

THE RELATIVE INFLUENCE OF HEREDITY AND ENVIRONMENT
ON THE EARLY GROWTH RATE OF THE CHICKEN

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PREFACE

The increasing demand of broiler growers on poultry breeders to supply better broiler chicks brings about the problem involved in this thesis. Improvement of early growth in the domestic fowl depends on the most efficient breeding system possible which, in turn, depends on an accurate estimate of heritability.

In June of 1949, the writer was assigned the thesis problem of obtaining an accurate estimate of early growth at 6 and 12 weeks of age in the Silver Orlabur chicken. The main purpose of this breed of chicken is to cross Silver Orlabur males with New Hampshire females to produce a columbian-patterned broiler chick.

The writer wishes to express his appreciation to the staff of the Poultry Department of Oklahoma Agricultural and Mechanical College for their helpful advice and cooperation and especially to Dr. George F. Godfrey, under whose supervision the experimental work was carried out. Dr. Godfrey has been a constant source of guidance and has offered invaluable constructive criticisms in the writing of this thesis. Also, to Professor R. B. Thompson is extended the most sincere appreciation for his excellent cooperation in making it possible for the writer to work out the above problem.

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INTRODUCTION

Poultry breeders in recent years have become increasingly aware of the need for greater improvement of early growth in the chicken. This has arisen, for the most part, from keener competition between poultry breeders as a result of the increased demand of broiler growers for better broiler chicks. For the breeder to obtain improvement in early growth, it is necessary to select the most efficient breeding plan possible. Selection of this breeding plan is dependent on an accurate estimate of heritability for the particular character in which one is interested. The objective of this thesis is to obtain an accurate estimate of the heritability of early growth in the domestic fowl so that the most efficient breeding plan for improving growth rate can be formulated.

LITERATURE REVIEW

To obtain an estimate of heritability one must determine the ratio of the genetic variance to the total variance in the population concerned. There are several different methods of calculating heritability estimates, the principle ones being by selection experiments, by the intra-sire regression of offspring on dam, by the analysis of variance technique, and by isogenic lines. Most estimates of heritability of growth in the chicken have been obtained by the use of the analysis of variance method. Regardless of the method used, there are advantages and disadvantages to each method. These will be discussed in the following pages.

Schnetzler (1936) divided one population of Barred Plymouth Rocks into rapid and slow growing lines based on weight at 8 or 9 weeks of age. Although no estimate of heritability was reported, the work demonstrates that a population of chickens can be separated into fast and slow growing lines with significant differences in weight between them by one or two generations of selection.

MacArthur (1944), using the laboratory mouse, divided one population in two lines. These were a slow line and a rapid line based on weight. After 21 generations of individual selection, the author concluded that even though some separation of lines occurred each generation most of the separation was obtained in the first 7 generations.

Krider, Fairbanks, Carroll, and Roberts (1946), working with Hampshire swine, divided one population in two lines--a rapid growing line and a slow growing line. This was done to measure the cumulative effects of selection based on rate of growth over several generations. The data includes four generations of which the heritability estimate for each generation is averaged to obtain one estimate. The estimates obtained were 16 percent for 150 days and 19 percent for 180 days. Heritability estimates were also calculated by

the analysis of variance method.

Hazel and Lamoreux (1947), using White Leghorns, obtained an estimate of heritability of growth of 31.6 percent at 22 weeks of age by the use of the analysis of variance technique which is based on paternal half sib correlation. Lerner, Asmundson, and Cruden (1947), using New Hampshire chickens, applied an analysis of variance to calculate three estimates of heritability. These were 41.5 percent for the variance between sires, 59.7 percent for the variance between dams, and 50.6 percent for the variance of sires and dams combined. The authors' conclusion was that 50 percent is a fair heritability estimate of growth at 12 weeks.

Shoffner and Sloan (1948), using the intra-sire regression method of estimating heritability, obtained an estimate of 75.2 percent for body weight at 300 days of age. Hurry (1949) utilized the analysis of variance method and computed a heritability estimate of 38 percent for Barred Plymouth Rocks and 30 percent for New Hampshires. This estimate was for both males and females at 8 weeks of age. With the same two breeds of chickens, an estimate of heritability of growth for 12-week-old males was 64 and 48 percent, respectively. The 8-week heritability was corrected for 22.2 percent inbreeding for the Barred Plymouth Rocks and 20.2 percent inbreeding for the New Hampshires, but the 12-week heritability for the males was not corrected for inbreeding which would make the estimate too high.

Lerner and Cruden (1951), using an analysis of variance, obtained a December body weight (adult body weight) heritability estimate of 15.3 percent. White Leghorns were used for this experiment. Glazener, Elow, Bostian, and Dearstyne (1951), using three strains of New Hampshires and two strains of Barred Plymouth Rocks, obtained estimates of heritability through the use of an analysis of variance from 51 to 79 percent for 12-week body weights.

El-Ibiary and Shaffner (1951), using an analysis of variance on body

weight data collected from a population of New Hampshire chickens, calculated heritability estimates of growth for 2, 6, 8, and 10 weeks of age. The authors were not interested in heritability estimates of body weight as such, but as a means to explain the effect of induced hypothyroidism on the genetics of growth in the chicken. Their estimates were divided into treated and control. The control estimates are reported here.

	Females		Males	
	h^2	g^2	h^2	g^2
2nd week	31.4%	0.0%	44.5%	5.6%
6th week	27.8%	14.3%	38.1%	13.1%
8th week	36.9%	22.5%	27.0%	10.7%
12th week	54.0%	25.9%	21.0%	12.8%

The authors stated that h^2 is the ratio of the genetic variance to the total observed variance, or the broad definition of heritability described by Lush (1948); and g^2 is the ratio of the additive genetic variance to the total observed variance, or the narrow definition of heritability described by Lush.

From the above review, heritability estimates of body weight range from 14 to 75 percent. This wide range could be caused by several reasons:

(1) The population used. In the above review there are eight different workers or groups of workers, and even though some of these workers used the same population of chickens, there are several different populations of chickens represented. This means there could be different genotypes as well as different environments involved.

(2) The age at which the heritability estimate is calculated. As it is shown in the work by El-Ibiary and Shoffner (1951), different ages have different estimates. The trend is in favor of the oldest age having the highest heritability estimate.

(3) The method of estimating heritability. Each method has varying amounts of dominance, epistasis, maternal effects, environmental peculiarities, and sampling error.

PROCEDURE

The experimental work discussed in this paper was with the Silver Oklabar chicken, one that is of the type that forms the American Class. It has a columbian-feather pattern resulting from the dominant sex-linked silver gene and the recessive autosomal black restriction gene. The main purpose of this breed of chicken is to cross Silver Oklabar males with New Hampshire females to produce a columbian-patterned broiler chick.

In the three years that this work was carried on, it was attempted to maintain management as uniform as possible from generation to generation. The regular starter ration that was fed on the College Experimental Farm was used. Each hatch of each line was brooded in one house which was equipped with gas brooders. Body weights at 6 and 12 weeks of age were taken on every individual, and sexes were determined at 12 weeks of age.

On January 9, 1950, 1057 chicks from flock matings on the College Experimental Farm were started to obtain the first generation selected parents. From the body weights obtained, a mean and standard deviation were calculated for each sex. The rapid growing males were selected from the males having weights at least one standard deviation above the mean of the males. The rapid growing females were selected from the females weighing at least one standard deviation above the mean of the females. Similarly, the slow growing males were selected from the males weighing at least one standard deviation below the mean of the males, and the slow growing females were selected from the females weighing at least one standard deviation below the mean of the females. These selected males and females comprised the first generation parents. The rapid growing selected males and females were housed in a separate flock-mated pen from the slow growing selected males and females.

Each line of the first generation parents produced two hatches, the first

September 2, 1950, and the second September 10, 1950. The eggs for each hatch were saved two weeks. The first hatch produced 195 rapid growing chicks and 166 slow growing chicks, and the second hatch produced 180 rapid growing chicks and 126 slow growing chicks. From the weights obtained at 6 and 12 weeks of age the chicks that comprised the second generation parents were selected. Although the goal for the selected parents was at least one standard deviation above or below the mean, this could not be followed completely. In order to maintain sufficient breeding stock, some breeders had to be selected that were less than one standard deviation above or below the mean of their respective line, but they were at least above or below the mean of their line.

The second generation parents were housed in individual mating pens, and the eggs produced by them were pedigree marked. These parents produced two hatches of which the first hatch produced 223 rapid growing chicks and 241 slow growing chicks. The second hatch produced 175 rapid growing chicks and 136 slow growing chicks. The first hatch was put in the brooder house July 3, 1951, and the second hatch July 30, 1951. The eggs for each of these two hatches were saved for two weeks.

The only weights that are considered in the analyses are the weights of chickens completing their first 12 weeks of growth. From the weight data collected, heritability estimates for early growth in the chicken are calculated by three methods. These are the selection experiment which is based on the differences between the two lines, and is patterned closely from the work of Krider, Fairbanks, Carroll, and Roberts (1946) on swine; the intra-sire regression of offspring on dam that is described by Lush (1940); and the analysis of variance which is patterned after that of Lerner, Asmundson, and Cruden (1947). Involved in this work are 2969 chicks from five hatches over a period of three years. The records of two complete generations plus the foundation generation are included. The two complete generations are the result of matings of 206 dams and 24 sires.

RESULTS AND DISCUSSION

Heritability is defined in the broad sense of the word as the function of the whole genotype of an individual in contrast to the heredity and environment combined. This definition includes the complete genotype in which is included not only the additive portion but also the portions due to dominance, epistasis, and maternal effects. The genotype is not transmitted as a unit because the genes segregate and recombine into new gene combinations and, therefore, only the additive gene effects are transmitted. The narrow sense of heritability, then, is the additive gene effects contrasted to heredity and environment. This includes only what is transmitted through the gamete.

Selection Experiment

Line Differences Resulting from Selection—The mean weights at each age by sex, line, and generation for all progeny are given in Table 1. There is an increase in the difference between lines of the second generation over the first generation progeny. This increased difference between lines is not due to the rapid line becoming heavier, but to the slow line decreasing in size. Also, not only the slow line decreased in size the second generation, but the rapid line decreased a small amount. This can be explained by the use of the data in Table 3 in which the selection differentials or the amount of selection pressure applied each generation is recorded. The selection differential was calculated by subtracting the mean for the whole population from which the parents were selected from the mean for selected parents. For example, the mean of the selected parents of the second generation rapid line is 3.002 pounds (Table 2), and the mean of the whole population from which they were selected or the first generation chicks at 12 weeks, rapid line, is 2.599

pounds (Table 1). The difference is 0.403 pounds which is the selection differential of the parents over the population from which they were selected. The mean of the parents of each generation should be weighted according to its number of progeny. Since the first generation in this work was a result of a flock mating, it was impossible to calculate a weighted mean, but the second generation was weighted according to each parents' number of offspring.

The first generation parents had, in most instances, a larger selection differential than the second generation. Not as much selection pressure was used in selecting the second generation parents as was used in selecting the first generation parents because, to obtain sufficient breeding stock, birds had to be used that were closer to the mean weight than were the first generation parents. This is shown again in Table 2, the mean weights of the parents by generations and lines. The parents of the second generation rapid line did not weigh as much at 6 and 12 weeks of age as the rapid line parents of the first generation and, in turn, the parents of the second generation slow line weighed more than the parents of the first generation slow line. Because the mean of the second generation parents is weighted by progeny, the mean of the combined parents of the second generation at 12 weeks of age, rapid line, is larger than the mean of the combined parents of the first generation at 12 weeks of age, rapid line. This is true regardless of the means of the sires and dams being larger in the first generation than the second. Possibly some gene combinations or epistatic effects were present in the first generation which were not in the second generation, causing this decrease in weight of the second generation parents.

Environment might be another reason for the difference in weight of the second generation from the first. Environment might affect one generation differently than another. Therefore, it should affect each line within the

generation about the same amount. This is the reason for two opposite lines being used for estimating heritability; that is, environment is eliminated leaving the difference between lines due to genetic causes.

The range of the first and second generation unselected progeny weights are shown graphically in Figures 1, 2, 3, and 4. These graphs show the overlapping of the weights of the two lines. The range in weights is about the same in the first generation at 6 weeks. In the second generation the upper range of weights of the slow line does not reach the upper range of the rapid line. In each generation the lower range of the two lines is about the same. In each generation at 12 weeks the upper range of the slow line does not reach the upper range of the rapid line. The lower ranges are about the same in both lines. At both 6 and 12 weeks there is less overlapping of weights in the second generation than in the first generation, indicating that progress was made in the separation of the two lines by mass selection.

Estimating Heritability from Data of the Selection Experiment--Heritability estimates by this method are calculated by dividing the amount of accumulated selection into the cumulative difference of the two lines. An estimate of heritability can be obtained for differences between individuals of the same line, and differences between parental means. These estimates are listed in Table 4.

The "A" portion of Table 4, or the intra-line heritability for each generation, is estimated by dividing the mean difference between unselected progeny of the two lines by the total amount of selection contributing to that line difference. For example, the mean 12-week weight (Table 1) for second generation chicks is 0.537 pounds heavier for the rapid than for the slow line. The cumulative superiority of the rapid line parents over the population from which they came (Table 3) is 0.357 and 0.403 pounds, and the cumulative inferiority of the slow line parents under the population from which they came

was -0.589 and -0.247 pounds. This is equivalent to an intra-line difference of 1.696 pounds between rapid and slow line parents of the second generation. Thus, heritability is estimated as $\frac{0.537}{1.696} \times 100 = 31.66$ percent for 12-week weight in the second generation.

The "B" portion of Table 4, or the inter-line heritability is estimated for each generation by dividing the mean difference for unselected progeny of the two lines by the difference between the means of their parents. For example, in the 12-week weight, parents of the second generation averaged 3.002 pounds for the rapid line and 2.025 pounds for the slow line (Table 2). The second generation progeny (Table 1) were 0.537 pounds heavier in the rapid than the slow line. Thus, $\frac{(0.537 \times 100)}{0.977} = 54.98$ percent of the difference between parental means in the second generation is estimated as heritable.

The "C" portion of Table 4 is for the most part self-explanatory. Since the first generation had no accrued selection, the figure is zero. In the second generation there has been some previous selection applied making some distinction between lines due to genetic differences.

Two things can be seen by these estimates. One, the estimates of heritability of the male birds each time is smaller than for the females except in the "C" portion at 12 weeks of age. On the other hand, in Table 1, the males of each generation have a larger coefficient of variation than the females. Two, the 6-week estimate of heritability is slightly lower than the 12-week, denoting that there is less genetic variability at 6 than at 12 weeks of age. An interesting observation is that the coefficient of variation (Table 1) of the unselected progeny is higher at 6 weeks, in most cases, than at 12 weeks. This indicates that just because the total variation is higher at one age, it does not necessarily mean that the genetic variation is higher also.

Estimates of heritability obtained from such a selection experiment as has been described are more accurate than most other methods because the

estimates are averages of several generations. When carried over several generations, it does two things---(1) tends to decrease sampling error, and (2) epistatic effects are diluted. If epistatic effects are important, the beginning gains made include this cause, but this tends to disappear in later generations. Genes in the gametes that are produced tend, in the following generations, to recombine and maintain a random distribution. Lush (1948) states that this procedure is probably the most effective method to measure additive genetic differences minus epistatic effects. To go further, Lush states that to get nearer the actual heritability in the narrow sense, discard the data of the first two generations and use only data beginning with the third generation. If this is true, then the estimates in Table 4 are probably high or in between the narrow and broad definitions of heritability. The question of validity of these estimates indicates that more generations are needed to erase any doubt. These two lines are being continued for this purpose.

The use of a selection experiment to determine estimates of heritability is rare in the literature compared to other methods of estimation. The chief difficulties are time, space, and expense, and it is good for only one trait at a time.

Intra-sire Regression of Offspring on Dam

This method of estimating heritability is a modified version of the regression between parent and offspring. The difference is that with the intra-sire regression environmental contributions and mating peculiarities are avoided by restricting the variance to that within the sire groups.

Procedure Followed in Determining Estimates of Heritability---The data used in the calculation of this method are the data collected from the second generation of the selection experiment. A total of 8 sires, 71 dams, and 366

offsprings in the rapid line and 3 sires, 65 dams, and 309 offsprings in the slow line comprised this second generation. Because of the question of the males, for the most part, weighing more than the females and thus biasing the regressions in favor of the males, all male and female weights were converted to a percent of an ideal weight. The ideal weights that were used at 6 weeks of age were 1.4 pounds for the males and 1.3 pounds for the females, and at 12 weeks of age 3.86 pounds for the males and 3.18 pounds for the females. The regression obtained from these data was then doubled to obtain an estimate of heritability. The regression is doubled to allow for the sires' contribution to the genetic variation. The intra-sire regressions and heritability estimates thus obtained are recorded in Table 5. One observation is that in both the rapid and slow lines the 12-week estimate is higher than the 6-week estimate.

The intra-sire regression for the slow line at 6 weeks of age is extremely low, and at 12 weeks it is a minus figure. This is brought about by selection in the opposite direction from the rapid line. These low regressions when doubled result in low heritability estimates.

Estimates of heritability by this method can contain varying amounts of maternal effects besides the additive gene effects. The amount can vary between two extremes. One extreme is that if the direct and complete transmission of cytoplasmic particles from dam to offspring is involved, the regression will include all of the maternal effects. On the other hand at the opposite extreme, effects due to environmental influences acting on the daughters, but not affecting the dam's own performance, will not be at all included in the regression. Intermediate amounts of variance due to maternal effects can appear from other causes such as maternal effects due to variations in the dam's genotype for maternal ability. Since there is no way at present to discriminate between these two possibilities, one has to assume

that a reasonable estimate is somewhere in between the two extremes.

Lush (1948) states that if there is a tendency to select mates of a sire because of similarity, there would be some increase in heritability. Since the sires and dams of each line in this work are selected on the basis of high or low weight, this positive assortive mating could affect the estimates of heritability. This will not enter into these estimates too greatly because of two reasons: (1) the parents are selected on the phenotype and not the genotype, and (2) the parents selected were not influenced by pedigree, progeny, or any other method that would influence selection other than the individual's weight at 6 and 12 weeks.

Probably the best estimate of the heritability of body weight at 6 and 12 weeks of age from this method is that calculated for the rapid line; that is, 31 percent at 6 weeks and 49 percent at 12 weeks. Since the rapid growth and not the slow growth is what the breeder desires, the rapid line estimate is the more practical.

Analysis of Variance

The third method for estimating heritability used in this thesis is the analysis of variance technique described by Lush (1948). This method is currently being used by many investigators for the study of genetic variability involved in quantitative inheritance. The inheritance of body weight in chickens is considered to be a multiple gene trait (Jull and Quinn, 1931; Lerner and Asmundson, 1932; and Asmundson and Lerner, 1933). The calculations used are from data of the second generation of the selection experiment. This involved weights of 366 offsprings resulting from the mating of 71 dams and 8 sires in the rapid line, and weights of 309 offsprings from 65 dams and 8 sires in the slow line. These weights, as in the intra-sire regression method, were converted to percentages of ideal weight.

In this method of estimating heritability, the amount of variance between sires, between dams within sires, and between full sibs are partitioned from the total variance in both the rapid and slow lines. Each line was treated separately instead of being combined, because even though they came originally from one population they are now two generations away from the beginning population. These two lines, for this purpose at least, because of selection in opposite directions probably have a different set or combination of genes affecting growth and can be considered two separate populations. Therefore, it was felt that the estimates of heritability obtained from data resulting from combining the two lines would not be valid.

With this method three estimates of heritability can be obtained--(1) from variance between dams, (2) from variance between sires, and (3) a combined estimate from variance between dams and sires. Each of these three estimates were calculated and are shown in Tables 6, 7, 8, and 9. The mean squares recorded in the above tables were calculated by dividing the sum of squares by their respective degrees of freedom, as shown in detail by Snedecor (1948).

The interpretation of the mean squares listed in Tables 6, 7, 8, and 9 are discussed by Lerner et al. (1947). The total mean square contains both the genetic (G) and the environmental (E) variance. The environmental portion also includes most of the non-additive deviations due to dominance and epistasis. The mean squares between sires (S) consist largely of one-quarter of the genetic variance, that between mates of each sire (D) another quarter, and the mean square for the families of full sisters (W) contains the remainder of the genetic variance and all of the environmental term. The total variance then consists of $S + D + W$.

The amount of genetic variance that is contributed by the dam (D) and sire (S) is calculated from the composition of mean squares in Tables 6, 7, 8, and 9. The average number of offsprings per dam is represented by the

letter "z", and the average number of dams per sire is represented by the letter "y". To calculate an estimate of heritability from the dam's variance, the amount of genetic variance contributed by the dam (D) is multiplied by four and divided by the total variance, as shown in the "a" part of the heritability estimates in Tables 6, 7, 8, and 9. Similarly, in the "b" part, a heritability estimate from the sires is calculated by multiplying by four the genetic variance contributed by the sires (S), and this is then divided by the total variance. The "c" part is calculated by multiplying by two the genetic variance contributed by the dam and sire and dividing by the total variance.

Since, as stated above, the contributions from sires and dams each contain one-quarter of the variance due to the average gene effects, the difference between them (D-S) provides a basis for estimating the importance of maternal effects. These are listed in Tables 6, 7, 8, and 9. The maternal effects listed are all minus except the 12-week slow line which is so low it can be disregarded for all practical purposes, and for the 12-week rapid line which is about 5 percent and could influence the estimate of heritability from dams.

The question arises, which of the three estimates of heritability (a, b, or c) is the best. Lerner, Axundson, and Cruden (1947) state that the estimates of heritability involved might be slightly larger than the true heritabilities if non-additive interactions such as epistasis or dominance are involved. In this analysis of variance no separation of variance due to non-additive effects such as epistasis or dominance was calculated. Hazel and Lamoreux (1947), working with White Leghorns, found that only an insignificant amount of non-additive effects were present. This work was with body weight at 22 weeks. If this type of variation is important, the estimates listed in Tables 6, 7, 8, and 9 could be slightly larger than the true

heritabilities. The exact amount is not known; therefore, the estimates obtained from the sires and dams contain all of the additive genetic variance plus whatever epistasis or dominance effects are left in the S and D portion of the genetic variance.

Discrepancies among the three estimates might be attributed in part to sex-linkage in cases where the estimates from the sires show an excess, and to maternal effects when the estimates from the dams are higher (Lerner et al., 1947). Evidence of sex-linkage has been found by Maw (1935) who concluded that one or maybe more than one sex-linked gene is involved in the inheritance of body weight in the chicken. Kaufman (1947) also found evidence that sex-linkage was involved in the growth of the domestic fowl. Maternal effects have been found by Lerner et al. (1947) to contribute about 5 percent of the total variance of the 12-week body weight of the chicken. These differences could in part be due to one or both of the reasons above mentioned. It is not believed that these reasons will account for all of the differences in some of the sets. It will be noticed that the 6-week rapid line estimate from sires is over 100 percent which is obviously incorrect. The exact reasons for this is not known. One reason could be a tremendous sampling error. For example, if there are 20 genes involved in the inheritance of body weight, there would be possible 3^{20} genotypes. The number of birds considered in this analyses for the rapid line is 366 and for the slow line 309; therefore, the sampling error could be considerable.

Another possibility is the mating system. This cannot be checked to see if there are any full brothers or sisters in any of the matings since the parents of the offsprings involved came from a flock mating. The probability of many full brother and sister matings is quite low, but it could happen and cause difficulty. The 6-week estimate of heritability from sires is also high in the 6-week slow line, but is far from 100 percent. The mean square

between sires is also very high. A reason the mean square is higher between sires than between dams is because of the difference between the number of males and females involved. Therefore, because of the difficulties involved in the estimates from sires, the estimates from dams seem to be the most adequate. These are 59 percent for the rapid line and 28 percent for the slow line at 6 weeks of age. Maternal effects for both lines are negative.

The 12-week estimates of heritability are considerably closer together, especially in the slow line. In this case if sex-linkage and maternal effects are involved, these could be canceling each other, thus, causing the estimates to be about the same. The positive maternal effects in the 12-week rapid line even though small (5 percent), could be the major reason the estimate from dams is larger than from sires.

Comparison of the Three Methods of Calculating Heritability Estimates

Estimates of heritability for body weight obtained in this work range from 2 percent (rapid 6-week intra-sire regression) to 81 percent (from sires 6-week rapid analysis of variance). This wide range can be explained somewhat as follows.

Three methods are used to calculate the heritability estimates. Each method varies in the amount of non-additive effects and sampling error that is included in the estimate. From the results, sampling error apparently is important in the analysis of variance method. In the calculating of this estimate, the genetic variance contributed by the sire or dam is multiplied by four. This is done because the mean square of either the sires or between dam within sires contains only one-quarter of the genetic variance, but at the same time the sampling error and any non-additive effects involved are multiplied by four. If these effects are present, the estimates calculated would be larger than the true heritability. Estimates obtained from the intra-sire

regression of offspring on dam method would also be too large, if these effects are present, because the regression is multiplied by two. This at the same time doubles any sampling error and non-additive effects that are present. The estimates from the selection experiment are not multiplied in any way; therefore, if any non-additive effects or sampling error are present, they would not be multiplied and thus the estimates would be closer to the true heritability than those obtained by the other methods. This is one of the major reasons estimates of heritability obtained from this method are considered nearer the true heritability. Other reasons why the selection experiment is considered one of the most accurate methods available to animal breeders are: (1) the elimination of the environmental factor because of the two opposite lines, (2) the tendency of reducing sampling error because of the averaging of several generations, and (3) the reducing of any epistatic effects that are present.

From the results obtained in this thesis, maternal effects are relatively unimportant except for the 12-week rapid line (Table 8) which shows that about 5 percent of the total variance is due to maternal effects. If this is subtracted from the estimate from dams, the estimate of course will be lower and nearer the narrow sense of heritability. The 12-week rapid line intra-sire regression estimate is 49 percent. If the 5 percent maternal effects obtained in Table 8 is subtracted from the regression before it is doubled, the resulting estimate will be about 38 percent. This is nearer the estimates obtained in the selection experiment at 12 weeks of age.

By comparing the heritability estimates calculated by the three methods, one can obtain an idea of the amount of non-additive interaction. Reviewing briefly the estimates obtained: selection experiment, 30 percent; intra-sire regression of offspring on dam, rapid line, 30 to 50 percent; and analysis of variance from dams, rapid line, 50 to 60 percent. The estimate obtained

from the selection experiment is made up of only two generations. Lush (1948) states that if epistasis is important, the first two generations will contain epistatic effects and from the third generation on less and less epistasis. For this reason considering this estimate alone, one would expect the estimate to be high. Considering, then, the estimates obtained from the other two methods, one could assume that epistasis is not very important for growth at 6 and 12 weeks of age, at least in the population concerned here. The high estimates obtained in the analysis of variance are attributed mainly to sampling error.

From the above data and discussion, the estimate of heritability that is probably nearer the true heritability is about 30 percent for both 6 and 12 weeks of age with the 6-week estimate being slightly lower than the 12-week estimate.

Variability of Growth at 6 and 12 Weeks of Age

From Table 1 the coefficient of variation of the first and second generations is recorded. In the first generation at 6 weeks of age, variability of both lines is about the same; whereas, at 12 weeks of age, the slow line has more variability than the rapid line. In the second generation at both 6 and 12 weeks of age, the slow line is more variable than the rapid line. This agrees with Schnetzler (1936) who states that there was more variability among his slower growing birds than among his rapid growing birds at 8 or 9 weeks.

Latimer (1924) states that variability in the live weight of White Leghorns is greatest at 5 weeks. Schroeder and Lawrence (1932) found that the variability reached a maximum by 6 weeks. Asmundson and Lerner (1934) state that the period from 2 to 8 weeks of age is considered most suitable for the purpose of studying genetic difference of rate of growth because variability is greatest. From the data in Table 1, the coefficient of variation is greater

at 6 weeks than 12 weeks. This is the total variability due to all causes. The heritability estimates listed in Tables 4, 5, 6, 7, 8, and 9 show that the 12-week estimate is slightly higher than at 6 weeks. Therefore, because the total variability is greater at 6 weeks of age, it does not necessarily mean that this is the best time to select breeders. The genetic variability, regardless of the total variability, is what most interests the breeder. Thus, selection of breeders for growth is slightly more efficient at 12 weeks of age than at 6 weeks of age in this population.

Choice of Breeding System

The question arises, now that an estimate of heritability of growth has been determined, which breeding system should be followed. There are two main breeding systems available for use by the breeder. One is selection on phenotypes or individual selection, and the other is genotypic selection based on the use of family averages and progeny tests. The relative efficiency of these two systems have been discussed rather thoroughly by Lerner, Cruden, and Taylor (1949). There are two main factors to consider when comparing the two systems--heritability and family size. The work by Lerner et al. (1949) shows that as heritability increases the relative efficiency of family selection over mass selection decreases, and also as family size decreases the relative efficiency of family selection over mass selection decreases. Therefore, from this work a trait such as 6 and 12-week body weight which has a heritability of 30 percent could be selected nearly as efficiently by mass selection as family selection, if the number of sisters is not over six.

With eight sisters, family selection becomes a little more efficient than mass selection. If the heritability is 60 percent, it is still more efficient to practice mass selection than family selection, even if as many as eight sisters are in the family. A major reason why mass selection is

preferred over family selection, if at all possible, is that in the use of mass selection there is no need of expensive record keeping. The increased expense, time, and labor necessary to use family selection efficiently can then be turned to other traits that have lower heritability estimates and require the use of family selection to obtain efficient gains.

TABLE 1. MEAN WEIGHT IN POUNDS OF ALL OFFSPRINGS BY GENERATION, SEX, LINE, AND AGE

Gen.	Sex	Line	6 Weeks				12 Weeks				
			No.	Mean	s*	C.V.**	No.	Mean	s*	C.V.**	
0	Male	R	322	.829			323	2.744			
		S									
		R-S									
	Female	R	394	.809			404	2.354			
		S									
		R-S									
Combined	R	716	.818			727	2.528				
	S										
	R-S										
1	Male	R	154	.902	.175	.194	154	2.802	.502	.179	
		S	127	.806	.157	.195	128	2.510	.463	.184	
		R-S		.096				.292			
		R	157	.855	.144	.168	156	2.399	.288	.120	
		S	138	.758	.124	.164	137	2.049	.311	.152	
		R-S		.097				.350			
	Female	R	311	.878	.162	.185	310	2.599	.455	.175	
		S	265	.781	.143	.183	265	2.272	.454	.200	
		R-S		.097				.327			
		Combined	R	189	.881	.170	.193	189	2.791	.439	.157
			S	161	.631	.167	.265	156	2.216	.413	.186
			R-S		.250				.575		
2	Male	R	178	.807	.148	.183	178	2.354	.298	.127	
		S	148	.586	.138	.235	144	1.854	.268	.145	
		R-S		.221				.500			
	Female	R	367	.845	.165	.195	367	2.579	.435	.169	
		S	309	.610	.155	.254	300	2.042	.416	.204	
		R-S		.235				.537			

* - standard deviation

** - coefficient of variation

TABLE 2. MEAN WEIGHT OF SELECTED PARENTS
BY GENERATION, LINE, AGE, AND SEX

Gen.	Line	Sex	6 Weeks		12 Weeks	
			No.	Mean	No.	Mean
1	Rapid	Sires	4	1.213	4	3.500
		Dams	39	1.045	39	2.822
		All Parents	43	1.061	43	2.885
	Slow	Sires	4	0.475	4	1.775
		Dams	31	0.550	31	1.847
		All Parents	35	0.541	35	1.839
2	Rapid	Sires	8	1.121	8	3.341
		Dams	71	0.982	71	2.664
		All Parents	79	1.051	79	3.002
	Slow	Sires	8	0.704	8	2.234
		Dams	65	0.675	65	1.816
		All Parents	73	0.690	73	2.025

TABLE 3. SELECTION DIFFERENTIALS OF SELECTED PARENTS,
IN WEIGHT FOR AGE (POUNDS)

Age When Weighed	Sex	Line	Parents of Generation	
			1	2
6 Weeks	Sires	Rapid	.384	.219
		Slow	-.354	-.102
	Dams	Rapid	.236	.127
		Slow	-.259	-.083
	All Parents	Rapid	.243	.173
		Slow	-.277	-.091
12 Weeks	Sires	Rapid	.756	.539
		Slow	-.969	-.276
	Dams	Rapid	.468	.265
		Slow	-.507	-.233
	All Parents	Rapid	.357	.403
		Slow	-.689	-.247

TABLE 4. HERITABILITY OF BODY WEIGHT BY AGE AND SEX OBTAINED FROM THE SELECTION EXPERIMENT

Item Studied	Genera- tion	Sex	Percentage Heritability for Weight at	
			6 Weeks	12 Weeks
A. For difference in weight between birds of same line.	1	Male	13.00	16.93
		Female	19.59	35.89
		Combined	18.65	31.26
	2	Male	23.61	22.64
		Female	31.34	33.94
		Combined	29.97	31.66
B. Differences in weight between birds of different lines.	1	Male	13.00	16.93
		Female	19.59	35.89
		Combined	18.65	31.26
	2	Male	59.95	51.94
		Female	71.98	58.96
		Combined	65.09	54.98
C. Excess of B over A (largely due to the genetic difference between lines, which has accrued from selection in previous generations)	1	Male	0.00	0.00
		Female	0.00	0.00
		Combined	0.00	0.00
	2	Male	36.34	29.30
		Female	40.64	25.02
		Combined	35.12	23.32

TABLE 5. ESTIMATES OF HERITABILITY OF BODY WEIGHTS AT
6 and 12 WEEKS OF AGE BY LINES CALCULATED FROM
INTRA-SIBS REGRESSIONS OF OFFSPRING OF DAM

Age Weighed	Line	b	h^2
6 Weeks	Rapid	.1523	.3046
	Slow	.0110	.0220
12 Weeks	Rapid	.2442	.4882
	Slow	-.0365	.1730

TABLE 6. ANALYSIS OF VARIANCE OF BODY WEIGHTS AT 6 WEEKS OF AGE, RAPID LINE

Source of Variation	d.f.	Mean Square	Interpre- tation	Composition of Mean Square
Total	365	160.82	E + G	
Between sires (S)	7	2181.37	0.25G	W + zD + yzS
Between dams	70	421.53		
within sires (D)	63	226.00	0.25G	W + zD
Between full sibs (W)	295	98.96	E + 0.5G	W

$$z = \text{average number of offsprings per dam } \frac{366}{71} = 5.16$$

$$y = \text{average number of dams per sire } \frac{71}{8} = 8.88$$

D = genetic variance contributed by the dams

S = genetic variance contributed by the sires

E = environmental variance

G = genetic variance

From the composition of mean squares:

$$D = \frac{(\text{M.S. of D}) - (\text{M.S. of W})}{z} = \frac{226.00 - 98.96}{5.16} = 24.62$$

$$S = \frac{(\text{M.S. of S}) - (\text{M.S. of D})}{yz} = \frac{2181.37 - 226.00}{(8.88)(5.16)} = 42.68$$

Heritability estimates:

$$(a) \text{ from dams } \frac{4D}{S+D+W} = \frac{98.48}{166.26} = .5923$$

$$(b) \text{ from sires } \frac{4S}{S+D+W} = \frac{170.72}{166.26} = 1.0268$$

$$(c) \text{ combined } \frac{2(D+S)}{S+D+W} = \frac{134.60}{166.26} = .8096$$

Maternal effects:

$$\frac{(D-S)}{S+D+W} = \frac{-18.06}{166.26} = -.1086$$

TABLE 7. ANALYSIS OF VARIANCE OF BODY WEIGHTS AT 6 WEEKS OF AGE, SLOW LINE

Source of Variation	d.f.	Mean Square	Interpretation	Composition of Mean Square
Total	308	172.13	E + G	
Between sires (S)	7	1026.26	0.25G	W + zD + yzS
Between dams	64	289.69		
Between dams within sires (D)	57	199.24	0.25G	W + zD
Between full sibs (W)	244	141.29	E + 0.5G	W

$$z = \text{average number of offsprings per dam} \frac{309}{65} = 4.75$$

$$y = \text{average number of dams per sire} \frac{65}{8} = 8.13$$

D = genetic variance contributed by the dams

S = genetic variance contributed by the sires

E = environmental variance

G = genetic variance

From the composition of mean squares:

$$D = \frac{(\text{M.S. of D}) - (\text{M.S. of W})}{z} = \frac{57.95}{4.75} = 12.20$$

$$S = \frac{(\text{M.S. of S}) - (\text{M.S. of D})}{yz} = \frac{827.02}{38.62} = 21.41$$

Heritability estimates:

$$(a) \text{ from dams } \frac{4D}{S+D+W} = \frac{48.80}{174.90} = .2790$$

$$(b) \text{ from sires } \frac{4S}{S+D+W} = \frac{85.64}{174.90} = .4897$$

$$(c) \text{ combined } \frac{2(D+S)}{S+D+W} = \frac{67.22}{174.90} = .3843$$

Maternal effects:

$$\frac{(D-S)}{S+D+W} = \frac{-9.21}{174.90} = -.0527$$

TABLE 8. ANALYSIS OF VARIANCE OF BODY WEIGHTS AT 12 WEEKS OF AGE, RAPID LINE

Source of Variation	d.f.	Mean Square	Interpretation	Composition of Mean Square
Total	365	133.08	E + G	
Between sires (S)	7	916.14	0.25G	W + zD + yzS
Between dams	70	202.95		
Between dams within sires (D)	63	212.57	0.25G	W + zD
Between full sibs (W)	295	97.52	E + 0.5G	W

$$z = \text{average number of offsprings per dam } \frac{366}{71} = 5.16$$

$$y = \text{average number of dams per sire } \frac{71}{8} = 8.88$$

D = genetic variance contributed by the dams

S = genetic variance contributed by the sires

E = environmental variance

G = genetic variance

From the composition of mean squares:

$$D = \frac{(\text{M.S. of D}) - (\text{M.S. of W})}{z} = \frac{115.05}{5.16} = 22.30$$

$$S = \frac{(\text{M.S. of S}) - (\text{M.S. of D})}{yz} = \frac{703.87}{45.82} = 15.36$$

Heritability estimates:

$$(a) \text{ from dams } \frac{4D}{S+D+W} = \frac{89.20}{135.18} = .6599$$

$$(b) \text{ from sires } \frac{4S}{S+D+W} = \frac{61.44}{135.18} = .4545$$

$$(c) \text{ combined } \frac{2(D+S)}{S+D+W} = \frac{75.32}{135.18} = .5572$$

Maternal effects:

$$\frac{(D-S)}{S+D+W} = \frac{6.94}{135.18} = .0513$$

TABLE 9. ANALYSIS OF VARIANCE OF BODY WEIGHTS AT 12 WEEKS OF AGE, SLOW LINE

Source of Variation	d.f.	Mean Square	Interpretation	Composition of Mean Square
Total	299	161.73	E + G	
Between sires (S)	7	605.89	0.25G	W + zD + yzS
Between dams	64	243.30		
Between dams within sires (D)	54	199.44	0.25G	W + zD
Between full sibs (W)	235	139.52	E + 0.5G	W

$$z = \text{average number of offsprings per dam } \frac{300}{65} = 4.62$$

$$y = \text{average number of dams per sire } \frac{65}{8} = 8.13$$

D = genetic variance contributed by the dams

S = genetic variance contributed by the sires

E = environmental variance

G = genetic variance

From the composition of mean squares:

$$D = \frac{(\text{M.S. of D}) - (\text{M.S. of W})}{z} = \frac{59.92}{4.62} = 12.97$$

$$S = \frac{(\text{M.S. of S}) - (\text{M.S. of D})}{yz} = \frac{486.45}{37.56} = 12.95$$

Heritability estimates:

$$(a) \text{ from dams } \frac{4D}{S+D+W} = \frac{51.88}{165.44} = .3136$$

$$(b) \text{ from sires } \frac{4S}{S+D+W} = \frac{51.80}{165.44} = .3131$$

$$(c) \text{ combined } \frac{2(D+S)}{S+D+W} = \frac{51.64}{165.44} = .3134$$

Maternal effects:

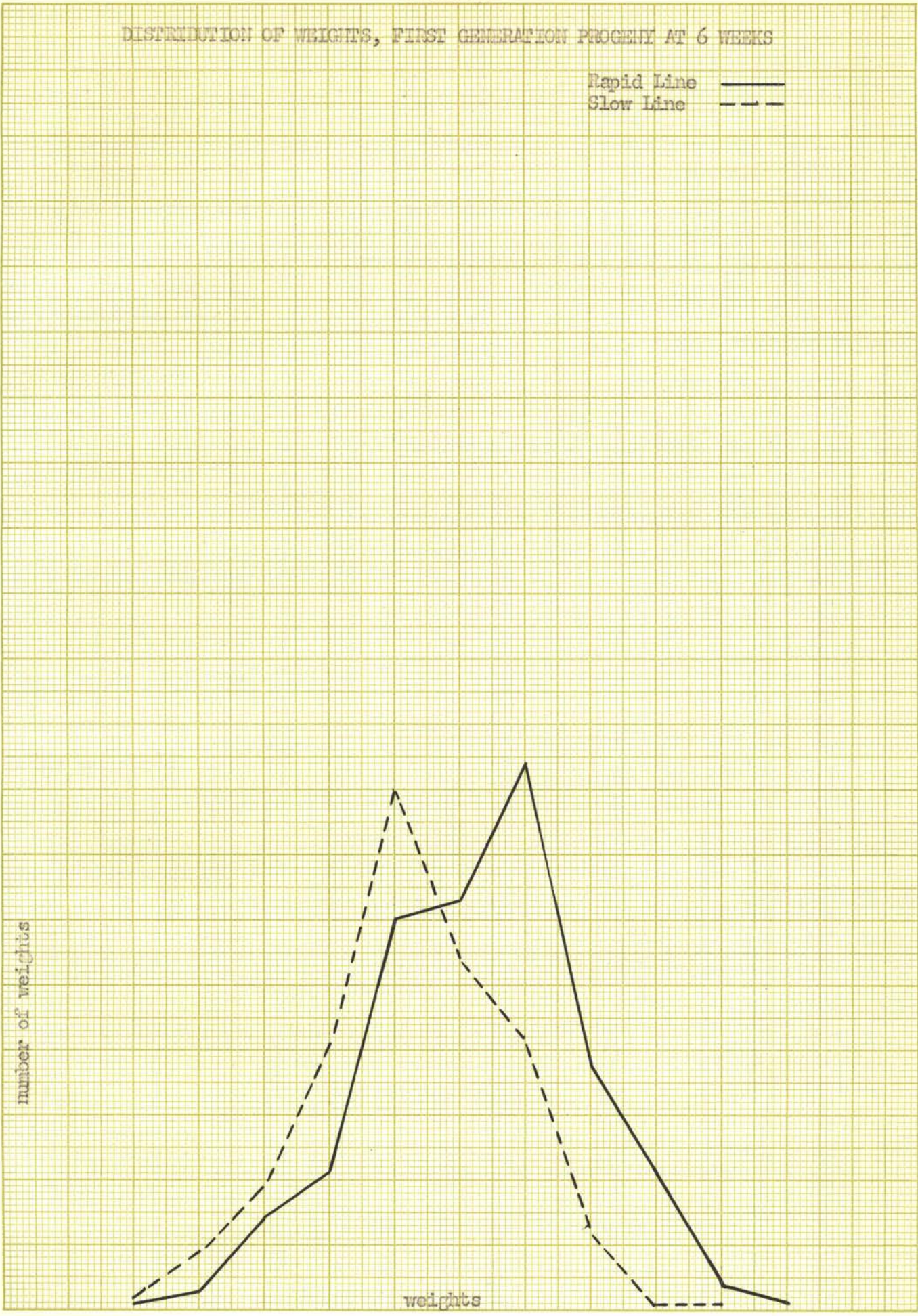
$$\frac{(D-S)}{S+D+W} = \frac{.03}{165.44} = .00018$$

FIGURE 1

DISTRIBUTION OF WEIGHTS, FIRST GENERATION PROGENY AT 6 WEEKS

Rapid Line ———
Slow Line - - - -

number of weights



.2 .3 .4 .5 .6 .7 .8 .9 1.0 1.1 1.2 1.3

weights

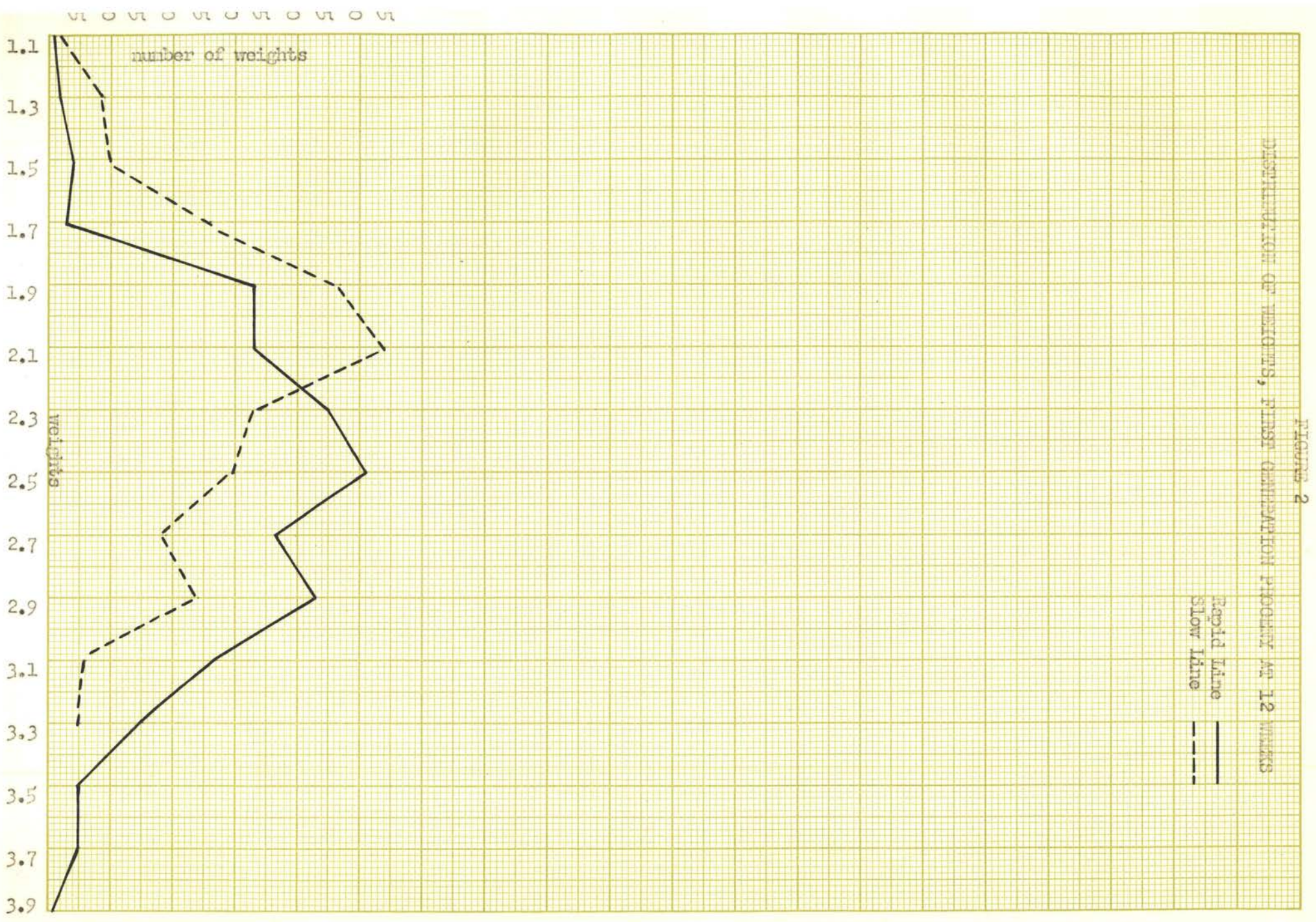


FIGURE 2
DISTRIBUTION OF WEIGHTS, FIRST GENERATION PROGENY AT 12 WEEKS

FIGURE 3

DISTRIBUTION OF WEIGHTS, SECOND GENERATION PROGENY AT 6 WEEKS

Rapid Line ———
 Slow Line - - - -



FIGURE 4

DISTRIBUTION OF WEIGHTS, SECOND GENERATION PROGENY AT 12 WEEKS

Rapid Line ———
 Slow Line - - - -



CONCLUSIONS AND SUMMARY

Data were analyzed on 2969 chicks hatched from Silver Oldfashions over a period of three years. The major objective was to establish as accurate a heritability estimate for early body weight in the domestic fowl as possible. This was accomplished by calculating heritability estimates by the use of three methods. These were selection experiment, intra-sire regression of offspring on dam, and analysis of variance technique.

A by-product of calculating an estimate of heritability, using the selection experiment method, was the establishment of two lines (rapid and slow growing) of poultry based on weight at two ages (6 and 12 weeks). These two lines originally were from the same population. Two generations of each line have been described in this thesis. Estimates of heritability obtained by the use of the intra-sire regression method and the analysis of variance method were calculated from the second generation body weights of birds involved in the selection experiment.

From these data the following was concluded:

1. The most reliable estimate of heritability for early body weight of the domestic fowl is about 30 percent with estimates obtained from 6-week body weights slightly lower than those calculated from the 12-week body weights.
2. Genetic variability is slightly higher at 12 weeks than at 6 weeks of age.
3. Five percent of the variance at 12 weeks of age in the rapid growing line was due to maternal effects.
4. Mass selection is more efficient than family selection for improving body weight at 6 and 12 weeks of age.

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