EFFECTS OF SELECTION AND OUTBREEDING
ON HATCHABILITY IN CHICKENS

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EFFECTS OF SELECTION AND OUTBREEDING
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INTRODUCTION

Normal hatchability expected in commercial strains of chickens, particularly within the broiler breeds, is approximately 65 percent to 70 percent of all eggs set. Discovery of how to increase this to 90 percent would be a definite contribution to the poultry industry.

Many factors have been found to influence hatchability. These could be grouped under management, nutrition, and breeding. Management and nutrition studies are the bases for much of the improvement in hatchability. However, there yet remains the problem of low hatchability due apparently to the genetic constitution of the stock involved.

To best improve hatchability by breeding would require much information concerning the genetic aspects of this trait. Little of this information seems to be currently available. The breeder needs to know the heritability of the trait in order to decide the type of selection best suited to his problem.

This thesis deals with an experiment on selection for hatchability. Objectives of the thesis are to indicate the population change per generation and relate certain aspects for the purpose of obtaining heritability estimates. An intra-sire comparison of inter- and intra-line offspring will be presented.

LITERATURE REVIEW

Heritability of Hatchability

Hatchability breeding experiments have received the attention of investigators from the beginning of present day poultry breeding. Earlier work centered around determining whether or not the "hatching quality" of eggs was a separate and heritable trait. Pearl (1910) first undertook this venture. He obtained a correlation coefficient of 0.031 ± 0.072 for 87 dam-daughter pairs. Among Pearl's interpretations was the conclusion that "hatching quality in eggs" is definitely inherited in the female line and probably also in the male line.

Hays and Sanborn (1924) conducted some correlation studies with Rhode Island Reds. They then suggested that hatchability is determined by one incompletely dominant gene, (H), that there is no sex linkage, and that all results are to be expected in a simple mono-hybrid ratio. They believed that the poultry could be grouped into three phenotypes as follows: (1) those showing hatchability of 85 percent or above, called high; (2) those with a hatchability of 55 to 84 percent called medium; and (3) those below 55 percent, called low. Since factor (H) was thought to have a cumulative effect, the range for the medium class was twice as great as for the high class. Hays and Sanborn concluded that hatchability is an inherited trait. Jull (1931), however, pointed out that the low values found by other workers for hatchability correlations between parent and offspring made invalid the assumption of simple inheritance.

Hays and Sanborn (1924) found a daughter-dam correlation coefficient of 0.21 ± 0.05 for 74 Rhode Island Red dams with their 148 daughters, and $\underline{r} = 0.16 \pm 0.06$ for 60 White Leghorn dams and their 105 daughters. Pearl and Surface (1909) obtained a correlation of 0.188 ± 0.06 between full sisters, a higher correlation than that obtained from other relationships within the same flock. They concluded that hatchability, although heritable, was obscured by some sort of "prepotency" factor which made genetic progress by selection based on ancestral records more difficult. Dunn (1921) demonstrated that hatchability and general vitality of the stock are separate components. He correlated pre- and post-natal mortality of a group of sixty-six progenies, each "progeny" being five or more chicks which actually hatched, and found the correlation to be nil.

Jull (1931) divided a mixed group of Rhode Island Reds and White Leghorns into two groups. One group's eggs had hatchability above the mean, the other group below. He then compared the hatching performance of the two groups of offspring. In both breeds, the higher performing daughters were from the higher performing group of dams.

Some of the above, and other, work was also intended to investigate the relative roles of the sire and the dam in the hatchability of eggs. Landauer (1951) stated that the only possible interpretation of published data seemed to be that the male plays a less important role than the female in determining hatchability.

Early workers determined that hatchability is an inherited trait. Other evidence to support this conclusion could be obtained from the observed differences in hatchability between breeds, strains, lines, and families.

Later work attempted to establish to what extent hatchability is inherited. Heritability estimates for hatchability in poultry were first calculated by Wilson and Johnson (1946) from data on turkeys. Using the intra-sire regression of daughters on dam, they estimated the heritability of hatch of fertile eggs to be 0.26. Shoffner and Sloan (1948) reported a heritability estimate of 0.134 which became 0.160 after correction for 16 percent inbreeding. This heritability estimate was obtained from the regression calculated on an intra-year, intra-sire basis for 474 sets of dam-daughters. Hill et al. (1954) estimated the heritability of hatchability to be 0.08 from 269 dams in three breeds in three years. This estimate of the heritability of family mean embryonic viability was based only on the sire variance component.

In a study of the effect of supplemental oxygen on hatchability and on selecting for hatchability in New Hampshire chicken eggs at high altitude, Davis (1955) obtained heritability estimates of 0.292 and 0.648 for the oxygen-hatched and the air-hatched lines, respectively. He concluded that the heritability was higher in the line hatched in air because variation caused by environment was smaller. The method in obtaining heritability estimates was that of doubling the regression of dam on daughter.

Brunson (1955) obtained heritability estimates of 0.05, which became 0.08 when transformed to the probit scale, based on the sire contribution to the genetic variance. Mean maternal effects were 0.14 which became 0.34 from the probit transformation. Brunson stated that maternal effects probably represented an overestimate of heritability; and since the hatchability data were collected on the parental generation, and the parental birds were selected for hatchability, the possibility of a biased estimate existed. Also, the heritability was lower at the higher hatchability percentages. Crittenden et al. (1957) obtained heritability estimates from data procured on a commercial poultry breeding farm. Estimates were based on both analysis of variance and regression techniques. The values for these estimates ranged from zero to ten percent. The percentage hatch of fertile eggs was ninety. The percentage data were all transformed to the arcsin $\sqrt{\text{proportion}}$ scale.

Effects of Inbreeding and Outbreeding on Hatchability

Although several studies relating inbreeding and heterosis to hatchability have been conducted, few investigations have been designed with a study of hatchability as the primary purpose. Cole and Halpin (1922) found that full sib mating with selection of a non-vital character (plumage color) resulted in a rapid deterioration of the stock. Hatchability declined from 67 to 18 percent, which made it impossible to continue the line. In a second trial the same intensity of inbreeding occurred, but selection was based on hatchability and viability. Although some effect of this selection was apparent, hatchability again declined in successive generations.

Dunn (1923) reported some inbreeding experiments with White Leghorns. Again no direct selection for the trait hatchability was practiced. Matings were limited to the offspring of that hen which had the largest number of daughters surviving at one year of age. In this experiment hatchability declined in all the inbred families. The decline was from 72 percent in the original flock to 18 percent after three generations of sib mating. There were differences, however, among families in the rate of decline in hatchability. One of the four families used in this experiment maintained a hatch percentage of 41.5 after five generations of inbreeding with selection.

Dumon (1931) mated closely related "high" performing birds for three generations. The performance of this stock dropped from 72 to 34 percent for the breeders, even though individual selection for hatchability was practiced. Matings of chickens between inbred but only slightly related strains increased hatchability back to approximately the pre-inbreeding level.

Warren (1927) found that the White Leghorn X Jersey Black Giant cross hatched better than either parent.

Jull (1929) made several full and half sib matings with two breeds and four lines. The results of these matings indicated that as the amount of inbreeding increased, the hatchability percentage decreased. This decrease was approximately the same whether the relationship of the particular mating was reached in one or two generations. Shoffner (1948) calculated the intra-sire regression of hatchability on inbreeding from 76 sire groups representing various lines and breeds. This regression was -0.436 ± 0.132. The interpretation was that for each ten percent increase in inbreeding, there was an average decline of 4.4 percent in hatchability.

Dumon (1931) also indicated that hatchability declined with inbreeding, even though selection was practiced. Waters and Lambert (1936) obtained contrasting results in regard to the effects of inbreeding on hatchability. They selected for hatchability, vigor, and family size. Data were presented on three families which had zygotic inbreeding coefficients of 83, 61, and 41 percent at the ninth generation mating. Different intensities of inbreeding were practiced between families and generations. The hatching performance of these families was maintained at 68 to 77 percent. This demonstrated that inbreeding *per se* does not necessarily lower hatchability. Later, Waters (1945), Knox (1946), and others substantiated that it is possible to inbreed without a subsequent decline in hatchability.

Warren (1934) improved hatchability by crossing breeds, as compared to intra-breed matings. Byerly *et al*. (1934) studied hatchability of the parental stock. They further concluded that crossing breeds with a hatchability above 80 percent lowered hatchability as often as it increased it among the flocks used.

Waters (1938) obtained a significant increase in hatchability from line-crossing inbred White Leghorn males with random bred females of the same breed. The progeny from this cross performed better than either the inbred or the random bred flocks.

Knox and Olsen (1938) found that crossbreds hatched better than inbreds in studies at the National Agricultural Center.

In broiler type birds, Horlacher *et al*. (1941) improved hatchability by crossing breeds. Knox *et al*. (1943) did not improve hatchability with two- and three-way crosses.

Jeffrey (1944) improved hatchability from 60 to 78 percent in six years of selection for egg production, hatchability, and adult viability.

Wilson (1948), using records obtained from various lines of White Leghorns, found that hatchability did not change appreciably for a ten year period. There was a selection differential of from approximately one-half to one standard deviation. Although rather wide yearly variation was noted, hatchability averaged 72.7 percent for the first year and 68.8 percent for the last year.

Discussion of Heritability

Heritability can be expressed as a ratio of variances. Variance can be thought of as one-half the average squared difference between the individuals in the population being compared. These are useful concepts because variation between individuals is a requisite for any population change to be brought about by the breeder (Lush, 1948). If there is no difference among the chickens, there is no basis for selecting or culling a chicken.

The observed phenotype is not directly inherited, even though the variation in simply inherited traits such as comb type is largely due to differences in genotype. The phenotype of an individual is the net result of the individual's genotype and environment. For an example of environment affecting a highly heritable trait, consider that a single comb could have been dubbed and appear to be a pea comb. The only thing directly inherited is the ability to respond in a certain manner to a particular environment, or set of environments. Lush (1948) showed that phenotype (P), in the simplest case, equals heredity (H) plus environment (E). H and E are measured in terms of their effects on P. In statistical terms $\sigma_P^2 = \sigma_E^2 + \sigma_H^2 + 2\text{Cov}_{HE}$, where σ_P^2 is the phenotypic variance, σ_E^2 is the variance due to environment, and σ_H^2 is the variance due to heredity. Again, if there is no correlation between heredity and environment, the observed phenotype is the result of adding the effects of heredity and environment. Heritability, in the broad sense, becomes the proportion of the phenotypic variance that is due to hereditary differences between the individuals concerned (heredity meaning the combination of genes, or genotype, of an individual measured in terms of their effects on the phenotype). Hence, heritability (h^2) is the ratio $\frac{\sigma_H^2}{\sigma_H^2 + \sigma_E^2}$ (Lush, 1948). From this, it can be seen that h^2 can range from zero to one in value. Any change in either σ_H^2 or σ_E^2 will change h^2. Any circumstance which increases σ_E^2 will tend to decrease h^2.

Genetic variance is that which can be attributed to differences in genotype. Heritability then depends upon how much more alike are relatives, than randomly selected individuals, because of greater similarity in genotypes of the relatives. Within certain limits, it really makes very little difference what absolute numbers of genes are alike and unlike. The interest lies in the proportion of like genes possessed by relatives that are unlike in the average of the population.

Jerome et al. (1956) presented some interesting illustrations showing the source of genetic variance. To best appreciate the illustration, assume a population which has so many alleles at a given locus that in random mating no identical allele will occur in the various matings involved in this illustration.

Sire genotype	Dam 1 genotype	Dam 2 genotype
A_1A_2	A_3A_4	A_5A_6

Progeny of Dam 1: A_1A_3, A_1A_4, A_2A_3, A_2A_4

Progeny of Dam 2: A_1A_5, A_1A_6, A_2A_5, A_2A_6

From the genotypes of the above paternal half sibs, a comparison is made to show the number of gene pairs between half sib groups identical by descent.

	A_1A_5	A_1A_6	A_2A_5	A_2A_6
A_1A_3	1	1	0	0
A_1A_4	1	1	0	0
A_2A_3	0	0	1	1
A_2A_4	0	0	1	1

The total number of genes present is 32. The total number of genes identical between half sib groups is eight. Thus, the average fraction of genes identical by descent between half sibs is one-fourth. Therefore, on the average, one-fourth of the genes in a group of half sib offspring from heterozygous parents are alike because of descent. If this group of half sib offspring would be compared with a similar group sired by a different male, one-fourth of the additive genetic variance (σ_G^2) would be due to the difference between sires. It may be noted that, as no more than one identical gene per comparison occurs, transmitted dominance does not occur. The same things apply to dams. Therefore one-fourth of the σ_G^2 is due to sires, and one-fourth σ_G^2 is due to dams. The remaining one-half σ_G^2 is accounted for by sampling at meiosis. This will be shown by a comparison between full sibs.

Sire genotype: A_1A_2 Dam genotype: A_3A_4

Progeny genotype: A_1A_3, A_1A_4, A_1A_3, A_1A_4,
A_2A_3, A_2A_4, A_2A_3, A_2A_4

Full sib comparisons showing the number of gene pairs identical by descent follow.

	A_1A_3	A_1A_4	A_2A_3	A_2A_4
A_1A_3	2	1	1	0
A_1A_4	1	2	0	1
A_2A_3	1	0	2	1
A_2A_4	0	1	1	2

For this group of full sibs there are 16 identical gene pairs. Therefore, one-half the additive genetic variance is contained within full sibs. Also, eight of the identical pairs are identical at both alleles. This will allow 8/32 of the parental dominance to be expressed by the progeny.

The above illustration can be expanded to include many locus sites with the same conclusions concerning additive genetic variance. Li (1955) derived the additive genetic variance using the binomial theorem. For discussions concerning non-additive genetic variance, the reader is referred to Lush (1948), Lerner (1958), and Jerome _et al_. (1956).

Jerome _et al_. (1956) have shown, from simple Mendelian genetic theory, that the additive genetic variance in a population mating at random is derived as follows; one-fourth from the sires, one-fourth from the dams, and one-half from sampling at meiosis. Under random environment for all individuals, the variance among full sibs (σ^2) contains all of the environmental variance (σ^2_E) in addition to one-half the additive genetic variance ($\sigma^2_G/2$). By definition, h^2 in the narrow sense equals $\sigma^2_G / (\sigma^2_G + \sigma^2_E)$.

Then

$$\hat{h}^2_S = \frac{4\hat{\sigma}^2_S}{\hat{\sigma}^2_S + \hat{\sigma}^2_D + \hat{\sigma}^2} , \text{ where}$$

$\hat{h}^2_S$ = an estimate of heritability based on the sire component of variance,

$\hat{\sigma}^2_S$ = an estimate of the sire component of variance,

$\hat{\sigma}^2_D$ = an estimate of the dam component of variance,

and $\hat{\sigma}^2$ = an estimate of the variance between full sibs of one batch.

In addition,

$$\hat{h}^2_D = \frac{4\,\hat{\sigma}^2_D}{\hat{\sigma}^2_S + \hat{\sigma}^2_D + \hat{\sigma}^2},$$

where $\hat{h}^2_D$ = an estimate of heritability based on the dam component of variance,

and

$$\hat{h}^2_{(S+D)} = \frac{2\,(\hat{\sigma}^2_S + \hat{\sigma}^2_D)}{\hat{\sigma}^2_S + \hat{\sigma}^2_D + \hat{\sigma}^2},$$

where $\hat{h}^2_{(S+D)}$ = an estimate of heritability based on the average of the sire and dam variance components.

Fredeen (1953) points out that the reliability of h^2_S depends upon; (1) the number of degrees of freedom available for the estimation of σ^2_S, (2) the contribution made to the sire component of variance by epistasis, (3) the validity of the assumption concerning random mating, and (4) the magnitude of environmental correlations between paternal half sibs. Also, the amount by which the estimate of $h^2_{(S+D)}$ exceeds the estimate $\hat{h}^2_S$ provides some measure of the importance of dominance and/or environmental correlations between full sibs.

EXPERIMENTAL PROCEDURE

Experimental Material and Methods

This study was conducted through five generations and five hatching seasons; the two were completely confounded. That is, no part of any one generation was used more than one year. Presented herein by generations are the means for both the unselected offspring generations and the selected parents. Results are also presented from another phase of the study comparing the inter- and intra-sire performance of the offspring (pullets) from the selected fourth generation birds. Heritability estimates obtained from an analysis of variance of the four groups of the unselected fifth generation pullets are included in the report.

The experimental material used in this study was a group of New Hampshires that had been a closed flock under selection for body weight, mortality, egg production, and egg quality values for a number of years. Inbreeding had been avoided as much as possible (Brunson, 1955). The initial population consisted of 930 daughters from 16 sires and 150 dams. These daughters were then tested for hatchability and fertility by being mated to a random sample of intra-line males in the fall. In the spring of 1955 these daughters were separated into three groups, known as Line 1, Line 2, and Controls. Preliminary $\hat{h}^2$ of hatchability of all eggs set averaged 9 percent based on a single egg per pullet and about 25 percent when based on about 14 eggs per pullet and an average of 6.4 daughters per dam family (Godfrey _et_ _al_., 1955). On the basis of these heritability estimates, family selection was indicated as the preferred breeding method to improve hatchability. In the fall of 1955, 731 pullets of Lines 1 and 2 and 300 Control pullets were housed and tested. From this, 10 sires and 70 dams were selected to continue both lines.

Essentially, the same procedure was followed the next year. In September of 1957, 820 pullets from Lines 1 and 2 and 100 pullets of the Control stock were housed. Lines 1 and 2 were tested and females of outstanding performance from superior families were selected for the individual male breeding pens.

Inter-line crosses were also made from these dams the following spring. Two hatches each were made from the inter- and intra-line matings. The egg production obtained in two weeks was used for all hatches. The inter-line chicks hatched February 27 and March 12, 1958. As soon as the last eggs for the second hatch were collected, the cross-matings were made by switching the Line 1 and Line 2 males. Two weeks later, paternity was credited to the new males. The cross-mated progeny hatched April 9 and April 23. Therefore there was a time differential between the inter- and the intra-line offspring of four, six, and eight weeks, according to which hatches are compared.

The pullets, then, were of four kinds. Besides the Lines 1 and 2, the Line 1 males X Line 2 females-cross was designated as Line 4, and its reciprocal, Line 3.

The Line 1 and Line 2 pullets were housed together, but separated by hatches. The Line 3 and Line 4 pullets were also housed together, but separated by hatches. The pullets were all mated to random samples of intra-line males, and as they reached the uniform age of 200 days were tested on "hatching power of eggs". Two hatches of two weeks' eggs each were then made to test these pullets. These test results are reported as the average of both hatches.

Prior to transferring, the eggs were candled. All "clears" were broken out and macroscopic examination provided the basis for classifying the eggs as either infertile or dead germ.

Method of Obtaining Heritability Estimates

The method used to obtain the heritability estimates is based upon certain variance components calculated from an analysis of variance. The statistical model given by King and Henderson (1954) was

$Y_{hijk} = \mu + A_h + S_{hi} + D_{hij} + \epsilon_{hijk}$, where

μ = the overall mean (a constant),

A_h = the h^{th} hatch effect,

S_{hi} = the effect of the i^{th} sire in the h^{th} hatch,

D_{hij} = the effect of the j^{th} dam mated to the i^{th} sire in the h^{th} hatch,

ϵ_{hijk} = the effect of the k^{th} progeny of the j^{th} dam mated to the i^{th} sire in the h^{th} hatch,

and Y_{hijk} = the record of the k^{th} progeny of the j^{th} dam mated to i^{th} sire in the h^{th} hatch.

In addition, σ_A^2 = the hatch variance component,

σ_S^2 = the sire in hatch variance component,

σ_D^2 = the dam in sire in hatch variance component,

σ^2 = the variance between full sibs of one hatch, where

$\sigma_A^2 \sim$ NID $(0, \sigma_A^2)$,

$\sigma_S^2 \sim$ NID $(0, \sigma_S^2)$,

$\sigma_D^2 \sim$ NID $(0, \sigma_D^2)$, and

$\sigma^2 \sim$ NID $(0, \sigma^2)$, with

$\sigma_A^2 = \sigma_S^2 = \sigma_D^2 = \sigma^2$ also being assumed. There are n_{hij} progeny in each dam within hatch subclass. Thus

$\sum_h\sum_i\sum_j n_{hij} = N$. The analysis of variance, with notation appropriate to the general case, for this model is presented in Table I.

King and Henderson (1954) pointed out that although the model used is appropriate for a hierarchical classification with unequal numbers, hatches are factorially arranged while the other elements are indeed hierarchical. They infer that basing the analysis on the incorrect model is permissible for their purposes. Their reasoning seems to be that fairly good estimates of heritability can be obtained by this model.

These data were analyzed by the hierarchical model. Computations were made by using the IBM 650 high speed computer. Pulley's (1959) program was utilized for this analysis. It was designed for this type of analysis. Estimates of the variance components were then obtained from the mean squares.

Although the number of pullet records available for analysis averaged approximately 355 for all four groups, the number actually making up the analysis was less than the total of each line. No records were included in the analysis if less than five eggs were set. For this reason, 53 records out of 369 pullets in Line 1 were not used, 26 were left out of 395 Line 2 pullets, 52 were left out of 361 Line 3 pullets, and 46 were left out of 334 Line 4 pullets. Although this restriction of five eggs with the potential to hatch (fertile eggs) was imposed for

TABLE I

ANALYSIS OF VARIANCE FOR HIERARCHICAL CLASSIFICATION[1]

Source	d.f.	S.S.	M.S.	Coefficients of variance components E(MS)				
Total	$N-1$	TSS		σ_E^2	σ_D^2	σ_C^2	σ_B^2	σ_A^2
A	$a-1$	SSA	$\frac{SSA}{a-1}$	1	a_3	a_4	a_5	a_6
B in A	$\sum_i b_i - a$	SSB	$\frac{SSB}{\sum_i b_i - 1}$	1	b_3	b_4	b_5	
C in B	$\sum_i \sum_j c_{ij} - \sum_i b_i$	SSC	$\frac{SSC}{\sum_i \sum_j c_{ij} - \sum_i b_i}$	1	c_3	c_4		
D in C	$\sum_i \sum_j \sum_k d_{ijk} - \sum_i \sum_j c_{ij}$	SSD	$\frac{SSD}{\sum\sum\sum d_{ijk} - \sum\sum c_{ij}}$	1	d_3			
E in D	$N - \sum\sum\sum d_{ijk}$	SSE	$\frac{SSE}{N - \sum\sum\sum d_{ijk}}$	1				

Assume there are a A units, each with n_i samples ($\sum_i n_i = N$); each A unit has b_i B units, each B unit having n_{ij} samples; each B unit has c_{ij} C units, each C unit having n_{ijk} samples; each C unit has d_{ijk} D units, each D unit having n_{ijkl} samples; each D unit has e_{ijklm} E units, each E unit being a sample.

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[1] Pulley (1959)

analyzing the hatch of fertile eggs, no additional records had to be left out for this reason.

The average zygotic inbreeding coefficient for the generation was computed by Wright's F (for details and bibliography concerning this procedure, consult Lerner, 1958). The 1955 generation was taken as the zero base for computing F. The F value for both lines was approximately five percent. The heritability estimates were then corrected for inbreeding by the formula $\frac{(1 + F)h^2}{1 + Fh^2}$ as given in Lerner (1958).

RESULTS AND DISCUSSION

Results from the selection phase of the experiment are presented in Table II. This was conducted by applying selection pressure for the same traits through four generations. The mean fertility and hatch of fertile eggs percentages of the three groups, Line 1, Line 2, and Controls, are listed by generations. As the generations are completely separate, they are identified by year. The data listed under "Spring-Breeders" were obtained from the hatches which produced the next generation. All live pullets were then housed in the fall and flock-mated to test for hatching performance. This performance is given under "Fall-Total Offspring Generation". From this test the parents of the next generation were selected. For the purpose of comparison, the record made by those breeders is also presented. The difference between analogous elements under "Fall-Selected to be Breeders" and "Fall-Total Offspring Generation" is a measure of the selection differential of each generation.

As the population was not separated into different breeding groups until Spring 1954, the performance for all groups was identical that year. The percentage fertility of the breeders in the spring exhibited a trend of higher performance each year, including the Control group. The average fertility of Lines 1 and 2 moved from 88.8 percent in 1954 to 97.8 percent in 1958. The two selected lines averaged approximately one to two percent higher fertility each spring than the Controls. The performance in percentage hatch of fertile eggs for all three groups

TABLE II

PERFORMANCE IN SELECTED TRAITS BY GENERATIONS

Generation:	1954			1955			1956			1957			1958		
Line:	1	2	Con.	1	2	Con.	1	2	Con.	1	2	Con.	1	2	Con.
Spring-Breeders															
% F:[1]	88.8	88.8	----	93.8	94.2[2]	90.9	95.9	97.9	93.4	95.5	97.0	94.0	97.6	98.1	96.8
% H of F:[3]	83.6	83.6	----	88.5	89.0[2]	88.6	80.5	75.4	76.7	93.4	90.7	85.7	90.6	90.5	88.5
Fall-Total Offspring Generation															
% F:[1]	----	----	----	96.8	94.2	95.2	94.9	95.1	94.7	98.8	99.4	95.8	97.6	97.6	92.1
% H of F:[3]	----	----	----	89.7	87.6	91.1	93.8	94.1	88.8	91.0	90.9	89.9	90.6	92.8	82.7
Fall-Selected to be Breeders															
% F:[1]	99.4	99.6	----	99.9	99.3	95.2	99.0	98.7	94.7	99.7	99.6	95.8	99.3	97.6	92.1
% H of F:[3]	97.8	97.6	----	97.4	96.7	91.1	98.2	97.9	88.8	96.2	97.1	89.9	99.2	99.9	82.7

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[1] % F = percentage fertility.

[2] One pen, number 32, was left out of these data, as fertility was approximately 5%.

[3] % H of F = percentage hatch of fertile eggs.

varied rather markedly from year to year. The average performance of the two selected lines, however, is approximately one to two percent higher than the Control group each year. It will also be noted that the performance of the selected lines averaged 83.6 percent hatch of fertile eggs in 1954 and 90.6 percent in 1958.

An important criterion of the effectiveness of selection experiments is the performance of the unselected, or total, offspring generation. The average fertility for the selected groups is very similar to that of the Control group through 1956. A spread of approximately one and two percent for the 1957 and 1958 generations, respectively, appeared in fertility between the selected lines and the Controls. The first offspring generation after selection was begun, 1955, the Controls averaged approximately 2.5 percent greater hatch of fertile eggs than the average of Lines 1 and 2. After this first generation, the selected groups performed better than the Controls in this trait. The amount by which the selected groups exceeded in percentage hatch of fertile eggs was one to nine percent each year.

The percentage fertility exhibited in the fall by all three groups that were selected to be breeders is relatively high through all five generations, averaging approximately 98 percent. The difference in performance between the Controls and the selected lines averaged approximately four percent, although the Control breeders declined so that there was a difference of 6.3 percent the last generation. The selected lines also performed better in respect to percent hatch of fertile eggs. This difference was approximately 5.5 percent until the last generation, 1958, when a difference of 16.9 percent appeared.

The data presented in Table II indicate a trend for the birds under selection pressure to improve their performance during the duration of this study. This rather slow but, in general, consistent improvement is accompanied by the reverse trend in the group that was mass-mated, without any artificial selection having been applied.

Any interpretation of the results of this study which includes a comparison of different generations should be made with caution. This is because the environmental conditions may vary from year to year. Some possible sources of variation which would be confounded with generations are: weather, ration, housing, disease, and whether an egg which was "clear" upon candling was called infertile or dead embryo when broken out by different personnel. The difficulty imposed by yearly environmental variations may be somewhat alleviated by also considering the Controls. The possibility of gene drift in the Controls is also present.

The writer's interpretation is that the trend for the selected lines to be superior in performance to the unselected group is representative of the results of genetic improvement due to breeding.

In Table III are presented various heritability estimates based on variance components. For the two traits, percentage fertility and percentage hatch of fertile eggs, all data were analyzed using the original percentage values and also the transformation arcsin $\sqrt{\text{percentage}}$ values. Since the possibility of hatch effect was indicated, all data were subjected to a separate analysis of variance for each hatch as well as an analysis of variance which included both hatches.

The heritability estimates for percentage fertility ranged from -0.251 to 1.420. The mean of the heritability estimates for fertility in the intra-line birds, designated as Lines 1 and 2 in Table III, is

TABLE III

HERITABILITY ESTIMATES BASED ON VARIANCE COMPONENTS

Line	Hatch[1]	% Fertility			Arcsin $\sqrt{\%\text{ Fertility}}$		
		h^2_S	h^2_D	$h^2_{(S+D)}$	h^2_S	h^2_D	$h^2_{(S+D)}$
1	H1	.130	1.420	.800	.088	.146	.333
1	H2	-.021	.458	.222	-.012	.246	.117
1	H1 & 2	.026	.724	.382	.024	.338	.182
2	H1	.124	.748	.441	.087	.466	.279
2	H2	.030	-.251	-.110	.053	-.116	-.032
2	H1 & 2	.052	-.055	.000	.064	.063	.063
3	H3	.079	.242	.161	.161	.009	.085
3	H4	-.131	.099	-.016	-.163	.532	.184
3	H3 & 4	-.079	.429	.175	-.019	.302	.142
4	H3	.165	-.181	-.008	.188	.053	.121
4	H4	-.212	.410	.099	-.203	.296	.046
4	H3 & 4	-.061	.254	.097	-.018	.223	.102
		% Hatch of F[2]			Arcsin $\sqrt{\%\text{ Hatch of F}}$		
1	H1	-.080	.378	.076	-.125	.234	.056
1	H2	-.061	.414	.179	.008	.184	.096
1	H1 & 2	-.072	.325	.129	-.056	.208	.077
2	H1	.321	-.004	.034	.198	.211	-.006
2	H2	.100	.061	.081	.236	.065	.151
2	H1 & 2	.213	-.004	.068	.219	-.050	.085
3	H3	.092	.122	.107	.108	.438	.273
3	H4	-.127	-.383	-.255	-.252	.268	.008
3	H3 & 4	-.102	.330	.114	-.023	.092	.034
4	H3	.176	-.000	.088	.113	.243	.178
4	H4	-.090	.748	.329	-.044	.419	.094
4	H3 & 4	.096	.175	.136	.054	.287	.170

[1] H1, H2, H3, H4, H1 & 2, and H3 & 4 = h^2 estimated from variance components obtained from an AOV of hatch 1, hatch 2, hatch 3, hatch 4, hatches 1 and 2 combined, and hatches 3 and 4 combined, respectively.

[2] % Hatch of F = percentage hatch of fertile eggs.

0.284. The mean of the heritability estimates for fertility in the inter-line offspring, designated as Lines 3 and 4 in Table III, is 0.085. The transformed data produced heritability estimates with means of 0.132 and 0.114 for the intra- and inter-line offspring, respectively. The range of the heritability estimates using transformed data was only -0.203 to 0.406.

The arcsin transformation not only stabilizes the variance (Federer, 1955) but also seemed to lower the range in the heritability estimates. The result of the transformation was that, in general, the higher heritability estimates were reduced somewhat and some of the lower estimates were raised. Using the transformed data, the means of the heritability estimates for fertility were approximately 0.13 in the Lines 1 and 2, and 0.11 in the Lines 3 and 4.

The mean heritability estimates for hatchability, using transformed data, were approximately 0.10 in the Lines 1 and 2, and approximately 0.14 in the Lines 3 and 4. It will be noted that transforming the data to degrees again decreased the range of the $\hat{h}^2$ obtained. The $\hat{h}^2$ for percentage hatch of fertile eggs had a range of -0.383 to 0.748, while the $\hat{h}^2$ of the transformed data was only -0.252 to 0.438. When it is recalled that the percentage data produced one obviously incorrect $\hat{h}^2$ of 1.420, it would appear that, with these data at least, h^2 estimated from variance components might be more meaningful when percentages are transformed to degrees.

Brunson (1955) found that a rather large maternal effect was present in the dam's contribution to the variance. He stated that any heritability estimates based on the dam or combination of sire and dam variance components will be in excess of the true estimate. Further, heritability estimates based on the sire components of variance would more accurately reflect the true additive genetic variance.

From this experiment, the heritability estimates for fertility from transformed data based on the sire component averaged 0.05 for Lines 1 and 2, and zero (negative 0.009) for Lines 3 and 4. These same values for hatchability averaged 0.08 for the Lines 1 and 2, and also zero (negative 0.008) for the Lines 3 and 4. King and Henderson (1954) pointed out that a difference between the two estimates might also be accounted for by the greater selection differential on the males.

A definite hatch effect in these data was indicated by the variation between analogous heritability estimates obtained from different hatches. Even so, the heritability estimates for the traits studied in this experiment are of the magnitude which indicates that the family selection method is preferred. Lerner (1958) is cited for a more thorough discussion. Also, any interpretation of these heritability estimates should be made with the realization that the variance components used were obtained from an analysis based on a mathematical model that did not allow for the presence of any sire-hatch interaction. A possibility of S X H interaction is shown by the crossing of the lines in the graph which follows. Since lines crossed in seven of the eight comparisons, only one comparison was illustrated here.

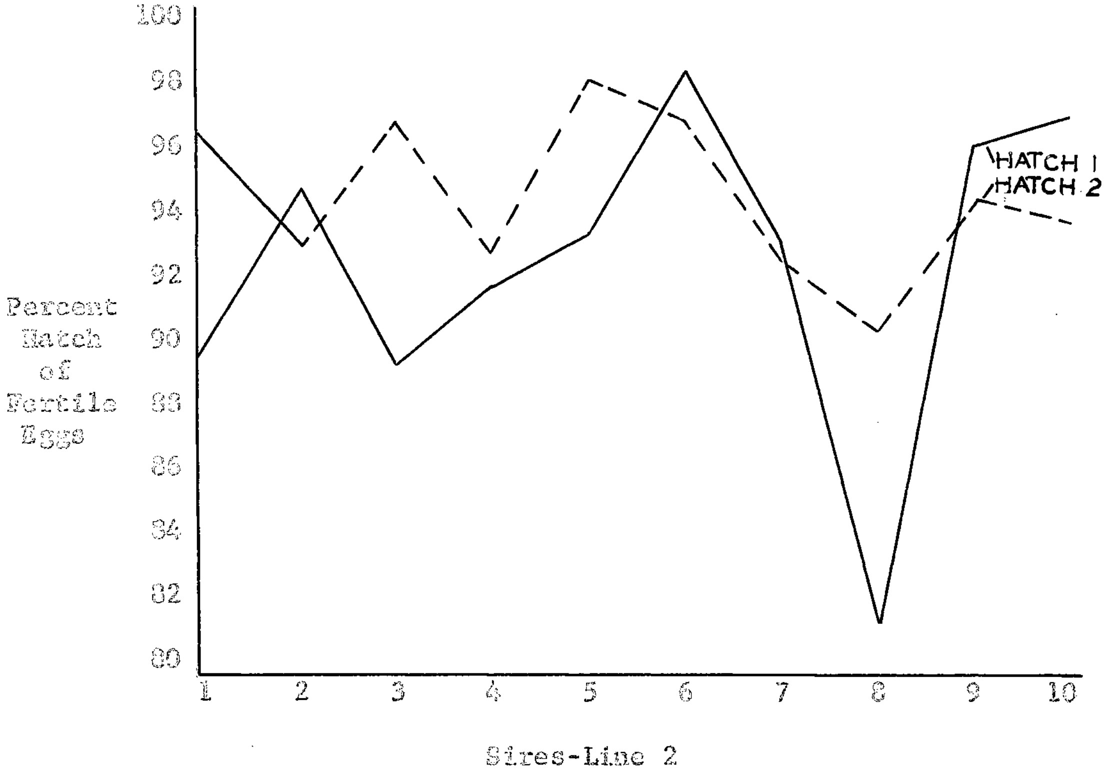

Figure 1. Graph of Sire X Hatch Interaction

In Table IV are presented the results of an intra-sire comparison in fall performance of Intra- and Inter-line offspring. The average fertility of the two groups of Inter-line offspring was approximately one percent higher than the average of the Intra-line offspring. The average hatch of fertile eggs of the Inter-line offspring was approximately 3 percent higher than the average of the Intra-line offspring. Also, in all cases, the offspring from Line 2 sires (Y) exhibited superior performance.

No statistical test was applied to these data because, as pointed out earlier, there was a difference in hatch dates between the Inter- and Intra-Line offspring. However, the writer's interpretation of these data is that the advantage of the line-crossed chickens is probably real. Experimental evidence that crossing tends to improve the traits which make up hatchability has been presented earlier.

TABLE IV

INTRA-SIRE COMPARISON IN FALL PERFORMANCE OF INTRA-LINE AND INTER-LINE OFFSPRING

	% Fertility		% Hatch of Fertile	
Sire	Intra-	Inter-	Intra-	Inter-
D30-5	97.9	97.7	94.4	91.9
D47-3	96.6	95.2	93.4	95.8
D30-10	96.8	95.7	90.4	91.4
D3-3[1]	95.0	----	91.6	----
D45-4	92.3	95.7	94.0	95.7
D54-13	97.2	95.4	88.4	92.6
D59-12	92.3	95.4	92.1	96.1
D72-8	92.2	97.9	91.1	96.0
D31-9	94.1	98.9	86.6	96.6
D48-7	93.3	98.3	85.9	94.0
Average	94.8	96.7	90.8	94.4
Y32-15	96.9	97.8	97.1	95.1
Y47-2	98.6	97.2	94.6	95.4
Y7-12[1]	98.1	----	94.8	----
Y5-1[1]	98.2	----	93.9	----
Y2-5	98.1	99.3	93.1	96.8
Y39-17	98.4	95.9	92.5	93.3
Y76-7	95.3	98.8	94.8	96.8
Y11-9	96.6	96.8	92.3	94.4
Y20-9	99.0	98.1	86.9	94.8
Y44-4	97.2	98.9	85.8	93.8
Y45-1[1]	----	97.5	----	96.0
Average	97.6	97.8	92.6	95.2

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[1] As these males did not produce both kinds of offspring because of death or other reasons, none of their offspring's performance is used in obtaining the average.

SUMMARY AND CONCLUSIONS

Three different phases of an investigation involving hatchability, fertility, and outbreeding were conducted with New Hampshire chickens. (1) The selection phase was conducted by applying selection for fertility and hatchability on a closed flock which was split into two separate lines for four generations. A Control (no selection) line was also maintained. (2) The outbreeding phase was conducted by crossing, at the fourth generation, the two lines that had been under selection pressure. (3) Heritabilities were estimated by using variance components of the performance records of each of the four groups (Line 1, Line 2, and their crosses) of approximately 350 pullets each.

The conclusions resulting from these data are as follows:

1. The performance of the selected lines was superior to that of the control line. This was due to the trend of improved performance exhibited by the selected lines, accompanied by the reverse trend in the control line.
2. The progeny resulting from the inter-line matings performed better than their intra-line half sibs.
3. The heritability estimates obtained were of the magnitude that would suggest that family selection is the preferred method. Definite indications of hatch effect were found. A possibility of Sire X Hatch interaction was also present. Further, heritabilities estimated from variance components might be more meaningful when percentages are transformed to degrees.

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