Egg Production Rate and Fertility in Inbred Chickens*

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(Received for publication April 9, 1948)

THERE has been an increasing amount of interest in inbreeding and hybridizing chickens which has become an important phase in many poultry breeding programs. The effect of inbreeding on the reproductive capacity of chickens influences the decision concerning the following: number and size of the inbred lines, ways of testing inbred lines, rates and ultimate levels of inbreeding and eventual commercial use of the surviving lines. As an example, if reproductive capacity is not greatly reduced, the most efficient methods will tend toward starting with many small lines, using intense inbreeding carried to high levels, practicing intense selection between lines continuously, and expanding the surviving lines rapidly in order to test in crosses. On the other hand, if reproductive capacity is greatly reduced, selection within lines would be emphasized instead of selection between lines. The lines would need to be larger and the process of making and testing lines would be slower.

Reproductive capacity is the product of four components: (1) egg production during the hatching season; (2) fertility; (3) hatchability, and (4) viability of offspring. A large reduction in any one of those factors seriously reduces reproductive capacity because the four components act multiplicatively to produce the replacements necessary to maintain inbred lines. Traits that are most seriously affected by inbreeding may require particular emphasis in selection. Likewise, traits possessing high heritability are capable of more improvement by individual selection.

This paper deals with the first two factors concerned in maintaining the reproductive capacity of inbred lines. Its purpose is to report estimates of heritability, the change in the traits with inbreeding and the amount of selection actually practiced during the maintenance of inbred lines of White Leghorns over a ten-year period. A subsequent paper will treat hatchability and viability of chicks.

REVIEW OF LITERATURE

Egg production expressed in percentage production over a short period is described as gross rate or intensity. A correlation of $+.48 \pm .01$ between winter rate and annual egg production was reported by Hays and Sanborn (1927). Lerner and Taylor (1943) gave the minimum estimate of heritability for rate of production as 16.1 percent under random mating. Their figure pertained to differences between means of families of four or more full sisters. Jull (1935) reported that fertility records of dams and daughters were significantly correlated in Rhode Island Reds, but not in White Leghorns or Barred Plymouth Rocks. Hays and Sanborn (1939) found the correlation between

* Journal paper No. J-1532 of the Iowa Agricultural Experiment Station, Ames, Iowa. Project No. 54.

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dam's and daughters's records of fertility to be +.02±.02 in Rhode Island Reds.

The effect of inbreeding on the rate of production was studied by Jull (1933), who found the rate of egg production decreased with inbreeding and by Hays (1924), who found that winter egg yield showed a tendency to decline after inbreeding coefficients exceeded 25 percent.

The published data concerning the influence of inbreeding on fertility were not so conclusive. No change in fertility due to inbreeding was observed by Cole and Halpin (1916). Jull (1933, 1939) found that inbred matings had higher fertility than did intercrossed matings. Waters and Lambert (1936) reported that no general decrease in fertility was noticed. Some families showed increased fertility.

EXPERIMENTAL MATERIAL

The data for the present study were obtained from the Iowa Agricultural Experiment Station's Poultry Section and were collected over a period of ten years (1936 to 1945) on birds in the inbreeding project.

Lines were not intentionally discarded but some were lost because of poor reproductive performance. When a line seemed near extinction it was crossed with another related line and continued in this manner. One of the lines was outcrossed in 1939 and 1940 so that it might be continued.

Since lines that became extinct were not included in the analysis, the number of them is larger in the more recent years. The number of lines as indicated by the number of sires used each year from 1936 through 1944 were 6, 8, 8, 10, 9, 10, 10, 13 and 13, respectively.

Egg production rate was calculated from the number of eggs set, divided by the number of days that eggs were saved for setting. There was little, if any, selection against small egg size, once the breeding pens were mated.

Generally, the hatching season lasted from January to June. Eggs were set each week in a forced draft incubator equipped with a separate hatcher. On the 18th day the eggs were individually candled and classified. The eggs classified as being dead germs or infertile were broken out to determine more accurately the date of embryonic death in 1938, 1939, and 1940. In other years the fertility and date of embryonic death were estimated by candling. The mating's total for all weeks of the hatching season constituted the fertility record.

If the male died or showed infertility to a high degree he was replaced. For this reason some females were mated to two or (in a few cases) three different males in one season. Hens producing less than ten eggs during the breeding season were not included in the study because of the discontinuity of percentage data when the numbers are small.

METHODS OF ANALYSIS

Inbreeding coefficients were calculated according to the method of Wright (1922). The inbreeding coefficients, rate of production and fertility were expressed as percentages.

A preliminary analysis of seasonal effects on infertility, hatchability and hatch of total eggs was made on the 1945 data. Since the preliminary analysis indicated there were no *general* weekly or seasonal trends, the entire record for the season was combined in the remaining analyses.

Regressions of egg production rate and fertility on inbreeding of the dam and on inbreeding of the offspring were computed on an intra-year, intra-sire basis because both yearly and sire effects were large. Partial regression coefficients for each of the two traits on the inbreeding of the offspring, taking into account the inbreeding of the dam, were calculated by the method given by Snedecor (1946). Partial regression coefficients were also calculated for each of the traits on the inbreeding of the dam independent of the inbreeding of the offspring.

Heritability estimates were based on the regression of offspring on dam as suggested by Lush (1940). The correlation between relatives is affected by the amount of inbreeding and by other aspects of the breeding structure of the population. These correlations were considered as if each of two widely different sets of conditions had prevailed. The first is that the population from which the data came had been produced by random mating, in which case no correction for inbreeding is used. The second is that the population consisted of partially inbred but unrelated and unselected lines, such as might theoretically be derived by inbreeding without selection from an originally random bred foundation. In that case correcting the observed regression for inbreeding actually practiced yields an estimate of heritability of individual differences applicable to the foundation population prior to inbreeding. The actual population from which the present data came was somewhat intermediate between these two conditions.

The average inbreeding of the hens which laid the eggs was 34 percent. But there had been some selection between inbred lines and most of the surviving lines were related to each other. The inbreeding would have increased the correlation between relatives but the discarding of lines and the relationship of the surviving lines would have decreased it. The relationship between five of the lines, according to Maw (1942), was between 30 and 60 percent. Under these circumstances, the only feasible method was to calculate heritability for each of the two rather extreme conditions described above. The estimates described as "adjusted for inbreeding" are probably underestimates, since this method neglects the reduction in genetic variance which almost surely resulted from discarding some lines. Those made without adjusting for inbreeding are almost surely overestimates of heritability of the individual differences that still remained in this population because the effect of the inbreeding was to make full sibs and other relatives more alike genetically. But the latter are not necessarily overestimates of heritability in the original foundation stock. Conceivably the effect of selection between lines could have reduced the observed correlations more than the inbreeding increased them.

Using path coefficients methods of Wright (1921), the correlation of offspring and dam shown in Figure 1 can be interpreted as

$$b_{popd} = \frac{g^2}{2} \frac{(1+f''+2f')}{\sqrt{(1+f')(1+f'')}} . \quad (1)$$

This formula was deduced with the assumption that there were no environmental tendencies which caused egg production or fertility of dam and offspring to be alike or unlike. When inbreeding is omitted, the interpretation of the correlation is $g^2/2$.

The *selection differential* is the average phenotypic superiority of the birds used as breeders over the average of the whole population for the year they were hatched. These were calculated for percentage of egg production and infertility and also for number of eggs and infertiles. To determine the selection differential in a given year (e.g., year 3) the year 3 matings, from which came the males used as breeders to sire the year 4 chicks, were averaged after weighting according to the number of daughters from each male. The same was done for the females used as breeders. The average of all matings for year 3 was subtracted from the average of those selected to be parents. The difference is the selection differential. In the case of egg production rate and fertility, the record of the mating from which breeding birds came was that of the dam. The sire's selection differential for egg production would be the difference between his dam's egg record and the average egg production of the population.

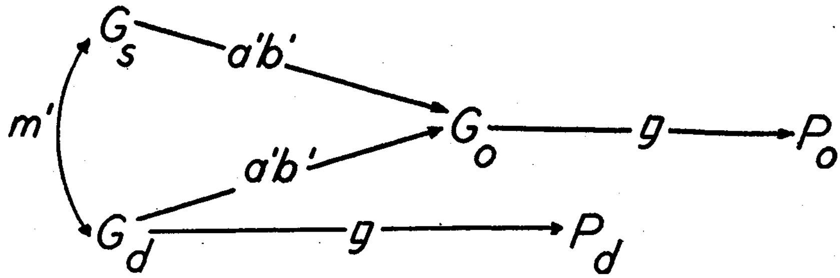

FIG. 1. Path coefficient diagram showing relations between phenotype of offspring and of dam.

RESULTS

The yearly means of the two traits are given in Table 1. The rate of production seemed to vary irregularly from year to year. If the first year's result is omitted, there is a gradual increase in percentage infertility.

Estimates of Heritability

Table 2 shows the results of the regression analysis of daughter on dam. The estimates of heritability for egg production rate and fertility were obtained by applying formula 1.

The regression of daughter's egg production rate on that of her dam when doubled to find the heritability gives an estimate of .42 without allowance for the amount of inbreeding present. When adjusted for the effect of inbreeding the estimate of heritability was .31.

The heritability of rate of egg production was 16 percent for differences between means of families of four or more,

TABLE 2.—*Regression of offspring on dam and estimates of heritability for egg production rate and fertility*

Trait	d.f.	b	Heritability on individual basis: Unadjusted for inbreeding	Heritability on individual basis: Adjusted for inbreeding
Egg production rate	813	.217	.43	.31
Fertility	813	.052	.10	.06

TABLE 1.—*Means of traits by years* (Percent)

Traits Years	1	2	3	4	5	6	7	8	9	Total
Egg production rate	37.2	37.5	36.6	44.8	50.7	33.1	42.2	47.1	41.0	41.5
Infertility	28.9	10.3	13.8	13.5	17.0	20.1	18.0	26.5	24.2	18.9
Inbreeding, dam	35.5	44.8	43.2	18.2	25.3	28.6	30.3	36.4	38.8	33.5
Inbreeding, offspring	40.6	52.1	41.7	35.9	42.6	45.5	46.7	39.9	46.6	43.5

TABLE 3.—*Simple and partial regressions of traits on inbreeding of dam and of offspring*

Independent variables	Egg production rate	Fertility
Simple regressions		
Inbreeding of dam	−.14±.04	+.11±.04
Inbreeding of offspring	−.06±.05	+.16±.04
Partial regressions		
Inbreeding of dam, independent of offspring's inbreeding	−.22±.06	+.01±.06
Inbreeding of offspring, independent of dam's inbreeding	+.12±.07	+.15±.06

according to Lerner and Taylor (1943). Shoffner (1946) gave the heritability of egg production to 500 days of age as 34 percent. Lerner and Cruden (1948) found heritability of accumulative egg production was nearly constant throughout the year and in the neighborhood of 33 percent.

The estimate of heritability of fertility from regression of daughter on dam was .06 when adjusted and .10 when not adjusted. Previous studies on the inheritance of fertility by Jull (1935) and by Hays and Sanborn (1939) have indicated that heritability was low or non-existent.

An intra-year correlation between rate of production and fertility was +.05±.03. The primary data were in percentages and the number of degrees of freedom was 924.

Table 3 shows the regressions of traits on inbreeding of dams and of offspring. The regressions were calculated on an intra-year, intra-sire basis and are followed by their standard errors. Egg production rate was negatively associated with the inbreeding of the dam. In the partial regression, the regression of egg production rate on the inbreeding of the dam (independent of the inbreeding of the offspring) becomes larger. The partial regression $b_y Fd \cdot Fo$ has a value of −.22±.06.

The partial regression of fertility on the inbreeding of the dam independent of the offspring's inbreeding was +.01±.06 which is much too low for statistical significance.

The selection differentials, given in Table 4 are, according to the interpretation, based on the hen's average. For each year the selection differentials for the sires were weighted and averaged. The same was done for the selection differentials for the dams. Then the two were combined and divided by two. The eight years were likewise averaged to give the results in Table 4.

The intensity of selection was not the same for sires and dams. For egg production the dams of the males had a selection differential of 6.7 eggs and the dams of the females 11.0 eggs. For fertility, the selection differentials were 9.5 and 8.0 percent for the sire and dam, respectively. Figure 2 shows graphically the selection differential in terms of standard deviations. Only once was the selection differential greater than one standard deviation.

DISCUSSION

It is not always clear whether a trait is really characteristic of the mating, the hen, the egg or the chick. The decision about this may greatly influence the re-

TABLE 4.—*Selection differentials from sires and dams combined*

Traits	Years 1	2	3	4	5	6	7	8	Average
Number of eggs	9.3	18.5	11.4	9.2	5.9	9.7	3.6	4.2	9.0
Number of infertile eggs	−6.1	−0.3	−0.2	−0.8	−2.7	−1.5	−4.4	−3.7	−2.4
Egg production rate (percent)	5.8	13.4	9.1	5.5	11.1	10.5	8.2	7.1	8.8
Infertility (percent)	−20.8	−2.6	−3.0	−5.0	−9.8	−7.4	−7.6	−14.0	−8.8

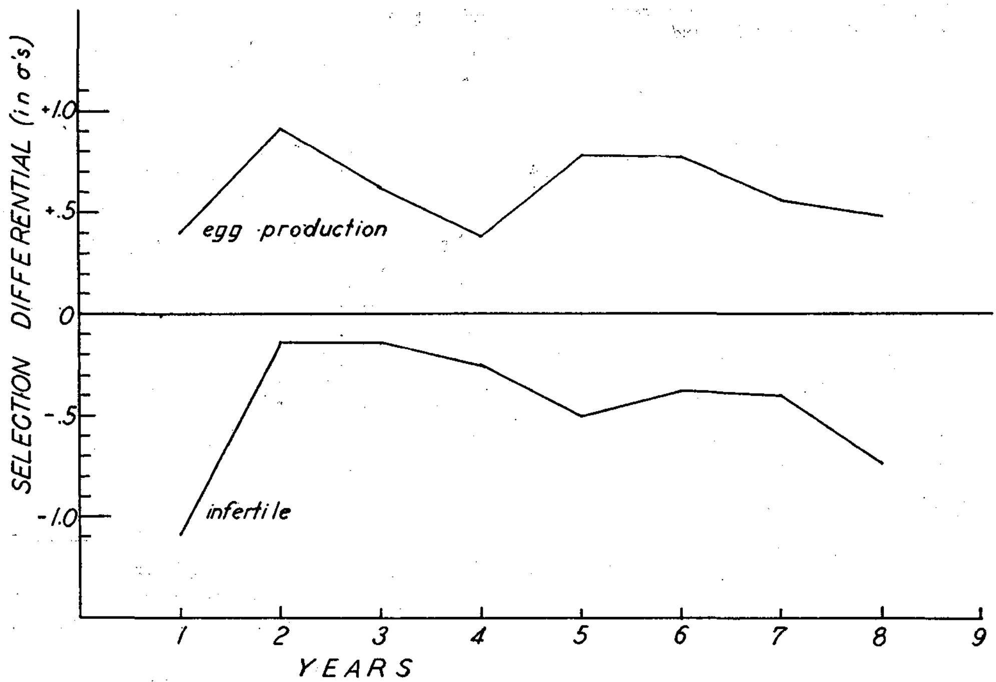

FIG. 2. Yearly selection differentials for egg production and infertility expressed in terms of standard deviations. Year 1 is 1936.

sults obtained in computing heritability and the selection differential. As a simple example of a characteristic which clearly belongs to the dam, rate of egg production is a trait of the individual hen. The hen will lay eggs without being mated to a male. That is, the male does not ordinarily influence the egg production of his mates. An example of characteristics which do not clearly belong wholly to the dam or wholly to the offspring is fertility. If a hen fails entirely to mate with a male the latter makes no genetic contribution and the egg remains a gamete instead of a zygote. Conceivably the cause of the failure to mate could be wholly environmental or it could be due to some real peculiarity of either the hen or the male. That in turn could be genetic or environmental in its causes.

It would appear sounder from the standpoint of biology to consider fertility as a characteristic of the dam. If repeatability is high, there is little reason to suppose that environmental effects which differ from one mating to another, even within the same pen, have important effects on egg fertility. The present data do not seem to offer a basis for estimating the extent to which these differences are environmental in the strictest sense of the word, or are partly caused by effects which the genes of the parents have on their phenotypes and behavior and thus on the fertility of the eggs.

In this study the corrections for inbreeding were based on the average inbreeding coefficients. The irregular mating system of the flock under study was brought about by: (1) crossing of inbred lines, (2) creation of new lines by subsequent inbreeding of birds from crosses between established inbred lines and (3) introduction of new stock into existing inbred lines. The new stock was either random-bred or inbred. When only random-bred stock is considered, certain generalizations may be made. As the result of any one of the above deviations in the mating system, the amount of variance between lines is decreased while that within the lines is increased in proportion to the amount of inbreeding. The correlation between full sibs within lines is increased and the inbreeding coefficient is decreased, as compared with the case where inbred lines are each bred entirely from within the line. It was not possible to estimate the relative effects of these irregularities in the breeding program. There was a hint from the fact that the average inbreeding coefficient of the offspring hcanged only a little over the nine years studied. This would indicate considerable irregularity in the breeding system. In addition, selection between inbred lines was probably a factor that would reduce the variance between lines.

The small postive intra-year correlation between egg production and fertility agrees with the findings of Lamoreux (1940) but is not statistically significant ($+.05 \pm .03$). A positive correlation between these traits would mean that the hen which lays at a rapid rate would lay a higher percentage of fertile eggs. This would result in a larger number of fertile eggs being produced, thereby simplifying the task of maintaining inbred lines.

The partial regression of egg production on the inbreeding coefficient of the dam means that for each increase of one percent in inbreeding, the egg production rate is lowered by 0.22 percent. This means that a line inbred 60 percent woud on the average decrease in egg production rate by $60 \times .22$ or roughly 13 percent. There are no reported results with which to compare this regression, but Hays (1924) and Jull (1933) found a decline in egg production with inbreeding.

Fertility, expressed as percentage, increased with increasing inbreeding although one might expect the reverse. There are a few circumstances that may change the slope of the regression but none that would change it entirely from negative to positive. A condition which would change the slope would be the selection of the more heterozygous individuals for breeders, especially if errors in pedigreeing allowed some hybrids to be produced. If this occurred the selection of the heterozygous individuals would most likely occur. The partial regression of fertility on the inbreeding of the offspring, independent of the dam's inbreeding ($b_{yFo.Fd}$), was larger than the partial regression of fertility on the inbreeding of the dam, independent of the offspring's inbreeding ($b_{yFd.Fo}$). This would appear to be due to the combined effect of sire and dam on fertility.

The selection differentials show what selection occurred in the process of maintaining inbred lines of poultry at Iowa State College. They may serve as a guide for future inbreeding programs. The fact that the selection differential was almost always less than one standard deviation is important in that it demonstrates that the selection practiced was not intense.

SUMMARY

Heritability estimates of individual differences in egg production rate and fertility were calculated from regression of daughter on dam in an inbred flock of White Leghorns. The values unadjusted for inbreeding were .43 and .10 for rate of production and fertility respectively. The values were lower when adjusted for the effects of inbreeding.

The decline in egg production rate re-

sulting from inbreeding is indicated by the regression $-.14 \pm .04$ which would signify an average reduction of 1.4% in egg production rate for each 1% inbreeding. The regression of fertility on inbreeding was practically zero. Partial regressions were also calculated.

Selection differentials when expressed in terms of their standard deviations were small. In only one case did the selection differential exceed one standard deviation.

ACKNOWLEDGMENT

It is a privilege to acknowledge the assistance and the use of unpublished notes of Drs. Jay L. Lush and L. N. Hazel in the preparation of this paper. Dr. Arne W. Nordskog helped check computations and gave many helpful suggestions for which I am grateful. The subject was presented in a more extended form as a thesis to the faculty of Iowa State College in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

REFERENCES

Cole, L. J., and J. G. Halpin, 1916. Preliminary report of an experiment of close inbreeding in fowl. Jour. Amer. Ass'n. Inst. Inv. in Poul. Husb. 3: 7.

Hays, F. A., 1924. Inbreeding the Rhode Island Red fowl with special reference to winter egg production. Amer. Nat. 58: 43–59.

———, and Ruby Sanborn, 1927. Intensity or rate of laying in relation to fecundity. Mass. Agr. Exp. Sta. Bull. 11.

Jull, M. A., 1930. Studies in hatchability. IV. The effect of intercrossing inbred strains of chickens on fertility and hatchability. Poultry Sci. 9: 149–156.

———, 1933. Inbreeding and intercrossing in poultry. Jour. Hered. 24: 37–41.

———, 1935. Studies in fertility in the domestic fowl. Poultry Sci. 14: 37–41.

Lamoreux, W. F., 1940. The influence of intensity of egg production upon infertility in the domestic fowl. Jour. Agr. Res. 61: 191–206.

Lerner, I. Michael, and Dorothy M. Cruden, 1948. The heritability of accumulative monthly and annual egg production. Poultry Sci. 27: 67–78.

———, and L. W. Taylor, 1943. The inheritance of egg production in the domestic fowl. Amer. Nat. 77: 119–132.

Lush, Jay L., 1936. Genetic aspects of the Danish system of progeny-testing swine. Ia. Agr. Exp. Sta. Res. Bull. 204.

———, 1940. Intra-sire correlations or regressions of offspring on dam as a method of estimating heritability of characteristics. Amer. Soc. An. Prod. Proc. 33: 293–301.

Maw, A. J. G., 1942. Crosses between inbred lines of the domestic fowl. Poultry Sci. 21: 548–553.

Shoffner, R. N., 1946. The heritability of egg production. Poultry Sci. 25: 412.

Snedcor, George W., 1946. Statistical methods applied to experiments in agriculture and biology. 4th ed. Sec. 13: 11. Ames, Iowa State College Press.

Waters, Nelson, F., and W. F. Lambert, 1936. Inbreeding in the White Leghorn fowl. Ia. Agr. Exp. Sta. Res. Bull, 202.

Wright Sewall, 1921. Systems of matings. I. The biometric relations between parent and offspring. Genetics. 6: 111–123.

———, 1922. Coefficients of inbreeding and relationship. Amer. Nat. 56: 330–338.