



An evaluation of the ability of three populations of Japanese quail to withstand severe inbreeding  
by Robert Patrick Webb

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

Japanese Quail from the University of California, Davis, and Japanese Quail from Dr. D. Douma, Bozeman, Montana, were crossed to form the foundation stock of Populations I and II while the foundation stock of Population III was made up of birds from the University of California. There were two replications per population. After the foundation stocks were formed, Population I was subjected to alternating generations of out-crossing and full-sib matings within the replications, while Populations II and III were randomly mated. Selection of parent birds in Populations I and II was done on the basis of the dam's egg mass per unit body weight and Population III (controls) was randomly selected. After 13 generations under their various mating systems, all 3 populations were in a non-inbred stage. Eggs set by generation 13 birds were hatched and those keets became generation 0 of the present study. When the keets were 4 weeks of age, they were sexed and full-sib mated. Each replication was assigned 16 mating cages at random. These matings were called families for a total of 32 families per population. After the first generation of full-sib matings, Population I was reduced to 12 families, Population II was reduced to 13 families and Population III reduced to 8 families.

Traits studied were age at first egg, number of eggs laid, number of eggs set, number of fertile eggs set, percent eggs set that were fertile, number of early and late embryonic deaths, percent of early and late embryonic deaths, number of keets hatched per mating, percent hatched, number of keets that died from hatch to 4 weeks of age and percent of keets hatched that died from hatch to 4 weeks of age. It was found that there was inbreeding depression in all traits except embryonic deaths. There seemed to be an inbreeding threshold for the population between 33 and 37.5%. Because this level was reached, the second generation of full-sib matings, the best estimate of the ability of the three populations to withstand severe inbreeding was the results of the first generation of full-sib matings.

In the first generation of full-sib matings, Population I was at a significant advantage over Populations II and III in number of eggs set per mating and hatch, fertility of eggs set and hatchability of eggs set. Population I was also at a significant advantage over Population II in early embryonic deaths. There was no significant difference among the three populations in late embryonic deaths and in post-hatching deaths. Selection in Populations I and II resulted in earlier sexual maturity in generation 0. From this study, it appeared that the alternating generations of outbreeding with full-sib matings within the replications of Population I adapted the population to withstand severe inbreeding better than the two random populations.

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Date May 23, 1972

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JAPANESE QUAIL TO WITHSTAND SEVERE INBREEDING

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ROBERT PATRICK WEBB

A thesis submitted to the Graduate Faculty in partial  
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of

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in

Animal Science

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## ABSTRACT

Japanese Quail from the University of California, Davis, and Japanese Quail from Dr. D. Douma, Bozeman, Montana, were crossed to form the foundation stock of Populations I and II while the foundation stock of Population III was made up of birds from the University of California. There were two replications per population. After the foundation stocks were formed, Population I was subjected to alternating generations of outcrossing and full-sib matings within the replications, while Populations II and III were randomly mated. Selection of parent birds in Populations I and II was done on the basis of the dam's egg mass per unit body weight and Population III (controls) was randomly selected. After 13 generations under their various mating systems, all 3 populations were in a non-inbred stage. Eggs set by generation 13 birds were hatched and those keets became generation 0 of the present study. When the keets were 4 weeks of age, they were sexed and full-sib mated. Each replication was assigned 16 mating cages at random. These matings were called families for a total of 32 families per population. After the first generation of full-sib matings, Population I was reduced to 12 families, Population II was reduced to 13 families and Population III reduced to 8 families.

Traits studied were age at first egg, number of eggs laid, number of eggs set, number of fertile eggs set, percent eggs set that were fertile, number of early and late embryonic deaths, percent of early and late embryonic deaths, number of keets hatched per mating, percent hatched, number of keets that died from hatch to 4 weeks of age and percent of keets hatched that died from hatch to 4 weeks of age. It was found that there was inbreeding depression in all traits except embryonic deaths. There seemed to be an inbreeding threshold for the population between 33 and 37.5%. Because this level was reached, the second generation of full-sib matings, the best estimate of the ability of the three populations to withstand severe inbreeding was the results of the first generation of full-sib matings.

In the first generation of full-sib matings, Population I was at a significant advantage over Populations II and III in number of eggs set per mating and hatch, fertility of eggs set and hatchability of eggs set. Population I was also at a significant advantage over Population II in early embryonic deaths. There was no significant difference among the three populations in late embryonic deaths and in post-hatching deaths. Selection in Populations I and II resulted in earlier sexual maturity in generation 0. From this study, it appeared that the alternating generations of outbreeding with full-sib matings within the replications of Population I adapted the population to withstand severe inbreeding better than the two random populations.

## INTRODUCTION

Inbreeding and its effects on plants and animals has been of interest to geneticists since the discovery of Mendelian inheritance and to breeders and producers since man first domesticated plants and animals. The reasons for this interest are primarily three-fold: (1) fixing of genes at specific production loci, (2) development of specific combining abilities by crossing inbred plants and animals and (3) reduction of deleterious genes in a population. Over the years, there have been many mating systems developed to fix genes at production loci ranging from full-sib matings to more sophisticated systems using less related individuals.

One of the more important recent developments in population genetics is the recognition of an inbreeding effect due to selection (McBride, 1965). Closed random-mated populations have an increase in degree of inbreeding due to limited population size and this increase per generation is equal to  $\frac{1}{2N_e}$  where  $N_e$  is the effective population size (Falconer, 1960). In populations under artificial selection, there is an additional decrease in the effective population size caused by selection of individuals or families to be used for breeding purposes. This additional decrease in the effective population size causes an additional increase in the inbreeding rate of the population. Robertson (1961) has shown that the proportionate decrease in effective population size due to individual selection ( $N/N_e$ ) becomes larger as the squared standardized selection differential and heritability increase. Since the change in

breeding value is also proportional to the selection differential and the heritability, maximizing the population's mean breeding value also means increasing the rate of inbreeding. There seems to be no way out of this dilemma (McBride, 1965).

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

The purpose of this study is to evaluate the ability of three populations of Coturnix coturnix japonica to withstand severe inbreeding after 13 generations under their various mating systems ranging from alternating generations of full-sib matings and wide outcrossing within the population to random mating within the population every generation. The hypothesis being tested is that the population subjected to alternating generations of inbreeding and outbreeding will adapt to inbreeding

more readily than the two random-mated populations.

## LITERATURE REVIEW

In most inbreeding experiments involving plants or animals, the phenomenon of "inbreeding depression" has generally been observed. Traits with low heritabilities have a tendency to show "inbreeding depression", heterosis in crossing and a great sensitivity to environmental fluctuations. McBride (1965) calls these symptoms the low heritability syndrome and they are generally associated with traits which have close connection with reproductive fitness or vigor. Such an association suggests a history of previous selection for the trait, either natural or artificial.

Animal productivity is related to fecundity and viability characters which are of the low heritability type. However, the fact that these characters show heterosis in crossing suggests that it would be desirable to select for low heritability traits between strains and breeds on their ability to produce superior commercial crosses. This would then allow selection within strains to be directed towards the improvement of high heritability characters (McBride, 1965).

### I. Inbreeding in Plants

In considering the effect inbreeding has on plants, the logical choice would be maize, since this plant has been more widely inbred experimentally than any other. Apparently the first inbreeding experiments with maize were those reported by Darwin in 1876. This inbreeding was, however, continued only a single generation, and the results were consequently not very informative. It was not until near the end of

the first decade of the twentieth century that precise data on the effects of inbreeding maize became available as the result of independent work of East (1908) and Shull (1909). The more important effects of continued self-fertilization reported by these investigators has been summarized by Allard (1960) as: (1) A large number of lethal and subvital types appear in the early generations of selfing. (2) The genetic material rapidly separates into distinct lines which show increasing within line uniformity for morphological and functional characteristics, for example, height, ear length and maturity. (3) Many of the lines decrease in vigor and fecundity until they cannot be maintained even under the most favorable cultural conditions. (4) The lines that survive show a general decline in size and vigor.

## II. Inbreeding in Animals

The classical study and analysis of the effect of inbreeding in animals was done with guinea pigs by a succession of workers in the United States Department of Agriculture. Wright's (1922) results were typical in showing an "inbreeding depression" for reproductive traits, with fertility (frequency and size of litters) being the trait most affected after 13 generations of full-sib matings. Wright's analysis of the data showed that sufficient selection pressure for fitness can overcome the deleterious effects of inbreeding. Thus, the effect of selection for production, whether conscious or unconscious, may be important in those experiments in which no apparent decline in fitness accompanies

inbreeding (Allard, 1960).

In swine, it has been reported that fertility (litter size) is much more difficult to maintain in lines being inbred than is growth rate (Comstock and Winters, 1944). Bereskin et al. (1970) found that inbreeding exhibited a significant curvilinear effect for average pig weight and total litter weight with the partial linear regression coefficients being -0.042 and -0.27, respectively. Inbreeding of the litter showed no significant influence on litter size at birth while inbreeding of the dam significantly lowered the number born per litter. The partial regression coefficients for litter size at birth on inbreeding of dam and inbreeding of litter were -0.31 and 0.06, respectively.

In a herd of Hungarian Pied Cattle, milk production was decreased by the effect of inbreeding, but with a probability level greater than 0.05 (Veress and Torok, 1969). This effect would probably become statistically significant with greater degrees of freedom.

Inbreeding may have different effects on lines, strains, breeds and species. For example, King (1918) conducted an experiment with Albino rats for 25 generations of full-sib matings and found that (1) inbreeding did not decrease the reproductiveness (frequency and size of litters) of the rats and (2) that under favorable nutritive conditions, the animals bred at a relatively early age.

### III. The Effect of Inbreeding on Avian Traits

#### A. Age at Sexual Maturity

As with other avian species, age of first egg is a measure of when sexual maturity is reached in Coturnix. The age of first egg is normally around 35-42 days of age (Wilson, 1961; Stanford, 1957), but is delayed as inbreeding increases (Sittman, Alplanalp and Fraser, 1966; Iton, 1967). Sittman et al. (1966) further reported that the age at sexual maturity was delayed more than one day for every 10% increase in inbreeding of the birds.

With chickens, in general, age at sexual maturity increased with an increase in inbreeding (Jull, 1933; Hays, 1924). Shoffner (1947) reported an increase in age at sexual maturity of 6 days for every 10% increase in inbreeding.

It has been shown in chickens by Waters (1945) and Waters and Lambert (1935) that it is not necessarily true that progressive increases in the intensity of inbreeding will show corresponding increases in age at sexual maturity. This could be due to the slower rate of inbreeding because no full-sib matings were made.

In work done with turkeys (Alplanalp and Woodward, 1967) it was reported that age at first egg appeared unaffected by an increase in inbreeding.

#### B. Egg Production

"Inbreeding depression" of egg production in Coturnix has been observed by Iton (1967) and Sittman et al. (1966). Sittman et al. (1966) attempted to place egg production on a percentage scale by taking the

number of eggs set per mating and hatch (the upper limit of 100% equals 14 eggs set). Based on this scale, for every 10% increase in inbreeding an average of 0.4 fewer eggs were set per mating and hatch.

In work done with Single Comb White Leghorn chickens (Duzgunes, 1949), it was reported that on the average, the more inbred females laid fewer eggs than their less inbred penmates. Hatching season production showed decreases with increased inbreeding in the two lines in which no selection for egg number was practiced, and showed increases in the lines selected for both high and low egg production in the month of November. The results of the low egg production line are somewhat surprising, but neither the data analyzed nor the scope of the study warranted a fuller discussion. The response of the high egg production line is another example that inbreeding coupled with selection could be useful in fixing genes for production loci.

Stephenson et al. (1952) showed that the inbreeding effect on egg production rate was non-linear for inbreeding coefficients under 25%, but essentially linear for inbreeding coefficients greater than 25%. The linear regression coefficient of egg production rate on inbreeding coefficient was  $-0.43 \pm .04$  after correcting for lines, years and interaction.

Egg production was measured by Shoffner (1947) as the number of eggs laid by an individual until she was 500 days of age. Those birds which died before that time failed to contribute to the family average.

The within-sire regression of the mean egg production of sister groups on their mean inbreeding was  $-0.926 \pm .068$ . The decline in egg production rate resulting from inbreeding in Wilson's (1948a) work was indicated by the regression coefficient of  $-0.14 \pm .04$  for a 6-month production period. Jull (1933) also reported that rate of egg production and total egg production of White Leghorn chickens decreased with an increase of the inbreeding coefficient.

Waters (1944) reported that there was no marked decrease in egg production for the families as a result of increased inbreeding. This could be due to the slower rate of inbreeding used in this study.

### C. Fertility

In work done with Coturnix, both Iton (1967) and Sittman et al. (1966) used the index of fertility of all matings minus the fertility of fertile matings as a measurement of the magnitude of complete male sterility. For a 10% increase in inbreeding, fertility of all matings decreased by approximately 11% of which 4% were due to complete male sterility. Also the percent of infertile females increased with an increase in inbreeding.

Fertility of chickens seems to be less affected by inbreeding than the fertility of Coturnix. Wilson (1948a), Jull (1933), Waters (1944) and Duzgunes (1949) all reported that fertility showed no significant decrease due to increased inbreeding to the authors knowledge. Hays (1924) was the only one that reported a decline in fertility as inbreeding

increased.

D. Hatchability

In Coturnix, maternal inbreeding and inbreeding of the embryo caused a decline in hatchability of approximately 3% and 7%, respectively, for every 10% increase in inbreeding (Sitman et al., 1966). Iton (1967) also indicated that hatchability was subject to inbreeding depression.

In Shoffner's (1947) study with chickens, the regressions were computed between the degree of inbreeding of a dam's offspring on the percentage hatch of the group of fertile eggs from which they came. The regression of hatchability on inbreeding was  $-0.436 \pm .132$ , a significant association. The regression of the hatchability of a dam's fertile eggs on her inbreeding coefficient was also computed and found to be  $-0.109 \pm .154$ , which was nonsignificant. There is no indication that because a dam is highly inbred the hatchability of her fertile eggs will be any lower than her lesser inbred contemporaries mated to the same sire. The inbreeding of the resultant zygotes has a more pronounced effect, which might be expected since the fowl is oviparous. The partial regression of the losses due to failure to hatch on the inbreeding coefficient of the zygote was calculated as 0.0044. No level of significance was reported.

The effect of inbreeding on the different lines of Single Comb White Leghorn chickens used in Duzgunes' (1949) study was found to be

homogeneous. The value of the partial regression of losses due to failure to hatch on inbreeding coefficient of the zygote (0.0044) was found to be identical with that reported by Shoffner (1947). The results obtained also support the previously reported result that it is the zygote's inbreeding rather than the dam's which has a deleterious effect on hatchability.

It was previously stated that inbreeding coupled with selection for fitness could be useful. Waters (1944) stated that despite continuous selection for high hatchability there has been, for nearly all lines of chickens in the study, a general decrease in hatchability as inbreeding increased. This decrease was not significant and demonstrated that it is possible to practice selective inbreeding and at the same time maintain a safe level of hatchability. Waters and Lambert (1935) also found no significant decrease in hatchability as the intensity of inbreeding increased. This could be due to the slower rate of inbreeding used in these studies.

In turkeys a decrease in hatchability as inbreeding increased was observed by Alplanalp and Woodward (1969). No significance as reported.

#### E. Survivability to Hatch

Wilson (1959) reported that the Coturnix is precocious in embryonic life. Embryonic feather papillae appear on the 7th day and the yolk transfer begins on the 15th day of incubation. Embryos under normal conditions had peaks of mortality between the 1st and 3rd days and

between the 15th and 17th days (hatch at 17.5 days), with a minor peak at midpoint in the incubation period.

During embryonic development maternal inbreeding had an affect on early mortality (1 to 8 days) which tended to increase at an accelerated rate with increased inbreeding of the dams. As with maternal inbreeding, the greatest losses due to inbreeding of the embryo were incurred in early mortality, which increased exponentially with inbreeding (Sittman et al., 1966).

Wilson (1948b) regressed chick mortality on inbreeding of the dam and obtained a regression coefficient of  $0.27 \pm .05$ . By regressing the same trait on inbreeding of the offspring, the regression coefficient was calculated as  $0.26 \pm .05$ .

#### F. Survivability from Hatch to Maturity

Sittamn et al. (1966) found that in Coturnix unfavorable effects of maternal inbreeding were evident in the first period after hatching from a comparison of the two types of non-inbred keets and also from the curvilinear increase in mortality with increased inbreeding. Mortality up to the 5th week of age was increased by approximately 2% and 4%, respectively, for each additional 10% increase in inbreeding of the dam and offspring. The same amount of the bird's own inbreeding decreased viability by about 0.8% and 1.9% in males and females, respectively, between the ages of 5 and 16 weeks.

A similar effect was found in chickens by Wilson (1948b). By

regressing survivability (number of pullets banded) on inbreeding of dam and offspring, regression coefficients of  $-0.20 \pm .04$  and  $-0.20 \pm .04$ , respectively, were calculated.

The results obtained by Jull (1933) showed that such close inbreeding as full-sib matings did not affect the viability of chicks to any marked extent. No significance level was reported.

Alplanalp and Woodward (1969) reported that viability of turkeys from hatch to maturity decreased as inbreeding increased. No significance level was reported.

## MATERIALS AND METHODS

### I. Experimental Animals

The Coturnix coturnix japonica used as the foundation stock in this study were hatched at the Montana Agricultural Experiment Station from eggs laid by generation 13 birds from the station's project 162. The eggs were the result of an outcrossed generation for all populations and were grouped according to the population, replication and family they represented. There were three populations with two replications per population.

Population I of project 162 was subjected to a mating system which alternated wide outcrossing within the Population I generation with full-sib matings the next generation. Selection of birds to be parents of the next generation was done on the basis of the dam's egg mass index. The egg mass index is equal to  $\frac{\text{Egg number} \times \text{mean egg weight}}{\text{Body weight of the bird}}$ . For additional information on the egg mass index one can refer to Hicks (1962).

Population II of project 162 was the result of a conventional selection program with no intentional inbreeding. Selection of the parent birds was based on the same index that was used for Population I and they were mated at random with the exception that no full-sib matings were made.

Population III was the control group for project 162. The parent birds were randomly selected and randomly mated with the exception that no full-sib matings were made. For additional details concerning the breeding procedures in project 162, refer to the masters thesis written

by Keller (1969).

In project 162, the foundation stock of Populations I and II were the result of a cross between birds obtained from the University of California, Davis campus and birds obtained from Dr. D. Douma, Bozeman, Montana. However, Population III (the controls) were strictly birds from the University of California. For more details on the foundation stock, one can refer to the doctoral dissertation written by Mahn (1968).

## II. Breeding Procedures

In this study, all of the matings in all of the generations and populations were full-sib. In generation 0, males and females were selected at random within families to be the parents of generation 1. Each replication of the three populations was assigned 16 mating cages and as many families as possible from each replication were represented. Population I was short 6 matings in both replications when the birds were housed. These matings were made up of birds from the same population and replication, but the birds were one week younger than the other birds in generation 0.

Generation I birds were selected at random within the surviving families to be the parents of generation 2. Full-sib matings from each of the 16 families (matings) per population replication were made whenever possible. Whenever a family could not contribute a full-sib mating to be parents of the next generation, replications of surviving families

were made.

Generation 2 birds were not mated and the study was terminated when the birds were 4 weeks of age.

### III. Experimental Procedure

The quail eggs were incubated at 99.5°F for 19 days with an average humidity of 87%. In project 162 and in the preliminary trial, there was little trouble in waiting until the 19th day before removing the keets from the incubator. In the first hatch of generation 1, there was essentially 100% mortality in the first week after hatching which contradicted the preliminary results. After some research and experimentation, it was found that the majority of the keets were hatched by the 18th day of incubation. This decrease in incubation time is thought to be due to the season (summer) in which they were incubated.

It is hypothesized by the author that the additional day in the incubator for the first hatch of generation 1 rendered the keets too weak to feed when placed in the brooders. Because of this, the majority of the keets (all that had hatched by day 18) were removed from the incubator on the 18th day, and the remaining keets were removed on the 19th day.

After the keets were removed from the incubator, they were banded and their identification recorded. The keets were then transferred to electrically heated batteries for 10 days at 100°F for the remaining 18 days.

At 28 days of age, the quail were sexed, mated and assigned to laying cages with their mates. They were housed at random with respect to population and replication in bank 8 of project 162. Bank 8 contained 96 individual mating cages and each replication of the three populations occupied 16 cages at the beginning of the study. When generation 1 was housed, there were extra cages available to house replications of surviving families due to reduction of number of families in all three populations.

Egg collection for the first hatch was done during the 5th and 6th weeks of age, with the eggs being incubated on the first day of the 7th week. Egg collection for the second hatch was done during the 7th and 8th weeks of age, with the eggs being incubated on the first day of the 9th week.

After incubation, those eggs which did not hatch were broken open and classified as to fertility, and if fertile, were classified as an early or late embryonic death.

#### IV. Traits Studied

In order to quantitate the effect of severe inbreeding on the three populations of quail, the following traits were studied: (1) age of first egg (sexual maturity), (2) egg production during the 5th, 6th and 7th weeks of age, (3) number of eggs set per mating and hatch, (4) fertility of eggs set per mating and hatch, (5) early embryonic deaths per mating and hatch, (6) late embryonic deaths per mating and hatch,

(7) hatchability per mating and hatch and (8) survivability of offspring per mating from hatch to 4 weeks of age.

Fertility was measured as an absolute number of fertile eggs and as a percentage based on number of eggs set. Early and late embryonic deaths were measured as absolute numbers and as percentages based on number of fertile eggs. Hatchability was measured as an absolute number of keets hatched and as two percentages based on number of eggs set and number of fertile eggs. Survivability was only studied for the second hatch of generation 1 and was measured as an absolute number and as a percentage based on number of keets hatched.

#### V. Method of Analysis

The experiment was factorial in design and the data were analyzed by least squares procedures (Harvey, 1960). The model for the analysis was:

$$Y_{ijklmnop} = \mu + A_i + B_j + C_k + D_l + E_m + F_n + G_o + \text{all two factor interactions} + b(X_{ijklmnop} - \bar{X}) + e_{ijklmnop}$$

where:

$Y_{ijklmnop}$  = the pth observation in the oth G class, in the nth F class, in the mth E class, in the lth D class, in the kth C class, in the jth B class and in the ith A class,

$\mu$  = the overall least squares mean,

$A_i$  = the effect of the ith population,

$B_j$  = the effect of the jth replication,

$C_k$  = the effect of the kth hatch,

$D_l$  = the effect of the  $l$ th side of housing,

$E_m$  = the effect of the  $m$ th row of housing,

$F_n$  = the effect of the  $n$ th cage of housing,

$G_0$  = the effect of the 0th generation (included only when both generations were analyzed together),

$b$  = partial regression of the dependent variable (Y) on age of first egg holding the discrete variables (A,B,C,D,E,F, and G) constant,

$e_{ijklmnop}$  = the random error.

Due to the size of the model and the limitations of the least squares program, all interactions could not be tested at the same time. They were tested in groups, with the significant interactions being tested with each additional group of interactions. When all interactions had been tested, the final model for each trait analyzed included only those interactions which were significant.

After the least squares analysis of variance was completed for each trait, a Duncan's Multiple-Range test was conducted as outlined by Harvey (1960) to determine the significance of individual differences among the least squares means for populations.

## RESULTS AND DISCUSSION

In most inbreeding studies, the traits measured are regressed on the inbreeding of the dam or sire and on the inbreeding of the individual. This type of regression was not calculated in this study because the inbreeding coefficients were only available for Population I. Therefore, the birds in generation 0 were assumed to have an inbreeding coefficient near zero, the birds in generation 1 had inbreeding coefficients of at least 25 percent and the birds in generation 2 were at least 37.5 percent inbred.

The results are from the analyses of each trait analyzed separately by generation and from the combined analysis of the two generations in which each trait was measured. In this study, a generation was considered to be all individuals from the time of fertilization through the subsequent egg production record of those individuals. The final least squares models for the traits measured in each generation are presented in tables 1-5 of the appendix. All least squares means and partial regression coefficients which are shown in tables 1-7 are from these least squares analyses of variance.

Hatch was a significant main effect for many of the analyses. The differences in time between the setting of the two hatches within each generation was two weeks. Since the incubator environment was uniform, the main differences between the two hatches should have been due to the additional two weeks of time and to the additional maturity of the parent birds. It was assumed that the additional two weeks had a negligible

effect, therefore, the majority of the hatch effect should have been due to the additional maturity of the parent birds.

The final models for each analysis sometimes contained significant interactions (appendix tables 1-5). The interactions of primary importance were the interactions with population. For example, if there was a significant population by generation interaction, the interpretation of resulting means for the three populations would depend on which generation they were taken from.

#### I. Traits Measured in Generations 0 and 1

The following traits were measured on birds in both generations 0 and 1: (1) age at first egg, (2) number of eggs laid during the 5th, 6th and 7th weeks of age, (3) number of eggs set per mating and hatch and (4) fertility of the eggs set per mating and hatch. The least squares population means and partial regression coefficients on age at first egg for these traits are presented in table 1. The least squares means for the first and second hatches for each of these traits, from the separate analysis of generations 0 and 1, are in table 2. The generation least squares constant estimates for these traits are in table 3.

##### A. Age at First Egg

Population was a significant ( $P < .05$ ) main effect for the separate analyses of the generations and for the combined analysis of both generations. In generation 0, Populations I and II were not significantly different from each other and both were significantly earlier in age at

TABLE 1. LEAST SQUARES MEANS AND REGRESSION COEFFICIENTS ON AGE AT FIRST EGG FOR TRAITS MEASURED IN GENERATIONS 0 AND 1

Trait	Genera- tion	Population			Regression on age at first egg
		I	II	III	
Age of first egg (days)	0	43.5 $\pm$ 1.9	43.2 $\pm$ 2.1	48.7 $\pm$ 2.1	
	1	51.8 $\pm$ 2.8	46.8 $\pm$ 3.0	55.0 $\pm$ 3.3	
No. eggs laid	0	14.8 $\pm$ 0.7	13.8 $\pm$ 0.7	12.6 $\pm$ 0.8	-.65 $\pm$ .07**
	1	9.0 $\pm$ 1.4	7.9 $\pm$ 1.1	8.4 $\pm$ 1.9	-.55 $\pm$ .13**
No. eggs set	0	11.9 $\pm$ 0.6	10.4 $\pm$ 0.5	7.5 $\pm$ 0.7	.00 $\pm$ .03
	1	5.4 $\pm$ 0.9	4.5 $\pm$ 0.7	4.9 $\pm$ 1.1	-.25 $\pm$ .07**
No. of fertile eggs	0	9.9 $\pm$ 0.6	8.0 $\pm$ 0.5	5.9 $\pm$ 0.6	.05 $\pm$ .03
	1	3.2 $\pm$ 0.7	2.6 $\pm$ 0.6	3.5 $\pm$ 0.9	-.15 $\pm$ .06*
Fertile eggs, %	0	87.7 $\pm$ 3.7	62.9 $\pm$ 3.4	61.9 $\pm$ 3.8	1.22 $\pm$ .19**
	1	37.0 $\pm$ 9.1	35.1 $\pm$ 7.4	49.6 $\pm$ 11.3	1.47 $\pm$ .77*

\* (P < .05)

\*\* (P < .01)

TABLE 2. LEAST SQUARES MEANS FOR HATCHES 1 AND 2 FOR TRAITS MEASURED IN GENERATIONS 0 AND 1

Trait	Generation	Hatch		F
		I	2	
No. eggs set	0	8.58 <sup>±</sup> .43	11.26 <sup>±</sup> .43	**
	1	3.90 <sup>±</sup> .63	5.97 <sup>±</sup> .63	**
No. fertile eggs	0	6.11 <sup>±</sup> .42	9.72 <sup>±</sup> .42	**
	1	2.32 <sup>±</sup> .49	3.87 <sup>±</sup> .49	*
% fertile	0	59.67 <sup>±</sup> 2.57	81.99 <sup>±</sup> 2.57	**
	1	35.10 <sup>±</sup> 6.50	45.96 <sup>±</sup> 6.50	

\* (P < .05)

\*\* (P < .01)

TABLE 3. GENERATION LEAST SQUARES MEANS FOR TRAITS MEASURED IN GENERATIONS 0 AND 1

Trait	Generation		F
	0	1	
Age at first egg	45.39 <sup>±</sup> 1.48	50.03 <sup>±</sup> 1.77	**
No. eggs laid	13.01 <sup>±</sup> .43	9.56 <sup>±</sup> .70	**
No. eggs set	8.95 <sup>±</sup> .31	3.57 <sup>±</sup> .54	**
No fertile eggs	7.88 <sup>±</sup> .31	2.00 <sup>±</sup> .57	**
% fertile	74.53 <sup>±</sup> 4.48	25.95 <sup>±</sup> 9.01	**

\*\* (P < .01)

first egg laid than Population III (table 1). In generation 1, Population II was significantly earlier than Populations I and III.

Generation was a significant ( $P < .05$ ) main effect for the combined analysis of both generations. This was thought to be due to the increase in age at first egg for all three populations in generation 1, caused by the increase in the inbreeding coefficients ("inbreeding depression") of generation 1.

B. Number of Eggs Laid

Population was not a significant main effect for any of the analyses of variance, but Population I laid a significantly greater number of eggs than did Population III in the analysis of generation 0 (table 1). In all analyses, the partial regression on age at first egg was significant ( $P < .05$ ). This was logical since the earlier a bird started laying eggs, the greater the chance that the bird would lay a larger total number of eggs by a given age.

Generation was a significant ( $P < .05$ ) main effect for the combined analysis of both generations. This reflected the drop in egg production from generation 0 to generation 1, and this drop was believed to be due to the increased inbreeding coefficient (approximately 25%) of generation 1. Population by row as a significant ( $P < .05$ ) interaction for the combined analysis of both generations.

C. Number of Eggs Set

Population was a significant ( $P < .05$ ) main effect for the analysis

of generation 0. In generation 0, all three least squares means were significantly different from each other with Population I (11.9 eggs) having the advantage over the other two populations. In generation 1, population was not a significant main effect and the three populations were not significantly different from each other when tested separately.

The partial regression on age at first egg was a significant effect in the analysis of generation 1, which indicated that the mature inbred bird laid more eggs than the younger (less mature) inbred bird. Generation was a significant ( $P < .01$ ) main effect for the combined analysis of both generations and this was a reflection on the "inbreeding depression" observed in egg production.

Population by row and population by cage were significant interactions for the analysis of generation 0.

#### D. Fertility of Eggs Set

Fertility of the eggs set per mating and hatch was measured as an absolute number and as a percentage based on the number of eggs set per mating and hatch. When fertility was measured as an absolute number, population was a significant ( $P < .05$ ) main effect only for the analysis of generation 0, with all three least squares means being significantly different from each other.

Hatch was a significant ( $P < .05$ ) main effect for all analyses, which was an indication that maturity influenced fertility in absolute numbers in that the mature birds laid more fertile eggs than the less

mature birds (the second hatch compared to the first hatch). The partial regression on age at first egg was significant ( $P < .05$ ) for the analysis of generation 1 and was further evidence that maturity influenced fertility of the eggs laid by generation 1 birds. Population by row and population by cage were significant ( $P < .01$ ) interactions for the analysis of generation 0.

When fertility was measured as a percentage of the eggs set per mating and hatch, population was a significant ( $P < .05$ ) main effect for the analysis of generation 0, with Population I (87.7%) having the advantage over Populations II and III (62.9 and 61.9%, respectively).

Hatch had a significant ( $P < .01$ ) effect on the percent fertile eggs for the analysis of generation 0. This indicated that the more mature the bird, the more fertile the eggs will be. The partial regression on age at first egg was positive and significant (table 1) for all three analyses, which was further indication that maturity had a significant influence on fertility.

Generation was a significant ( $P < .01$ ) main effect for the combined analysis of both generations and this was thought to be due to the increase in inbreeding from generation 0 to generation 1. Also, when both generations were analyzed, there were significant ( $P < .05$ ) population by generation and population by cage interactions.

## II. Traits Measured in Generations 1 and 2

Early and late embryonic deaths were classified macroscopically

after the 19th day of the incubation period and were classified according to figure 1. Due to the method of classification, there was a possibility that some of the eggs that were classified as infertile might in fact have been zygotes which died at an extremely early age. Embryonic deaths were measured as absolute numbers and as percentages based on number of fertile eggs set per mating and hatch. Hatchability was measured as an absolute number and as percentages based on number of fertile eggs set per mating and hatch and on the number of eggs set per mating and hatch. The least squares means and the partial regression coefficients on age at first egg are presented in table 4.

The least squares means for the first and second hatches for each of these traits, from the separate analysis of generations 1 and 2, are in table 5. The generation least squares constant estimates for these traits are in table 6.

A. Early Embryonic Deaths

When early embryonic deaths were measured as an absolute number, population was not a significant main effect in any of the analyses and the least squares means in each analysis were not significantly different from each other.

Hatch was a significant ( $P < .05$ ) main effect for the analysis of generation 2. This indicated that early embryonic deaths in absolute numbers were in part a function of the fertility of the eggs set and the number of eggs set per mating and hatch. The older the parent

























































