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

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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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 $\frac{1}{2\ N_e}$ 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 dilema (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 nonsignficant. 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 papilae 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 $\frac{\text{Egg number x mean egg weight}}{\text{Body weight of the bird}}$. 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 indentification 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:

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

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 lth A class,

μ = 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 lth side of housing,

E_m = the effect of the mth row of housing,

F_n = the effect of the nth cage of housing,

G_o = 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	Generation	Population I	Population II	Population III	Regression on age at first egg
Age of first egg (days)	0	43.5±1.9	43.2±2.1	48.7± 2.1	
	1	51.8±2.8	46.8±3.0	55.0± 3.3	
No. eggs laid	0	14.8±0.7	13.8±0.7	12.6± 0.8	-.65±.07**
	1	9.0±1.4	7.9±1.1	8.4± 1.9	-.55±.13**
No. eggs set	0	11.9±0.6	10.4±0.5	7.5± 0.7	00±.03
	1	5.4±0.9	4.5±0.7	4.9± 1.1	-.25±.07**
No. of fertile eggs	0	9.9±0.6	8.0±0.5	5.9± 0.6	.05±.03
	1	3.2±0.7	2.6±0.6	3.5± 0.9	-.15±.06*
Fertile eggs, %	0	87.7±3.7	62.9±3.4	61.9± 3.8	1.22±.19**
	1	37.0±9.1	35.1±7.4	49.6±11.3	1.47±.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 1	Hatch 2	F
No. eggs set	0	8.58 ± .43	11.26 ± .43	**
	1	3.90 ± .63	5.97 ± .63	**
No. fertile eggs	0	6.11 ± .42	9.72 ± .42	**
	1	2.32 ± .49	3.87 ± .49	*
% fertile	0	59.67 ± 2.57	81.99 ± 2.57	**
	1	35.10 ± 6.50	45.96 ± 6.50	

* ($P < .05$)
** ($P < .01$)

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

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

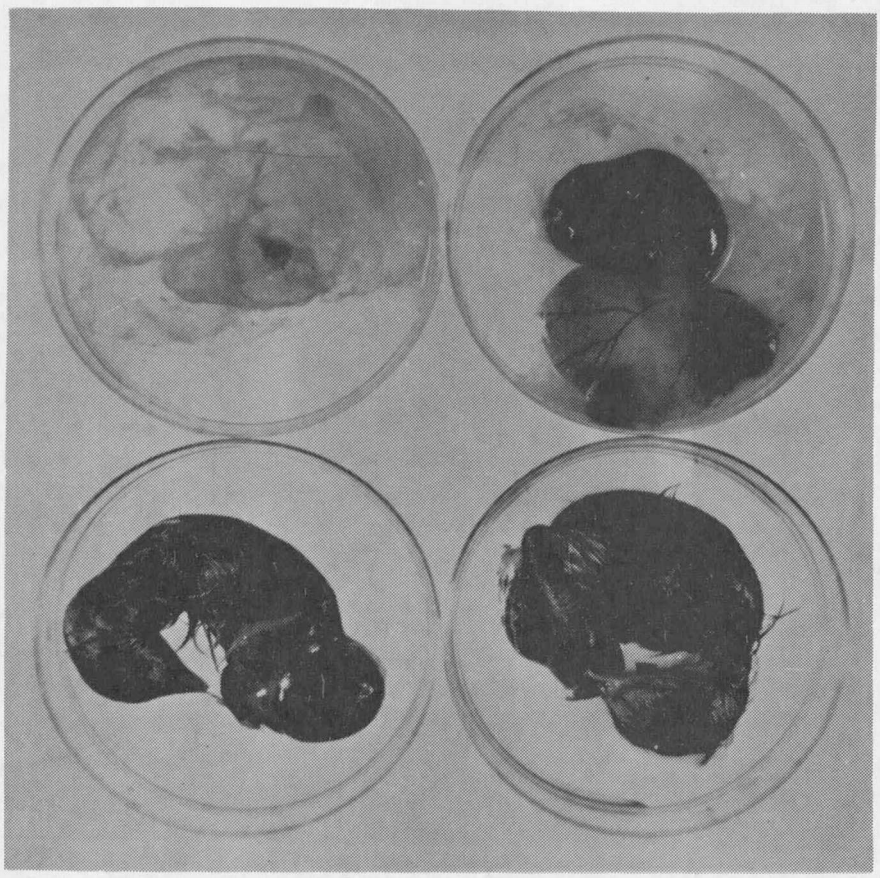


Figure 1. Embryonic deaths were classified as early if the embryos died during the stages shown in the top row and they were classified as late if they died during the stages shown in the bottom row.

TABLE 4. THE LEAST SQUARES MEANS AND REGRESSION COEFFICIENTS ON AGE AT FIRST EGG FOR TRAITS MEASURED IN GENERATION 1 AND 2

Traits	Generation	Population I	Population II	Population III	Regression on age at first egg
No. early embryonic deaths[a]	1	1.59±0.37	2.03±0.32	1-97± 0.37	2.56±1.66**
	2	1.90±0.46	1.03±0.37	1.44± 0.57	7.22±3.86
Early embryonic deaths, %	1	14.01±4.24	25.28±3.94	23.26± 4.55	..81±0.20**
	2	26.98±9.85	20.78±7.95	27.98±12.24	1.47±0.83
No. late enbryonic deaths[a]	1	2.13±0.26	2.38±0.23	1.53± 0.27	.36±1.31
	2	1.11±0.41	1.33±0.33	0.84± 0.50	4.13±3.40
Late embryonic deaths, %	1	21.25±4.09	23.89±3.80	26.05± 4.39	.22±0.19
	2	16.68±8.86	23.21±7.15	30.14±11.01	.44±0.74
No. hatch[a]	1	5.41±0.51	3.07±0.42	2.70± 0.49	2.26±2.50
	2	.20±0.14	.24±0.12	.18± 0.18	3.46±1.21**
Hatch of fertile eggs, %	1	61.61±5.37	33.75±4.39	30.23± 5.18	-.09±0.25
	2	0.19±4.14	5.02±3.34	3.51± 5.15	-.41±0.35**
Hatch of number eggs set, %	1	44.91±4.48	32.16±4.25	22.26± 4.94	-.00±0.00
		.95±1.34	2.86±1.09	1.91± 1.66	-.29±0.11*

[a] The regression coefficients and standard errors have been multiplied by 100.

* ($P < .05$)

** ($P < .01$)

TABLE 5. LEAST SQUARES MEANS FOR HATCHES 1 AND 2 FOR TRAITS MEASURED IN GENERATIONS 1 AND 2

Trait	Generation	Hatch 1	Hatch 2	F
No. early deaths	1	1.62 ± .20	2.11 ± .20	
	2	.98 ± .33	1.93 ± .33	*
% early deaths	1	21.30 ± 2.52	20.46 ± 2.52	
	2	22.15 ± 7.01	28.35 ± 7.01	
No. late deaths	1	1.63 ± .19	2.40 ± .19	**
	2	1.15 ± .29	1.70 ± .29	
% late deaths	1	21.17 ± 2.43	26.29 ± 2.43	
	2	23.70 ± 6.31	23.00 ± 6.31	
No. hatch	1	2.56 ± .34	4.89 ± .34	**
	2	.18 ± .10	.23 ± .10	
% hatch of fertile eggs	1	35.38 ± 3.48	48.34 ± 3.48	**
	2	1.51 ± 3.09	4.30 ± 3.09	
% hatch of No. of eggs set	1	25.05 ± 2.66	41.18 ± 2.66	**
	2	1.44 ± .95	2.37 ± .95	

* ($P < .05$)
** ($P < .01$)

TABLE 6. GENERATION LEAST SQUARES MEANS FOR TRAITS MEASURED IN GENERATIONS 1 AND 2

Trait	Generation 1	Generation 2	F
No. early deaths	1.83± .15	1.17± .27	*
% early deaths	21.83±2.41	23.52±4.32	
No. late deaths	2.00± .14	1.05± .24	
% late deaths	23.11±2.09	22.14±3.48	**
No. hatch	3.60± .19	.06± .33	
% hatch of fertile eggs	40.17±1.93	1.11±3.37	**
% hatch of eggs set	33.61±1.60	-4.93±3.18	**

* ($P < .05$)
** ($P < .01$)

birds, the greater the number of fertile eggs set, therefore a greater chance of an early embryonic death occurring.

Generation was a significant ($P < .05$) main effect for the combined analysis of both generations. This may have been due to the decrease in number of eggs set per mating and hatch by the parents of generation 2 (generation 1). Population by row was a significant ($P < .01$) interaction for the analysis of generation 1 and for the combined analysis of both generations.

When early embryonic deaths were measured as a percentage, population was not a significant main effect in the analysis of generation 1, but Population I showed a significant advantage over Population II (table 4). In the analysis of generation 2, population was not a significant main effect and the least squares means were not significantly different from each other. The regression on age at first egg was significant ($P < .01$) for the analysis of generation 1 (table 4), which indicated that the maturity of the embryo's dam influenced early embryonic environment. This could have been due to the fact that the more mature females laid larger eggs which might have been better suited for early embryonic development.

B. Late Embryonic Deaths

When late embryonic deaths were measured as an absolute number, population was not a significant main effect for any of the analyses. In generation 1, Population III (1.53 deaths) had a significant advantage

over Populations I and II (2.13 and 2.38 deaths, respectively), but this was probably due to the greater number of eggs set per mating and hatch by the latter two populations.

Hatch was a significant ($P < .05$) main effect for the analysis of generation 1. This seemed to reflect the increase in the number of eggs set per mating and hatch as the parent birds matured, therefore providing a greater chance for late embryonic deaths.

Generation was a significant ($P < .05$) main effect for the combined analysis of both generations. This reflected the drop in the number of eggs set per mating and hatch from generation 0 to generation 1 (parent generations). The partial regression on age at first egg was not significant for any of the analyses.

When late embryonic deaths were analyzed as a percentage, population, hatch, generation and the regression on age at first egg were not significant effects in any of the analyses.

C. Hatchability

When total number of eggs hatched per mating and hatch were analyzed, population was significant ($P < .01$) for the analysis of generation 1. In the analysis of generation 1, Population I (5.41 keets hatched) possessed a significant advantage over Populations II and III (3.07 and 2.70 keets hatched, respectively).

Hatch was a significant ($P < .01$) main effect and for the analysis of generation 1. This reflected the increase in the number of eggs set per

mating as the parent birds matured. The partial regression on age at first egg was significant only in the analysis of generation 2 and was an indication that maturity of the parent birds affected number hatched. Generation was a significant ($P < .01$) main effect for the analysis of both generations and reflected on the lower number of eggs set for, and lower number of eggs hatched in generation 2. Population by cage was a significant ($P < .01$) interaction for the analysis of generation 1.

When hatchability was measured as a percentage based on the number of fertile eggs set per mating and hatch, population was a significant ($P < .01$) main effect for the analysis of generation 1 with Population I (61.61%) having a significant advantage over Populations II and III (33.75 and 30.23%, respectively).

Hatch was a significant ($P < .05$) main effect for the analysis of generation 1. This indicated that effect of maturity on reproductive performance because the more mature birds laid more fertile eggs and possibly provided a better embryonic environment. The partial regression on age at first egg was significant ($P < .05$) for the analysis of generation 2 only and was a further indication of the effect the parent's maturity had on the percentage of the fertile eggs that hatched. Generation was a significant ($P < .01$) main effect for the combined analysis of both generations and it reflected the drop in percent hatched from generation 1 to generation 2. Population by cage was a significant ($P < .01$) interaction for the analysis of generation 1.

Hatchability was also measured as a percentage of the number of eggs set per mating and hatch to get an overall measurement of a population's ability to withstand severe inbreeding by incorporating embryonic deaths and fertility of the eggs set into one value. Population was a significant ($P < .05$) main effect for the analysis of generation 1. Population I showed a significantly greater percentage of eggs hatched over Populations II and III, and Population II had a significant advantage over Population III (table 4).

Hatch was a significant ($P < .05$) main effect for the analysis of generation 1. This indicated that as the parent birds matured, the eggs that they laid had a better chance of hatching. The regression on age at first egg (table 4) was significant for the analysis of generation 2. This indicated that the sooner the female parent started laying eggs, the lesser the chance it had in leaving offspring to continue the next generation. This could in part be due to the female birds laying eggs before their mates reached puberty, therefore, lowering the percent of eggs set that are fertile and the percent of eggs set that will hatch.

III. Survival from Hatch to 4 Weeks of Age

Because there was essentially 100% mortality in the first hatch of generation 1 and because the populations became extinct in generation 2, survival data were only available for the second hatch of generation 1 birds. The effects of interest in the analysis of this trait were population and the partial regression on age at first egg. The trait

was measured as an absolute number and as a percentage based on the number of keets hatched per mating (table 3). In both analyses, neither population or the regression on age at first egg were significant effects. Even though the overall population effect was not significant, in the analysis of number died, Population II had a significant advantage over Populations I and III. This in part was due to the differences in the number of keets hatched per population mating (table 4).

TABLE 7. LEAST SQUARES MEANS AND PARTIAL REGRESSION COEFFICIENTS ON AGE AT FIRST EGG FOR SURVIVAL FROM MATCH TO 4 WEEKS OF AGE

Trait	Generation	Population I	Population II	Population III	Regression on age at first egg
Number died	1	$2.7 \pm .4$	$1.5 \pm .4$	$2.2 \pm .4$	$.03 \pm .02$
Percent died[a]	1	40.7 ± 6.2	37.5 ± 5.6	45.2 ± 6.2	$.57 \pm .32$

[a] The regression coefficient and standard error are multiplied by 100.

IV. Family Survival

In generation 0, each population replication consisted of 16 families (matings) or a total of 32 families per population. Identification of the families was done in order to select as broad a sample from the matings (full-sib) as possible each generation. Due to the reproductive performance and deaths of the birds in generation 0, and due to the generation 1 zygote's performance in surviving until 4 weeks of age, when the matings were made in generation 1, Population I was reduced to 12 families, Population II was reduced to 13 families, and Population III

was reduced to 8 families. A Chi-square analysis of the number of families per population in generation 1 indicated no significant population effect. It must be noted that more matings were made in each population because replications of families were made whenever possible in order to better evaluate the ability of each population to withstand severe inbreeding.

In generation 2, due to "inbreeding depression" observed in the parent birds of generation 2 and in the zygotes of generation 2, the three populations became extinct. The keets that did hatch in generation 2 had a noticeable increase in the percent of abnormalities such as wry-necks and spraddle-legs (figures 1-2 in the appendix). This was explained by the expected increase in homozygosity of the deleterious genes due to increased inbreeding in the populations. Why these abnormalities did not show up in as large a percentage in generation 1 birds might have been due to a low frequency of these deleterious genes in the populations when the study started.

V. Discussion

The combined analysis of both generations that exhibited each trait was done only to get an indication of the generation (inbreeding) effect. In most of the traits measured, generation was a significant effect indicating the presence of "inbreeding depression". Due to this "inbreeding depression", in the last generation in which each trait was measured, the three population least squares means were not significantly different

from each other. For these reasons, only the first generation in which each trait was measured will be discussed. Comparisons among all three populations were of interest, but due to the ancestry of the three populations, the comparison between Populations I and II was considered to be the most informative.

Percent died was the best indication of survivability from hatch to 4 weeks of age because number died was a function of the number of keets hatched per mating. Since percent died (table 7) was not significantly different for the three populations, the key to surviving the first generation of inbreeding seemed to be in the number and fertility of the eggs set by the parents, and in the ability of the zygotes to overcome early and late embryonic deaths (hatchability of fertile eggs).

In number of eggs set per mating and hatch in generation 0, both Populations I and II, which had previously been selected for increased egg mass, had a significant advantage (11.9 and 10.4 eggs set, respectively) over Population III (7.5 eggs set) which had no previous selection for egg production. Population I had a significantly greater number of eggs set per mating and hatch than Population II. This could in part be due to heterosis, since the females in Population I were the result of a cross between inbred parents.

Population I also had a significant advantage over Populations II and III in number of fertile eggs set per mating and hatch and in the percent of the eggs set per mating and hatch that were fertile (table 1).

This again in part could be due to heterosis since both parents are the result of a cross between inbred parents.

Embryonic deaths as an absolute number was a function of the number of fertile eggs set per mating and hatch, and it has been established that Population I was superior to both Populations II and III in number of fertile eggs set per mating and hatch. Therefore, percent of early and late embryonic deaths based on number of fertile eggs set per mating and hatch was the best indication of how the three populations were able to withstand inbreeding at this stage of development. In generation 1, Population I (14.01%) was at a significant advantage over Population II (25.28%) in early embryonic deaths and was approaching a significant advantage over Population III (23.26%). None of the three populations had an advantage in the percent of late embryonic deaths. The ability of Population I to overcome early embryonic deaths better than the other two populations may have been related to the alternating generations of inbreeding and outbreeding within each replication. It is postulated that this mating system deleted or decreased in frequency the deleterious genes that affect reproductive performance and early embryonic survival.

With the above in mind, it is easy to understand why Population I possessed a significant advantage over Populations II and III in number of keets hatched per mating and hatch, in the percent hatched based on the number of fertile eggs set per mating and hatch, and in the percent

hatched based on the number of eggs set per mating and hatch.

Population I was 33 percent inbred in generation 1 and 39.5 percent inbred in generation 2. Populations II and III were at least 25 percent inbred in generation 1 and at least 37.5 percent inbred in generation 2. Since the three populations became extinct in generation 2 and the difference in the three population inbreeding coefficients was small, it appeared that there was a population inbreeding threshold between 33 and 37 percent. Above this threshold level of inbreeding, the populations succumbed to "inbreeding depression".

Population I's overall advantage over Populations II and II seemed to be due to its history of alternating generations of inbreeding with outbreeding coupled with selection for increased egg mass per unit body weight.

SUMMARY

Japanese Quail from the University of California, Davis, and Japanese Quail from Dr. D. Douma, Bozeman, Montana were crossed to form the foundation stock for Populations I and II. Population III (control) was made up entirely of birds from the University of California. There were two replications per population. After the formation of the foundation stocks, Population I was subjected to a mating system of alternating generations of outbreeding with full-sib matings within each replication, while Populations II and III were randomly mated. Selection of the parent birds of each generation in Populations I and II was done on the basis of an index consisting of the dam's egg mass per body mass, while there was no applied selection in Population III.

After 13 generations under their various mating systems, all three 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 allowed 16 matings (families) for a total of 32 families per population. After the first generation of full-sub matings, attrition reduced Populations I, II and II to 12, 13, and 8 families, respectively. In order to better evaluate the populations' ability to withstand severe inbreeding, replications of families were made whenever possible in the second generation of full-sib matings.

Traits studied were age at first egg, number of eggs laid during the 5th, 6th and 7th weeks of age, number of eggs set per mating and

hatch, number of fertile eggs set per mating and hatch, percent of eggs set that were fertile per mating and hatch, number of early and late embryonic deaths per mating and hatch, percent of early and late embryonic deaths based on the number of fertile eggs set per mating and hatch, number of keets hatched per mating and hatch, percent hatched based on number of fertile eggs and number of eggs set per mating and hatch, mortality of keets from hatch to 4 weeks of age per mating and hatch, and percent mortality of keets from hatch to 4 weeks of age per mating and hatch.

The traits were analyzed by generation and then the two generations in which each trait was measured were combined to get an indication of a generation (inbreeding) effect. From these combined analyses, it appeared that there was "inbreeding depression" in all traits except embryonic deaths. In the separate analysis of the second generation in which each trait was measured, the population means were not significantly different from each other. Since the three populations reached a threshold level (33-37%) of inbreeding, beyond which survival did not occur, after the second generation of full-sib matings and since there was no significant difference among the populations, the first generation of full-sib matings was the best indication of the ability of the populations to withstand severe inbreeding.

The key to surviving the first generation of inbreeding appeared to be in the number and fertility of the eggs set by the parents, and in

the ability of the zygotes to overcome early and late embryonic deaths. Population I was at a significant advantage over Populations II and III in number of eggs set per mating and hatch, number of fertile eggs set per mating and hatch, and percent of eggs set that were fertile. Population I was also at a significant advantage over Population II in early embryonic deaths. None of the populations had an advantage in late embryonic deaths. Since hatchability was a function of the above, Population I was at a significant advantage over Populations II and III in number of keets hatched per mating and hatch and in percent hatched based on number of fertile eggs and number of eggs set per mating and hatch.

It is postulated that the alternating generations of outbreeding with full-sib matings coupled with selection, differentially decreased the frequency of deleterious genes that affected reproductive performance, thus making Population I more adaptable to severe inbreeding than the populations with a history of random mating.

The hatch effect and the partial regression on age at first egg were significant in many of the analyses and they were indications of how maturity or age of the parent birds influenced the traits studied. It appeared that the older the parent bird, the more fertile the eggs, and the more likely the fertile eggs would hatch.

APPENDIX

APPENDIX TABLE 1. THE MEAN SQUARES FOR THE FINAL ANALYSIS OF TRAITS MEASURED IN GENERATION 0[a]

Source \ Trait	Number of eggs laid	Number of eggs set	Number of fertile eggs	Percent fertile eggs set	Age at first egg
Population	23.66	120.68**	97.96**	0.5522**	211.16**
Replication	13.57	20.95	11.57	0.3251**	18.75
Hatch		290.67**	526.32**	1.9765	
Survival					4.58
Side	11.50	22.62	0.67	0.1070**	4.39
Row	0.92	8.23	22.06	0.1011**	20.67
Cage	7.83	32.02**	24.54**	0.1432**	34.91
Regression on age at first egg	1092.08**	0.04	21.60	1.2099**	
Pop x Side				0.1588**	
Pop x Row		49.26**	39.88**	0.1467**	
Pop x Cage		41.06**	42.37**	0.2457**	
Rep x Hatch				0.0916**	
Rep x Row				0.1461**	
Rep x Cage		42.65**	19.65*	0.1574**	
Hatch x Cage				0.0382**	
Side x Row				0.0777**	
Remainder	11.98	10.00	9.63	0.0030	42.40

[a] Those two factor interactions not included in the model were not significant.

* ($P < .05$)

** ($P < .01$)

APPENDIX TABLE 2. MEAN SQUARES FOR TRAITS MEASURED IN GENERATION 1[a]

Source \ Trait	Number early deaths	Percent early deaths of fertile eggs	Number late deaths	Percent late deaths fertile eggs	Number keets hatched	Percent fertile eggs hatched	Percent eggs set hatched
Population	.94	.0742	8.49	.0111	63.35**	.8120**	.2414*
Replication	.03	.1333	.64	.0269	1.39	.0013	.1933
Hatch	9.88	.0029	24.50**	.1061	220.50**	.6803**	1.0337**
Survival							
Side	.58	.1052	3.56	.1125	3.22	.3585**	.0410
Row	8.15*	.0353	6.69	.0508	10.09	.0652	.1019
Cage	9.73**	.1377**	6.69*	.0437	13.00*	.1111*	.1022*
Regression on age of first egg	6.72	.7687**	.22	.0567	5.43	.0092	.0695
Pop x Row	8.61**						
Pop x Cage					14.71**	.1435**	
Rep x Side			17.67*				
Rep x Row					22.77*	.2202**	
Rep x Cage					12.93*	.2246**	
Side x Row						.1755*	
Row x Cage	4.24[b]	.0795*		.0673[b]			.1056**
Remainder	2.82	.0469	2.99	.0446	6.61	.0487	

APPENDIX TABLE 2. (CONTINUED)

Source \ Trait	Number deaths hatch to 4 wks of age	Percent keets hatched that died 1st 4 wks of age	Number eggs laid	Number eggs set	Number fertile eggs set	Percent eggs set fertile	Age of first egg
Population	7.45	.0367	2.79	3.47	2.61	.0699	174.23*
Replication	1.03	.0391	2.69	2.06	5.23	.0582	.76
Hatch				86.11**	48.05*	.2357	
Survival							1.68
Side	.22	.6106*	26.72	79.87*	63.25**	.0929	1.38
Row	4.63	.0943	16.26	7.63	1.59	.0383	29.59
Cage	1.89	.0965	12.30	14.68	23.40**	.3278	59.35
Regression on age of first egg	5.57	.2789	341.24**	132.39**	47.02*	.4566*	
Remainder	3.49	.0866	18.04	11.72	7.07	.1135	42.08

a Those two factor interactions not included in the model were not significant.
b ($P < .1$)
* ($P < .05$)
** ($P < .01$)

APPENDIX TABLE 3. MEAN SQUARES FOR TRAITS MEASURED IN GENERATION 2[a]

Source \ Trait	Number early deaths	Percent early deaths of fertile eggs	Number late deaths	Percent late deaths fertile eggs	Number keets hatched	Percent fertile eggs hatched	Percent eggs set hatched
Population	3.07	.0210	1.73	.0590	.01	.0099	.0015
Replication	.05	.0155	2.66	.0070	.18	.0168	.0036
Hatch	18.05*	.0767	6.05	.0010	.05	.0122	.0017
Side	11.56	.0529	10.05*	.0364	1.91*	.0043	.0080
Row	1.37	.1001	.06	.0167	.32	.0217	.0041
Cage	3.75	.1150	7.70**	.1069	1.09**	.0384**	.0110**
Regression on age at first egg	11.03	.4603	3.61	.0423	2.68**	.0361**	.0173*
Hatch x Cage						.0183*	
Remainder	3.15	.1437	2.45	.1167	.31	.0089	.0027

a Those two factor interactions no included in the model were not significant.

* ($P < .05$)

** ($P < .01$)

APPENDIX TABLE 4. MEAN SQUARES FOR THE COMBINED ANALYSIS OF TRAITS MEASURED ONLY IN GENERATIONS 1 AND 2[a]

Source \ Trait	Number eggs laid	Number eggs set	Number fertile eggs	Percent eggs set fertile	Age at first egg
Population	17.83	104.83**	16.14	.1229	299.23**
Replication	45.06	33.99	20.05	.0008	36.01
Generation	228.00**	1070.53**	766.53**	4.9644**	537.01**
Hatch		371.90**	355.78**	2.0806**	
Side	3.81	.50	59.26*	.0971	4.77
Row	4.83	47.21*	26.50	.0109	38.92
Cage	15.63	12.56	35.68**	.1782**	66.83
Survival					15.94
Regression on age at first egg	118.75**	1.40	.70	.8670**	
Pop x Gen				.2521*	
Pop x Row	28.32*		31.41**		
Pop x Cage			33.13**	.1983**	
Gen x Hatch			56.54*		
Gen X Cage			19.35*	.2237**	
Side x Row				.1541*	
Side x Cage			26.35**	.1698**	
Row x Cage		25.40**			
Remainder	12.55	13.85	9.61	.0585	39.06

[a] Those two factor interactions not included in the model were not significant.

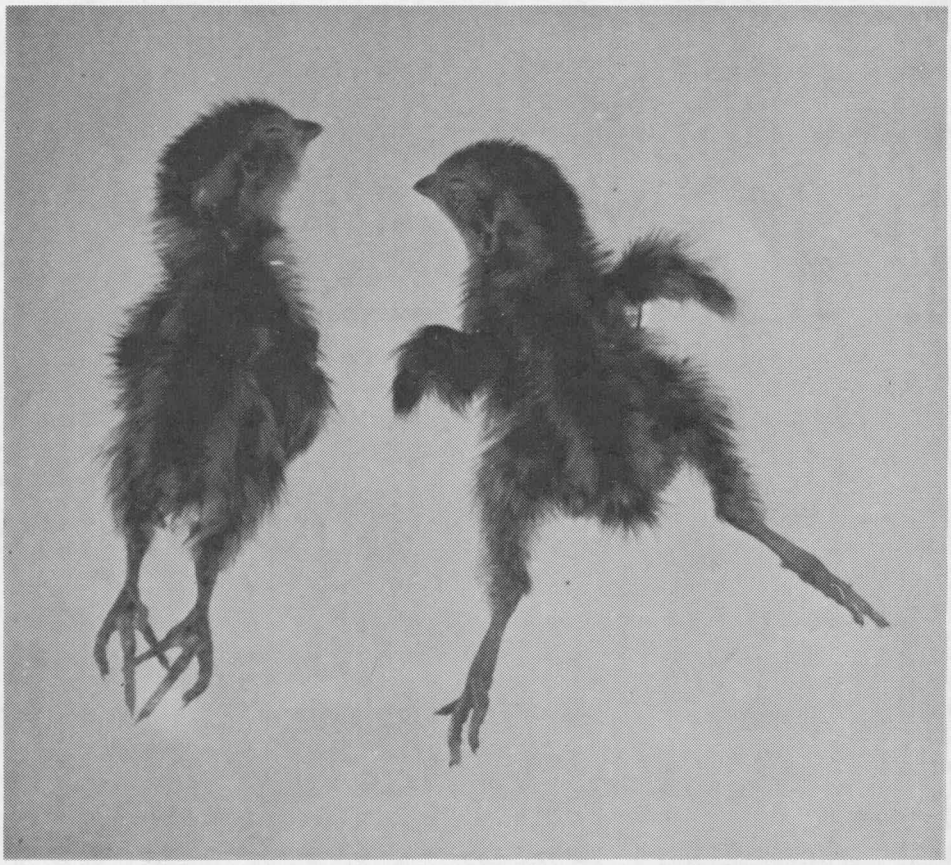
* ($P < .05$)

** ($P < .01$)

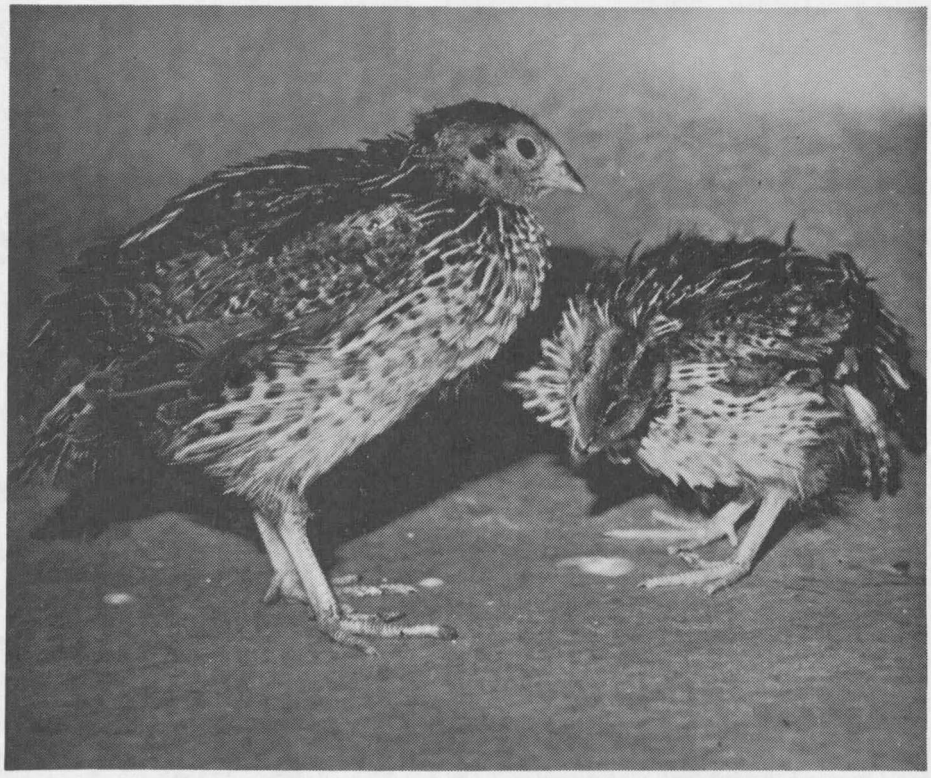
APPENDIX TABLE 5. MEAN SQUARES FOR TRAITS MEASURED ONLY IN GENERATION 1 AND 2[a]

Source \ Trait	Number early deaths	Percent early deaths of fertile eggs	Number late deaths	Percent late deaths fertile eggs	Number keets hatched	Percent fertile eggs hatched	Percent eggs set hatched
Population	1.65	.0685	5.61	.1224	20.18	.1877	.2737**
Replication	.14	.0527	2.96	.0567	.93	.0348	.1389
Generation	14.66*	.0105	33.14**	.0038	460.95**	5.6209**	4.7152**
Hatch	25.14**	.0133	29.86**	.0616	76.05**	.5275**	.3898**
Side	1.67	.0905	11.29*	.1644	.38	.0008	.0958
Row	7.74	.0493	7.19*	.0429	8.11	.0582	.1038*
Cage	4.86	.0892	7.68**	.0912	14.42**	.1013*	.0675[b]
Regression on age at first egg	.50	.1124		.0002	1.62	.0001	.1455*
Pop x Row	12.52**						
Gen x Hatch					69.80**		.3092**
Gen x Cage	9.10**	.2164**					.0785*
Side x Cage				.1463*			
Row x Cage			4.96**		10.96**	.0939**	.0972**
Remainder	3.16	.0813	.17	.0657	5.04	.0459	.0371

a Those two factor interactions not included in the model were not significant.
b ($P < .1$)
* ($P < .05$)
** ($P < .01$)



Appendix figure 1. Normal keet's leg structure (left) compared to a spraddle legged keet's leg structure (right).



Appendix figure 2. Normal 4-week-old quail (left) compared to a wry-neck 4-week-old quail (right).

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