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# Effects of mating system in Japanese quail

## 1. Inbreeding and fitness *

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**Summary.** A selection experiment, conducted for 17 generations, compared a selected population mated in a cyclic manner with alternating generations of inbreeding and outbreeding, a selected population mated at random and a randomly mated, randomly selected control population. Trends in the number of birds available for selection and number selected are presented for each population. Actual and theoretical levels of inbreeding for each population were similar. Samples of all populations were subjected to continuous full-sib inbreeding at generation 12. All populations were sensitive to inbreeding depression. However, the cyclic mated population had greater reproductive fitness after continued intensive breeding.

**Key words:** Japanese quail – Inbreeding – Mating system – Fitness

## Introduction

The degree of inbreeding in closed populations increases each generation due to finite population size. In populations under selection there is an additional increase in the degree of inbreeding due to the effect of selection on effective population size. Effective population size changes inversely with the square of the standardized selection differential and the heritability (Robertson 1964).

Mating systems in which close relatives within a line are mated lead to greater initial levels of inbreeding but to a lower rate of final approach to the limit. Conversely, mating systems which attempt to minimize genetic covariance among mates lead to lower initial levels of inbreeding but to a higher final rate of approach to the limit (Robertson 1964; Robinson and Bray 1965).

The possible usefulness of inbreeding to increase the rate of response to selection for additive gene effects depends on the expected increase in total genetic variance and selection among sublines, but is limited by cycle interval and any consequent reduction in selection intensity or effective population size (Dickerson 1977).

Objectives of this study were to describe the populations, characterize differences in levels of inbreeding attributable to differences in mating system and selection intensity and evaluate the effect of prior mating system on ability to withstand continuous inbreeding.

## Materials and methods

Three populations (designated I, II, and III) of Japanese quail (*Coturnix coturnix japonica*), each composed of two replicates, were studied. A flow chart showing the general management schemes applicable to Populations I and II are outlined in Fig. 1. The selection criterion for females of Population I and II was an index equal to the number of eggs laid by the female from 28 to 78 days of age multiplied by the average egg weight taken from a sample of eggs and divided by her 78-day body weight. Hicks (1962) called this a biomass index.

Generation 0 of Population I was the $F_2$ of a cross between a stock from the University of California at Davis and a stock from a Bozeman, Montana, fancier. At generation 0, each replicate of the population was closed and in each succeeding generation selection was practiced. The proportion selected, averaged over replicates and generations, was 39%. Individuals in odd numbered generations were the result of full-sib matings and individuals in even numbered generations were the result of wide-outbreeding within the closed replicates. Wide outbreeding was determined by minimizing the genetic covariance between the prospective mates. The final

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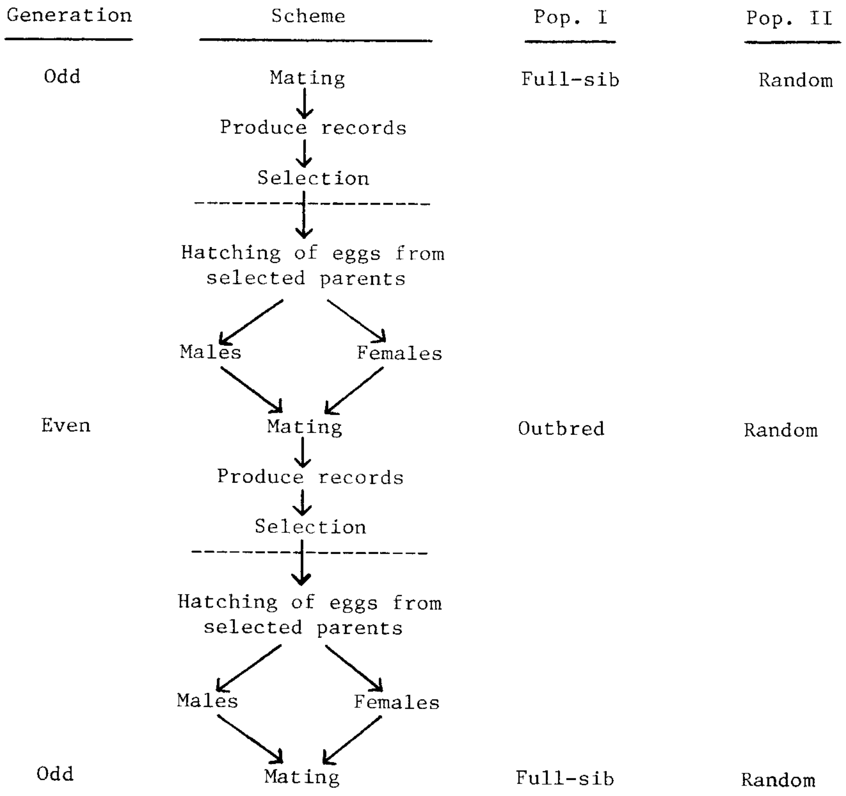

**Fig. 1.** Management scheme for the selected populations

two generations, 16 and 17, were mated at random and the parents of generation 17 were unselected.

Population II was formed in the same manner as Population I. At generation 0 both replicates of Population II were closed and in the succeeding generations selection was practiced. The proportion selected, averaged over replicates and a generation, was 24%. Mating of individuals was at random except that no full-sib matings were made. Half-sib mating was not possible because only full-sib families were produced. The parents of generation 17 were unselected.

The two replicates of Population III were continuations of the University of California stock. In each generation the selection of individuals and choice of mates was at random. Averaged over replicates and generations the proportion selected was 51%. Population III was used as a control to measure environmental changes across generations.

The birds were housed in male-female pairs at 28 days of age. No females had reached sexual maturity at this time. Egg production was recorded during a subsequent 50-day test period and at 78 days of age all birds were weighted.

The entire colony was treated alike, except for differences in mating system and selection procedures. The generation interval was held constant at about 4 months, a period which was not believed to place differential selection pressure on any population. An attempt was made to keep the effective population sizes of each replicate of all populations equal and constant over time. The harmonic means of the numbers of keets alive at 78 days each generation were 164, 201 and 105 for each replicate of Populations I, II and III, respectively. The actual number of pairs producing summed over replicates, in each generation and population are shown in Fig. 2. With only minor exceptions each replicate constituted approximately one-half the total number of reproducing pairs of each population.

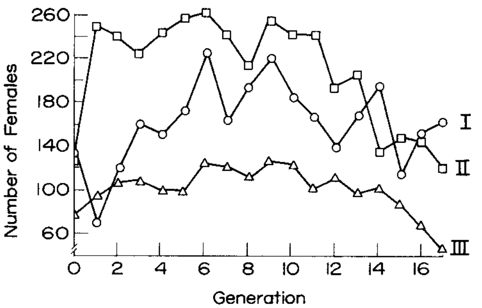

**Fig. 2.** Trends in the total number of females available for selection for each population

It was required that a female produce eggs in order to be selected. Therefore, the selection of females, whether for high index values or at random, occurred after eggs were laid. The number of females in each population, summed over replicates, after selection is shown in Fig. 3. The ratio of the number of females for a given population in a given generation in Fig. 3 to the comparable number of females in Fig. 2 equals the proportion selected for that population and generation. In Population I, it was necessary to increase the number of females selected during the earlier generations in order to produce as many progeny as in Population II. This was due to adverse effects of inbreeding depression of reproductive fitness in Population I.

For the purpose of calculating theoretical levels of inbreeding, a constant number of individuals equal to the effective population size appropriate to the population being considered was used as the number of individuals present in each generation. The restriction of no sib matings results in

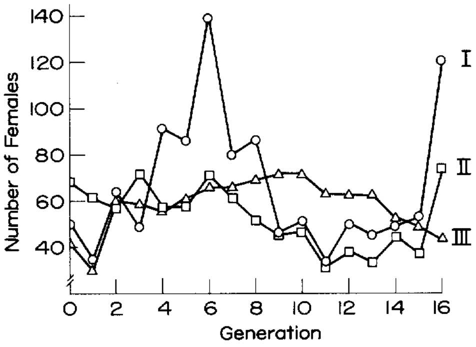

**Fig. 3.** Trends in the number of females that produced progeny contributing to the next generation for each population summed over replicates

minimal decrease in the rate of inbreeding in large lines (Wright 1951; Robinson and Bray 1965; Sather et al. 1977). Therefore, mating was assumed to be at random in populations II and III for calculating the increase in inbreeding due to finite populations size and selection intensity. Selection acts to reduce the effective number by the ratio $N/N_e$, where N is the number of individuals prior to considerating the effect of selection and Ne is the effective number of individuals after selection (Robertson 1964). The theoretical change in the level of inbreeding per generation was calculated as $1/2\,N_e$ after adjusting $N_e$ for selection. In Population I the effect of mating system on the theoretical inbreeding coefficients was calculated from a simulated pedigree population in the classical manner (Wright 1922). Mating system and selection effects on inbreeding were assumed to be additive and independent for Population I. Observed levels of inbreeding were calculated for each bird using the pedigree as described by Wright (1922).

The possible effect of mating system on response to continuous inbreeding was studied at generation 12 (Webb 1972). Sublines for each population of size 64 (32 pairs) were developed with stock drawn from as many families as possible in each replication of each population. Three sublines were subjected to a test of genetic load by continued full-sib mating. These generation 12 birds were designated generation 0′. These birds were full-sib mated to produce generation 1′. Data were collected from two hatches each generation on embryonic death (early vs. late) and hatchability of eggs set. Embryonic death was determined microscopically after eggs failed to hatch and was classified as early (less than approximately 9 days) and late (greater than approximately 9 days).

**Table 1.** Levels of inbreeding for each population

| Generation | Population I | | Population II | | Population III | |
|---|---|---|---|---|---|---|
| | Observed | Theoretical | Observed | Theoretical | Observed | Theoretical |
| 0 | 0.012 | 0.005 | 0.009 | 0.004 | 0.000 | 0.000 |
| 1 | 0.254 | 0.250 | 0.019 | 0.006 | 0.033 | 0.005 |
| 2 | 0.010 | 0.006 | 0.027 | 0.010 | 0.025 | 0.010 |
| 3 | 0.324 | 0.315 | 0.025 | 0.012 | 0.037 | 0.014 |
| 4 | 0.013 | 0.008 | 0.023 | 0.016 | 0.038 | 0.019 |
| 5 | 0.334 | 0.331 | 0.020 | 0.018 | 0.035 | 0.024 |
| 6 | 0.024 | 0.009 | 0.028 | 0.021 | 0.034 | 0.029 |
| 7 | 0.335 | 0.337 | 0.028 | 0.024 | 0.019 | 0.033 |
| 8 | 0.020 | 0.010 | 0.028 | 0.027 | 0.016 | 0.038 |
| 9 | 0.336 | 0.338 | 0.027 | 0.029 | 0.018 | 0.043 |
| 10 | 0.022 | 0.011 | 0.024 | 0.031 | 0.015 | 0.048 |
| 11 | 0.339 | 0.340 | 0.024 | 0.033 | 0.011 | 0.052 |
| 12 | 0.048 | 0.012 | 0.024 | 0.039 | 0.017 | 0.057 |
| 13 | 0.338 | 0.341 | 0.033 | 0.042 | 0.016 | 0.062 |
| 14 | 0.044 | 0.014 | 0.037 | 0.044 | 0.016 | 0.067 |
| 15 | 0.341 | 0.343 | 0.040 | 0.049 | 0.012 | 0.071 |
| 16 | 0.067 | 0.015 | 0.040 | 0.051 | 0.017 | 0.076 |
| 17 | 0.074 | 0.018 | 0.045 | 0.053 | 0.026 | 0.081 |

The population means for age at first egg, number laid, precent early and late embryonic death and percent hatchability, were estimated by least squares procedure (Harvey 1975). The main effects were population, replication, hatch, cage location and the appropriate two factor interactions. The covariate age at first egg was also included in the analyses of number laid, percent early and late embryonic death and percent hatchability. All possible interactions could not be fit at one time due to limitations of the computer program. Therefore, multiple analyses were made of the data with different sets of two factor interactions and those that were significant ($P < 0.05$) in one of the preliminary analyses were used in the final model. Higher order interactions were assumed neglible and ignored.

## Results and discussion

### *Inbreeding levels*

The observed levels of inbreeding in the experimental populations and the theoretical levels are shown in Table 1. There was good agreement in most cases between theoretical and observed inbreeding coefficients.

In inbred generations of Population I, observed levels of inbreeding were always within 0.01 of their expectation and inbreeding quickly reached the level of 0.34. When a cyclic mated population of assumed infinite size is considered, the theoretical level of inbreeding in the full-sib progeny quickly approaches ⅓ and remains constant at that value for all subsequent progeny of full-sib matings. Levels of inbreeding in outbred generations of population I deviated somewhat further from theoretical values, by as much as 0.05. These differences may be due to sampling errors; otherwise they are difficult to explain.

In Population II and III, agreement between theoretically expected levels of inbreeding and those actually observed was quite good. However, there was a consistent tendency in both populations for theoretical levels of inbreeding to be greater than observed levels, especially during later generations when this difference was as large as 0.06. Woodard et al. (1973) reported that Japanese quail are more sensitive to the effects of inbreeding than are other domestic fowl. It is conceivable that in Population II, the more highly inbred individuals had lower indices and were not selected, thus lowering the average level of inbreeding. However, differences between theoretical levels of inbreeding and those observed for Population III cannot be explained by the same argument. Another possible explanation applicable to both populations II and III is that more highly inbred individuals failed to survive as well as individuals with lower levels of inbreeding. This would not explain the results from Population I, but perhaps Population I was less "susceptible" to inbreeding depression (see later results). Other possibilities are (1) that the differences occurred by chance, or (2) the theoretical considerations failed to adequately describe the biological situation. Comparison of theoretical inbreeding coefficients for Population II and III showed the relatively small effect of selection on effective population size in this study where population size was quite large.

### *Fitness*

The trial initiated at generation 12 to study the effects of previous mating system on response to continuous inbreeding was terminated after two generations because an average of 0.2 quail were hatched per family during generation 2′; hence, no families had sufficient members to continue. This result agrees with those of Sittman et al. (1966) where a complete loss of reproductive fitness was observed by the third generation of successive full-sib mating of Japanese quail. The number of surviving families of each generation is shown in Table 2. A chi square contingency test showed the populations to be homogenous in this respect. These results indicated that all populations were sensitive to inbreeding depression for fitness traits. Sittman et al. (1966) and Iton (1967) observed inbreeding depression for fertility and hatchability in Japanese quail.

Analyses of variance for each trait indicated that the mean squares for replication and interactions of replication with other main effects rarely approached significance ($P > 0.10$). Therefore, the results presented herein have been averaged over replications.

Shown in Table 3 are means for age at first egg, number of eggs laid, embryonic death and hatchability for each population at generation 1′. Population II had significantly younger age at first egg than did populations I and II, however, the number of eggs laid to 78 days adjusted for age at first egg was similar for all populations. Overall, embryonic death rate was somewhat higher and rate of hatch lower than observed by Sittman et al. (1966). A significant advantage in fitness for Population I was observed (Table 3). Population I had significantly lower early embryonic death loss and greater percent hatch than Population II and III. This suggested that Population I was less "susceptible" to inbreeding depression than the populations with no history of inbreeding. Greater reproductive fitness in Population I could be attributed to a beneficial alteration of allelic frequencies via natural selection. The cyclic mating system was probably more effective in bringing together undesirable allelic combinations and in permitting natural selection to eliminate them than were the random mating systems.

**Table 2.** Number of surviving families of each generation under continuous inbreeding in samples from the three populations

| Generation[a] | Pop. I | Pop. II | Pop. III |
|---|---|---|---|
| 0′ | 32 | 32 | 32 |
| 1′ | 12 | 13 | 8 |
| 2′ | 0 | 0 | 0 |

[a] 0′ corresponds to generation 12 of the selection experiment

**Table 3.** Effect of inbreeding on some components of reproductive fitness[a]

| Trait | Pop. I | Pop. II | Pop. III |
|---|---|---|---|
| Age at first egg (days) | $52 \pm 3^{b}$ | $47 \pm 3^{c}$ | $55 \pm 3^{b}$ |
| Number of eggs laid[e] | $9.0 \pm 1.4$ | $7.9 \pm 1.1$ | $8.4 \pm 1.9$ |
| Early embryonic death (%) | $14 \pm 4^{b}$ | $25 \pm 4^{c}$ | $23 \pm 5^{bc}$ |
| Late embryonic death (%) | $21 \pm 4$ | $24 \pm 4$ | $26 \pm 4$ |
| Hatchability (%) | $45 \pm 4^{b}$ | $32 \pm 4^{c}$ | $22 \pm 5^{d}$ |

[a] Generation 1′

[b c d] Means within row with different superscripts are significantly ($P < 0.05$) different

[e] Adjusted for age at first egg

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