

Effects of mating system in Japanese quail

2. Genetic parameters, response and correlated response to selection *

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Received August 1, 1983

Communicated by H. Abplanalp

Summary. A 17-generation selection experiment was conducted to study direct and correlated responses to mass selection under a mating system with alternating generations of full-sib inbreeding and wide outbreeding (population I) as compared with a mass selected, randomly mated population (population II). The selection criterion was an index of total egg mass to 78 days divided by adult female body weight. Estimates of heritabilities and genetic correlations are reported. Estimated heritabilities for the index were 0.38 ± 0.04 and 0.29 ± 0.05 in population I and II, respectively. Realized heritabilities were 0.10 ± 0.05 and 0.12 ± 0.03 . For most traits studied the mean phenotypic values in the cyclic mated population decreased for inbred generations. Increased inbreeding levels also caused outbred generation means of population I to decrease through the first six or seven generations. After this period of adaptation to inbreeding selection response was positive for the index and positively correlated traits. Total response to selection under the cyclic inbred-outbred mating system did not exceed selection response made under random mating. However, the rate of response in the cyclically mated population exceeded that in the randomly mated population in later generations when the cyclically mated population had apparently adapted to inbreeding.

Key words: Japanese quail – Selection – Mating system – Heritability

Introduction

Selection is the only means available to a breeder to make long-term directed genetic change within large

populations. When response to selection is likely to be small due to low heritability, different systems of mating may be considered to help identify animals of superior genetic merit.

Inbreeding thus may be useful in augmenting effects of selection because it increases the genetic variance among inbred families. Dickerson has stated (1973) and shown theoretically (1977) that response to selection with an alternate generation full-sib inbreeding mating system can be expected to exceed that for a random mating system if heritability is less than 0.20 and selection intensity per generation is not reduced. The usefulness of inbreeding in such a program would be limited by any consequent reduction in selection intensity or effective population size (Dickerson 1977).

The objective of this study was to compare response to mass selection in a population under alternate generation full-sib inbreeding with response to mass selection in a population under continuous random mating.

Materials and methods

Three populations of Japanese quail (*Coturnix coturnix japonica*) previously described by MacNeil et al. (1984) were studied for 17 generations. Selection was applied to populations I and II and population III served as an unselected control. The selection criterion was an index calculated as egg mass divided by 78-day body weight, hence, only females were artificially selected. Egg mass was the number of eggs produced by a female during a 50-day period beginning at 28 days of age multiplied by average egg weight.

Each generation, beginning in generation zero, Population I was selected for a larger index and full-sib mated in alternate generations. This cyclic mating system resulted in the production of inbred progeny in odd numbered generations. Individuals in even numbered generations resulted from wide outbreeding determined by minimizing the genetic covariance among prospective mates. The final two generations (16 and 17) were produced by random mating and the parents of generation 17 were unselected.

* Published with approval of the Director of the Montana Agricultural Experiment Station, Journal Series No. 1221

Population II was selected by the same criterion as population I. Mating was at random in every generation, except that no full-sib matings were made. As in Population I, parents of generation 17 were not selected.

Population III was mated and selected at random every generation. Therefore, only natural selection, chance and environmental events should have influenced this population. Population III was used as a control throughout the study.

Attempts were made to keep effective population size equal for each replicate of all populations. This necessitated retaining more females in Population I during early generations due to mortality from inbreeding depression. The average number of female keets alive at 78 days per replicate per generation were 179, 228 and 97 for population I, II and III, respectively. Proportions of these females selected were 39, 24 and 51% for Populations I, II and III, respectively.

Selection differentials were computed within each replicate of each population as the difference between the mean index for all females which produced progeny in generation $k+1$ weighted by the number of progeny left and the mean index for all females in generation k .

Generation means and analyses of variance were computed by least-squares procedures for a fixed model (Harvey 1975). The independent variables were population, generation, replication, row and bank of housing, sex where applicable and two factor interactions among the main effects. Dependent variables were the index, egg number, egg weight, egg mass, body weight, shank length and shank width. Body weight, shank length and shank width were measured at 78 days of age. Direct and correlated responses were calculated as deviations from Population III, the control.

Genetic parameters and their standard errors were estimated according to methodology given by Falconer (1960). Heritability estimates were calculated as twice the regression coefficient of offspring on parent which should minimize any bias due to selection (Falconer 1960). For sex-limited traits only the regression of daughter on dam was used. For those traits which were not sex-limited the regressions of daughter on dam and son on sire were pooled. Pooling was thought to be legitimate because the two regressions were similar and these traits were measured at maturity and were not likely to be influenced by maternal effects.

The standard error for each heritability estimate was calculated as:

$$\sigma_h^2 = \left[\left(\frac{4}{N-2} \right) \left(\frac{1+(n-1)t}{n} - b^2 \right) \right]^{1/2}$$

where

N = the number of parents,

n = the average number of progeny per family,

t = the product of the relationship between offspring and parent (assumed = 0.5) and the estimated heritability and

b = the appropriate regression coefficient.

Genetic correlations were calculated as:

$$r_a = \frac{\text{COV}_{xy}}{\sqrt{\text{COV}_{xx'} \text{COV}_{yy'}}$$

Standard errors for genetic correlation were calculated as:

$$\frac{1-r_a^2}{\sqrt{2}} \sqrt{\frac{\sigma_{h_x}^2 \sigma_{h_y}^2}{h_x^2 h_y^2}}$$

Results and discussion

In order to minimize bias and sampling error in the estimates of selection applied and genetic response, adjustments were made for important influences in sampling birds from the various rows and banks of the house. Krehbiel et al. (1971) have provided further justification of least squares adjustment for environmental effects in estimates of selection applied and response. In the analysis of variance for the selection index, all sources of variation were significant. However, only population, generation and their interaction accounted for more than 1.0% of the total variation. Replication and interactions of replication with population and generation when taken together accounted for less than 1.5% of the total variation for all traits. Generation means were thus nearly similar for both replications within each population. Therefore, the unweighted average over replication of the replication – population – generation subclass means was used to estimate the population-generation subclass means. Overall means and standard deviations have been provided (Table 1) to benchmark the level of performance achieved over the course of this experiment.

Cumulative selection responses and cumulative selection differentials of index values (Table 2) indicate that Population I had significantly lower selection differentials than Population II. However, the realized heritabilities (regression of cumulative response on one-half the cumulative female selection differential) for Populations I and II were similar; 0.10 ± 0.05 and 0.12 ± 0.03 respectively. Therefore, when all generations were considered, linear response per unit of selection differential was not different between Population I and II. The realized heritabilities of the index were about half the magnitude of the parent-offspring regression estimated heritabilities.

Direct response to selection in Population I was best described by a quadratic equation (Fig. 1). The initial decrease in index values for Population I during generations one to six was probably due to inbreeding depression masking the effect of selection for higher values and reduced opportunity for selection due to inbreeding depression of fitness traits (MacNeil et al.

Table 1. Arithmetic means and residual standard deviations for traits studied

Trait	n	Mean	SD
Index	9,017	1.82	0.71
Body wt	18,070	123.60	11.90
Egg no.	9,017	9.31	2.55
Egg wt	9,017	24.92	9.18
Egg mass	9,017	248.02	96.67

Table 2. Selection differentials (*SD*) and selection response (*R*) for the index

Generation	Population I		Population II	
	R	SD	R	SD
1	-0.205	0.475	0.064	0.658
2	0.127	-0.004	-0.347	0.593
3	-0.390	0.162	0.457	0.777
4	0.479	0.689	-0.146	0.547
5	-0.625	0.228	0.108	0.638
6	0.638	0.483	-0.287	0.492
7	-0.635	0.270	0.411	0.595
8	0.660	0.580	-0.093	0.493
9	-0.624	0.528	0.055	0.534
10	0.645	0.847	0.032	0.548
11	-0.341	0.564	0.165	0.619
12	0.362	0.774	0.001	0.757
13	-0.296	0.570	0.201	0.724
14	0.502	0.788	-0.265	0.735
15	-0.428	0.603	0.036	0.566
16	0.340	0.569	0.098	0.683

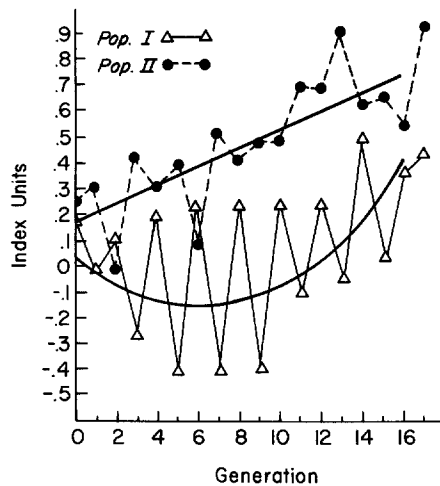


Fig. 1. Direct response to selection for the index as a deviation from the control

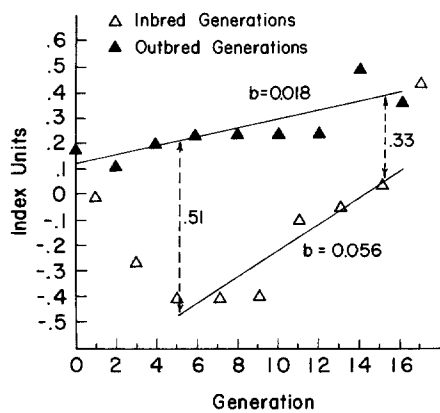


Fig. 2. Population I response to selection in inbred and outbred generations

1984). Following generation six the response to selection for larger index values was observed as a rapid and nearly linear increase of 0.065 units per generation. A large part of this increased response was due to the increase in inbred generation means relative to adjacent outbred generation means. Apparently, Population I became “adapted” to inbreeding during the early generations such that inbreeding depression was no longer of sufficient magnitude to override the response to selection during later generations. When inbred and outbred generations of Populations I were considered separately (Fig. 2), the response to selection was observed to be linear for outbred generations (0.018 ± 0.004 units per generation) and quadratic from inbred generations with the curvature the result of inbreeding depression in generation 1 and 3. The linear regression of index value on generation number was 0.056 ± 0.006 for inbred generations 5 through 15. In addition to the increase in between family additive genetic variance, the greater rate of response in inbred generation may also be attributed to the greater selection differentials achieved in selecting among outbred females to serve as parents. At generation 5, inbreeding resulted in a predicted difference between inbred and outbred phases of population I of 0.51 index units. At generation 16, 35% of this difference had been recovered due to the greater rate of selection response in inbred generations.

Response to selection in Population II was essentially linear. The linear regression of the index on generations was 0.034 ± 0.007 units per generation and approached being significantly larger ($P = 0.13$) than the 0.018 value for the outbred generations of Population I, and was significantly smaller than the regression of the index as generation number for the inbred generations. Interestingly, the average of the regressions of index on generation number for inbred and outbred generations of population I (0.037) was similar to the 0.034 units per generation of population II.

The mean index in Population II was significantly greater than the mean index of Population I at generation 17. The difference between the two populations at generation 17 was five times larger than at generation zero (0.46 vs. 0.08). This comparison should be free of inbreeding effects since Population I quail in generation 17 were produced by outbred parents mated at random. Hence, it was concluded that after 16 generations of selection, response in the random mated population was greater than response in the population that was inbred in alternate generations. The lower response in Population I was probably due to significantly lower selection differentials, especially in the early generations.

Figures 3 through 6 show correlated responses in egg weight, egg number, egg mass, and body weight, re-

spectively. The smooth continuous lines reflect the respective regressions of generation means on generation number for each trait. In general, the observed correlated responses agreed with estimated genetic correlations. As with the index, the effects of inbreeding are clearly evident by the decrease in the mean of most traits in the inbred generations of Population I. The difference between inbred and outbred generation means tended to decrease in later generations and supported the hypothesis that Population I became less sensitive to inbreeding.

Egg weight was a component of the numerator of the index. In Population I, the quadratic term of the regression of egg weight on generation was significant, probably due to the effects of inbreeding in early generations and subsequent recovery (Fig. 3). In Population II there was no significant correlated response in egg weight. In light of the small genetic correlations observed between egg weight and the index, the expected correlated response in egg weight would also be small. Previous work (Insko et al. 1971; Lucotte 1975) has indicated strong natural selection for egg weight at some optimum, intermediate value.

The correlated response in egg number (Fig. 4) under the cyclic mating system was quadratic and decreased through generation 6 at an approximate rate of 0.43 eggs per generation and then increased by 0.70 eggs per generation through the end of the study. In Population II the correlated response was such that egg number increased at a linear rate of 0.29 ± 0.07 eggs per generation. This rate of change was not significantly different from the overall rate of increase for Population I.

Egg mass was the multiplicative combination of egg weight and egg number and the numerator of the index. In Population I the correlated response in egg mass (Fig. 5) followed a pattern similar to the correlated response in egg number by decreasing through generation 7 at an average rate of 3.71 g per generation

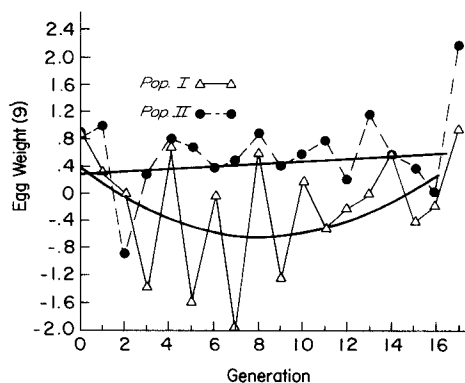


Fig. 3. Correlated response in egg weight to selection for the index as a deviation from the control

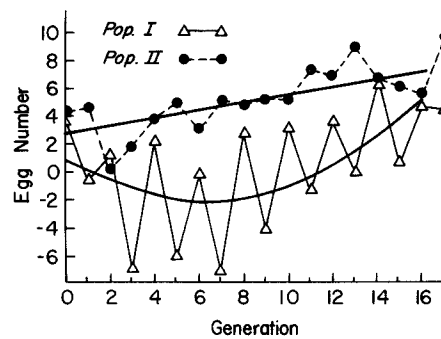


Fig. 4. Correlated response in egg number during a 50-day period to selection for the index as a deviation from the control

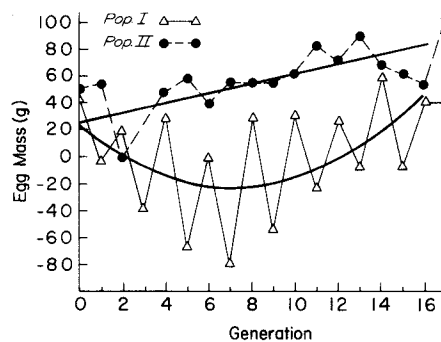


Fig. 5. Correlated response in egg mass to selection for the index as a deviation from the control

and then subsequently increasing by 7.54 g per generation. The correlated response in egg mass for Population II was positive and linear at a rate of 2.95 ± 0.80 g per generation. The overall rates of increase were not significantly different between Populations I and II. In both populations correlated response in egg mass closely followed the direct response of the index.

In both Population I and II body weight decreased linearly as correlated responses to selection for the index (Fig. 6). Population II decreased at a significantly greater rate than did Population I: 0.96 ± 0.09 g per generation versus 0.66 ± 0.11 g per generation. There was some evidence of curvilinearity in both populations as body weight tend to remain somewhat constant from generation 12 on. It is unlikely the genetic variation in body weight had been exhausted. However, the directional selection applied may have sufficiently altered the body weight-egg interrelationship to affect fecundity (Wright 1977).

Table 3 contains estimates of heritability for all traits. Estimates for Population I are not reported because of bias introduced by the mating system. Estimates for Population II were consistently, but usually not significantly, higher than those for Popula-

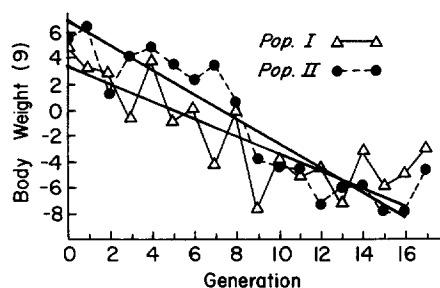


Fig. 6. Correlated response in 78-day body weight to selection for the index as a deviation from the control

Table 3. Estimates of heritability (h^2) in populations II and III

Trait	Population II		Population III	
	n ^a	h^2	n ^a	h^2
Index	916	0.38 ± 0.04	985	0.29 ± 0.05
Body wt	1,832	0.60 ± 0.04	1,970	0.52 ± 0.04
Egg no.	916	0.33 ± 0.04	985	0.30 ± 0.05
Egg wt	916	0.16 ± 0.04	985	0.03 ± 0.05
Egg mass	916	0.32 ± 0.04	985	0.28 ± 0.05

^a n = the number of parents

Table 4. Estimates of genetic correlations in populations II and III

Trait 1	Trait 2	Population II r_a	Population III r_a
Body wt	Egg mass	-0.21 ± 0.06	0.27 ± 0.07
	Egg no.	-0.50 ± 0.04	0.03 ± 0.08
	Egg wt	0.67 ± 0.04	^a
	Index	-0.65 ± 0.03	-0.06 ± 0.08
Egg mass	Egg no.	0.83 ± 0.03	0.94 ± 0.01
	Egg wt	0.57 ± 0.09	0.28 ± 0.31
	Index	0.85 ± 0.02	0.98 ± 0.01
Egg no.	Egg wt	0.19 ± 0.11	-0.09 ± 0.33
	Index	0.94 ± 0.01	^a
Egg wt	Index	0.20 ± 0.10	-0.11 ± 0.33

^a $r_a > 1.0$

tion III. This might be due to the fact that the foundation stock for Population II was from a broader genetic base than that for Population III.

Both heritability estimates for mature body weight of 0.60 and 0.52 of this study are higher than the estimates of 0.36 by Marks and Kenney (1964), 0.42 by Kawahara and Inone (1966) and 0.48 by Sefton and Siegel (1974). Estimates of the heritability of body

weight reported here were similar to the 0.57 and 0.45 reported by Wilhelmson (1975) for male body weight at 56 and 84 days of age, respectively. Estimates of 0.45 and 0.49 for female body weight at 56 and 84 days of age, respectively, were also reported by Wilhelmson (1975). Kawahara and Saito (1976) reported estimates of 0.69 for males and 0.30 for females for 25-week body weight.

The estimates of heritability for egg number of 0.30 and 0.33 from this study are in good agreement with literature estimates of 0.38 and 0.49 (Marks and Kenney 1964), 0.20 to 0.25 (Sittman et al. 1966) and 0.42 (Strong et al. 1978). Wilhelmson (1975) reported six estimates for heritability of number of eggs from first egg that ranged from 0.21 to 0.40 with an average of 0.31.

Present estimates of heritability for egg weight of 0.16 and 0.03 are lower than previous estimates of 0.54, 0.65 and 0.50 (Kawahara and Inone 1966; Sittman et al. 1966; Strong et al. 1978, respectively). The average of four estimates for the heritability of egg weight by Wilhelmson (1975) was 0.47.

Estimates of genetic correlations among the traits studied are shown in Table 4. Several part-whole relationships exist between egg mass, egg weight, egg number and the index. Therefore, it was expected that these genetic correlations would be both positive and high. The only exceptions to this expectation were the genetic correlation between egg weight and the index in Population II and the genetic correlations of egg weight with the index and egg mass weight in Population III.

Strong et al. (1978) reported genetic correlations that agreed reasonably well (when one considers size of standard errors) with present estimates. They were 0.54 ± 0.31 for body weight at sexual maturity and egg weight, 0.05 ± 0.13 for body weight and egg number and -0.08 ± 0.54 for egg number and egg weight. Wilhelmson (1975) has reported moderately to highly positive genetic correlations of egg number from first egg with body weight and egg weight were generally near zero.

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