Effect of mating system on selection response in Japanese quail
by Michael David MacNeil

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Animal Science
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Abstract:
Records from 17 generations of three replicated populations of Japanese quail were analyzed by least squares procedures. Population I was selected and mated in a cyclic fashion with alternating generations of full sib inbreeding and wide outbreeding. Population II was selected and randomly mated. Population III was randomly mated and randomly selected for use as a control. Population, replication, generation, sex interactions among these factors and regressions on Fx were analyzed in various combinations as independent variables in fixed effect models. Response variables were the selection index, body weight, egg mass, egg number, egg weight, shank length and shank width. The objectives of this study were to 1) examine differences in direct and correlated responses to selection between. populations I and II, 2) determine the importance of each of the components of the selection index: egg number x egg weight/ body weight to the index, 3) estimate genetic parameters and 4) describe possible modes of gene action for each of the characters studied. Selection response was equally efficient for both mating systems. The realized heritabilities for the selection index were .21±.04 for population I and .16±.01 for population II. The correlated responses of all characters in population I moved in the same overall direction as the correlated responses in population II.

Egg number was the most important component of the index followed in order by body weight and egg weight. The average heritability estimates for the index, body weight, egg mass, egg number, egg weight, shank length and shank width were .62, .51, .57, .60, .54 and .35, respectively. The genetic correlations were generally in good agreement with the literature estimates. Additivity was a major influence in the inheritance of egg mass, egg number, egg weight and shank width. Dominance was an influence in the inheritance of the index, body weight, egg number and egg weight. Epistatic effects were of some importance to the index and body weight.

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MICHAEL DAVID MACNEIL

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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Approved:

D D Kress
Chairperson, Graduate Committee

J L Van Horn
Head, Major Department
Act

Henry L Parsons
Graduate Dean

MONTANA STATE UNIVERSITY
Bozeman, Montana

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ABSTRACT

Records from 17 generations of three replicated populations of Japanese quail were analyzed by least squares procedures. Population I was selected and mated in a cyclic fashion with alternating generations of full sib inbreeding and wide outbreeding. Population II was selected and randomly mated. Population III was randomly mated and randomly selected for use as a control. Population, replication, generation, sex interactions among these factors and regressions on F_x were analyzed in various combinations as independent variables in fixed effect models. Response variables were the selection index, body weight, egg mass, egg number, egg weight, shank length and shank width. The objectives of this study were to 1) examine differences in direct and correlated responses to selection between populations I and II, 2) determine the importance of each of the components of the selection index:

$$\frac{\text{egg number x egg weight}}{\text{body weight}}$$

to the index, 3) estimate genetic parameters and 4) describe possible modes of gene action for each of the characters studied. Selection response was equally efficient for both mating systems. The realized heritabilities for the selection index were .21±.04 for population I and .16±.01 for population II. The correlated responses of all characters in population I moved in the same overall direction as the correlated responses in population II. Egg number was the most important component of the index followed in order by body weight and egg weight. The average heritability estimates for the index, body weight, egg mass, egg number, egg weight, shank length and shank width were .62, .51, .57, .60, .54 and .35, respectively. The genetic correlations were generally in good agreement with the literature estimates. Additivity was a major influence in the inheritance of egg mass, egg number, egg weight and shank width. Dominance was an influence in the inheritance of the index, body weight, egg number and egg weight. Epistatic effects were of some importance to the index and body weight.

INTRODUCTION

Inbreeding has been shown to reduce productivity in most breeding programs and yet heterosis generally results when inbred lines are crossed. It has been proposed that the increment of inbreeding rather than the total amount of inbreeding may provide opportunity for a combination of selection and genetic drift to exert maximum effect in producing phenotypes and thus genotypes yielding progress toward desirable goals (Keller, 1969). Over a large number of generations, alternating generations of full sib mating and wide outcrossing maximizes this increment, given the biological constraint that selfing is impossible and the constraint imposed by a limited effective population size. By using reasonably large populations the researcher can effectively hedge against the loss of alleles with minor effects which subsequently might be responsible for increased productivity.

The progress from individual selection is dependent on the mode of gene action. If only a small portion of the phenotypic variance is derived from additive gene action, then selection progress can be slow and inefficient, and other selection criteria should be found or other methods of selection employed.

The present experiment with Japanese quail compares selection response in a population undergoing alternating generations of inbreeding and outbreeding with selection response in a population under random mating. Additionally, genetic parameters were estimated and an attempt was made to define the principle mode of gene action for each of the characters studied.

LITERATURE REVIEW

Selection

Selection is the process by which directional changes in gene frequency occur and is the result of differential reproductive success of genetically different individuals:

> Selection whether in mortality, mating or fecundity applies to the organism as a whole. A gene which is more favorable than its allelomorph in one combination may be less favorable in another. Even in the case of cummulative effects, there is generally an optimum grade of development of the character and a given plus gene will be favorably selected in combinations below this optimum but selected against in combinations above the optimum (Wright, 1931).

The change in allelic frequency is in approximate proportion to the portion of the population selected and the square of the allelic frequency. Selection should ultimately decrease the variance of the population with respect to the selected trait. Inbreeding is accelerated under selection because of the effect of selection on limiting population size and an inbreeding effect due to selection itself (Robertson, 1961).

Selection of Japanese Quail. Much of the reviewed literature dealt solely with selection for body weight at a certain age, typically between four and six weeks. Stress conditions have been used to intensify the selection pressure in some experiments; however, the performance of the stressed lines was either the same or only slightly better than unstressed lines when compared in a non-stressed environment (Marks and Lepore, 1967; Collins _et al._, 1970; Marks, 1971; Cahil _et al._, 1975). The discussion therefore will be limited to unstressed lines.

Tables 1 and 2 show the heritabilities for body weight within weekly age classes and some other characters of Japanese quail. In general the heritabilities for body weight are about 5% greater for females than for males.

Between family selection for 3-week body weight with a selection differential computed as 2.94 grams per generation resulted in a response of 1.5 grams per generation (Collins _et al._, 1968). They observed positive correlated responses for adult body weight and egg weight. No change was reported for fertility, hatchability, liveability and egg production. In another study (Collins _et al._, 1970) individuals were selected for 6-week body weight with selection differentials per generation in the range of 6.77 to 7.85 grams and response per generation was 1.08 to 1.38 grams. A decline in body weight of the controls in this study was attributed to natural selection against large body size in the given environment.

TABLE 1. HERITABILITIES OF BODY WEIGHT OF JAPANESE QUAIL

Age	Sex[a]	h^2	Method[b]	Source
3 weeks	B	.34	o-mp	Collins *et al.* (1968)
	B	.51	R/S	Collins *et al.* (1968)
4 weeks	M	.25	R/S	Marks (1971)
	M	.29	o-pf	Marks (1971)
	F	.30	o-pm	Marks (1971)
	F	.30	o-mp	Marks (1971)
	M	.31	R/S	Marks (1971)
	M	.33	o-mp	Marks (1971)
	F	.34	R/S	Marks (1971)
	F	.34	o-pf	Marks (1971)
	M	.35	o-pm	Marks (1971)
	F	.36	R/S	Yosida and Collins (1967)
	M	.38	R/S	Yosida and Collins (1967)
	F	.41	R/S	Marks (1971)
5 weeks	M	.34	R/S	Chahil *et al.* (1975)
	F	.53	R/S	Chahil *et al.* (1975)
6 weeks	B	.25	R/S	Collins *et al.* (1970)
	B	.25	R/S	Marks and Lepore (1968)
	B	.42	---	Kawahara and Inuoe (1966)
	B	.43	R/S	Abplanalp (1967)
Mature	B	.36	---	Marks and Kinney (1964)

[a] M = males; F = females; B = both.

[b] R/S = realized; o-mp = regression of offspring on the midparent; o-pm = regression of offspring on the male parent; o-pf = regression of offspring on the female parent.

TABLE 2. HERITABILITIES OF OTHER TRAITS OF JAPANESE QUAIL

Trait	h^2	Source
Egg production	.20	Kawahara and Inoue (1966)
	.46	Marks and Kinney (1964)
Age at sexual maturity	.33	Kawahara and Inoue (1966)
	.36	Marks and Kinney (1964)
Egg weight	.54	Kawahara and Inoue (1966)
Egg number	.39	Marks and Kinney (1964)

Marks (1971) used individual selection for 4-week body weight and observed a response over 15 generations of 40.4 grams. The selection differential per generation was reported as 10.0 grams, resulting in a selection intensity value (i) of 1.01. During the study the control line decreased in weight by an average of 10.6 grams.

In saving approximately one of four females and one of eight males, Abplanalp (1967) observed a response to selection for body weight of approximately 6.4 grams per generation for males during generations 13 to 17. The previous generations had been confounded by changes in other practices.

Simultaneous selection for body weight and shank length at 8 weeks of age over five generations was practiced by Isogai *et al*. (1974a). Approximately the top 40% were selected in each generation. Response to selection per generation expressed as percentage deviations of the nonselected control in a high shank length, constant body weight line was .26% for body weight and .91% for shank length. In a line selected for high body weight and a constant shank length response to selection per generation was 1.5% for body weight and .2% for shank length. The ratio of shank length to the cube root of body weight was significantly different among treatments and among each treatment and control. In another report (Isogai _et_ _al_., (1974b) the correlated response of mature skeletal length to selection for longer shanks was not consistent among parts of the skeleton, being greater in the anterior and posterior extremities. Overall correlated response of the mature skeletal length was 3.3% in the high shank length line and 1.5% in the high body weight line. It was concluded that selection pressure for shank length might result in a disruption of the balance among skeletal bones. Correlated response of mature body weight in the high shank length selected line was 3.5%, while in the high body weight selected line the correlated response in mature body weight was a 12.2% increase.

Keller (1969) selected a group of birds for an index (total egg mass ÷ weight of the female parent) and observed no response to selection over five generations. A possible reason for no response suggested by the author was the response to selection was "being masked or compounded by environment and/or natural selection."

Abplanalp (1967), selecting for egg number during a test period, had selection differentials of 0.0 for males and 12.0 for females over 12 generations. During the 6 to 12 week period the controls laid an average of 16.8 eggs compared to 28.1 eggs for the selected group. From 12 to 16 weeks the controls averaged 25.1 eggs, whereas the selected group averaged 24.5 eggs. Egg mass was decreased by .07 grams per generation in the selected group.

Genetic correlations among several traits have been reported by Kawahara and Inoue (1966) and El-Ibiary, et al., (1966). These correlations are summarized in table 3. Age at sexual maturity shows a moderately high negative correlation with egg production. Results seem to differ between studies as to whether or not age at sexual maturity is positively correlated with body weight; this could be due in part to the different times when body weight was measured. All other correlations, except egg weight with egg production, reported as significant were positive.

Body weight has been examined in relationship to a sexual dimorphism by several researchers. It has been suggested by Collins and Abplanalp (1968) and Wilson et al., (1961) that this is due at least in part to the more rapid development of the heavier female reproductive tract. Yosida and Collins (1967) reported a similar correlation for 4-week body weight between male and female birds of .9. Becker et al., (1964) reported a similar correlation

TABLE 3. GENETIC CORRELATIONS BETWEEN CHARACTERS OF JAPANESE QUAIL

Trait	r	Source
Egg weight x egg production	-.39	Kawahara and Inoue (1966)
x age at sexual maturity	.39	Kawahara and Inoue (1966)
x adult body weight	.47	El-Ibiary *et al.* (1966)
x immature body weight	.87	Kawahara and Inoue (1966)
Age at sexual maturity x body weight	.54	Kawahara and Inoue (1966)
x adult body weight	-.22	El-Ibiary *et al.* (1966)
x egg production	-.51	Kawahara and Inoue (1966)
x % growth 3-4 weeks	.29	El-Ibiary *et al.* (1966)
x egg number	-.63	El-Ibiary *et al.* (1966)
Egg number x adult body weight	.34	El-Ibiary *et al.* (1966)

of 1.00; in arriving at this correlation the assumption of no sex-linked effects was made. Sex linked effects along with maternal effects were subsequently found to be important to the determination of body weight (Collins and Abplanalp, 1968). El-Ibiary _et_ _al_. (1966) first found significant differences in body weight between sexes at 6 weeks of age of 6% in favor of the female which continued to increase to 22% at adulthood. The coefficients of variation were comparable for both sexes at all ages. Collins and Abplanalp (1968) reported this dimorphism to have decreased between 7 and 8 weeks of age.

Lucotte (1975) reported egg weight to be normally distributed about a mean of 11.2 grams, where hatchability was also optimum. Optimum hatchability was at an only slightly lighter egg weight in a study by Insko _et_ _al_. (1971).

Selection of Chickens. The selection of chickens has been mainly conducted for two traits: egg production and body weight at some age. The desirable effects attributed to selection for fucundity have been greatly augmented by favorable changes in environmental conditions raising some question as to the importance of the selection itself (Clayton, 1972). Summary tables of heritabilities are presented in tables 4, 5 and 6. Arithmetic mean heritabilities for body weight, egg production, egg weight and age

TABLE 4. HERITABILITIES OF BODY WEIGHT OF CHICKENS

Age	Sex[a]	h^2	Method[b]	Source
4 weeks	-	.48	fs-r	Siegal (1963)
	-	.49	d-var	Kan *et al*. (1958)
	M	.75	s-var	Thomas *et al*. (1958)
	F	.75	d-var	Thomas et al. (1958)
	B	.44	o-fp	Maloney *et al*. (1967)
	B	.50	o-fp	Maloney *et al*. (1967)
	M	.67	s-var	Thomas *et al*. (1958)
	F	.83	d-var	Thomas *et al*. (1958)
8 weeks	F	.22	o-p	Kinney and Shoffner (1965)
	F	.22	o-p	Kinney and Shoffner (1965)
	M	.24	s-var	Kinney and Shoffner (1965)
	F	.27	R/S	Siegal (1962)
	M	.30	R/S	Siegal (1962)
	F	.31	s-var	Kinney and Shoffner (1965)
	M	.33	o-p	Kinney and Shoffner (1965)
	F	.33	o-p	Kinney and Shoffner (1965)
	M	.36	d-var	Kinney and Shoffner (1965)
	M	.37	d-var	Kinney and Shoffner (1965)
	-	.40	o-fp	Wyatt (1954)
	-	.46	fs-r	Wyatt (1954)
	M	.70	s-var	Thomas *et al*. (1958)
	F	.79	d-var	Thomas *et al*. (1958)
10 weeks	-	.17	o-fp	Krueger *et al*. (1952)
	-	.28	fs-r	Krueger *et al*. (1952)
	-	.33	o-fp	Krueger *et al*. (1952)
	B	.34	d-var	Brunson *et al*. (1956)
	-	.41	ms-E	Lankford and McLung (1952)
	-	.46	fs-r	Krueger *et al*. (1952)
	M	.62	s-var	Thomas *et al*. (1958)
	F	.76	d-var	Thomas *et al*. (1958)
12 weeks	-	.07	R/S l	Maloney *et al*. (1963)
	F	.27	R/S	Maloney *et al*. (1967)
	-	.34	R/S h	Maloney *et al*. (1963)
	M	.35	R/S	Maloney *et al*. (1967)
	B	.37	R/S l	Maloney *et al*. (1967)
	B	.50	R/S h	Maloney *et al*. (1967)

(Table 4, cont'd)

Age	Sex[a]	h^2	Method[b]	Source
24 weeks	-	.38	fs-r	Ideta and Siegal (1966a)
	-	.44	R/S	Ideta and Siegal (1966a)
	-	.46	fs-r	Siegal (1963)
38 weeks	-	.36	fs-r	Ideta and Siegal (1966a)
	-	.38	fs-r	Siegal (1963)
	-	.54	R/S	Ideta and Siegal (1966a)
Unknown	F	.17	s-var	Lerner and Cruden (1951)
	-	.31	o-fp	McClung (1958)
	F	.46	d-var	Lerner and Cruden (1951)
	-	.48	o-fp	Dillard *et al.* (1953)
	-	.49	fs-r	Dillard *et al.* (1953)
	F	.49	o-fp c	Lerner and Cruden (1951)
	F	.80	o-fp	Lerner and Cruden (1951)

[a] - = unspecified, M = male, F = female, B = both.

[b] fs-r = full sib correlation, o-fp = regression offspring on female parent, o-p = regression offspring on parent, R/S = realized, ms-E = mean square expectations, m-var = variance component, d-var = dam variance component, h = high line, l = low line, c = corrected for maternal effects.

TABLE 5. HERITABILITIES OF EGG PRODUCTION OF CHICKENS

h^2	Method[a]	Source
.00	o-fp	Wyatt (1954)
.13	s-var	Kinney and Shoffner (1965)
.14	fs-r	Ideta and Siegal (1966a)
.17	o-fp	Krueger _et_ _al_. (1952)
.18	d-var	Kinney and Shoffner (1965)
.20	s-var	King and Henderson (1953)
.21	fs-r	Siegal (1963)
.23	o-p	Kinney and Shoffner (1965)
.25	fs-r	Dillard _et_ _al_. (1953)
.28	fs-r	Krueger _et_ _al_. (1952)
.32	o-fp	McClung (1958)
.41	d-var	King and Henderson (1953)
.48	R/S	Ideta and Siegal (1966a)
.51	fs-r	Wyatt (1954)
.66	o-fp	Taketomi _et_ _al_. (1974)

[a] s-var = sire variance component, d-var = dam variance component, fs-r = full sib correlation, o-fp = regression of offspring on female parent, o-p = regression of offspring on parent, R/S = realized.

TABLE 6. HERITABILITIES OF OTHER TRAITS OF CHICKENS

Trait	h^2	Method[a]	Source
Age at sexual maturity	.06	sd-var	Kinney and Shoffner (1965)
	.16	fs-r	Dillard *et al.* (1953)
	.16	d-var	Kinney and Shoffner (1965)
	.19	o-fp	Dillard *et al.* (1953)
	.19	R/S	Ideta and Siegal (1966a)
	.24	d-var	Lerner and Cruden (1951)
	.28	fs-r	Ideta and Siegal (1966a)
	.29	o-fp c	Lerner and Cruden (1951)
	.33	d-var	Lerner and Cruden (1951)
	.38	fs-r	Siegal (1963)
	.52	s-var	King and Henderson (1953)
Egg weight	.34	s-var	King and Henderson (1953)
	.48	d-var	King and Henderson (1953)
	.55	d-var	Lerner and Cruden (1951)
	.53	R/S	Ideta and Siegal (1966a)
	.60	o-fp	Lerner and Cruden (1951)
	.63	fs-r	Siegal (1963)
	.67	fs-r	Ideta and Siegal (1966a)
	.71	o-fp c	Lerner and Cruden (1951)
Shank length	.57	s-var	Kan *et al.* (1958)

[a] d-var = dam variance component, s-var = sire variance components, fs-r = full sib correlation, o-fp = regression offspring on female parent, R/S = realized, c = corrected for maternal effects.

at sexual maturity are .37, .28, .56 and .26 respectively. There is some evidence for non-additive gene effects being involved in the inheritance of body weight, egg production and shank length.

Evaluation of individual selection, sire and dam family selection and index selection based on sire and dam families and individual record for short term egg production resulted in individual selection showing the most response when standardized for the amount of selection and the phenotypic variance within the population (Kinney et al., 1970). The standardized response per generation of .10 ± .04 phenotypic standard deviations for individual selection was not significantly greater than the standardized response per generation to sire family selection of .08 ± .03 standard deviations or to index selection of .06 ± .02 standard deviations. The standardized response per generation to dam family selection was .04 ± .05 standard deviations. Though heritabilities were not reported in this study, these results seemingly contradict the theory of index selection being the most efficient for traits of low heritability. However, as was pointed out, the individually selected population was subject to less inbreeding than the other populations due to the use of a random sample of males as parents for the next generation. Further, the dam family selected population was not restricted with respect to half and full sib matings, whereas the sire family and index selected populations were. The intensity of selection per generation expressed as the selection differential in standard deviation units for each selection system was .98 for sire family, 1.08 for index, .92 for dam family and .51 for individual. Direct responses per generation were: .89 ± .34% for sire family selection, .77 ± .20% for index selection, .55 ± .21% for individual selection and .38 ± .20% for dam family selection. Correlated responses expressed as coefficients of linear regression on generation were negative and significant for egg weight and body weight in the sire family, dam family and index selected lines (-.55 and -.18; -.43 and -.12; -.60 and -.25, respectively). Regression coefficients on generation were positive and significant for long term production rate in the sire family line (1.29) and the index selected line (.64).

Divergent selection for 12-week body weight by Maloney _et_ _al_., (1967) showed response to be greater in the high line than in the low line. A difference in the rate of response was also noted between males and females in the high line. The high line responses for males and females were 99.8 grams and 72.5 grams per generation, respectively. The responses per generation in the low line for males and females respectively were -20.4 grams and -21.3 grams. The difference between sexes in the high line and among lines led to the analysis of the selection intensities within and among lines. No significant differences in selection intensity were found between lines or sexes. The average i values for the males and females of the high and low lines, respectively, were 1.24, 1.16, .96 and .92. Throughout the 15 generations of the study the realized heritability of 12-week body weight changed very little. Correlated response of 6-week body weight was found to be 46.27 grams per generation in the high line males and 36.29 grams per generation in the high line females. The response in the low line was reported at -4.54 grams per generation in both sexes. March egg weight was decreased by .47 gram per generation in the low line selected females. This decrease stabilized after the second generation of selection. Selected female parents in both lines exhibited a decrease in percentage egg production, percent fertility, and hatchability of fertile eggs. Age at sexual maturity was reduced in the high line by a non-significant amount, while it was increased in the low line by eight days.

Short term divergent selection results for 8-week body weight with sufficient numbers so as to have a negligible inbreeding effect were reported by Siegel (1962). The average effective selection differentials were 120.1 and 145.5 grams for the high line males and females, respectively, and -112.6 and -113.6 grams for the low line males and females. The average response per generation measured as the difference between lines within sexes was calculated to be 80.25 grams for the males and 73.50 grams for the males. Response to selection was not broken out by line and sex.

Dickerson (1963) summarized the comparisons between all stock on the Random Sample Tests and a "carefully unselected strain of White Leghorns developed by King." Deviations from this control furnished the method used to estimate genetic change in those stocks placed on test by commercial breeders regardless of selection criteria. The major changes reflect increased efficiencies in production, pounds of feed per pound of eggs, (-1.5% per year), pounds of eggs per hen housed, (1.8% per year), egg number per hen housed, (1.4% per year) and percent production per hen-day, (.8% per year). Relatively minor changes of .3 to .4% per year were made in egg weight, length of period in production and percent viability.

Cole and Hutt (1973) reported on a long term selection project with White Leghorns. The first criterion for selection was disease resistance. However, significant selection pressure was applied with respect to production. The method of evaluating progress was to compare the most recent three generations with the original three. While the use of three generation averages would minimize individual year effects, the admitted improvements in environment due to managerial changes would still be a source of bias. Thus, the changes reported must be considered as a consequence of confounded genetic and environmental improvements. During the initial period, 1936 to 1938, average egg production for the C and K lines, respectively, was 169 and 165 eggs per hen completing test or 116 and 120 eggs per hen housed. For the years 1967 to 1969 average egg production per hen completing test was 243 and 229 eggs for the C and K lines, respectively, and 228 and 220 eggs per hen housed for the C and K lines, respectively. Egg weight was increased during the 33-year period by 3.9 grams in the C line and 1.9 grams in the K line. Body weight remained unchanged for both lines during the course of the project. Yoa (1961) made use of the statistical model and analysis of variance derived by Hayman (1954) to estimate the significance of additive and dominance effects of genes with respect to egg production and 10-week body weight. In this analysis epistatic effects are assumed to be of no importance. With crossbred chickens total dominance effects were more important than additive effects for egg production; however, additive effects were more important than dominance effects for body weight. When purebreds were used as controls both additive and dominance effects were of significant importance. The additive effects were more important to body weight than to egg production. With inbreds as controls "moderately significant" additive effects were shown for egg production, but not for body weight. Dominance effects were highly significant for body characters.

The ratio of the sire by dam interaction variance component to the between dams variance component was used by Kan _et_ _al_., (1958) to detect non-additive gene effects for body weight at 4 and 9 weeks and for shank length. The data were taken from full diallel sets between the White leghorn and New Hampshire breeds and the analytical model was Eisenhart's model II (Eisenhart, 1947). It was concluded that non-additive effects were important to shank length, but of relatively little importance to body weight at either age studied. A study by Brunson et al., (1956) was not conclusive with regard to the importance of non-additive effects for 10-week body weight. Siegal (1962) concluded that the higher heritabilities for 8-week body weight obtained by full and half sib correlations than are realized in response to selection were indicative of non-additive gene effects. Epistatic effects were discounted due to the similarity of realized heritabilities over generations and also the similarity of realized heritabilities to heritability estimates from daughter on dam regression analysis. Since selection yielded slightly higher realized heritabilities for males than females sex linked effects might be indicated. A comparison of the heritabilities from the sire and dam components of the analysis of variance resulted in higher heritabilities in 7 of 8 cases from the dam component indicating possible maternal and/or dominance effects. Brunson et al., (1956) observed maternal effects for body weight amounting to only 2% of the total genetic variance.

Lerner and Cruden (1951) detected significant maternal effects for egg weight in one line. Maternal effects were defined as those due to factors which increase the resemblance of half sisters by the same sire by more than twice the amount they increase the resemblance between full sisters. The hypothesis of maternal effects was put forward only hesitantly.

Thomas _et_ _al_., (1958) reported the difference of heritability estimates from male and female progeny for the same character presented some evidence that sex linked genes might be of importance in the expression of those characters, in this case body weight. Sex linked effects for body weight were also reported by Brunson _et_ _al_., (1956) in this case accounting for 10% of the total genetic variance.

Some genetic correlations among characters reported by various authors are presented in table 7. Age at sexual maturity shows a moderate negative correlation with 8-week body weight and a high negative correlation with egg production. Eight-week body weight also shows a moderate to high negative correlations with age at sexual maturity, egg production and body weight at other unspecified ages. Shank length is moderately correlated with both body weight and egg number. It was noted that in one case genetic improve-

TABLE 7. GENETIC CORRELATIONS BETWEEN CHARACTERS OF CHICKENS

Traits		Sex[a]	f	Source
Age at sexual maturity	x 8 week body wt.	m	-.81	Kinney and Shoffner (1965)
		f	-.33	Kinney and Shoffner (1965)
			-.24	Ideta and Siegal (1966a)
			-.22	Siegal (1963)
		f	-.06	Kinney and Shoffner (1965)
		m	.21	Kinney and Shoffner (1965)
	x body wt.	f	-.03	Lerner and Cruden (1951)
	x egg wt.	f	.59	Lerner and Cruden (1951)
	x egg production	f	-1.00	Kinney and Shoffner (1965)
8 week body wt.	x egg wt.	f	.23	Ideta and Siegal (1966b)
			.33	Siegal (1963)
	x egg production	f	-1.00	Kinney and Shoffner (1965)
		f	-.47	Kinney and Shoffner (1965)
		f	-.32	Siegal (1963)
Body wt.	x egg wt.	f	.34	Lerner and Cruden (1951)
		f	.35	Buvanendran and Merrit (1972)
	x shank length	?	.55	Tierce and Nordskog (1973)
Shank length	x egg number	f	.39-.54	Telloni _et al_. (1973)

[a] m = males, f = females

ment for 9-week body weight would have been 14% more efficient with selection practiced on shank length at 9-weeks than on 9-week weight itself (Kan et al., 1958). This was due to the higher heritability of shank length than 9-week weight and a high genetic correlation between the two traits.

Although the chicken and Japanese quail are both of the same family and should show some genetic similarity, chickens have been subjected to many kinds of artificial selection and mating systems, whereas quail have not. The pronounced migratory instinct of the quail (Bannerman, 1963) is almost totally absent in the chicken. This and other behavioral differences may affect production and reproduction of quail under certain management systems and not necessarily the chicken.

Inbreeding

Inbreeding is the mating of individuals in a population that may have alleles at certain loci that are identical by descent; implied is a base population in which no two individuals are related by ancestry. The degree of inbreeding can be measured as the coefficient of inbreeding (F_x) which is the probability of two alleles at a locus being identical by descent. In an infinite, random mating population change in mean allelic frequencies and thus a change in the population mean does not follow as a direct consequence of forming inbred lines. Any change in the mean line phenotype caused by inbreeding is rather the result of dominance deviations at the loci concerned, and the direction of change is toward the more recessive alleles (Falconer, 1960). The total variance of a population with dominance increases as inbreeding increases, except with a sufficiently large frequency of the recessive allele in which case the total variance decreases as inbreeding increases (Wright, 1969). The within-line variance with dominance decreases as inbreeding increases, except with a sufficiently small frequency of the recessive allele, in which case the within-line variance increases to a limit then decreases with further increases in inbreeding (Wright, 1969).

Inbreeding of Japanese Quail. Studies of Japanese Quail have indicated a pronounced sensitivity to inbreeding. Adverse effects of inbreeding on hatchability, viability and egg production were reported to be about double in comparison with chickens (Woodward *et al.*, 1973). Inbreeding depression of egg number, age at first egg, fertility and hatchability have been observed in many studies (Sittman _et_ _al_., 1966; Iton, 1967; Boesiger, 1969; Keller, 1969; Shinje _et_ _al_., 1971; Webb, 1972; Kulenkamp _et_ _al_., 1973; Lucotte, 1975). Sittman _et_ _al_., (1966) reported hatchability was decreased by 7%, viability by 4% and fertility by 11% for each 10% increase in inbreeding in the progeny. Kulenkamp _et_ _al_., (1973) compared full sib matings with outbred controls for 5 generations and reported regression coefficients on percent inbreeding that were negative for fertility (-.08), egg production (-.02), hatchability (-26), 3 and 7 week livability (-.26 in both cases) and 3 and 7 week body weight (-.12 and -.06 respectively). Positive regression coefficients on percent inbreeding were reported for 3-week body weight (.06) and egg weight (.04). The latter observation was in conflict with that of Iton (1967) who reported, but did not quantify an inbreeding depression for egg weight. The observations of Lucotte (1975) support the position that egg weight and body weight are not affected by inbreeding.

Non linear depression of all depressed traits at higher levels of inbreeding, $F_x = .25$, has been reported by Sittman _et_ _al_., (1966) and Kulenkamp _et_ _al_., (1973). Sittman _et_ _al_. (1966) further described the depression as an accelerating decline. Linear declines in performance would be expected if the decline were due to dominance effects alone (Lush, 1948; Kempthorne, 1957). Assuming gene frequencies to be unchanged, curvilinear response can be attributed to dominance interactions (Lush, 1948; Kempthorne, 1957), or to a parent-progeny interaction (Stittman _et_ _al_., 1966). Natural selection, causing a possible change in gene frequencies, played an important part in both the aforementioned studies. In one (Sittman _et_ _al_., 1966) reproductive fitness was lost completely at the third generation, F_x=.5, and in the other (Kulenkamp _et_ _al_., 1973) 11 of 17 inbred lines were lost by the fifth generation.

Sittman _et_ _al_., (1966) reported briefly on the parental effects which they attributed to the female parent. Maternal inbreeding caused a decrease in hatchability of 3% and in viability of 2% for each 10% increase in F_x.

Inbreeding of chickens. Hays (1924) reported that a scheme of linebreeding to a specific sire caused the resulting inbred progeny to exhibit a delayed sexual maturity and a decrease in egg production, but no change in body weight relative to non-inbred progeny of the same sires. In another study (Hays, 1935) daughters of inbred males were older, 7.2 ± .92 days, and heavier, .79 ± .06 kg, than non-inbred contemporaries at the laying of their first egg. Annual egg production was lower for the daughters of the inbred males by 16.9 ± 2.02 eggs. The daughters of the inbred males were less variable with respect to age and weight at first egg.

Inbreeding depression of immature body weight has been reported by Glazener et al., (1951) and MacLaury and Johnson (1971). MacLaury and Johnson (1971) found a regression of -1.32 ± .44g for 8-week body weight on percent inbreeding and Glazener et al., (1951) found a regression of -.13 ± .01 ounces for 12-week body weight on percent inbreeding.

Shoffner (1948a) reported a significant regression of -.44 ± .13 for egg hatchability on the zygote's inbreeding coefficient, but a non-significant regression on the female parents inbreeding coefficient. Significant regressions were also reported for egg production on the hen's inbreeding coefficient of .93 ± .07 and age at sexual maturity on the inbreeding coefficient of .60 ± .11. Non-significant regressions were reported for mature bird weight and egg weight. The average inbreeding coefficient during the last generation of the study was approximately .60.

The findings of Duzgunes (1950) with respect to hatchability were in agreement with those of Shoffner (1948a).

He did not, however, quantify a regression as the study contained too few individuals to be conclusive.

Wilson (1948b) reported significant regression for egg production rate on the hen's inbreeding coefficient of -1.4 ± .04 eggs and significant partial regressions for hatchability on dam's inbreeding coefficient of 19 ± .07 and for chick mortality on dam's inbreeding coefficient of 20 ± .07.

In examining the effect of inbreeding on production characters Blow and Glazener (1953) found significant regressions for age at sexual maturity, egg production, and hatchability on percent inbreeding of .32 ± .10 days, -.30 ± .11 eggs and -.37 ± .11% respectively. Non-significant regressions on percent inbreeding were found for body and egg weights.

Macha et al., (1971) reported that egg production, egg mass, body weight and hatchability of fertile eggs were lower in inbred hens than in random mated controls. Egg weight, mortality and hatchability of eggs set were not affected by inbreeding of the hens.

El-Ibairy and Rizk (1969) found hybrid to inbred ratios for male and female Fayomi if 1.07 and 1.24, respectively, for body weight and 1.04 and 1.10, respectively, for shank length. Similar ratios for body weight of 1.14 and 1.08, respectively, were reported by Stonaker (1963).

In a 10-year inbreeding experiment with selection for increased hatchability and "the general vigor of the individual bird," Waters and Lambert (1936) observed that the inbreeding did not result in significant inbreeding depression of age at first egg, egg production, fertility, or hatchability. This may be due to the mating systems all utilizing more distant relatives than full sibs. Inbreeding coefficients in the final year of the study ranged from .4 to .7.

Lines selected for high and low body weights and for high and low egg weights for 11 generations were studied by Casey and Nordskog (1971). When corrected for inbreeding the high and low body weight lines had decreased in egg production. Linecrosses show this decrease not due to the loss of genetic capacity. The low egg weight selected line showed no change from the control with respect to egg production, which when corrected for breeding was in effect an increase in egg production. The high egg weight line showed both actual and corrected for inbreeding increases in egg production. Regression coefficients for the combined lines on percent inbreeding were: -.53 ± .07, .40 ± .17 and .21 ± .08 for hen day egg production, age at sexual maturity and adult mortality, respectively. Analysis via reciprocal crosses showed maternal and sex linked effects to be relatively unimportant. The geometric midparent mean was a better estimator than the arithmetic mean of the actual F_1 value, implicating multiplicative gene action.

After five generations of full sib matings, little overall change as a result of selection was reported in hatchability, egg weight, or age at sexual maturity (Waters, 1945a,b,c,). A reduction in variability in egg weight and age at sexual maturity was noted in the respective studies where they were the traits under selection.

Wessels (1971) reported hatchability, viability, egg production and spring egg weight to be unchanged by increasing the percent inbreeding from 31.25 to 45.3. The weight of the first 14 eggs was significantly depressed by the same change in inbreeding.

Outbreeding

Outbreeding can be considered as the mating of individuals within a population or immigrants to that population that would be less likely than the average of the base population to have alleles at a locus identical by descent. If the population under consideration remains closed then a change in allelic frequencies and thus a change in the population mean cannot be a result of outbreeding. In the first filial (F_1) generation, heterosis, or the deviation of the observed value from the midparent value, depends for its occurrence on directional dominance (Falconer, 1960). The degree of heterosis is dependent on the square of the difference in allelic frequencies of the families crossed, and the direction of the deviation must be toward the more dominant alleles. Heterosis shown by the second filial (F_2) generation is expected to drop back toward the midparent by one half the difference between the midparent and the F_1, provided epistatic effects are unimportant. If new individuals are brought into a population, then allelic frequencies and the population mean can change as a result of outbreeding.

Outbreeding of Japanese Quail. Keller (1969) in a five generation study with cyclic inbreeding and outbreeding observed increases greater than one standard deviation on the second cycle outcross for total egg weight, egg number and an index of biomass (total egg weight ÷ weight of the female parent).

Outbreeding of Chickens. Cole and Hutt (1973) compared interstrain hybrids at 10-year intervals during the course of a 34-year selection study, with one generation per year. Hybrid hens showed higher production records of 25 eggs to 500 days of age, and increases of egg and body weights over the within strain hens of 1.2 and 74.5 grams, respectively. Age at sexual maturity was decreased by 5.6 days in the straincrosses. Mortality from 1 to 42 days of age was reduced by 1.0% and from 43 to 160 days by 1.5% for the straincrosses in comparison to the straightbreds. However, from 161 to 500 days the mortality of the straincrosses was .63% greater than that of the straightbreds.

In comparing topcross Leghorn progeny with inbred and randombred progeny, Waters (1938) found the topcross progeny significantly superior to both the inbred and randombred progeny with respect to hatchability, 85% vs 72% and 81%, respectively. The topcross progeny also had a lower mortality to 8 weeks than did the inbred progeny, 6% vs 14%. There were no significant differences in this study between groups with respect to fertility. The inbreeding levels in this study ranged from 25% to 85%.

Crosses among related inbred lines showed little improvement over parental lines with respect to growth, egg production and liveability (Maw, 1941). Crosses among unrelated inbred lines resulted in progeny which had superior records for growth, egg production and liveability in comparison with the parental stock and randombred control birds.

Shoffner (1948b) reported that, with respect to hatchability, linecrosses were superior to within line matings and that three and four way crosses exceeded two way crosses.

Wessels _et_ _al_., (1971) found outcross individuals to be consistently superior to highly inbred half sibs with respect to embryo and chick viability, egg production, age at sexual maturity, 6 week body weight at sexual maturity, 6 week body weight and adult egg weight. Outcrossing had little effect on fertility, body weight at sexual maturity or the weight of the first 14 eggs.

Wessels (1971) reported hatchability, viability, egg production and spring egg weight to be higher in the outbred rather than the inbred half sibs at the 31.25% level of inbreeding but not at the 12.5% level of inbreeding. This in contradiction to Wessels _et_ _al_., (1971) who had observed that a higher degree of inbreeding did not result in a greater degree of heterosis than lower degrees of inbreeding with respect to the same traits.

MATERIALS AND METHODS

Management Procedures

Three populations of Japanese quail (Coturnix coturnix japonica), each replicated (making six groups in all), were studied. Populations I and II were the result of a cross between a stock from the University of California at Davis and one from a local (Bozeman, Montana) fancier. Generation 0 was the result of this cross for these populations. Population III was made up of birds from the University of California at Davis stock.

In all respects except for the mating system and selection differences, the entire colony was treated exactly alike at all times. The generation interval was held constant at about 4 months, a period which was not believed to place any unwanted selection pressure on any population differently. An attempt was made to keep the effective population size of each population constant for the duration of the study. The harmonic means of the generation effective population sizes were 328, 403, and 210 for populations I, II, and III, respectively.

Each generation, beginning in generation 0, of population I was selected for an index and mated in a cyclic manner with the individuals in the odd generation being the result of full sib mating and the even generations the result of wide outbreedings. The wide outbred matings were determined by minimizing the genetic covariance between the prospective mates. Approximately 39% of the progeny were selected as parents for the subsequent generation. The final two generations, 16 and 17, were random mated to equalize the individual and parental inbreeding effects, and the parents of generation 17 were unselected in order to compare endpoints with the other two populations to be subsequently described.

Population II was selected on the same criteria and in the same manner as population I and was random mated every generation. Approximately 24% of the progeny were selected to be parents of the following generation. The only exception to the random mating was that no full sib matings were made at any time.

The selection and mating schemes are outlined in figure 1.

Population III was selected and mated at random and was used as a control to measure changes in environmental influences from generation to generation. Fifty-one percent of the progeny in this population subsequently became parents. Due to the somewhat different genetic stock used

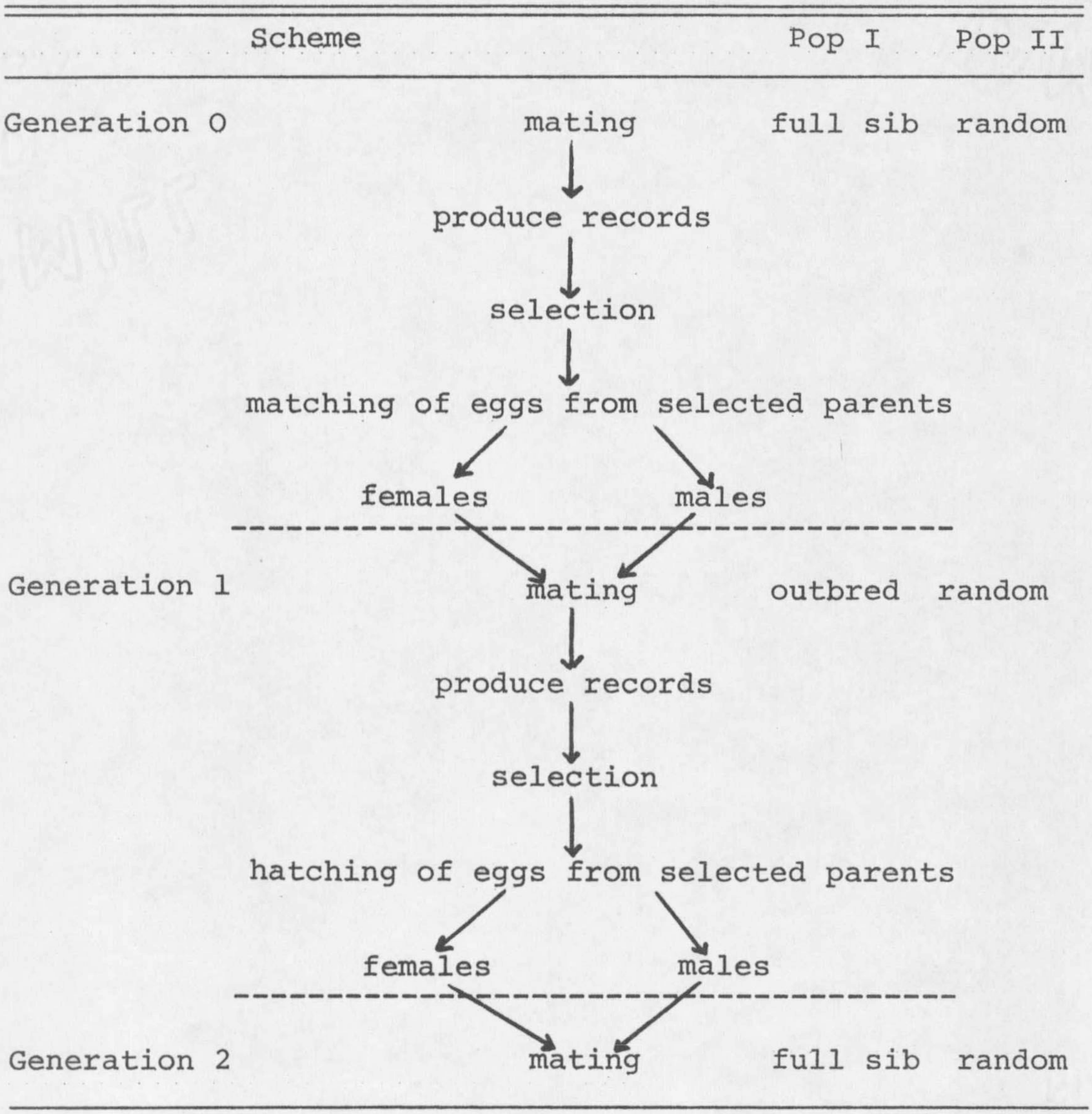

Figure 1. Illustration of the management scheme for the selected populations.

for the control, if a genotype by environment interaction was important with respect to any of the traits studied, then this control may be somewhat biased. It was assumed that interactions of this type were unimportant and that population III was in all respects a satisfactory control.

The selection index, which Hicks (1962) called a biomass index, was equal to the number of eggs laid by a female, during a 50-day test period beginning when she was 28 days old, multiplied by the average egg weight from a weekly sample divided by her 78-day body weight. In population II the selection pressure was thus placed on the female and none was placed on the male. In population I there was some selection pressure placed on the males due to their having to be full sibs to selected females in the inbred generations. Also, the minimizing of the genetic covariance in the outbred generations caused negative selection pressure to have been placed on the males in those generations.

Eggs were collected for hatching and stored so as to be set in the incubator in one of two settings during each generation's test period. There may have been some inadvertent selection against large eggs because of an unknown but seemingly differential number were broken in the storage trays. The eggs were incubated at 37.5°C for 19 days at an average humidity of 87%. Upon hatching keets were banded and identification recorded, and placed in electric breeding batteries for 10 days at 37.8°C and a subsequent 18 days at 26.7°C. During this time the keets were fed a starter-grower ration (table 8). At 28 days after hatching the matings were made (1 male to 1 female) and each pair was placed at random in an individual cage in the laying house. The cages were arranged in eight batteries with four double banks of 12 cages each in a room 6.1 meters square with a 2.44 meter high ceiling with continuous light, forced draft ventilation and a constant temperature of approximately 21°C. During the laying period a layer ration (table 8) was fed.

An outbreak of quail enteritis was diagnosed in the laying house during generation 14 which resulted in some amount of additional mortality across all populations. By using the effective population sizes for generations 7 to 12 it was found that population I suffered only a 16% decrease while populations II and III had 40% and 37% decreases, respectively. There has been some work done with the genetics of disease resistance (Cole and Hutt, 1973) which indicates possible genetic control of

TABLE 8. JAPANESE QUAIL RATIONS

Ingredient	Starter-grower	Laying
Ground wheat (%)	45.75	46.10
Soybean oil meal (%)	46.00	37.00
Fish meal (%)	3.00	3.00
Dicalcium phosphate (%)	2.60	4.10
Limestone (%)	1.00	8.30
Salt (%)	1.00	1.00
Trace minerals (%)	.05	.05
Vitamin Premix (%)	.40	.40
Methionine (%)	.20	.05

susceptibility, and since the difference between populations I and II was so great, perhaps the cyclic mating system was effective in decreasing susceptibility to enteritis. Since these apparently differing mortality rates are not based on solid data, and no such data was available, no attempt was made to separate out any mortality effect. When the outbreak occurred Furacin was added to the water as a remedy and was subsequently maintained in the feed at prophylactic levels. The enteritis was found only in the laying house and never posed a problem in the brooders.

Analytical Procedures

A least-squares multiple linear regression program (Dixon, 1970) was used in a stepwise manner which removes the most important component first to determine the importance of the components of the index to the index itself. Thus the variable added to the multiple regression was the one which made the greatest reduction in the residual regression sum of squares. Equivalently the variable added was the one which had the highest partial correlation with the index partialed on the variables that had already been added.

The traits under study in addition to the components of the index were: total egg mass during the test period (egg number multiplied by average egg weight) and shank length and width at 78 days of age.

All analyses of variance were performed by the least-squares procedure of Harvey (1975). A sample analysis of variance table illustrating the expected mean squares from which the variance component estimates were calculated is shown in table 9. The model which was the basis for the majority of the analyses was:

$$Y_{ijklm} = M + P_i + R_j + G_k + S_l + (\text{two factor interactions}) + E_{ijklm}$$

where: Y_{ijklm} was a normally and independently distributed observation,

M = the overall mean,

R_i, R_j, G_k and S_l = the sets of fixed main effects for the ith population, jth replication, kth generation and lth sex, respectively.

(two factor interactions) = all possible two factor interactions among the main effects,

E_{ijklm} = the variance not accounted for elsewhere in the model, assumed to be NID $(0, \sigma_e^2)$.

TABLE 9. SAMPLE ANALYSIS OF VARIANCE TABLE

Source	D.F.	EMS
Pop.	p-1	${}^{2}_{e} + rg\Sigma\Pi^{2}/p-1$
Rep.	r-1	${}^{2}_{e} + pg\Sigma p^{2}/r-1$
Gen.	g-1	${}^{2}_{e} + pr\Sigma\gamma^{2}/g-1$
Pop x rep	(p-1)(r-1)	${}^{2}_{e} + g\Sigma(\Pi\rho)^{2}/p-1)(r-1)$
Pop x gen	(p-1)(g-1)	${}^{2}_{e} + r\Sigma(\Pi\gamma)^{2}/(p-1)(g-1)$
Rep x gen	(r-1)(g-1)	${}^{2}_{e} + p\Sigma(\rho\gamma)^{2}/r-1)(g-1)$
Residual	difference	${}^{2}_{e}$
Total	$N - a^{b} - 1$	----------

[a] Steel & Torrie (1960)

[b] a = the number of degrees of freedom absorbed.

The appropriate test in all cases is against the error mean square.

Additionally, in all analyses by the least-squares procedures, the battery and bank of housing were absorbed by "ordinary least-squares absorption."

For the sex limited traits, sex was omitted from the model and the particular analysis was run on only individuals of the appropriate sex.

The mating system effect and the selection effect together can be considered to have been the summation of the population effect, the generation effect and the interaction between the two. If population III was genetically different from populations I and II originally or became genetically different in the course of the study such that a genotype by environment interaction was of some importance, the model may be inadequate. Such a genotype by environment interaction is not believed to have existed. The direct and correlated responses were therefore reported as deviations from the control (population III) to adjust for generation to generation environmental effects. By reporting the data in this manner, the difference between populations I and II should reflect genetic differences unless a genotype by environment interaction did exist.

Subsequent to the overall analyses the inbreeding effects were determined by linear and non-linear regression of each trait on the coefficient of inbreeding. The cubic level was fitted first, then the quadratic level and finally the linear component. The highest significant level was deemed appropriated to use in the determination of the mode of gene action.

The female selection differentials were calculated within generations as the selected parents mean for the index minus the mean for all parents multiplied by the number of progeny produced by that female summed over all female parents and divided by the number of total progeny.

The responses to selection and the correlated responses were estimated by using the cubic, quadratic and linear levels of regression for the trait under consideration on generation. The responses and correlated responses to selection always were taken as deviations from population III, the control.

Heritability estimates were calculated by three methods. Realized heritabilities were calculated by the linear regression of the generation cummulative response on the respective cummulative selection differential. The regression coefficient from the regression of offspring on one parent was taken as an estimate of one half the heritability for that character. The regression coefficient from the regression of offspring on the mid-parent value was also used as a heritability estimate for those traits that were not sex limited.

Residual phenotypic correlations were calculated using the residual variances and covariances from the least-squares analyses (Harvey, 1975). Genetic correlations were obtained as:

$$r_g = \frac{\text{cov}_{xy}}{\text{cov}_{xx}\text{cov}_{yy}} \quad \text{(Falconer, 1960)}$$

where: cov_{xy} = the parent-progeny crosscovariance for those two traits and cov_{xx} and cov_{yy} = the parent-progeny trait covariances for the respective traits. The covariance components were obtained by the use of an option available in the stepwise regression program.

RESULTS AND DISCUSSION

Genetic Parameters

Heritability Estimates. Heritability estimates obtained by all methods are shown in table 10. The heritability estimates for body weight were found to be somewhat higher than those previously reported. Collins et al., (1970), Marks and Lepore (1968) and Abplanalp (1967) reported the realized heritability of body weight at 6 weeks of age to be .25, .25 and .43, respectively. All of these estimates are realized heritabilities which are characteristically lower than heritability estimates made by other methods. The influences of maternal and paternal effects may also account for the seemingly elevated estimates reported here. Other estimates of the heritability of body weight at or near maturity were also lower. They were .42 (Kawahara and Inuoe, 1966) and .36 (Marks and Kinney, 1964). The estimates reported here appear to be well in line with the estimates of the heritability of mature body weight in the chicken (table 4). Egg number was also found to be more highly heritable in this study than in the study of Marks and Kinney (1964) where they reported the heritability of egg number as .39 compared to the estimate of .58 reported here. The heritability estimate reported

TABLE 10. HERITABILITY ESTIMATES FOR THE TRAITS UNDER STUDY FROM ALL THREE POPULATIONS

Trait	h^2	N[a]	Method[b]
78-day body weight	.45 ± .01	17,360	o-mp
	.51 ± .01	17,360	o-pf
	.58 ± .01	17,360	o-pm
78-day shank length	.50 ± .01	17,360	o-mp
	.56 ± .01	17,360	o-pf
	.56 ± .01	17,360	o-pm
78-day shank width	.28 ± .01	17,360	o-mp
	.38 ± .01	17,360	o-pf
	.39 ± .01	17,360	o-pm
50-day egg mass	.57 ± .01	8,595	o-pf
Egg weight	.60 ± .04	8,595	o-pf
Egg number	.58 ± .02	8,595	o-pf
Index	.16 ± .01	3,904	R/S (pop. II)
	.21 ± .04	3,189	R/S (pop. I)
	.62 ± .01	8,595	o-pf

[a] N = number of progeny records

[b] R/S = realized; o-mp = regression of offspring on midparent; o-pf = regression of offspring on female parent; o-pm = regression of offspring on male parent.

here agrees well with an estimate of .54 reported by Kawahara and Inuoe (1966). No previously published estimates for the heritability of shank length, shank width or the index were found in the quail literature. The heritabilities reported here do agree with the heritability estimate for the same traits in chickens (tables 4, 5, and 6).

Correlations. Presented in table 11 are the genetic and phenotypic correlations for these populations.

The genetic correlations indicate that selection for the index was not antagonistic with the correlated responses in the components of the index that would be expected from the signs of these correlations (i.e., the signs of the genetic correlations of the index and those components of the index in the numerator were positive and the sign of the correlation of the index and the component in the denominator was negative).

In general there was good agreement between the phenotypic and genetic correlations reported here and those previously reported in the quail and chicken literature (tables 3 and 7, respectively). Body weight was positively correlated with egg weight (r_g = .40) in agreement with El-Ibiary *et al*., (1966) and Kawahara and Inoue (1966).

TABLE 11. PHENOTYPIC (r_p) AND GENETIC (r_g) CORRELATIONS AMONG VARIOUS TRAITS UNDER STUDY FROM ALL THREE POPULATIONS

First trait	Second trait	r_p	r_g
78-day body weight	Shank length	.38	.48
	Shank width	.32	.53
	50-day egg mass	.26	-.07
	Egg weight	.31	.40
	Egg number	.20	-.29
	Index	.04	-.39
78-day shank length	Shank width	.27	.25
	50-day egg mass	.14	.12
	Egg weight	.13	.29
	Egg number	.10	-.06
	Index	.07	-.17
78-day shank width	50-day egg mass	.04	.09
	Egg weight	.13	.22
	Egg number	.02	-.03
	Index	.02	-.09
50-day egg mass	Egg weight	.68	.72
	Egg number	.97	.95
	Index	.97	.95
Egg weight	Egg number	.60	.29
	Index	.65	.51
Egg number	Index	.96	.97

Positive phenotypic correlations were found for body weight and the egg production characters, but only the body weight-egg weight genetic correlation was positive, suggesting that those environmental conditions which were conducive to the production of larger numbers of eggs were also conducive to heavier body weights. Body weight was positively correlated both phenotypicly and genetically with shank length and width. The correlations of shank length and width with the other characters were generally low. The egg production characters were all highly correlated with each other with the exception of egg number and egg weight where the genetic correlation was only moderate. No negative correlations were found among the egg production characters.

In conflict with the .29 genetic correlation of egg weight and egg number found for these data was the previously reported -.39 genetic correlation of Kawahara and Inoue (1966). This positive genetic correlation was also in seeming conflict with the negative genetic correlation of body weight and egg weight reported here. This conflict can be explained in the light of the negative genetic correlations between age at sexual maturity and body weight and age at sexual maturity and egg number (El-Ibiary _et al_., 1966). Since the 50 day test period for this study began prior to sexual maturity the indication from the genetic correlations with sexual maturity was that heavier birds matured at a younger age and birds that matured earlier laid the most eggs. Since heavier birds laid heavier eggs it follows that birds that matured earlier and thus laid more eggs should have laid heavier eggs.

A situation similar to the one in beef cattle where selection for 365 day weight will yield faster progress in weaning weight than will selection for weaning weight itself was found in these data. Given the heritabilities of table 10 and the genetic correlations of table 11 and assuming similar selection intensity can be applied regardless of the selection criteria, response in the index would be increased by 26% over the direct response by selecting for egg number alone.

Response and Gene Action

Index. Response to selection for the index (figure 2) resulted in population I decreasing through generation six and then increasing at an approximate rate of .065 units per generation to the end of the study. It was felt that the initial decrease in the index is probably due to the effect of inbreeding on the index. It has been previously

$$Y_{II} = .447 + .072(x - \bar{x}) - .0006(x - \bar{x})^2 - .0009(x - \bar{x})^3$$

$$R^2_{II} = .85$$

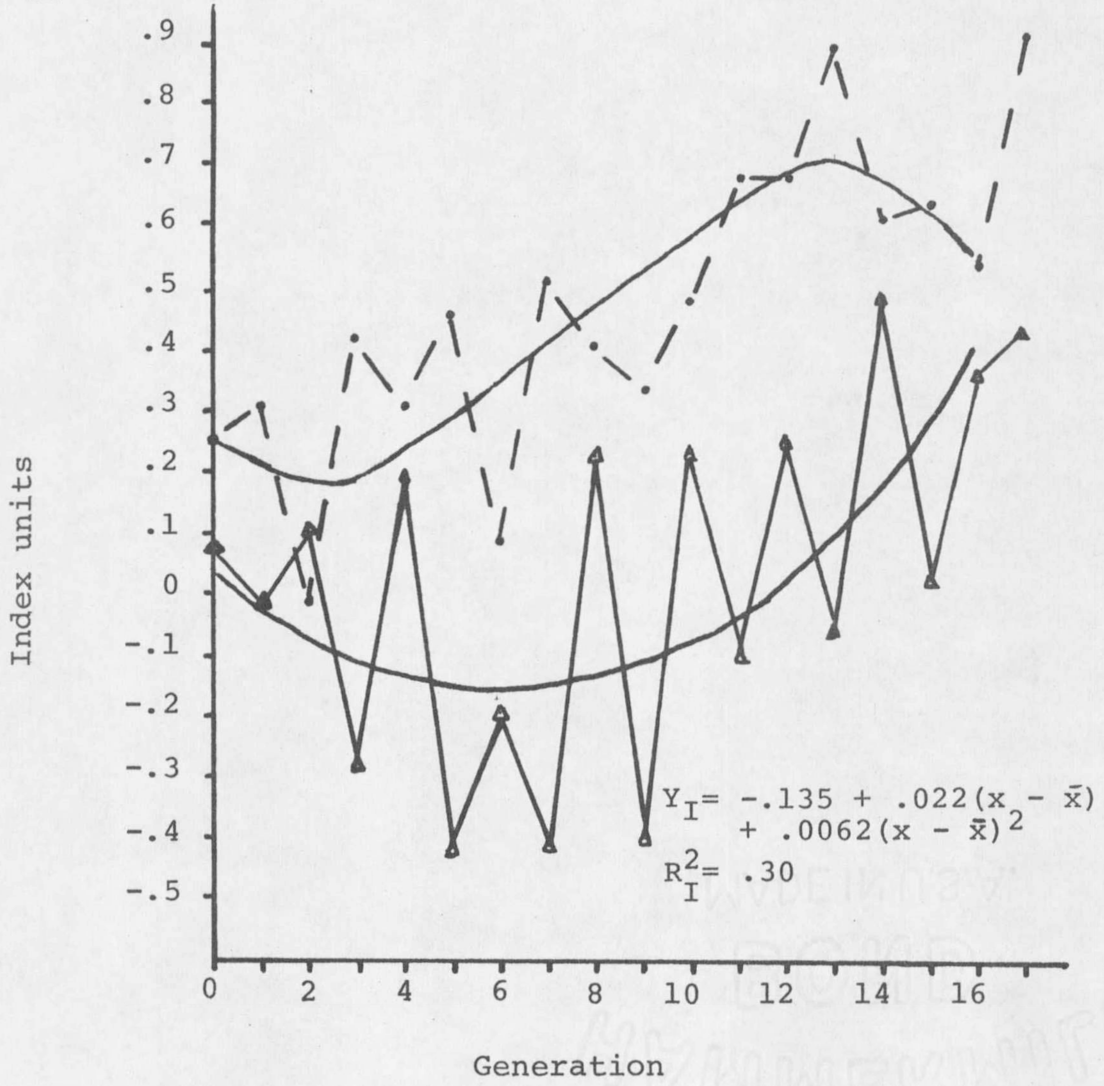

Figure 2. Changes in the index over time as deviations from the control.

observed (Keller, 1969) that almost no selection pressure could be applied to this population during the early portion of the study due to poor reproductive fitness attributed to inbreeding depression. Population II responded to selection by increasing in an essentially linear manner at a rate of .035 ± .006 units per generation. However, the actual regression equation estimating response was cubic but the significance of the cubic term is contended by the author to be an artifact.

Cumulative responses and cumulative female selection differentials (table 12) show that population I had the smaller selection differentials and made less total response than did population II. The realized heritabilities of .21 ± .04 and .16 ± .01 for populations I and II, respectively, indicate that the response per unit selection differential was similar in both populations.

The analysis of variance (appendix, table 13) showed that the population, generation and the population by generation interaction effects accounted for 21% of the total variation in the index, with population being the most important source of variation followed by the interaction and generation in that order. The error variance accounted for an additional 78% of the total variance.

TABLE 12. CUMMULATIVE RESPONSES AND SELECTION DIFFERENTIALS

Generation	Population I Response	Population I Selection Differential	Population II Response	Population II Selection Differential
1	-.0408	.0183	.0738	.2791
2	.0317	-.4959	-.2627	.5124
3	-.2997	-.2736	.0950	1.2150
4	.1409	-.0269	.0442	1.6085
5	-.4426	.0177	.1507	2.0379
6	-.0423	.1390	.0663	2.3753
7	-.5903	.2205	.1596	2.7328
8	.2068	.5716	.1808	3.0897
9	-.2758	.9808	.2367	3.5079
10	.2336	1.1364	.2726	3.9782
11	-.1119	1.6414	.4507	4.5268
12	.2534	2.1914	.4448	5.0631
13	.0065	2.5900	.5655	5.5791
14	.4576	3.2643	.3756	6.1213
15	.0192	3.6907	.4069	6.5109
16	.3712	4.4477	.3051	7.2389

All the other sources of variation were also significant.

Stepwise multiple regression showed the numerator of the index (total egg mass) to be more important than the denominator (body weight) to the index. R^2 values for all populations fell in the range of .91 to .95 for the regression of the index on total egg mass.

The addition of body weight to the prediction equation increased R^2 to .98 in all populations. Subdividing total egg mass into egg weight and egg number and rerunning the stepwise regression again showed the same marked similarity among populations. Egg number was the most important component of the index. This was in agreement with the very high phenotypic and genetic correlations between egg number and the index. R^2 for the regression of the index on egg number ranged from .85 ± .05 in population II to a high of .90 ± .04 in populations I and III. In all populations the next component to enter the multiple regression model was body weight. Again there was no significant difference in the R^2 values associated with the different populations: .93 ± .03 in population I, .91 ± .03 in population II and .94 ± .02 in population III. The addition of egg weight to the model increased the R^2 to .98 in all three populations. That egg weight was of the least importance to an index which causes selective pressure to favor increased egg weight and correlations and heritabilities which would seem to place egg weight in a more favorable situation for correlated response than body weight was not wholly unexpected. In these data the phenotypic standard deviation of body weight was 5.4 times as great as the phenotypic standard deviation for egg weight. Secondly, Flower (personal communication) stated that there may have been some uncontrolled selection for small or average size eggs as the larger eggs seemed more prone to breakage in the storage trays. Lucotte (1975) and Insko et al., (1971) have also indicated that natural selection tends to favor an intermediate size egg and thus may have countered some of the selection imposed here.

Significant curvilinear regression of the index on F_x was found in populations I and III, while in population II no significant regression on F_x was found. In addition, population I shows a cyclic response pattern which closely follows the level of inbreeding. The significant curvilinear regression was suggestive of gene action that was other than additive or dominance, and the inbreeding depression must be attributed to dominance interactions (Lush, 1948 and Kempthorne, 1957). The realized heritabilities further suggest that 80% of the phenotypic variation was due to non-additive variation. Therefore, the conclusion put forth was that the mode of gene action for the inheritance of the index was at least somewhat complex.

Body Weight. Selection for an index in which body weight was the denominator makes the expected correlated response in body weight negative unless the covariance between the numerator and body weight were high enough that the numerator would increase at a faster rate than body weight. The expected correlated response to selection in body weight still depends on the sign of the genetic correlation. The sign of this genetic correlation was negative. Thus the expected correlated response was negative, a condition which would cause the index to increase even if the numerator were held fixed.

In populations I and II the correlated response of body weight to selection (figure 3) was to decrease throughout most of the time period. Population II decreased at a significantly faster rate than did population I: .96 ± .09 grams per generation versus .66 ± 11 grams per generation.

All sources of variation in body weight (appendix,

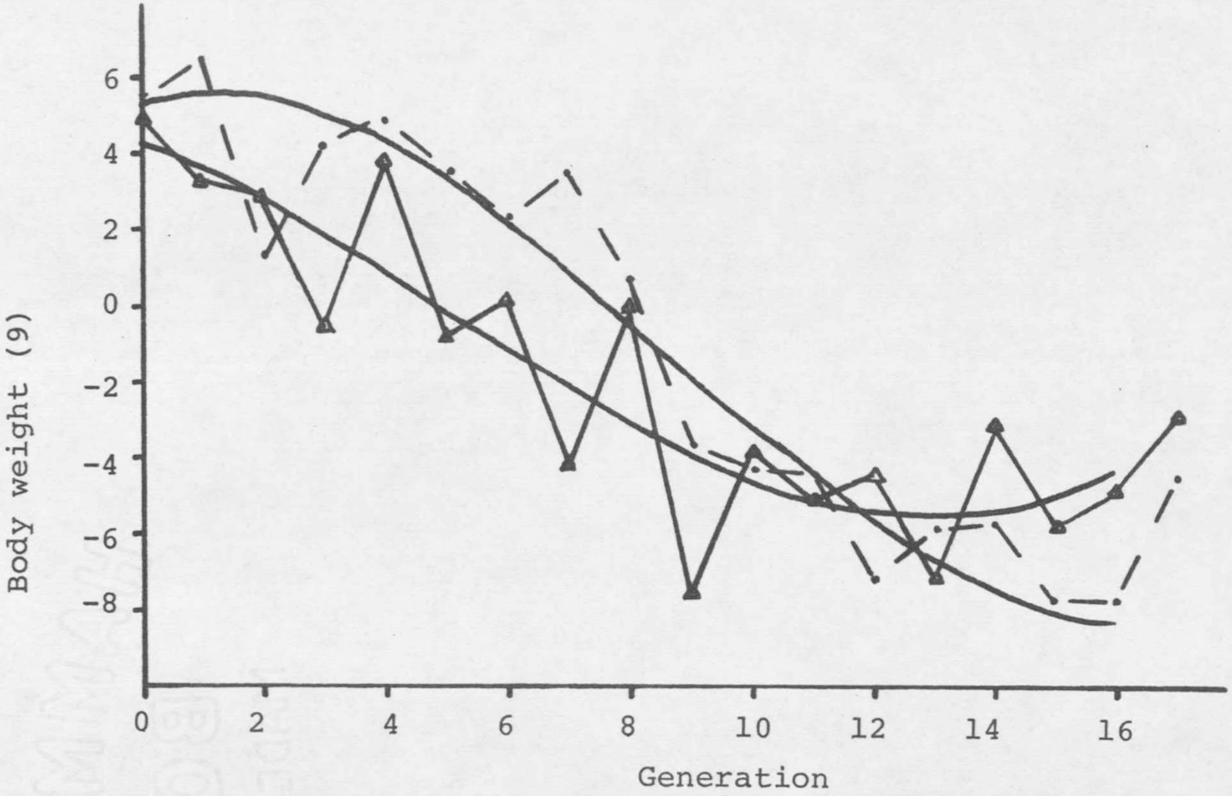

Figure 3. Changes in body weight over time as deviations from the control.

$$Y_{I} = -3.110 - .859(x - \bar{x}) + .0471(x - \bar{x})^{2} + .00457(x - \bar{x})^{3} \qquad R^{2}_{I} = .77$$

$$Y_{II} = -.553 - 1.368(x - \bar{x}) - .0157(x - \bar{x})^{2} + .00947(x - \bar{x})^{3} \qquad R^{2}_{II} = .91$$

table 14) were significant except the replication by sex interaction. Sex was by far the most important effect, accounting for 62% of the total variation. The generation and population effects, together with their interaction, accounted for 7% of the variation in body weight, with the error variance accounting for 31% of the total. Among the other effects, the generation main effect was most important followed by the population by generation interaction and the population main effect.

In all three populations significant non-linear regression on F_X was found. This implied that the inheritance of body weight in these populations had an important genetic component not due to additivity or dominance deviations alone. The non-linear regression component accounted for 5.6% of the variation in the body weights of population II and 3.7% of the variation in population III. The heritability estimates (table 9) for body weight averaged .51 and indicated that 51% of the phenotypic variance was due to the additive genetic variance. The cyclic nature of the correlated response in population I corresponding to the cyclic nature of the inbred-outbred mating system also suggested that dominance deviations were important.

Total Egg Mass

With total egg mass being comprised of egg weight multiplied by egg number and making up the numerator of the index, the expected correlated response of total egg mass would be upward if the covariance of total egg mass and the index were positive but downward if the covariance were negative. In all of the populations studied the covariance of total egg mass and the index was positive, and as previously noted, both the phenotypic and genetic correlations between the two traits approach unity.

In population I the correlated response in total egg mass to selection (figure 4) was to decrease through generation seven at an approximate rate of 5.71 grams per generation and then increase to the end of the study at an average of 7.54 grams per generation. The overall effect thus was to increase by 1.83 grams per generation. The correlated response in total egg mass of population II (figure 4) to selection was to increase linearly at a rate of 2.95 ± .80 grams per generation for the duration of the study. A rate of increase that was not significantly different from the overall rate of increase in population I. In both populations the correlated response in total egg

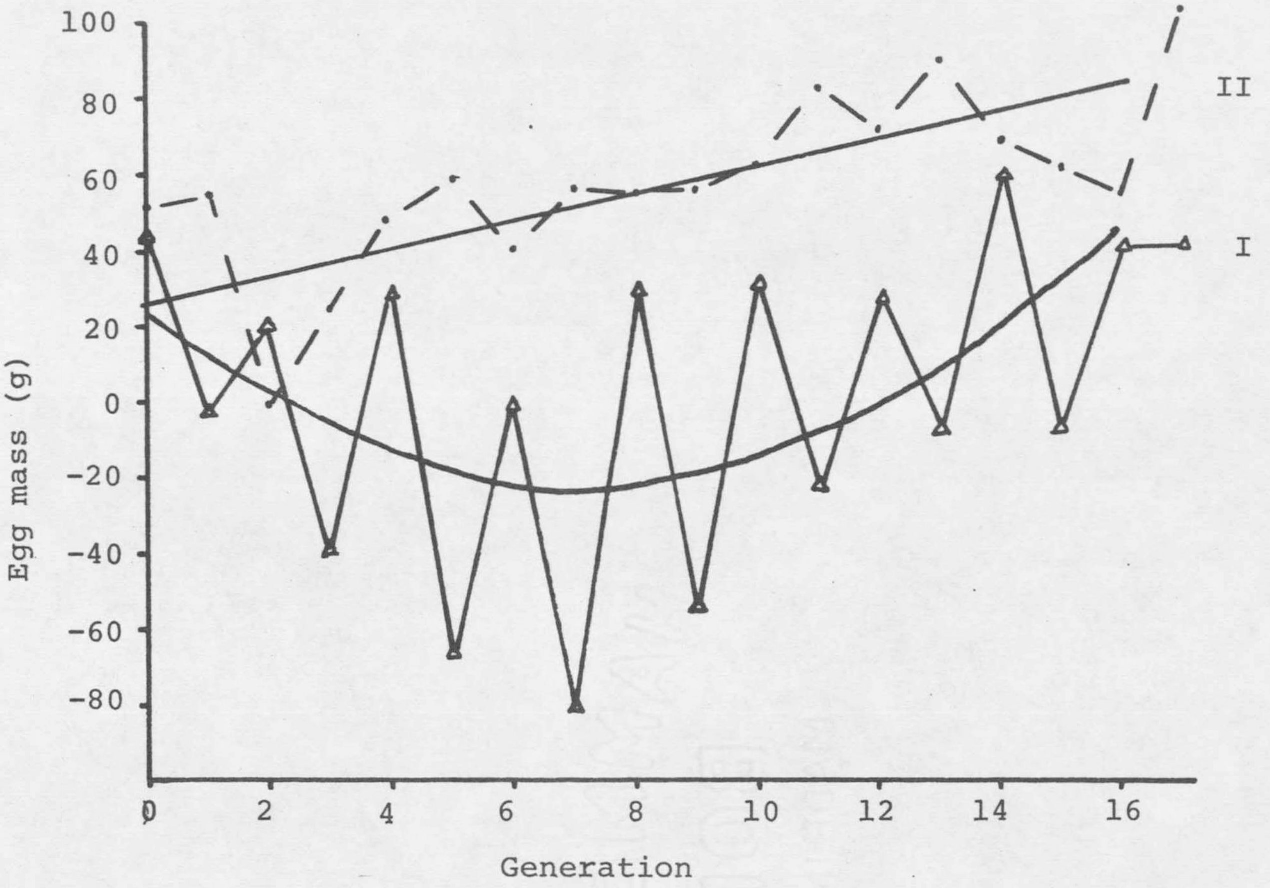

Figure 4. Changes in total egg mass over time as deviations from the control.

$Y_I = -21.07 + 1.317(x - \bar{x}) + .8669(x - \bar{x})^2$ $R_I^2 = .24$

$Y_{II} = 54.76 + 2.502(x - \bar{x})$ $R_{II}^2 = .37$

mass closely followed the direct response of the index as expected.

The analysis of variance for egg mass (appendix, table 15) showed 21% of the variation in total egg mass was accounted for by the main effects and interactions of the main effects. Of the 21% population was the most important, 9.4% of the total variation.

In the determination of the principal modes of gene action relative to total egg mass the cyclic pattern of the correlated response of population I inversely following the degree of inbreeding up and down were present, indicating dominance. Population II exhibited a linear inbreeding depression characteristic of dominance gene action which accounted for less than one percent of the variation in egg mass. However, populations I and III exhibited significant quadratic inbreeding depression which requires at least dominance interactions to explain. In population III the regressions in inbreeding again accounted for less than one percent of the variations. Also the heritability of total egg mass, .57, which may be biased upward by maternal effects, was indicative of a large portion of the variance. Thus, additivity was probably the major form of gene action involved in the inheritance of total egg mass.

Egg Number. As egg number was a portion of the numerator of the selection index, its correlated response should follow that of total egg mass under the same conditions. The covariance of egg number and the index had been observed to be positive and the phenotypic and genetic correlations approached unity.

The observed correlated response in egg number to selection are shown in figure 5. In population I the correlated response in egg number was to decrease through generation six at an approximate rate of .43 eggs per generation and then increasing by .70 eggs per generation through the end of the study. The correlated response in egg number of population II and eventually to increase throughout the study at a rate of .29 ± .07 eggs per generation, an increase which was not significantly different from the .30 eggs per generation increase of population I over the duration of the entire study.

The total variation in egg number when subdivided showed 80% of the variation to be unaccounted for in the main effects and interactions of the analysis of variance model (appendix, table 16). Population accounted for 8.3% of the variation, generation accounted for 4.0% and the interaction between the two accounted for 5.8% of the variation.

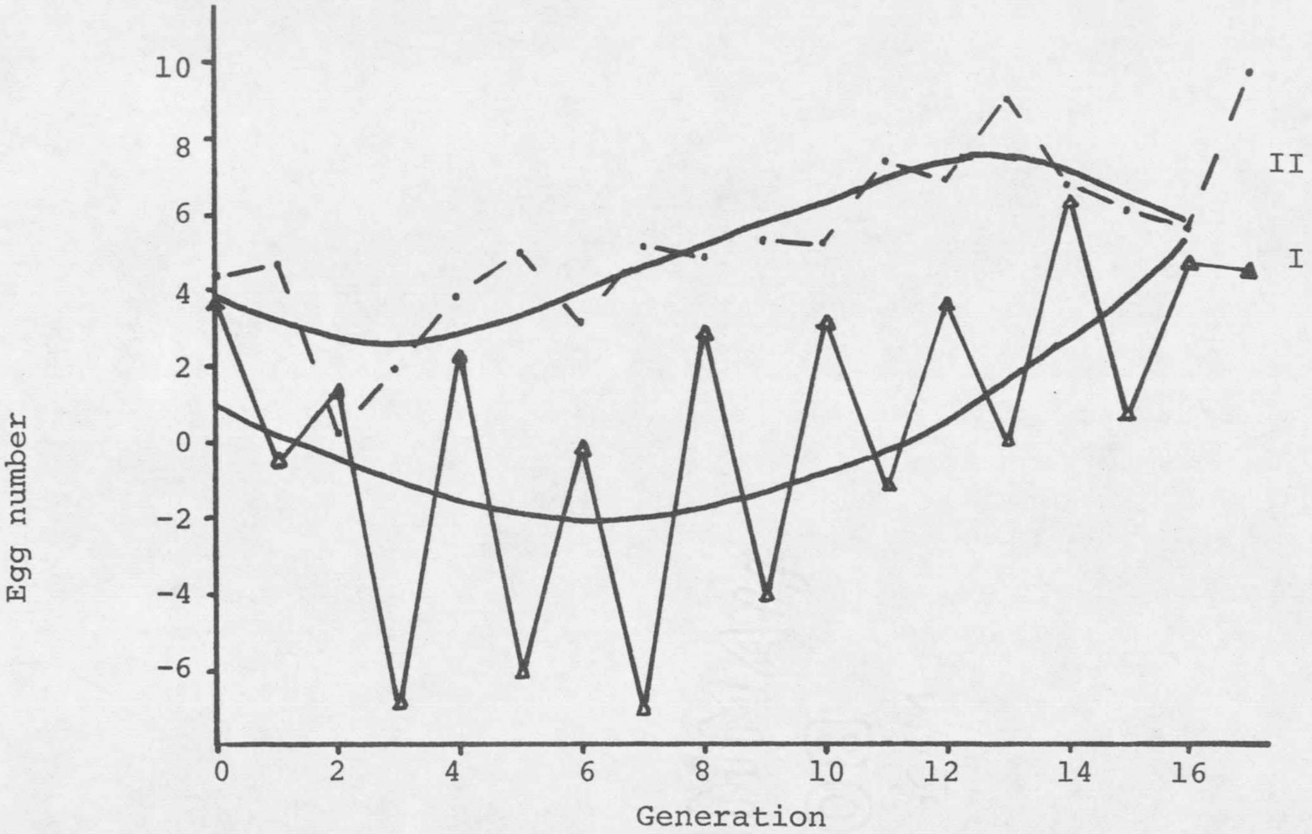

Figure 5. Changes in egg number over time as deviations from the control.

$Y_I = -1.71 + .2568(x - \bar{x}) + .0773(x - \bar{x})^2$ $R_I^2 = .28$

$Y_{II} = 5.116 + .6975(x - \bar{x}) - .0039(x - \bar{x})^2 - .00958(x - \bar{x})^3$ $R_{II}^2 = .70$

Reproductive rate is of major economic and/or evolutionary importance to every species. Egg number, an indication of potential reproductive rate, has been and will continue to be the trait most often selected in most fowl. As such it would be convenient if the mode of gene action influencing egg number were primarily additive. The heritability of egg number appears fairly high (.58) from these data, a direct reflection of the proportion of the total variance due to the additive variance. Unfortunately the cyclic, up and down correlated response pattern inversely following the increases and decreases in inbreeding in population II seem indicative of dominance. The quadratic regression of egg number on inbreeding in populations I and III suggest dominance interactions.

The variance components show the variation in egg number due to the regression on inbreeding accounted for less than 3% of the variation in egg number in populations II and III. The indication was that major portions of the gene action influencing the inheritance of egg number were additive and dominance.

<u>Egg Weight</u>. Egg weight was the second component of the numerator of the index. Given the positive covariance between egg weight and the index, egg weight should have

increased as the index increased. However, previous work (Lucotte, 1975 and Insko et al., 1971) has indicated strong natural selection pressure for the egg weight of the Japanese quail egg to stay around 11 grams.

The correlated responses in egg weight to selection for the index (figure 6) were somewhat different than would be expected from a correlated response formula. In population I the overall correlated response in egg weight was an increase of .018 ± .038 grams per generation. It was curious that generations two and 13 did not respond in the expected characteristic manner. Generation two should have had a higher average egg weight than the inbred generation it followed, but it did not. Population II also showed a significant, unexpected drop in the average egg weight in this generation. The most likely explanation for this drop was sampling error. However it is possible that this drop was caused by an environmental influence that the control population failed to respond to, thus yielding the only evidence of a possible flaw in the control stemming from the different origin than the experimental populations. In light of the previous observations about the influence of natural selection on egg weight the unexpected rise of generation 13 may be another example of natural selection.

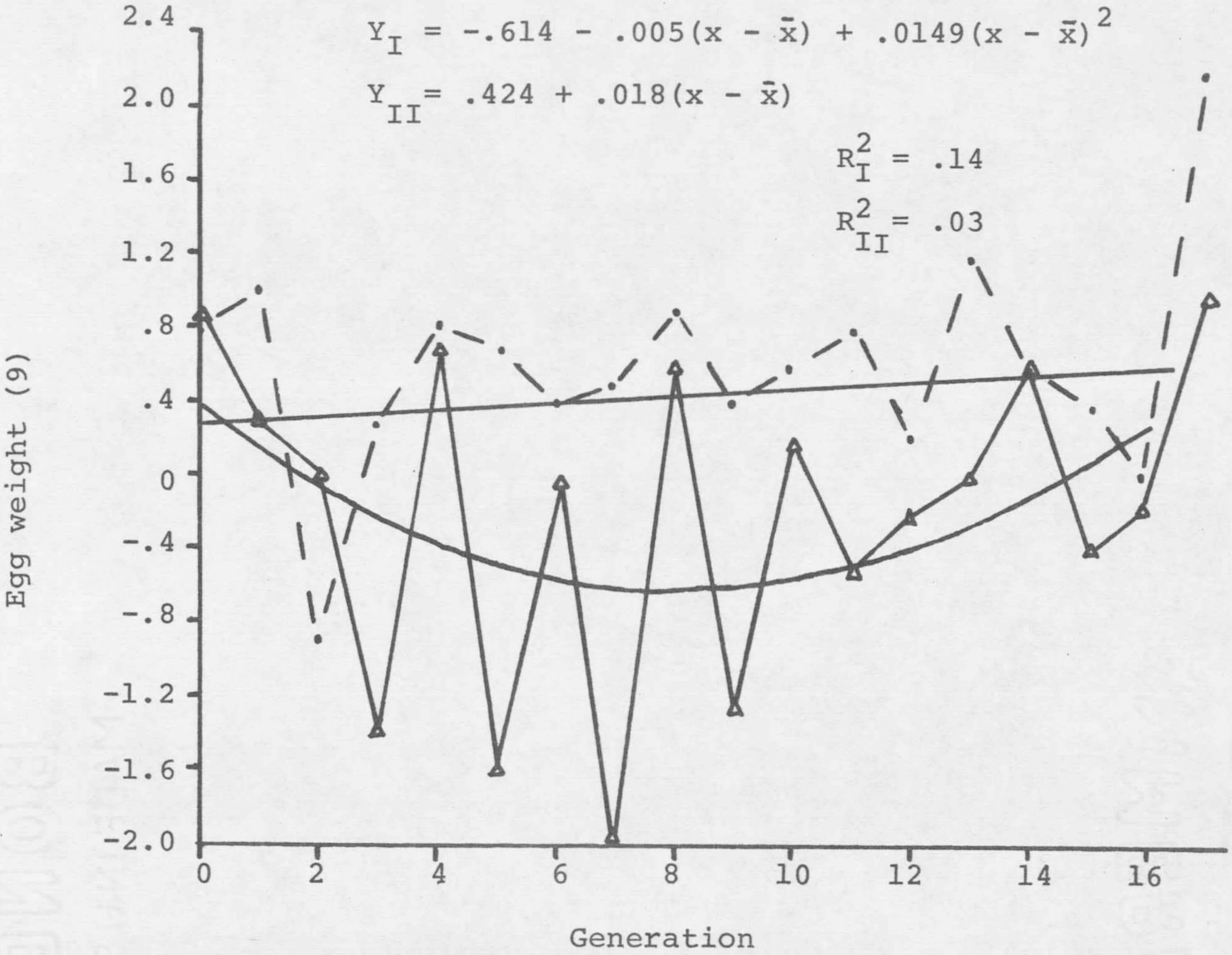

Figure 6. Changes in egg weight over time as deviations from the control.

Noting that generation 12 had the lowest average egg weight of any outbred generation, possibly natural selection completely overrode the inbreeding effect, which was decreasing in magnitude with each cycle. A further example of natural selection for some mean egg weight can be seen in the correlated response to selection in population II. No significant regression of egg weight on generation was found. The regression coefficient was also within one standard error of the .018 gram per generation increase in population I. The conclusion most likely drawn is that the difference between the mating systems was responsible for the decreased egg weights observed in the early generations contrary to the expected correlated response, but was ineffective in bringing about any long-term change in egg weight.

Significant sources of variation to egg weight were (appendix, table 17) population, generation and the interactions, population by generation and replication by generation. The first three sources accounted for 8.5% of the total variation, while the replication by generation interaction accounted for less than .2%.

The plot of population I egg weight over time (figure 6), excluding the abnormalities previously discussed, did exhibit inbreeding depression of egg weights. The regression of egg weight on generation in population II was not significant. In population III the quadratic level of the regression of egg weight on inbreeding was significant, but accounted for less than .1% of the total variation. The linear partial regression, however, accounted for 3.7% of the variation. The heritability of egg weight indicates that 60% of the phenotypic variance was additive. Thus, the inheritance of egg weight was influenced by gene with both dominance and additive effects.

Shank Length

The correlated response of shank length to selection for the index in populations I and II is illustrated in figure 7. In population I the response was to decrease significantly in a linear fashion at a rate of .003 centimeter per generation during the study. In population II the quadratic term of the regression equation approached significance (p .10), while its omission resulted in an equation which failed to describe the response adequately (p .10).

The error variance component was the only variance component that was greater than 10% of the total variance

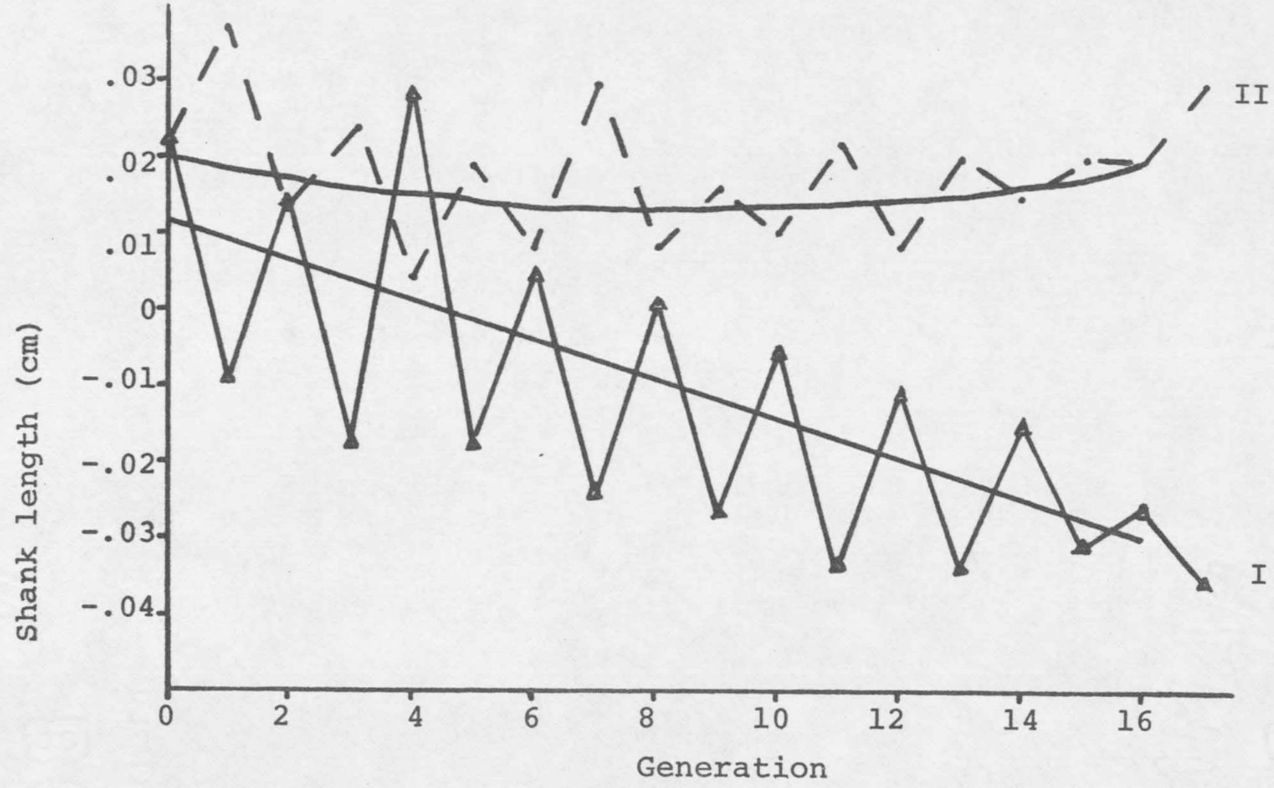

Figure 7. Changes in shank length over time as deviations from the control.

$Y_I = -.0087 - .00274(x - \bar{x})$ $R_I^2 = .46$

$Y_{II} = .0141 - .00006(x - \bar{x}) + .00009(x - \bar{x})^2$ $R_{II}^2 = .08$

of shank length and accounted for 82% of that variance (appendix, table 18). Sex and generation were the next two most important effects making up 8% and 6% of the total variance, respectively. Together, the components: population, replication, generation, sex and the population by generation interaction made up 18% of the total variance.

The estimation of a mode of gene action for shank length was rather inconclusive. The pronounced cyclic pattern of correlated response in population I leads to the conclusion that dominance was a factor. In population III the regression of shank length on F_x was quadratic, and the non-linear component of the regression accounted for more than 10% of the variation, thus indicating some gene action other than additivity or dominance. However, in population II no significant regression of shank length on F_x was found, which would be indicative of additive gene action. The average of the heritability estimates for shank length was .54, also indicating that over one half the phenotypic variation in shank length was due to the additive variation.

Shank Width

In both populations I and II the correlated response of shank width (figure 8) to selection for the index was to decrease over time. Population II decreased at a significantly faster rate than did population I, .00040 ± .00006 centimeters per generation, respectively. Population I did not exhibit the characteristic correlated response pattern that was common to the other traits studied under the cyclic inbred-outbred mating system. From the analysis of variance (appendix, table 17) the generation and sex variance components accounted for 18% and 9% of the total variance of shank width, respectively. The error variance component accounted for an additional 70% of the total variance, while population, replication and the population by generation interaction effects made up two of the remaining 3% of the total variance.

In population I the regression of shank width on F_x showed the shape of the regression line to be cubic, while in population II the same regression line was linear and in population III no significant regression was found. It may have been that the cubic response in population I was circumstantial and should, in fact, be linear, and that no significant regression was found in population III due to

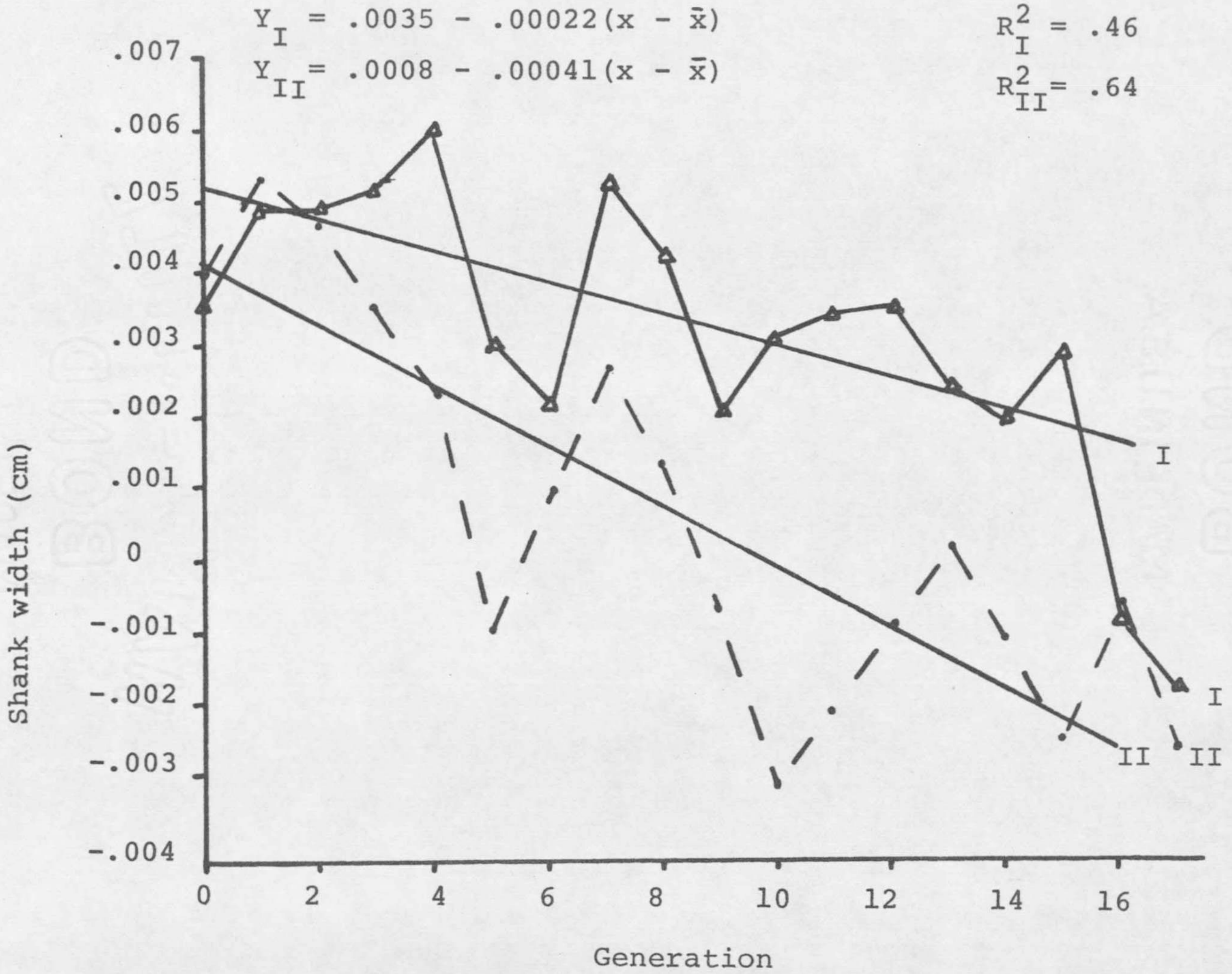

Figure 8. Changes in shank width over time as deviations from the control.

the limited range of values for F_x. Thus it was theorized that the mode of gene action for the inheritance of shank width was additivity. This would account for the absence of the cyclic response pattern under the inbred-outbred rating system. The only moderate heritability estimates for shank width would seem to be evidence counter to this conclusion.

General Discussion

The differences between the regression lines illustrating the direct responses to selection at the beginning and end of the experiment were not significantly different from each other. Thus neither mating system was shown to be superior to the other for total responses to selection. If, in violation of one of the assumptions of regression, the regression lines estimating the responses are extrapolated into the future generations then it appears that the mean index of the females under the cyclic mating system would surpass the mean index of the females under the random mating system.

Keller (1969) utilized the same populations, mating systems and selection criteria and was unable to detect significant response in the index over 5 generations. With the greater number of generations available for this study, significant responses to selection were detected as well as significant differences in response patterns. Examination of the response pattern of the cyclic mated population showed inbreeding caused a decrease in the mean index during the early generations. In a situation where income would be dependent on productivity this would be a serious drawback to a cyclic mating scheme as income would be reduced in the early generations.

Egg number was shown to have been the most important component of the index and accounted for more than 80% of the total variation. Previously, Abplanalp (1967), during a test period from 36 to 72 days of age, demonstrated an 11.7 egg superiority for an egg number selected line when compared to a random mated control after 12 generations of selection. Over the same number of generations of this study, the index selection and cyclic rating scheme were ineffective in changing egg number while the index selection alone increased egg number by about 4.5 eggs. As was previously noted, given the heritabilities and genetic correlations found for these data, the response in the index would have been 26% more efficient had the selection criterion been egg number.

In the study of Abplanalp (1967) egg weight decreased slightly as a correlated response. In the first 12 generations of the present study, egg weight was unchanged by the selection for the index alone, but decreased due to inbreeding depression under the cyclic mating system. The genetic correlation of egg weight with the index indicates that egg weight should increase as a correlated response to selection. That egg weight was unchanged by selection for the index might be an advantage in that Lucotte (1975) and Insko _et al._, (1971) have shown an optimum egg weight to exist in populations of Japanese quail.

SUMMARY

The objectives of this study were to 1) examine differences in direct and correlated responses between an alternating generation inbred-outbred mating system and a random mating system, 2) determine the importance of each of the components of an index:

$$\frac{\text{egg number x egg weight}}{\text{body weight}}$$

to the index, 3) estimate genetic parameters and 4) describe possible modes of gene action for each of the characters studied.

Records from 17 generations of three replicated populations of Japanese quail were analyzed by least squares procedures. Population I was selected and mated in a cyclic fashion with alternating generations of full sib inbreeding and wide outbreeding. Population II was selected and randomly mated. Population III was randomly mated and randomly selected for use as a control. Population, replication, generation, sex, interactions among these factors and regressions on F_X were analyzed in various combinations as independent variables in fixed effect least-squares models. Response variables were the index, body weight, egg mass, egg number, egg weight, shank length and shank width.

Selection response was equally efficient for both mating systems when measured as response per unit of selection differential. The realized heritabilities for the selection index were .21 ± .04 for the cyclic mated population and .16 ± .01 for the random mated population. When the selection responses as average response per generation were compared, then neither population was superior. In the cyclic mated population the regression equation estimating response per generation was quadratic, decreasing through generation six and then increasing to the end of the study. In the random mated population the regression equation estimating direct response had a significant cubic term, but was essentially a linear increase throughout. The correlated responses of all characters in the cyclic mated population moved in the same overall direction as the correlated responses in the randomly mated population, only at a slower rate. In the characters egg number, egg weight and egg mass, the correlated responses under the cyclic mating system were quadratic, decreasing in the early generations due to inbreeding depression and the subsequently increasing as selection had a greater effect. Contrasted with the quadratic correlated responses under the cyclic mating system, the correlated responses under random mating were essentially linear.

Egg number was the most important component of the index and accounted for an average of 88% of the variation in the index. Body weight was the second most important component of the index and accounted for an additional 5% of the total variation. The third and final component of the index, egg weight, also accounted for an average of 5% of the variation in the index.

The average heritability estimates for the index, body weight, egg mass, egg number, egg weight, shank length and shank width were .62, .51, .57, .60, .54 and .35, respectively. Genetic correlations among the response variables were high and positive for all the egg production variables with each other. The body structure variables were also positively correlated with each other but of lesser magnitude. Body weight had negative genetic correlations of moderate value with egg number and the index and of lesser magnitude with egg mass. The genetic correlation of body weight with egg weight was moderate and positive. The shank characters in general exhibited low genetic correlations with all the other variables except each other and egg weight where they were moderate and positive.

Additivity was a major influence in the inheritance of egg mass, egg number, egg weight and shank width. Dominance was an influence in the inheritance of the index, body weight, egg number and egg weight. Epistatic effects were of some importance to the index and body weight. The information for the estimation of modes of gene action for shank length was less conclusive.

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APPENDIX

TABLE 13. ANALYSIS OF VARIANCE FOR THE INDEX

Source	D.F.	Sum of Squares	Mean Squares	F
Total	9016	5494.9		
Population	2	399.5	199.82	399.6**
Replication	1	6.7	6.75	13.5**
Generation	17	247.9	14.58	29.1**
Pop. x Rep.	2	19.6	9.63	19.2**
Pop. x Gen.	34	248.9	7.32	14.6**
Rep. x Gen.	17	17.3	1.02	2.0**
Residual	8943	4471.3	.49	

**p<.01

TABLE 14. ANALYSIS OF VARIANCE FOR BODY WEIGHT

Source	D.F.	Sum of Squares	Mean Squares	F
Total	18089	5810375		
Population	2	9496	4748	33.5**
Replication	1	15066	15066	106.3**
Generation	17	221903	13053	92.1**
Sex	1	2542460	2542460	17941.5**
Pop. x Rep.	2	10097	5048	35.6**
Pop. x Gen.	34	76579	2252	15.8**
Pop. x Sex	2	1508	754	5.3**
Rep. x Gen.	17	5733	337	2.3**
Rep. x Sex	1			.0
Gen. x Sex	17	26689	1569	11.0**
Residual	17995	2550029	141	

**p<.01

TABLE 15. ANALYSIS OF VARIANCE FOR TOTAL EGG MASS

Source	D.F.	Sum of Squares	Mean Squares	F
Total	9016	101705586		
Population	2	6722970	3361485	359.6**
Replication	1	48717	48717	5.2**
Generation	17	4608536	271090	29.0**
Pop. x Rep.	2	248411	124205	13.2**
Pop. x Gen.	34	4597697	135226	14.4**
Rep. x Gen.	17	326799	19223	2.0**
Residual	8943	83577456	9345	

**p<.01

TABLE 16. ANALYSIS OF VARIANCE FOR EGG NUMBER

Source	D.F.	Sum of Squares	Mean Squares	F
Total	9016	899538		
Population	2	52628	26314	312.3**
Replication	1	841	841	9.9**
Generation	17	37241	2190	26.0**
Pop. x Rep.	2	4319	2159	25.6**
Pop. x Gen.	34	37750	1110	13.1**
Rep. x Gen.	17	2531	148	1.7*
Residual	8943	753441	84	

*p<.05
**p<.01

TABLE 17. ANALYSIS OF VARIANCE FOR EGG WEIGHT

Source	D.F.	Sum of Squares	Mean Squares	F
Total	9016	63010.5		
Population	2	1045.9	522.9	80.1**
Replication	1	3.9	3.9	.6
Generation	17	1247.5	73.3	11.2**
Pop. x Rep.	2	2.2	1.1	.1
Pop. x Gen.	34	1790.1	52.6	8.0**
Rep. x Gen.	17	151.7	8.9	1.3
Residual	8943	58321.7	6.5	

**p<.01

TABLE 18. ANALYSIS OF VARIANCE FOR SHANK LENGTH

	D.F.	Sum of Squares	Mean Squares	F
Total	18089	247.0896		
Population	2	3.2326	1.6163	139.8**
Replication	1	.3859	.3859	33.3**
Generation	17	13.8158	.8127	70.3**
Sex	1	10.5163	10.5163	909.8**
Pop. x Rep.	2	.8909	.4454	38.5**
Pop. x Gen.	34	3.6384	.1070	9.2**
Pop. x Sex	2	.0024	.0012	.1
Rep. x Gen.	17	.9404	.0553	4.7**
Rep. x Sex	1	.0030	.0030	.2
Gen. x Sex	17	.2866	.0169	1.4
Residual	17995	207.9826	.0116	

**p<.01

TABLE 19. ANALYSIS OF VARIANCE FOR SHANK WIDTH

Source	D.F.	Sum of Squares	Mean Squares	F
Total	18098	5.8725		
Population	2	.0261	.0130	54.5**
Replication	1	.0033	.0033	13.7**
Generation	17	1.0648	.0626	262.2**
Sex	1	.2819	.2819	1180.4**
Pop. x Rep.	2	.0109	.0054	22.7**
Pop. x Gen.	34	.0318	.0009	3.9**
Pop. x Sex	2	.0001	.0001	.2
Rep. x Gen.	17	.0146	.0009	3.6**
Rep. x Sex	1	.0011	.0011	4.5**
Gen. x Sex	17	.0071	.0004	1.7*
Residual	17995	4.2973	.0002	

*$p<.05$
**$p<.01$

TABLE 20. OVERALL MEANS AND SEX CONSTANTS FOR EACH TRAIT

Trait	Constant	Male	Female
Body Weight (g)	123.60	-12.52	12.52
Shank length (cm)	3.39	- .025	.025
Shank width (cm)	.27	- .0042	.0042
Egg mass (g)	248.02		
Egg number	24.92		
Egg weight (g)	9.31		
Index	1.82		

TABLE 21. CONSTANT ESTIMATES FOR ALL TRAITS AS DEVIATIONS FROM THE CONTROL FOR POPULATION I

Generation	Body Weight Units	Shank Length Units	Shank Width Units	Egg Mass Units	Egg Number Units	Egg Weight Units	Index Units
0	4.85	.022	.0036	44.14	3.68	.90	.179
1	3.25	-.010	.0049	- 3.47	- .60	.27	-.026
2	2.79	.014	.0049	20.63	1.34	.00	.101
3	- .65	-.018	.0052	-40.03	-6.96	-1.41	-.289
4	3.87	.028	.0060	30.09	2.33	.66	.190
5	- .76	.018	.0031	-66.90	-6.08	-1.63	-.435
6	.13	.005	.0022	- .67	.02	.05	.203
7	-4.35	-.025	.0053	-81.13	-7.07	-2.01	-.432
8	.02	.001	.0043	29.75	3.01	.63	.228
9	-7.79	-.027	.0022	-55.23	-4.13	-1.32	-.396
10	-3.93	-.005	.0032	30.94	3.22	.24	.249
11	-5.13	-.034	.0035	-21.89	-1.23	- .53	-.092
12	-4.54	-.011	.0036	25.73	3.59	- .22	.270
13	-7.37	-.034	.0025	- 8.99	- .01	.02	-.026
14	-3.19	-.015	.0020	60.14	6.27	.60	.476
15	-5.89	-.031	.0030	- 8.22	.42	- .45	.048
16	-4.97	-.026	-.0007	40.61	4.74	- .16	.388

TABLE 22. CONSTANT ESTIMATES FOR ALL TRAITS AS DEVIATIONS FROM THE CONTROL FOR POPULATION II

Generation	Body Weight g	Shank Length cm	Shank Width cm	Egg Mass g	Egg Number	Egg Weight g	Index
0	5.44	.021	.0039	51.29	4.29	.78	.250
1	6.38	.021	.0053	53.63	4.73	1.03	.314
2	1.23	.013	.0047	- 1.07	.24	-.88	-.033
3	4.07	.024	.0035	24.72	2.06	.34	.424
4	4.83	.004	.0024	47.52	4.00	- .80	.278
5	3.52	.019	-.0010	58.68	4.98	.67	.386
6	2.24	.007	.0008	40.03	3.10	.36	.099
7	3.44	.030	.0028	56.11	5.02	.51	.510
8	.64	.008	.0014	54.64	4.88	.86	.417
9	-3.73	.016	-.0007	56.01	5.31	.44	.472
10	-4.41	.010	-.0031	61.97	5.21	.61	.504
11	-4.59	.022	-.0020	83.09	7.32	.80	.669
12	-7.28	.007	-.0009	72.46	6.81	.32	.670
13	-6.01	.020	.0003	89.51	8.95	1.23	.871
14	-5.84	.015	-.0011	68.35	6.80	.58	.606
15	-7.82	.019	-.0024	62.34	6.08	.39	.642
16	-7.90	.019	-.0005	51.61	5.61	- .04	.544

TABLE 23. REGRESSION COEFFICIENTS FOR EACH TRAIT ON F_x x 100

Trait	Pop.	Linear	Quadratic	Cubic
Index	I	- 2.214	7.025	N.S.
	II	N.S.	N.S.	N.S.
	III	- 3.795	17.677	N.S.
Body Weight	I	- 25.38	172.52	-211.71
	II	- 58.73	653.06	-2042.97
	III	25.37	- 23.97	N.S.
Shank Length	I	- .279	1.917	- 3.245
	II	N.S.	N.S.	N.S.
	III	- .049	.048	N.S.
Shank Width	I	.0044	- .0324	.0656
	II	.0005	N.S.	N.S.
	III	N.S.	N.S.	N.S.
Egg Mass	I	-300.7	941.2	N.S.
	II	-111.4	N.S.	N.S.
	III	-531.4	2283.1	N.S.
Egg Number	I	- 28.42	93.56	N.S.
	II	- 12.06	N.S.	N.S.
	III	- 46.36	212.49	N.S.
Egg Weight	I	- 4.978	17.261	N.S.
	II	N.S.	N.S.	N.S.
	III	- 15.744	55.456	N.S.

Average Inbreeding Level

Population I = .170
Population II = .027
Population III = .023

N.S. = Non-significant

[redacted]

MacNeil, Michael D
Effect of mating system on selection response in Japanese quail

DATE	ISSUED TO

[redacted]