



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

Montana State University

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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: egg number \times 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 $.21 \pm .04$ for population I and $.16 \pm .01$ 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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IN JAPANESE QUAIL

by

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A thesis submitted in partial fulfillment
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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:

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

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 $.21 \pm .04$ for population I and $.16 \pm .01$ 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 cumulative 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 <u>et al.</u> (1968)
	B	.51	R/S	Collins <u>et al.</u> (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 <u>et al.</u> (1975)
	F	.53	R/S	Chahil <u>et al.</u> (1975)
6 weeks	B	.25	R/S	Collins <u>et al.</u> (1970)
	B	.25	R/S	Marks and Lepore (1968)
	B	.42	---	Kawahara and Inuo (1966)
	B	.43	R/S	Abplanalp (1967)
Mature	B	.36	---	Marks and Kinney (1964)

^aM = males; F = females; B = both.

^bR/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 <u>et al.</u> (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 <u>et al.</u> (1966)
x egg production	-.51	Kawahara and Inoue (1966)
x % growth 3-4 weeks	.29	El-Ibiary <u>et al.</u> (1966)
x egg number	-.63	El-Ibiary <u>et al.</u> (1966)
Egg number x adult body weight	.34	El-Ibiary <u>et al.</u> (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 fecundity 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 <u>et al.</u> (1958)
	M	.75	s-var	Thomas <u>et al.</u> (1958)
	F	.75	d-var	Thomas <u>et al.</u> (1958)
	B	.44	o-fp	Maloney <u>et al.</u> (1967)
	B	.50	o-fp	Maloney <u>et al.</u> (1967)
	M	.67	s-var	Thomas <u>et al.</u> (1958)
	F	.83	d-var	Thomas <u>et al.</u> (1958)
	8 weeks	F	.22	o-p
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 <u>et al.</u> (1958)
F		.79	d-var	Thomas <u>et al.</u> (1958)
10 weeks	-	.17	o-fp	Krueger <u>et al.</u> (1952)
	-	.28	fs-r	Krueger <u>et al.</u> (1952)
	-	.33	o-fp	Krueger <u>et al.</u> (1952)
	B	.34	d-var	Brunson <u>et al.</u> (1956)
	-	.41	ms-E	Lankford and McLung (1952)
	-	.46	fs-r	Krueger <u>et al.</u> (1952)
	M	.62	s-var	Thomas <u>et al.</u> (1958)
	F	.76	d-var	Thomas <u>et al.</u> (1958)
12 weeks	-	.07	R/S l	Maloney <u>et al.</u> (1963)
	F	.27	R/S	Maloney <u>et al.</u> (1967)
	-	.34	R/S h	Maloney <u>et al.</u> (1963)
	M	.35	R/S	Maloney <u>et al.</u> (1967)
	B	.37	R/S l	Maloney <u>et al.</u> (1967)
	B	.50	R/S h	Maloney <u>et al.</u> (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 <i>et al.</i> (1953)
	-	.49	fs-r	Dillard <i>et al.</i> (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.

^bfs-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 <u>et al.</u> (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 <u>et al.</u> (1953)
.28	fs-r	Krueger <u>et al.</u> (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 <u>et al.</u> (1974)

^as-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)	
Shank length	.71	o-fp c	Lerner and Cruden (1951)	
	.57	s-var	Kan et al. (1958)	

^ad-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 $.10 \pm .04$ phenotypic standard deviations for individual selection was not significantly greater than the standardized response per generation to sire family selection of $.08 \pm .03$ standard deviations or to index selection of $.06 \pm .02$ standard deviations. The standardized response per generation to dam family selection was $.04 \pm .05$ 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: $.89 \pm .34\%$ for sire family selection, $.77 \pm .20\%$ for index selection, $.55 \pm .21\%$ for individual selection and $.38 \pm .20\%$ 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 females. 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	r	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 <u>et al.</u> (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 (Stittman 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, $7.2 \pm .92$ days, and heavier, $.79 \pm .06$ 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 $-1.32 \pm .44g$ for 8-week body weight on percent inbreeding and Glazener et al., (1951) found a regression of $-.13 \pm .01$ ounces for 12-week body weight on percent inbreeding.

Shoffner (1948a) reported a significant regression of $-.44 \pm .13$ 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 $.93 \pm .07$ and age at sexual maturity on the inbreeding coefficient of $.60 \pm .11$. 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 $-1.4 \pm .04$ eggs and significant partial regressions for hatchability on dam's inbreeding coefficient of $19 \pm .07$ and for chick mortality on dam's inbreeding coefficient of $20 \pm .07$.

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 $.32 \pm .10$ days, $-.30 \pm .11$ eggs and $-.37 \pm .11\%$ 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 of 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: $-.53 \pm .07$, $.40 \pm .17$ and $.21 \pm .08$ 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 \div 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

