BEHAVIOR-GENETIC ANALYSES IN JAPANESE QUAIL CHICKS

by

Fred Harold Benoff

Thesis submitted to the Graduate Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Poultry Science

APPROVED:

Paul B. Siegel
Chairman Dr. P. B. Siegel

W L Beane
Dr. W. L. Beane

R. W. Young
Dr. R. W. Young

H. P. Van Krey
Dr. H. P. Van Krey

May, 1975

Blacksburg, Virginia

ACKNOWLEDGEMENT

The author wishes to express his sincere thanks and appreciation to Professor P. B. Siegel, major advisor, for his suggestions, guidance and encouragement throughout this course of study. Thanks are also expressed to Professors W. L. Beane, H. P. Van Krey and R. W. Young for their help in reviewing this thesis. The assistance of several technicians and graduate students in the collection of data is most appreciated.

Special thanks are extended to the author's family, Mr. and Mrs. Martin Benoff, Rhona and Cheryl for their support and encouragement during these years of college.

This research was in part supported by NSF grant GB-40060.

TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

Domestic animals were removed many centuries ago from their natural habitat and placed in environments designed and managed by man. Although during the process of domestication there was conscious and unconscious selection for needed behaviors and against others, many behaviors remained unaltered. As a result, man has had to adapt his management practices to fit the animal's behavior. Experiment 1 was designed to evaluate several management schemes on livability in newly hatched Japanese quail (*Coturnix coturnix japonica*) chicks.

There is a growing interest in understanding genetic and evolutionary aspects of animal behaviors. Genetic procedures developed for studying morphological and physiological characters can also be used for evaluating the genetic aspects of behavior. Japanese quail are unique study material for investigating the interfacing of genetics and domestication on behaviors. This is because although domesticated for the last several hundred years, there are also wild birds of this same species in Japan. Wild and domestic quail, while similar in physical appearance, are known to differ considerably in physiology (Kawahara, 1973). Experiment 2 involved such a genetic analysis of tonic immobility, a behavior occurring in both wild and domestic animals.

REVIEW OF LITERATURE

Tonic Immobility:

Tonic immobility, or animal hypnosis, is a behavior observed over a wide range of organisms representing the highest classes of invertebrates and extending through every class of vertebrates in the phylum chordata. Only those aspects of the behavior most relevant to this thesis will be alluded to here. This is because much of the research and theory regarding tonic immobility was reviewed by Ratner (1967) and updated by Gallup (1974a).

Descriptively, tonic immobility in birds can be characterized as a reversible physical immobility with accompanying muscle hypertonicity during which time the animal is unable to respond to external stimulation. Ratner (1967) elaborated on several hypotheses concerning the nature of this behavior. Data amassed since then indicate the phenomenon to be related in some way to fear. Factors such as repeated testing and handling tend to decrease the duration and incidence of immobility in birds (Ratner and Thompson, 1960; Gilman et al., 1950), whereas conditions thought to induce fear ; unfamiliar testing conditions, separation from conspecifics, loud noises and electrical shock produce just the opposite effect (Rovee et al., 1973; Salzen, 1963; Gallup et al., 1970a; Gallup et al., 1970b).

From an ecological vantage point, tonic immobility has been implicated as an adaptive reaction to predation. Investigators have shown that the presence of a looming object (Ginsburg et al., 1974) or simulation of the predator-prey relationship (Gallup et al., 1971; Gallup, 1973) will prolong the immobility reflex. Another approach to the study of tonic immobility as an evolutionary significant behavior involves a determination of the genetic components influencing the behavior and will be discussed in further detail below.

Behavior Genetics:

Wilcock (1969) noted that many behaviors of interest exhibit a continuous variability and are "governed by the effects of many genes acting together". Behavior traits, therefore, can be subjected to the same types of genetical analysis as physiological and morphological traits. Quantitative genetic analyses permits the estimation of both additive and nonadditive genetic variation. Since the severity of the selection pressure to which a trait has been exposed is a direct function of its adaptive significance, behaviors most closely related to fitness will have little additive genetic variation and will be inherited in a heterotic manner (Falconer, 1960; Bruell, 1964; 1967). Thus, it follows that neutral traits will have a relatively large additive variance and will be inherited in an intermediate way.

The ratio of the total genetic variance to the phenotypic variance is known as the heritability in the broad sense. Genetic variance may be broken down further into additive, dominance and epistatic variances. Heritability in the narrow sense is the ratio of the additive genetic variance to the phenotypic variance. Although there are many methods used to measure heritability, most are less than ideal and provide estimates that lie somewhere between the narrow and the broad sense. Much detail on the concept of heritability, interpretations and methodologies is covered by Falconer (1960) and Pirchner (1969).

To date, two studies have been published that assess genetic influences on tonic immobility. McGraw and Klemm (1973) found significant differences in duration of immobility in two lines of rats previously selected for different maze learning capabilities. There was no response to two generations of individual phenotypic selection for high and low duration of immobility. They then inbred the populations for three generations and obtained two lines that differed in duration of immobility. In a two-way selection experiment for duration of immobility in chickens, Gallup (1974b) reported realized heritabilities of .58 and .59 in the upward and downward directions, respectively. Although these data indicate that tonic immobility in at least one strain of chickens has little survival value, Gallup attributed the result to domestication which reduced selection pressure for the trait.

Feeding and Watering Behavior:

Shreck *et al.*, (1963) discussed how hunger and thirst may arouse "random" behavior, and that relief of hunger and thirst serves as a reinforcer of this behavior. In an experiment with lighting and rearing conditions as independent variables, Shreck *et al.*, (1963) observed higher mortalities and lower body weights in young cockerels raised in isolation as well as under poor illumination. That extraceptive stimulation influences the behavior of young chicks comes as no surprise, because precocial birds have well developed sensory organs at hatching. Many studies have demonstrated the facilitating effect of social interaction on feeding behavior in young chicks (Tolman, 1964; Tolman and Wilson, 1965; Wilson, 1968; Strobel *et al.*, 1970; Strobel and MacDonald, 1974). Social facilitation of feeding depends on at least two stimuli; tapping sounds (Tolman, 1967), and movement of the head (Strobel and MacDonald, 1974) which attract the chick to the food source.

Dawkins (1971) in a series of experiments found that although chicks shift their attention from cryptic to conspicuous grains during feeding, preference in a choice situation was for grains that were familiar in appearance. In contrast, water attracts birds by its visual properties of movement and brightness from a reflecting surface (Rheingold and Hess, 1957). From a husbandry viewpoint, information is needed on the effects of providing feed and water either simultaneously or sequentially to newly hatched chicks.

EXPERIMENT 1: FEEDING AND WATERING BEHAVIOR IN NEWLY HATCHED CHICKS

MATERIALS AND METHODS

Stock:

Quail used in this experiment were from a randombred control population and from S_{10} generation matings of replicated lines selected for high and low mating frequency (Sefton and Siegel, 1973; Stroemer, 1973). Data were obtained for chicks from three hatches. There were 373, 645, and 583 quail in hatches one, two, and three, respectively.

Management and Experimental Procedures:

Pedigreed eggs were incubated in a Petersime model S6-PH incubator-hatcher. Eggs were transferred from the incubator to the hatcher on the 16th day of incubation. Wet bulb readings were 29.3°C during incubation and 32.2°C during hatching, while dry bulb readings were 37.7°C during incubation and 37.2°C during hatching. Three days subsequent to the transfer, newly hatched chicks were removed from the hatcher, wingbanded, randomized, and placed in the brooder facilities.

Quail were raised in heterosexual flocks in a modified chick battery brooder. The battery consisted of five levels with two pens per level, each pen being 88 cm long and 77 cm wide. Pen temperatures under the hover were maintained at 37°C for the first three days, and 35°C for nine days thereafter. Room temperature was 30°C. Continuous illumination was provided throughout the experiment.

Lines were equally divided and randomized into groups. These groups were then randomly assigned to treatment pens. Treatments consisted of the following feed and water combinations:

(a) feed at time zero (time when the chick was initially introduced into the pen) and water six hours later,

(b) water at time zero and feed six hours later, and

(c) feed and water simultaneously at time zero.

Assignments of these treatments over the three hatches followed a Latin Square arrangement.

All chicks were provided with feed and water *ad libitum* six hours after being placed in a treatment pen. Quail were fed the VPI&SU quail starter ration (Table 1).

Measurements and Statistical Analysis:

The development of feeding and watering behavior was inferred from body weight and mortality data. Body weights at seven days of age were analyzed according to a nested design with unequal subclass numbers. Hatches were analyzed individually. The statistical model was:

$$Y_{ijk} = \mu + T_i + P_{j(i)} + e_{ijk}$$

The subscripts assume the following values: i = 1, 2, 3; j = 1, 2; and k = 1, . . . mijk, where mijk equals the number of observations in the ij*th* cell.

Y_{ijk} is the k*th* observation in the ij*th* cell,

μ is the overall mean,

T_i is the i*th* treatment effect,

$P_{j(i)}$ is the j*th* pen within the i*th* treatment, and

e_{ijk} is the random error associated with the measurement of the ijk*th* observation.

Mortality during the first six days posthatch were analyzed using a Chi square test to determine the significance of differences between the three treatment groups.

Table 1. Formulation of the VPI&SU Starter Ration

Ingredients		Composition[1] (g)
Ground yellow corn		445.80
49% Protein solvent extracted soybean oil meal		364.60
Meat and bone meal		50.00
60% protein fish meal		50.00
Limestone		5.20
Fat		33.30
Dehydrated alfalfa meal		20.80
Defluorinated phosphate		15.60
Vitamin premix		5.20
Corn gluten meal		4.20
Salt		4.20
Methionine		0.52
Trace minerals		0.52
	TOTAL	999.94

[1] Ration contains 28% protein

RESULTS AND DISCUSSION

Mortality:

Mortalities to six days of age were pooled over hatches for each feeding-watering treatment (Table 2). The percentage mortality was 2.3 for Treatment a, 2.9 for Treatment b, and 2.5 for Treatment c. Differences between the treatments for mortality were not significant ($\chi^2 = .33$) demonstrating that these procedures for starting quail had no differential effect on mortality. It should be pointed out that livability was excellent in all hatches. Therefore, the effect of these treatments in situations where higher mortality is more typical is not known.

Body Weight:

Mean body weights at seven days of age for quail in Hatch one were 22.2, 22.6 and 23.5 g for Treatments a, b and c, respectively. None of the differences among means was significant (Table 3), showing that the procedure for starting quail had no effect on growth at seven days of age.

In hatches two and three variances were heterogeneous (Table 4) according to Bartlett's test. The heterogeneity of variances appears to be caused by differences between pens within a treatment rather than differences between treatments. The heterogeneity of variances precluded further analysis of these data. It may, however, be interesting to continue this study in an effort to find the biological causes of the heterogeneity.

Table 2. Numbers of Quail, Alive and Dead at Six Days of Age for the Three Treatments

	Treatments		
	a	b	c
Alive	539	536	538
Dead	13	16	14
Total	552	552	552

a = Feed was available when quail were placed in the pen and water was given six hours later.

b = Water was available when quail were placed in the pen and feed was given six hours later.

c = Feed and water were available when quail were placed in the pen.

Table 3. Analysis of Variance of Body Weight at Seven Days of Age for Quail From Hatch 1

Source of Variation	d.f.	M.S
Among treatments	2	9.29
Within treatments	3	9.03[2]
Sampling error	367	8.79[1]

[1]Sampling error MS is the denominator for the within treatment's F test.

[2]Within treatments MS is the denominator for the between treatment's F test.

Table 4. Means and Variances for Body Weight at Seven Days of Age for Treatments for Hatches 2 and 3

		Hatch 2		Hatch 3	
Treatment	Pens	$\bar{x}$	s^2*	$\bar{x}$	s^2**
a	1	22.1	11.5	21.5	8.2
	2	20.3	8.9	22.1	4.7
b	1	21.0	9.2	21.6	8.9
	2	20.9	6.4	22.6	5.6
c	1	22.1	9.0	21.7	4.9
	2	21.2	6.8	23.0	4.6

*Bartlett's Test, $\chi^2 = 13.1$ ($P \leq .025$).

**Bartlett's Test, $\chi^2 = 21.7$ ($P \leq .005$).

SUMMARY AND CONCLUSIONS

Comparisons were made among three procedures for starting day-old quail; (a) water initially, followed by feed six hours latter, (b) feed initially, followed by water six hours latter, (c) feed and water both given initially. No differences were found among procedures for livability to six days of age and body weight at seven days of age. These results suggest that under excellent husbandry newly hatched quail are capable of learning to eat and drink regardless of which one they are exposed to first.

EXPERIMENT 2: GENETIC ANALYSES OF TONIC IMMOBILITY

MATERIALS AND METHODS

Stock and Management:

The quail used in this experiment were the same as those from hatches one and two in Experiment 1. Husbandry of these birds was described in the previous section.

Testing Procedures:

At 6 and again at 12 days of age each quail was carried by hand from its brooding pen to a testing platform that was located in the same room. Each subject was placed on its right side and manually restrained for 15 seconds. When immobility did not occur following the first restraint, successive 15-second sessions were initiated with a maximum of five attempts. Each quail received an induction number based on the number of restraints required to induce immobility. The temporal duration of immobility was measured in seconds from the time restraint was terminated to the time the chick righted itself. Individuals that failed to immobilize received an induction number of five with a duration of zero.

Each chick was in clear view of an observer that was seated approximately one m from it. Direct eye contact between the experimenter and quail was avoided because Gallup *et al*. (1972) demonstrated a prolonging influence from such contact on the duration of tonic immobility.

Statistical Analysis:

Durations of tonic immobility at 6 and 12 days of age were considered as different traits. Data were transformed to square roots prior to analysis. Quantitative data were analyzed in two steps. The first was a factorial analysis using the method of least squares adapted for non-orthogonal data (Stevens, 1948) to determine the importance of sex effects. The statistical model was:

$$Y_{ijkl} = \mu + S_i + L_j + H_k + (SL)_{ij} + (SH)_{ik} + (LH)_{jk} + (SLH)_{ijk} + e_{ijkl}$$

The subscripts assume the following values: i, k = 1, 2; j = 1, . . . 5; l = 1, . . . mijk, where mijk equals the number of observations in the ijk<u>th</u> cell.

Y_{ijkl} is the l<u>th</u> observation in the ijk<u>th</u> cell,

μ is the overall mean,

S_i is the i<u>th</u> sex effect,

L_j is the j<u>th</u> line effect,

H_k is the k<u>th</u> hatch effect,

$(SL)_{ij}$ is the interaction between the i<u>th</u> sex and j<u>th</u> line,

$(SH)_{ik}$ is the interaction between the i<u>th</u> sex and k<u>th</u> hatch,

$(LH)_{jk}$ is the interaction between the j<u>th</u> line and k<u>th</u> hatch,

$(SLH)_{ijk}$ is the second order interaction between the i<u>th</u> sex, j<u>th</u> line and k<u>th</u> hatch, and

e_{ijkl} is the random error associated with the measurement of the ijkl<u>th</u> observation.

Duncan's multiple range test (Kramer, 1956) was used to separate means when significant differences were found for variables with more than two means.

The second analysis was a hierarchial classification following that of King and Henderson (1954) to provide components of variance and covariance for use in estimating heritabilities and correlations. The statistical model was:

$$Y_{ijklm} = \mu + h_i + l_{j(i)} + s_{k(ij)} + d_{l(ijk)} + e_{ijklm}$$

The subscripts assume the following values: i = 1, 2; j = 1, . . . 5; k = 1, . . . s_{ijk}, where s_{ijk} equals the number of sires within the jth line and ith hatch; l = 1, . . . d_{ijkl}, where d_{ijkl} equals the number of dams within the kth sire, jth line, and ith hatch; m = 1, . . . e_{ijklm}, where e_{ijklm} equals the number of progeny within the lth dam, kth sire, jth line and ith hatch.

Y_{ijklm} is the record of the mth progeny of the lth dam mated to the kth sire from the jth line within the ith hatch,

μ is the overall mean,

h_i is the ith hatch effect

$l_{j(i)}$ is the effect of the jth line within the ith hatch,

$s_{k(ij)}$ is the effect of the kth sire of the jth line and ith hatch,

$d_{l(ijk)}$ is the effect of the lth dam mated to the kth sire of the jth line and ith hatch, and

e_{ijklm} is the random error associated with the measurement of the ijklmth observation.

Heritability estimates from the component analysis were based on paternal half sib correlations [$h^2_S = 4S \div (S + D + E)$], maternal half sib correlations [($h^2_D = 4D \div (S + D + E)$] , and full sib correlations

$[h^2_{S+D} = 2(S + D) \div (S + D + E)]$. The genetic correlations between the duration of tonic immobility at 6 and 12 days of age were estimated using sire and dam components of variance and covariance $[r_{GG} = (\text{Cov } S + \text{Cov } D) \div (\sqrt{S_x + D_x}\ \sqrt{S_y + D_y})]$. Standard errors for the heritability estimates and genetic correlations were calculated by the method described by Becker (1964).

RESULTS AND DISCUSSION

Lines:

Differences among lines for duration of immobility at 6 and 12 days of age were significant (Table 5), suggesting a genetic basis for this trait. Rankings of lines by the size of their means indicate that there is no relationship between the duration of tonic immobility and prior selection for mating ability (Table 6). The duration of immobility increased over age for all lines except Line C. Lines H2 and L1 had the longest durations at both ages with the rankings of Lines H1 and L2 and C, shifting somewhat with age.

The incidence of tonic immobility for line and age groups is presented in Table 7 as the cummulative percentage incidence over five restraints. The range among lines for percentage of quail responding to the immobility reflex on the first restraint was considerably greater at 12 days (82 to 97%) than at six days (80 to 86%) of age. The range among lines narrowed by the second restraint as values approached 100 percent. At both ages, the ranking of lines for percentage incidence on the first restraint was similar to the rankings of these lines for duration of immobility. Lines with larger mean durations of immobility had a greater proportion of birds responding on the first restraint; likewise those with smaller mean durations had a lower incidence of immobility. These results are in agreement with those of Ratner and Thompson (1960) who found a positive correlation between the percentage of chickens responding and the duration of immobility.

Table 5. Analyses of Variance for Duration of Tonic Immobility at 6 and 12 Days of Age

Source of Variation	df	MS 6-day	MS 12-day
Among Lines (L)	4	108.12**	148.33**
Among Hatches (H)	1	164.73**	725.16**
Among Sexes (S)	1	52.13	1.55
L X H	4	13.64	30.64
L X S	4	38.95*	12.86
H X S	1	40.01	3.74
L X H X S	4	7.78	7.19
Residual[1]	783	14.94	16.31

**$P \leq 0.01$.

*$P \leq 0.05$.

[1]Residual mean square was used as the denominator for all F tests.

Table 6. Mean[1] Duration (sec) of Immobility by Line and Age

Age (Days)	Lines				
	H1	H2	C	L1	L2
6	32.50[a]	80.78[c]	46.54[ab]	58.60[b]	43.27[a]
12	44.21[a]	92.91[c]	41.87[a]	63.18[b]	56.94[ab]

[1]Means within a row with the same superscript are not significantly different ($P \leq 0.05$).

Table 7. Cumulative % Incidence by the 1st, 2nd, 3rd, 4th and 5th Restraint, by Line and Age

Line	n	6-Day					12-Day				
		1st	2nd	3rd	4th	5th	1st	2nd	3rd	4th	5th
L1	232	85	94	96	98	100	91	99	100	100	100
L2	154	82	93	98	98	100	94	98	99	100	100
C	192	82	95	97	97	100	83	98	100	100	100
H1	137	80	93	98	99	100	82	94	98	100	100
H2	88	86	96	96	97	100	97	100	100	100	100

Individuals that failed to respond received an induction number of five with a duration of zero sec.

There was an inverse relationship between the number of inductions and the mean duration of immobility within each line (Tables 8 and 9). That is, as the mean durations within a line decreased in magnitude the number of inductions increased. This relationship existed at both 6 and 12 days of age and is consistent with the observations of Ratner (1967) and McGraw and Klemm (1973) who noted an inverse relationship between induction time (number of inductions is a crude measure of induction time) and duration of immobility. Longer durations and fewer numbers of induction are suggestive of a higher degree of susceptability. Percentage incidence of immobility on the first restraint increased with age as did duration of immobility, an effect commonly observed by other investigators (Ratner and Thompson, 1960; Salzen, 1963; Rovee et al., 1973; Borchelt and Ratner, 1973; Braud and Ginsburg, 1973; Rovee and Kleinman, 1974). At this point, however, the biological mechanisms underlying this age effect are poorly understood.

Sex:

There was no significant sexual dimorphism at either age for percentage incidence of tonic immobility. Further, there were no differences among sexes for duration of immobility at 6 and 12 days of age (Table 5). Mean duration of immobility was 46.3 sec for males and 54.9 sec for females at six days of age. At 12 days of age means were 58.4 for males and 55.6 for females. These findings are consistent with those of Borchelt and Ratner (1973) and Gallup (1974b) who reported lack of sexual dimorphism for the trait in quail and chickens.

Table 8. Means and Standard Errors of Duration (sec) of Tonic Immobility by Lines and Number of Inductions at 6 Days of Age

No. Induct	Line				
	L_1	L_2	C	H_1	H_2
1	61.6 ± 5.2	46.5 ± 4.9	49.3 ± 4.7	32.3 + 3.7	87.2 ± 11.2
2	50.6 ± 10.3	32.1 ± 11.9	41.9 ± 8.2	37.2 ± 8.0	46.0 ± 13.3
3	34.6 ± 9.2	30.3 ± 15.2	30.7 ± 28.2	23.1 ± 11.3	———
4	25.5 ± 14.2	———	———	13.5 ± 2.5	1.0 ± 0.0
5	2.0 ± 2.0	0.3 ± 0.3	7.7 ± 7.7	68.0 ± 0.0	33.0 ± 3.0

Table 9. Means and Standard Errors of Durations (sec) of Tonic Immobility by Lines and Number of Inductions at 12 Days of Age

No. Induct	Line				
	L_1	L_2	C	H_1	H_2
1	66.3 ± 4.6	58.1 ± 4.8	46.3 ± 3.9	50.3 ± 6.6	95.0 ± 13.3
2	37.6 ± 7.5	39.3 ± 16.1	19.7 ± 4.0	17.4 ± 6.1	33.0 ± 24.7
3	1.5 ± 0.5	2.0 ± 0.0	22.0 ± 19.5	10.6 ± 9.1	—
4	—	—	40.0 ± 0.0	16.0 ± 10.8	—
5	18.0 ± 0.0	50.0 ± 50.0	—	—	—

No difference between sexes would be expected if tonic immobility was a defensive behavior.

A significant line by sex interaction was found at six days, but not at 12 days of age (Table 5). The interaction at six days may be attributed to the differential response of sexes in line L1 which was in contrast to that observed in the other lines (Table 10).

Heritabilities:

Heritability estimates based on full and half sib correlations are presented in Table 11 for the duration of tonic immobility at 6 and 12 days of age. Estimates from full sib correlations were comparable for males and females at both ages. These estimates are composed of sizable amounts of additive and nonadditive genetic effects plus maternal influences.

At six days of age the heritabilities from maternal and paternal half sib correlations were of the same magnitude for males suggesting additive gene effects on duration of tonic immobility. On the other hand, for female progeny, the estimates based on maternal half sib correlations were larger than those calculated from paternal half sib correlations. Heritabilities based on maternal half sib correlations, while containing an additive genic component also provides information on nonadditive gene effects and maternal effects, and are in principle supposed to be at least as large as the sire based estimates which include additive gene effects and some epistatic deviations. The negative paternal half sib estimate for female progeny at 6 days of age may be due to the small sample size.

Table 10. Means Duration (sec) of Tonic Immobility at Six Days of Age by Line and Sex

Line	Sex	
	Male	Female
L1	40.7	72.2
L2	46.0	40.7
C	47.1	46.0
H1	30.8	34.3
H2	79.6	82.1

Table 11. Heritabilities and Standard Errors for Duration of Tonic Immobility at 6 and 12 Days of Age by Sex

Sex	6-Day			12-Day		
	4S	4D	2(S + D)	4S	4D	2(S + D
Male	.24 ± .24	.23 ± .36	.24 ± .15	.03 ± .23	.22 ± .38	.12 ± .15
Female	-.18 ± .20	.49 ± .34	.15 ± .12	.65 ± .25	.03 ± .27	.34 ± .14
$\bar{x}$	.03	.36	.20	.34	.13	.23

Heritability estimates of tonic immobility at 12 days of age also suggest that nonadditive gene action, maternal effects, or a combination of both influence this trait. Since, however, the estimate from maternal half sib correlations for females is small, it would seem that maternal effects have been eliminated by this age. The posthatching environment of the chick may mask the influence of the egg environment (maternal effects). Since such would be a function of time, maternal effects would become less with increasing chronological age of the chicks.

The large standard errors associated with the heritability estimates may be due to the size of the dam and sire families. When the heritability is unknown, the optimum dam family size in a sire and dam analysis is 10 with 3 or 4 dams per sire (Robertson, 1959). In this experiment the mean number of offspring per dam was 2.9 and there were 2.3 dams per sire. In retrospect, these numbers are insufficient and therefore may contribute to large variability associated with the heritability estimates.

Since heritability estimates based on full and half sib correlations are not precise, male and female estimates within a sib type were pooled and the average heritability calculated. At six days of age the mean estimate based on maternal half sib correlations was .33 greater than the mean estimate from paternal half sib correlations. This is indicative of sizable maternal and/or dominance effects with some additive effects. By 12 days of age maternal effects were small, if existant at all, and there were indications of considerable amounts of genetic additivity. The amount of genic additivity, however, is still considerably smaller than that indicated from realized heritabilities obtained by Gallup (1974b) for the domestic fowl. His values, which were in the range of .55 to .60, are unusually high for the additive genetic variance of any quantitative trait. A relatively recent summary of all published estimates obtained for a multitude of traits in the chicken was compiled by Kinney (1969).

Correlations:

Phenotypic correlations between tonic immobility at 6 and 12 days of age were .34 for males and .11 for females suggesting a low to moderate positive relation. Genetic correlations are due to either the transient effect of linkage or the more permanent effects of pleitropy. The latter effect is more readily implicated as a cause for correlation of duration of tonic immobility at 6 and 12 days of age because the trait is being measured at both ages. The genetic correlation between tonic immobility at 6 and 12 days of age was greater than unity for males and .18 for females. This diversity suggests that the estimates may be unreliable. The sampling errors inherent to heritability estimates are compounded in the estimation of genetic correlations because included are the variances of both traits and the covariances between them. Accordingly, a bank of data may be needed to obtain reliable estimates of the genetic correlations between tonic immobility measured at 6 and 12 days of age in Japanese quail.

SUMMARY AND CONCLUSION

The investigation reported here involved an analysis of some of the biological factors affecting tonic immobility in young Japanese quail. Both duration and incidence of tonic immobility were measured on each bird at six days and again at 12 days of age.

A significant line effect was found at both ages, and rankings of these lines for duration and incidence followed a similar pattern. Number of inductions and duration of immobility were inversely related, while the percentage incidence was positively associated with duration of immobility. A large maternal effect found at six days of age disappeared by 12 days of age. Additive genic effects were low to moderate which is indicative that tonic immobility is associated with fitness.

LITERATURE CITED

Becker, W. A., 1964. Manual of procedures in quantitative genetics. Program of Genetics, Washington State University, Pullman.

Borchelt, P. L. and S. C. Ratner. 1973. Development of freezing and immobility, predation defenses, in the Bobwhite quail (Colinus virginianus). Behav. Biol. 8:83-92.

Braud, W. G. and H. J. Ginsburg. 1973. Immobility reactions in domestic fowl (Gallus gallus) less than 7 days old: Resolution of a paradox. Anim. Behav. 21:104-108.

Bruell, J. H. 1964. Inheritance of behavioral and physiological characters of mice and the problem of heterosis. Am. Zool. 4:125-138.

Bruell, J. H. 1967. Behavioral heterosis. p. 272-286. In J. Hirsch (ed.), Behavior-genetics analysis. McGraw-Hill, New York.

Dawkins, M. 1971. Shifts of "attention" in chicks during feeding. Anim. Behav. 19:575-582.

Falconer, D. S. 1960. Introduction to quantitative genetics. Edinburg and London; Oliver and Boyd Ltd.

Gallup, G. G., Jr. 1973. Simulated predation and tonic immobility in lizards (Anolis carolinensis). Copeia 3:623-624.

Gallup, G. G., Jr. 1974a. Animal hypnosis: Factual status of a fictional concept. Psychol. Bull. 81:836-853.

Gallup, G. G., Jr. 1974b. Genetic influence on tonic immobility in chickens. Anim. Learn. and Behav. 2:145-147.

Gallup, G. G., Jr., H. S. Creekmore, and W. E. Hill III. 1970a. Shock-enhanced immobility reactions in chickens: Support for the fear hypothesis. Psychol. Record 20:243-245.

Gallup, G. G., Jr., R. F. Nash, R. J. Potter, and N. H. Donegan. 1970b. Effects of varying conditions of fear on immobility reactions in domestic chickens (Gallus gallus). J. Comp. Physiol. Psychol. 73:442-445.

Gallup, G. G., Jr., R. F. Nash, N. H. Donegan, and M. K. McClure. 1971. The immobility response: A predator-induced reaction in chickens. Psychol. Record 21:513-519.

Gallup, G. G., Jr., W. H. Cummings, and R. F. Nash. 1972. The experimenter as an independent variable in studies of animal hypnosis in chickens (Gallus gallus). Anim. Behav. 20:166-169.

Gilman, T. T., F. L. Marcuse, and A. U. Moore. 1950. Animal hypnosis: A study in the induction of tonic immobility in animals. J. Comp. Physiol. Psychol. 43:99-111.

Ginsburg, H. J., W. G. Braud, and R. D. Taylor. 1974. Effect of looming object on immobility reaction in Gallinaceous birds (Gallus gallus). J. Comp. Physiol. Psychol. 86:146-150.

Kawahara, T. 1973. Comparative study of quantitative traits between wild and domestic Japanese quail (Coturnix coturnix japonica). Exp. Anim. Suppl. 22:139-150.

King, S. C. and C. R. Henderson. 1954. Variance components analysis in heritability studies. Poul. Sci. 33:147-154.

Kinney, T. B., Jr. 1969. A summary of reported estimates of heritabilities and of genetic and phenotypic correlations for traits of chickens. U. S. Dept. Agr. handbook 363.

Kramer, C. Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. Biometrics 12:307-310.

McGraw, C. P. and W. R. Klemm. 1973. Genetic differences in susceptability of rats to the immobility reflex ("animal hypnosis"). Behav.-Genet. 3:155-161.

Pirchner, F. 1969. Population genetics in animal improvement. W. H. Freeman Co.

Ratner, S. C. 1967. Comparative aspects of hypnosis. In J. E. Gordon (ed.), Handbook of clinical and experimental hypnosis. MacMillan, New York. p. 550-587.

Ratner, S. C. and R. W. Thompson. 1960. Immobility reaction (fear) of domestic fowl as a function of age and prior experience. Anim. Behav. 8:186-191.

Rheingold, H. L. and E. H. Hess. 1957. The chicks "preference" for some visual properties of water. J. Comp. Physiol. Psychol. 50:417-421.

Robertson, A. 1951. Experimental design in the evaluation of genetic parameters. Biometrics 15:219-226.

Rovee, C. K. and J. M. Kleinman. 1974. Developmental changes in tonic immobility in young chicks (Gallus gallus). Develop. Psychol. 7:71-77.

Rovee, C. K., A. Agnello, and B. Smith. 1973. Environmental influences on tonic immobility in three and seven day old chicks (Gallus gallus). Psychol. Record 23:539-546.

Salzen, E. A., 1963. Imprinting and the immobility reaction of domestic fowl. Anim. Behav. 11:66-71.

Sefton, A. E. and P. B. Siegel. 1973. Mating behavior of Japanese quail. Poul. Sci. 52:1001-1007.

Schreck, P. K., G. M. Sterritt, M. P. Smith, and D. W. Stilson. 1963. Environmental factors in the development of eating in chicks. Anim. Behav. 11:306-309.

Stevens W. L. 1948. Statistical analysis of a non-orthogonal tri-factorial experiment. Biometrika 35:346-368.

Strobel, M. G. and G. E. MacDonald. 1974. Induction of eating in newly hatched chicks. J. Comp. Physiol. Psychol. 86:493-502.

Strobel, M. G., S. L. Freeman, and G. E. MacDonald. 1970. Social facilitation of feeding in newly hatched chickens as a function of imprinting. Canad. J. Psychol. 24:207-215.

Stroemer, G. R. 1973. Genetic variation of mating behavior of Japanese quail (Coturnix coturnix japonica). Unpublished Master thesis, VPI&SU.

Tolman, C. W. 1964. Social facilitation of feeding behavior in the domestic chick. Anim. Behav. 12:245-251.

Tolman, C. W. 1967. The effects of tapping sounds on feeding behavior of domestic chicks. Anim. Behav. 15:145-148.

Tolman, C. W. and Wilson, G. F. 1965. Social feeding in domestic chicks. Anim. Behav. 13:134-142.

Wilcock, J. 1969. Gene action and behavior: An evaluation of major gene pleitropisms. Psychol. Bull. 72:1-29.

Wilson, G. F. 1968. Early experience and facilitation of feeding in domestic chicks. J. Comp. Physiol. Psychol. 66:800-802.

VITA

The author, Fred Harold Benoff, was born in Philadelphia, Pennsylvania on April 30, 1952. He was raised in Pennsylvania and was graduated from Penn Center Academy, Philadelphia in June 1969. Fred entered Southeastern Massachusetts University where he remained for two years. Subsequently he entered The Pennsylvania State University where he received the degree of Bachelor of Science in Animal Science in June 1973. He is a member of Gamma Sigma Delta, the Phi Sigma Society, the Sigma Xi Society, Poultry Science Association, World Poultry Science Association, Association for the Advancement of Science, Animal Behavior Society, the American Genetic Association and the Genetic Society of America.

Fred H. Benoff

BEHAVIOR-GENETIC ANALYSES IN
JAPANESE QUAIL CHICKS

by

Fred H. Benoff

(ABSTRACT)

Several behaviors in Japanese quail (Coturnix coturnix japonica) were analyzed. Tonic immobility was examined in an evolutionary context, while feeding and watering behaviors were studied for husbandry implications under laboratory conditions.

Data were obtained from replicated lines selected for high and low mating ability and a randombred control population. Comparisons of growth and livability were made for chicks started on three different feeding and watering schemes; a). water initially with feed six hours later, b). feed initially with water six hours later, and c). feed and water simultaneously. At six, and again at 12 days of age each bird was immobilized. Measurement criteria were induction number and duration of immobility. A variance component analysis was used to estimate the genetics underlying tonic immobility.

There were no significant differences among feeding and watering regimes for mortality and seven day body weight. This indicates that birds learned to eat and drink equally well for the three treatments.

Although sexes were not different, lines differed significantly for duration and % incidence to the immobility response at both ages. Birds that responded faster also exhibited longer durations of

immobility suggesting a high degree of susceptability. Heritability estimates indicate that nonadditive gene effects and/or maternal effects are more important than additive gene effects. These results suggest that tonic immobility is a fitness trait and is therefore an adaptive behavior.