## IMPRINTING IN THE QUAIL, COTURNIX COTURNIX

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#### ABSTRACT

#### IMFRINTING IN THE QUAIL, COTURNIX COTURNIX

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This study investigated imprinting in the Japanese quail (<u>Coturnix coturnix</u>). Filot experiments indicated that these birds do not exhibit the following response, heretofore used to indicate imprinting. The present study proposed to show that the phenomena is not dependent on the following response, and to obtain preliminary information regarding the sensitive period for imprinting in this species.

Isolated quail poults of two post-hatch ages were individually exposed to a moving, flashing, clicking stimulus on the day of hatching. Two other groups received identical treatment except for exposure to the stimulus, and a fifth group was given no initial treatment. On the following day each bird received two test sessions in which distress calls, time showing fear responses, and time spent near the stimulus were measured with the stimulus both present and functionally absent.

The results indicate that imprinting does occur in the Japanese quail, and that it occurs during a sensitive peroid in the young bird's development. Birds exposed to the imprinting stimulus 5 - 9 hours after hatching exhibited reliably fewer distress calls and reliably less fear behavior when the stimulus was present than each of the other groups including those birds exposed to the stimulus 10 - 14 hours post-hatch. The topographical characteristics of the phenomena differ from birds previously studied in that following did not occur. It is suggested that the following response is only one of an array of responses involved in imprinting. Which of these responses manifest themselves in any experiment will depend upon the ecology and natural parent-young behavior of the species in question.

## IMPRINTING IN THE QUAIL, COTURNIX COTURNIX

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## TABLE OF CONTENTS

ACKNOWLEDGEMENTS	page 11
LIST OF TABLES	iv
LIST OF FIGURES	v
LIST OF APPENDICES	vi
INTROLUCTION	1
METHOD	10
RESULTS	16
DISCUSSION	31
REFERENCES	42
APPENDICES	46

## LIST OF TABLES

Table			Page
1.	Analysis distress	of Variance summary table of calls in test 1	20
2.	Analysis distress	of Variance summary table of calls in test 2	24

## LIST OF FIGURES

Figure		Page
1.	Distress calls emitted by each subject during test l	17
2.	Mean number of distress calls in test 1 as a function of treatment, stimulus condition and trials	18
3.	Distress calls emitted by each subject in test	22
4.	Mean number of distress calls in test 2 as a function of treatment, stimulus condition and trials	23
5.	Time showing fear behavior in test 1 as a function of treatment, stimulus condition and trials	26
6.	Mean difference (S-ON — S-OFF) in proportion of time exhibiting fear behavior as a function of treatment and trials in test l	28
7.	Mean proportion of time spent with the stimulus in test 2 as a function of treatment, stimulus condition, and trials	30

## LIST OF APPENDICES

Appendix	Page
A. Apparatus	47
B. Postures	53

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#### Introduction

In 1873 D. A. Spalding reported his observations on incubator hatched, visually isolated chicks. He noted that chicks, less than four days old, would follow the first moving object they encountered. On the other hand, if the birds remained in visual isolation until the forth day, they actively avoided objects which previously would have elicited following. Subsequently, Heinroth (1911) noted that incubator hatched goslings followed humans in preference to adults of their own species, if exposed to a human being just after hatching. Several years later, Konrad Lorenz, interested in "innate releasing mechanisms" involved in the social behavior of birds, extended these earlier empirical observations and provided a theoretical framework for their interpretation.

Lorenz proposed that young precocial birds do not instinctively recognize members of their own species. However, during a particular period of early development, the young bird will instinctively follow the first moving object it encounters, and form a "lasting attachment" to that object. Lorenz emphasized that this attachment is of a filial nature; can only be formed during "a brief critical period in the life of the individual"; and occurs in the absence of any conventional reinforcing agent. This phenomenon was presumed responsible for species identification in avian neonates. Lorenz called this phenomenon "imprinting", to distinguish it from conventional forms of learning. He considered imprinting of theoretical importance

since it appeared as an example of the interaction between following, an instinctive response, and selection of the object to follow, a plastic, acquired response.

#### Generality of "Imprinting"

In the last two decades a vast amount of literature has accumulated on imprinting in birds and similar behavioral , phenomenon in other species, including mammals and invertebrates. The majority of these studies have dealt with approach and following behavior in domestic chicks and ducklings. Following of moving objects has also been reported for young coots, moorhens, geese, turkeys, and swans. In addition, many nidicolous species have shown inappropriate courtship fixations which have been interpreted as imprinting, although following behavior was not measured, (see Slucken, 1965).

The properties of imprinting are often used to explain the attachment of young mammals to a parent or parent-surrogate. Following responses to a human handler have been observed in young sheep and goats (Hersher, Richmond and Moore, 1963; Scott, 1945), moufflons (Hediger, 1955), moose. (Altmann, 1958), and guinea pig (Hess, 1959). Marr (1964) studied the effects of external stimulation on what he considered imprinting in 3 week old puppies. Each subject was exposed to a white circle for 9 minutes on 7 consecutive days. During this treatment, one group of dogs was rubbed and rocked by the experimenter. Another groups had a flashing light present and the control animals were given no extra stimulation. Tests, carried out on the two days

following training, indicated that the pupples exposed to external stimulation spent more time near the circle than subjects not given the external stimulation. Thus, many of the characteristics of imprinting in precocial birds can be demonstrated in pupples. Marr and Gardner (1965) have also shown that early olfactory experience will affect later social preferences in the albino rat. Harlow (1962) has repeatedly shown imprinting like behaviors in the infant rhesus monkey. Other authors (see Sluckin, 1965) claim imprinting occurs in the human neonate. Furthermore Thorpe (1945) suggests that some insects become imprinted to their habitat, and Hess (1964) states that, "We have found what appears to be an imprinting of young birds to the characteristics of food objects." (p.1134). Some Relevant Factors in Imprinting

One of the main distinctions that has been made between imprinting and other types of learning is that imprinting can only occur during a specific period in the development of the organism; usually called the critical or sensitive period (see Hess, 1959; or Sluckin, 1965). The notion of critical periods in ontogeny is not exclusive to imprinting, nor to the development of social behaviors. The term has been borrowed from embryologists by students of behavior to refer to optimal periods for learning, infantile stimulation, and the "formation of basic social relationships" (Scott, 1962). It should be stressed that the term, critical period, does not refer to an all-or-none phenomenon, but to a gradual change in the

occurence probability of a behavioral event, depending on both environmental and organismic conditions. Moltz (1960) points out the widespread occurence of critical periods in the development of social behaviors in both mammals and birds. Within mammalian development, J. P. Scott (1962) has extensively investigated and behaviorally defined critical periods in the development of puppies.

The critical period for imprinting has been extensively studied for domestic chicks, and wild and domestic ducklings. Sluckin (1965) cautions that the age at which a bird follows a moving object and age at which imprinting occurs may be different. The critical age for imprinting must be determined by a test situation in which "imprinted" birds are compared with controls who were not given exposure to the stimulus early in life, or were given exposure to the stimulus at different ages. That is, the behavior of a bird during training is irrelevant. It is the behavior of a bird during testing that determines whether or not it became imprinted to the stimulus configuration. Ramsay and Hess (1954) demonstrated that the critical period for imprinting in mallard ducklings is 1 - 24 hours after hatching, and an optimal age for imprinting occurs at 13 - 16 hours post-hatch for both chicks and ducklings. Unfortunately, no comparative data exists on critical periods for imprinting in other species.

Most investigators concur that at least one factor involved in the termination of the critical period for imprinting in

birds and primary socialization in mammals is the development of fear responses (Moltz, 1960; Sluckin, 1965). Unfortunately, a definitive statement regarding fear behaviors in young birds is not available. However, several behavioral responses have been traditionally used as indicators of fear and will be regarded as such here. These behaviors include freezing, distress calls, running from an object, excessive activity and immobility reactions. Hess (1959) presents evidence that the development of fear is a limiting factor by extending the critical period for imprinting using injections of tranquilizing drugs in chicks. Schaller and Emlen (1962) studied the development of avoidance behavior in precocial birds including domestic fowl, turkeys, ducks, pheasants, and coturnix quail. Their results indicated a gradual rise in avoidance behavior up to the forth or sixth day, which concurs with the fact that the probability of imprinting declines over this time. Ratner and Thompson (1960) found similar results for the development of immobility reactions in domestic fowl.

As noted above, the vast majority of imprinting studies have used either domestic chicks or ducklings in determining stimulus and response characteristics in imprinting. It has generally been found (Sluckin, 1965) that any readily apparent stimulus, such as a moving object or a flashing light, will elicit following and imprinting in domestic chicks. Smith and Bird (1963) found that a stimulus containing both visual and auditory components was more effective in eliciting and

sustaining approach responses by chicks than either stimulus alone. Gottlieb (1963) found the same results using domestic ducklings. Results of a series of studies on hole nesting and surface nesting ducks (Gottlieb, 1963 a and b; Klopfer, 1959; and Gottlieb and Klopfer, 1962) have shown that the primacy of audio and visual stimulation is probably dependent on the ecology and natural behavior of the species in question. For example, in surface nesting species, the function of sounds made by the parent may be primarily to direct the young's attention. Whereas, in other species, such as the Woodduck, the auditory stimulus may be the necessary and sufficient condition for imprinting. Other stimulus parameters such as size, shape and color of the stimulus object have proven to be of rather small importance in the establishment of imprinting (see Sluckin, 1965).

#### Pilot Experiments

Because of the lack of comparative information on imprinting in ground nesting birds, I proposed to study the development of the phenomenon in the Japanese quail (<u>Coturnix</u> coturnix).

In order to demonstrate imprinting in this species, thirty poults were individually exposed to a wide variety of stimuli within 5 to 20 hours after hatching. The stimuli ranged from a rubber ball 4 inches in diameter, moving silently around a circular runway to a flashing light moving back and forth within a large rectangular runway. Few of the 30 birds exposed to

these stimuli followed the moving stimulus during the initial training period and none followed during testing which occured one to two days later. Schaller and Emlen (1962), on the other hand, reported that 31% of their coturnix quail were observed to follow a moving object. However, these authors failed to report the total number of birds, or whether the following response was maintained.

When an auditory stimulus (either a click or the experimenter saying chirp-chirp-chirp-) was paired with the moving stimulus, no following occured. However, there was a noticible reduction of fear behavior during both initial exposure and testing. This reduction was evidenced by fewer distress calls and less escape behavior. The distress call of the young coturnix quail is an intense series of high pitched, one syllable notes. It is easily recognized by its intensity and readily discriminated from soft chirping sounds, also emitted by these birds when young. Collias (1952) reports that domestic chicks tend to approach objects to which contentment calls are given, and avoid objects which elicit distress calls.

Moltz (1960) defined imprinting as "a procedure" which "has been found to evoke close following of the object in such precocial avian species as ducks, geese, coots, moorhens, and domestic fowl." Other investigators have not limited the definition of the phenomenon to the topographical characteristics of following. Scott (1962) defines imprinting as "attachment" to an object "to which they (the birds) are long exposed during

the critical period". Sluckin (1965) states that there is no reason why "attachments" built on responses other than following should not be classified as imprinting. Furthermore, Gottlieb and Klopfer (1962), as discussed above, have shown that the effective stimulus characteristics are species dependent. This suggests that response characteristics may also be species dependent and the following response may not be the only behavioral event indicating that imprinting has occurred.

As discussed above, fear responses limit the sensitive period for imprinting. That is, the development of these responses prevent the occurance of imprinting. Furthermore, several investigators have reported a relationship between fear responses, such as distress calls, and following behavior during a test situation. Hoffman (1966) showed that imprinted Peking ducklings emit more distress calls when the imprinting stimulus is absent than in its presence. Collias (1952) showed that chicks tend to approach objects to which contentment calls are made and avoid objects to which distress calls are made. He also demonstrated that the rate of distress calling in newly hatched chicks can be lowered by presenting it with clucking sounds or a moving object. Hess and Schaeffer (1959) recorded the number of chicks in each of eleven age groups that emitted contentment or distress calls in the presence of an imprinting object. They found that the percentage of animals giving distress calls increased rapidly with age, from 15 to 30 hours old. This result is strongly correlated with a decreased

tendency to become imprinted to the stimulus. Bermant (1963) showed that the frequency of distress calling in chicks decreases as maternal contact increases. These reports suggested that when following does not occur, imprinting can be measured by the amount of fear behavior shown in a testing situation.

In the final pilot study I exposed six coturnix quail, 5 -15 hours old, to a flashing, clicking, moving light suspended about 1 inch above the floor of a large rectangular box. Upon testing, 24 hours later, each of these birds showed considerably fewer distress calls when the stimulus was present than in its absence, which suggested imprinting had occurred.

#### Purpose of the Present Study

The purpose of the present experiment was to demonstrate that imprinting can occur in the Japanese quail (<u>Coturnix</u> <u>coturnix</u>), and thereby show that the phenomenon is not dependent on the following response. We also wish to obtain preliminary information about the critical period and the primacy of visual and auditory dimensions of the stimulus.

Isolated quail poults of two post hatch ages were individually exposed to a moving, flashing, clicking stimulus on the day of hatching. Two other groups received identical treatment except for exposure to the stimulus, and a fifth group was given no initial treatment. On the following day each bird was given two tests in which distress calls, time showing fear responses, and time near the stimulus were measured with the stimulus both present and absent. Comparisons were then made between and within groups.

Method

#### Subjects

The subjects were 30 Japanese quail poults (Coturnix Coturnix). Eggs were collected daily from the coturnix breeding colony in the psychology laboratories at Michigan State University and set within two days after collection. The eggs were incubated at 100°F in a Sears Model 165 pan type incubator and turned automatically every 3 hours. (See appendix A for description and photograph of egg turner). Within two hours of hatching the young poults were removed from the incubator and placed in individual isolation cages where they resided for the entire experiment, except during treatment or testing. Food and water were available ad libitum. Thus, each animal was housed in visual but not auditory isolation from the other animals. The mean ambient noise level in the isolation cages was 50db (A) measured with a Bruel and Kjaer model 2203 Sound Level Meter.

#### Apparatus

The inside demensions of the isolation boxes were  $9x9\frac{1}{2}xll$  inches. (See appendix A for diagram) The sides and top were white pine and  $\frac{1}{2}$  inch plywood respectively. The floor was made of  $\frac{1}{2}$  inch hardware cloth. Each box was heated and lighted by one 40 watt bulb burning continuously. A variac was used in conjunction with the light bulbs to maintain a constant temperature of  $98\pm 3^{\circ}F$ .

Food and water could be supplied from outside the box without disturbing the animal. Since newly hatched quail will drown in the water containers, the containers were also filled with small pebbles about  $\frac{1}{4}$  inch in diameter.

Subjects and recording equipment were housed separately from the treatment and testing room. The treatment and testing room was an environmental chamber kept between 95 and 98°F for the duration of the experiment: The room is 8x7 feet. The light intensity was kept at 1.5 foot candles and the ambient noise level was 37db (A).

The imprinting alley was a  $6x2\frac{1}{2}x2$  foot wooden box (see photograph in appendix A). The sides were painted flat white and the floor covered with green "Kraft" paper obtained from the poultry science department of Michigan State University. The top of the box was open and the stimulus was suspended from a string which was attached to pulleys at each end of the box. The stimulus traveled up and down the center of the alley  $\frac{1}{2}$  to 3 inches above the floor at a rate of approximately 4 inches per second.

The testing box (see photograph in appendix A) was essentially two l2xl8xl2 inch wooden boxes separated by an alley 8 inches wide, l2 inches high, and l6 inches long. The inside of the box was painted dark grey (Krylon-

Dove Grey Spray enamel, No. 1605) and the top and bottom were constructed out of  $\frac{1}{4}$  inch hardware cloth. The stimulus was positioned in one of the boxes in such a way that it could only be seen from that compartment and could not be seen either from the alley or from the other box. Thus, this testing box was, except for the stimulus, a completely new environment for the poult.

The stimuli were 5 inch high, red-orange translucent plastic cylinders 2½ inches in diameter with a closed bottom and an open top. This color was chosen since Smith and Bird (1964) found red to be the most effective eliciter of following in the domestic chick. Within each cylinder, ½ inch above the base was a 6v. bulb which was wired through a Lafayette Model 400B Combination Repeat Cycle and Interval Timer in such a way that when the stimulus was moving the light flashed for a duration of .124 seconds with an inter-flash interval of .40 seconds. The light intensity 6 inches from the stimulus was 6.2 foot candles. The auditory stimulus (26.5db (A) above ambient) was supplied by the click of the Lafayette timer mounted between the imprinting alley and the testing box.

#### Procedure

<u>Treatment</u> On days when a hatch was expected, the incubator was checked once every 3 hours. When a chick was found, the hatching time was estimated as the middle of that 3 hour period so the maximum error of estimation

was 12 hours. When a poult was found, it was taken from the incubator and placed into an isolation cage. If it appeared normal and healthy, it was randomly assigned to one of the five treatment groups listed below. There were 6 birds in each group.

- Group E1 Each bird was removed from its isolation 1. cage 5-9 hours after hatching, carried by hand into the testing room and placed into the imprinting alley. The stimulus was then turned on and set in such a way that for  $\frac{1}{2}$  of each minute the stimulus moved back and forth down the middle of the alley, the light flashed on and off, and relay clicked. (This condition will hereafter be referred to as S-ON). During the other half of each minute the stimulus was turned off so that it hung, relatively motionless, somewhere in the alley without the light flashing, or the clicking noise present. (This condition will hereafter be referred to as S-OFF). The S-ON and S-OFF conditions alternated in order to allow equal habituation times in the alley under each condition. Each bird remained in the alley with S-ON and S-OFF conditions alternating each  $\frac{1}{2}$  minute for 1 hour, and then the bird was returned to its isolation cage. This group will be referred to as the early-imprinted group.
- 2. Group  $E_2$  Each bird was given the same treatment as those in Group  $E_1$  except that it was given the

imprinting treatment 11 - 15 hours after hatching. This group will be referred to as the late-imprinted group.

- 3. Groups  $C_1$  and  $C_2$  were given the same treatment as  $E_1$ and  $E_2$  respectively. But the stimulus remained in the S-OFF condition during the entire 1 hour treatment.
- 4. Group C<sub>3</sub> These birds remained in their isolation cages and did not receive any exposure to the alley or to the stimulus.

<u>Testing</u> After the appropriate treatment each bird was individually given two test sessions. Each test session was 18 minutes long and consisted of three 3-minute trials with the stimulus in the S-ON condition and three 3-minute trials with the stimulus in the S-OFF condition. The S-ON and S-OFF trials were alternated so that each subject received either ON-OFF-ON-OFF-ON-OFF or OFF-ON-OFF-ON in a test session. The order (for each test for each bird) was decided randomly by the flip of a coin.

The first test session was 36-42 hours after hatching. In this test each bird was placed in the imprinting alley and the experimenter recorded the number of distress calls during each 3-minute trial. The stimulus conditions for each trial are described above. For twenty-five of the thirty subjects the experimenter also recorded the amount of time in each trial that the subject was either making distress calls, running about the perimeter of the alley or pecking at the walls.

Total time making any of these responses was taken as an indicator of total fear or total fear behavior.

The second test session was conducted 48 - 54 hours after hatching. In this test the bird was run in the test box (see appendix A), but the same procedure for presenting the stimulus conditions was used as in test 1. Distress calls were measured as above. The total amount of time in each trial that the subject was in the compartment with the imprinting stimulus was also recorded. This measure was included to get some idea of the relative importance of audio and visual properties of the stimulus. One would assume that if the visual properties were of primary importance, the subjects who had been successfully imprinted would spend more time in the compartment with the stimulus than subjects not imprinted.

Distress calls were counted by means of a panel of six push buttons, one for each trial (see appendix A). Each time the subject emitted a distress call the appropriate button was pressed by the experimenter. The buttons activated counters situated in a soundproof box outside the testing room. The duration of fear behavior and time spent near the stimulus were recorded by holding down a lever which activated a Gerbrant event recorder next to the soundproof box.

After the second test each bird was weighed and most were sexed by cloacal examination (Hemma, Siopes, Wilson and McFarland, 1965).

#### Results

All statistical procedures were taken from either Winer (1963) or Siegel (1959) and the probabilities reported for the individual comparisons are for bi-directional statistical significance.

#### Distress calls - Test 1

The distress call data from test 1 are shown in Figures 1 and 2. In Figure 1 the bars represent the mean number of distress calls in each stimulus condition for each group. The numbers (1-6 in each group) reveal the total number of distress calls that each subject made in each of the stimulus conditions. The trend for each subject within any treatment group can be determined by comparing the position of numbers in the S-ON and S-OFF conditions. Figure 2 shows the mean number of distress calls for each treatment group as a function of the two stimulus conditions and the three trials within each condition. Table 1 represents the analysis of variance summary table for these data.

Figure 1 reveals that in each group, except the lateimprinted group (E<sub>2</sub>), more distress calls are emitted during the S-OFF condition than during the S-ON condition. The overall F for stimulus condition was highly significant (F=71.377, p<.001) and individual comparisons using the studentized range statistic indicate that the effect is reliable within the early-imprinted group (E<sub>1</sub>) and each of the control groups (p<.01 for each group).



Figure 1. Distress calls emitted during test 1. The bars represent the mean number of distress calls in each stimulus condition for each group. The numbers (1 - 6) in each group) reveal the total number of distress calls that each subject made in each stimulus condition.



<u>Figure 2.</u> Mean number of distress calls in test 1 for each treatment group as a function of the three trials in each stimulus condition.

When the five treatment groups are compared with each other, Figure 1 indicates that within the S-OFF condition only small differences occur. However, within the S-ON condition, the early-imprinted group  $(E_1)$  produced fewer distress calls than each of the other groups, and the late-imprinted groups  $(E_2)$ produced more distress calls than each of the other groups. In Figure 2 (S-ON condition) this effect is more evident. Statistical evidence is furnished by the significant treatment by stimulus condition interaction (F=5.254, p>.01), indicating that the treatment groups did not respond alike to the different stimulus conditions. Individual comparisons (Duncan's test) within the S-ON condition yield exactly the conclusions drawn from Figure 2: The early-imprinted group  $(E_1)$  makes reliably less distress calls than the control groups (p < .05) and than the late-imprinted group (p < .01); The late-imprinted group  $(E_2)$ makes significantly more distress calls than the control groups (p < .025). Differences between the control groups within the S-ON condition do not approach statistical significance, and the variability within the S-OFF condition can also be attributed to random sampling.

The overall tests on trials and trials by treatment are also signifcant (p < .05 and p < .01 respectively). Figure 2 indicates that there may be a slight downward trend in distress calls over time, and that this trend depends on the particular group observed. Individual comparisons using the Newman-Keuls method reveal that the numbers of distress calls emitted in

## TABLE 1

Analysis of Variance summary table of distress calls in test 1.

SOURCE	Eta <sup>2</sup>	SS	df	MS	F
Between subjects		,96884.583	29		
Treatments ss w/ treatments	.091 .331	20722.167 76162.416	4 25	5180.542 3046.497	1.700
Within subjects		132863.167	150		
Stimulus condition Stim. Cond. X Treatment error	.144 .044 .052	33265.606 9794.255 11651.306	1 4 25	33265.60 2448.564 466.052	71.377** 5.254**
Trials Treatment X Trials error	.071 .057 .117	4026.433 12596.233 26720.001	2 8 50	2013 <b>.21</b> 6 1574 <b>.5</b> 29 534 <b>.</b> 400	3.767* 2.946**
Trials X Stim. Cond. Trials X Stim. Cond. X treatment	.013 .013	3154.078 3073.811	2 8	1577.039 384.226	2.759* N.S.
error	.122	28581.444	50	571.629	

#= p < .05
\*\*= p < .01</pre>

trial 1 and 2 are greater than those emitted in trial 3 (p<.05,  $p_{\neg}$ .01 respectively), while the difference between trials 1 and 2 is not significant. As can be seen from Figure 2 this trend is mostly due to the sharp decline shown by group E<sub>1</sub> in the S-OFF condition. The trials by stimulus condition interaction is also significant (F=2.759, p<.05) indicating that the trend over trials is influenced by the stimulus condition, as can be seen in Figure 2.

#### Distress calls - Test 2

Figures 3 and 4 are analogous to Figures 1 and 2 respectively, except that they represent the results of the second test. Table 2 is the analysis of variance summary table for the distress call data obtained from test 2.

Figure 3 reveals that within each of the treatment groups, except C<sub>3</sub>, more distress calls were emitted during the S-OFF condition than during the S-ON condition. This effect, although statistically significant (F=5.062, p<.05), is not nearly as large as in test 1.

Figures 3 and 4 show that in the S-ON condition, the earlyimprinted group produced fewer distress calls than each of the other groups. Due to the marked heterogeneity of variance between groups, as can be observed from Figure 3, the statistical comparisons between treatment groups, within the stimulus conditions, entailed the use of non-parametric procedures. A Kruskal-Wallis one way analysis of variance comparing the total distress calls of all groups within the S-ON condition yielded



Figure 3. Distress calls emitted during test 2. The bars represent the mean number of distress calls in each stimulus condition for each group. The numbers (1 - 6 in each group) reveal the total number of distress calls that each subject made in each of the stimulus conditions.



Figure 4. Mean number of distress calls in test 2 for each treatment group as a function of the three trials in each stimulus condition.

# TABLE 2

Analysis of Variance summary table of distress calls in test 2.

SOURCE	Eta <sup>2</sup>	SS	df	MS	F
Between subjects		83726.161	29		
Treatments ss w/ treatments	.136 .327	23864.634 59861.527	4 25	5966 <b>.1</b> 58 2394 <b>.</b> 461	2.492 NS
Within subjects		99618.167	150		
Stim. Cond. Stim. Cond. x treatment error	.019 .022 .095	_ 3528.939 4056.922 17426.973	1 4 25	3528.939 1014.230 697.079	5.062* 1.455 NS
Trials Trials x Treatment error	.072 .019 .205	13117.878 3435.233 37559.556	2 8 50	6558.939 429.404 751.191	8.731** < 1 NS
Trials x Stim. Cond. Trials x Stim. Cond. x Treatment	.003 .007	560.411 1242.478	2 8	280.205 155.310	<1 NS <1 NS
error	.102	18689.777	50	373•796	

\*=p<.05 \*\*=p<.01

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24

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a significant H (H=12.582, .01<p<.02). Mann Whitney U tests yielded significant differences between the early-imprinted group and each of the other treatment groups (all p's <.01). No other differences between groups even approached statistical significance indicating that in the S-ON condition, the earlyimprinted group emits less distress calls than each of the other groups, which do not differ. In the S-OFF condition the Kruskal-Wallis one way analysis of variance yielded non-significant results indicating that the differences observed in the S-OFF condition in Figures 3 and 4 are probably due to random sampling error.

The significant trials effect (F=8.731, p<.01) again indicates the downward trend over trials evident in both stimulus conditions in Figure 4.

#### Fear Behavior

The measure of the total fear behavior shown by each animal is the proportion of time in each trial of test 1 that was spent either making distress calls or running about the perimeter of the alley and/or pecking at the wall. Again, nonparametric statistical tests were used since these data were collected on only twenty-five of the thirty subjects and the number of subjects differed between the treatment groups. In Figure 5 these results are plotted in terms of mean proportion of trial time (3 minutes) showing fear behavior, as a function of the three trials in each stimulus condition.

Figure 6 indicates whether the greater amount of time



<u>Figure 5.</u> Mean proportion of trial time (3 minutes) showing fear behavior in test 1 as a function of treatment group and stimulus condition.

showing fear behavior was in the S-ON or S-OFF condition, for each trial in each treatment group. It is constructed by plotting the mean difference (S-ON minus S-OFF) between the proportions of time spent showing fear behavior during the S-ON and S-OFF conditions in each trial, for each treatment group. The width of each bar indicates the trial represented; narrowest bar - trial 1, middle bar-trial 2, widest bar - trial 3.

Figure 5 indicates that during each trial within the S-ON condition, the early-imprinted group  $(E_1)$  shows less fear behavior than each of the other groups. The overall Kruskal-Wallis test was significant (H=11.439, .02<p<.05) and individual comparisons within each trial revealed that the difference between the early-imprinted group and the other groups is reliable at each point within the S-ON condition of Figure 5 (p<.032 for each comparison). When the early-imprinted group  $(E_1)$  is excluded from the analysis, no significant differences exist (H=0.612), suggesting that the other four groups do not differ in total fear behavior in the S-ON condition.

In the S-OFF condition none of the differences observed in Figure 5 prove reliable, (overall H=7.8974, p>.05; trial 3, H=6.43, p>.05) indicating that the treatment groups do not differ in fear behavior during the S-OFF conditions.

When the S-ON and S-OFF conditions are compared to each other, Figure 6 shows that within the early-imprinted group there is more total fear behavior in the S-OFF condition than



<u>Figure 6</u>. Mean difference (S-ON-S-OFF) in the proportion of time exhibiting fear behavior, as a function of trials and treatment group. Positive going bars indicate a greater amount of fear behavior was shown in the S-ON condition than during S-OFF. Negative bars indicate the opposite. Width of the bar. indicates the trial: Narrow bartrial 1; Middle bar-trial 2; widest bar--trial 3. the S-ON condition. However, when the remaining groups are combined, Figure 6 indicates that there is slightly less fear behavior exibited in the S-OFF condition than the S-ON condition. A Wilcoxon test reveals that this difference is reliable  $(p_{<.}01)$ .

#### Time Spent with Stimulus

Figure 7 shows the mean proportions of trial time that the subjects in each group spent in the box with the stimulus. As can be seen from the figure, none of the treatment groups differed significantly from each other and the time spent with the stimulus in the two conditions does not differ.

#### Weight and Sex

Of the birds sexed there were 12 males and 14 females (each group split 3 - 3 or 4 - 2). There were not enough subjects to estimate differences between sexes as to imprintability. The only difference between sexes that was observed is that, in birds raised under these conditions, females weigh more than males. The mean weights for females and males were 7.89 and 6.96 grams respectively (t=2.97, p<.05).



Figure 7. Mean proportion of trial time (3 minutes) in test 2 that the subjects in each treatment group spent in sight of the stimulus as a function of stimulus condition.

#### Discussion

The results of this experiment indicate that imprinting does occur in the Japanese quail (<u>Coturnix</u> <u>coturnix</u>). In both tests the early-imprinted group  $(E_1)$  showed considerably fewer distress calls in the presence of the imprinting stimulus than each of the other groups. In addition, the amount of fear behavior evoked by the stimulus is reliably less in the earlyimprinted group than in each of the other groups. The earlyimprinted group  $(E_1)$  made fewer distress calls and showed less fear behavior during the S-ON condition than the S-OFF condition, whereas the other groups show greater fear behavior while the stimulus is present (S-ON) than in its absence (S-OFF). That the control groups also exhibit more distress calls in the S-OFF condition will be discussed later. No reliable differences in distress calls or fear behavior during the S-OFF condition suggests that, in the absence of the stimulus, all of the groups are approximately equal in their reaction to the environment. The sharp decline of the early-imprinted group between trials 2 and 3 in the S-OFF condition (Figures 2 and 5) can be explained by the observation that many of the poults from this group appeared to fall asleep during the preceding S-ON trial and continue sleeping throughout most of the final S-OFF trial. Comparison of the results obtained from the early and late-imprinted birds  $(E_1 \text{ vs. } E_2)$  eliminates habituation to the imprinting stimulus as an explanation for these data, since both of these groups had the same amount of exposure to the stimulus. Also, the comparison

between the early-imprinted group  $(E_1)$  and the early nonimprinted group (C1) indicates that fewer distress calls and less fear behavior are due to early exposure to the stimulus and not a general effect of early exposure to the alley. One other observation indicated that the early-imprinted group did become imprinted on the stimulus; the subjects in the earlyimprinted group (E<sub>1</sub>) frequently emitted soft peeping notes while the stimulus was in the S-ON condition. None of the birds from the other groups showed this type of vocalization during the tests. These vocalizations (see Farris, 1964) sound much like the vocalizations Collias (1952) calls "contentment notes" emitted by chicks when approaching familiar objects, eating or moving about undisturbed. Collias reports that "chicks tend to approach objects which stimulate contentment notes" and Bermant (1963) suggest that contentment calls indicate a chick is in a "suitable environment". Other investigators (Hess, 1959; Moltz, 1960) have noted that chicks tend to make contentment calls in the presence of an object to which they have imprinted.

All of these results lead to the conclusion that the earlyimprinted group (E1) did form an attachment to the stimulus analogous to the attachment of imprinted chicks or ducklings, regardless of the fact that the following response was not observed. That is, the young birds did imprint and only the topography of the response was different. Several investigators have found that the stimulus perameters needed to establish imprinting may differ depending on the natural behavior and

habitat of the species in question. Klopfer (1959) for example. compared the audio and visual components of imprinting stimuli in surface nesting species of waterfowl, the Woodduck (Aix spansa) which is a hole nester, and domestic Muscovy duck, a quackless species. He found that the surface nesting species required a visual stimulus in order for imprinting to occur. whereas the hole nesting Woodduck demonstrated auditory imprinting and would not respond to a visual stimulus which did not have an auditory component. These results were explained by the fact that the young Woodducks' first response to their mother in the nest is based on auditory stimuli while in surface nesting species visual cues play a much larger role in initiating following in the young duckling. The coturnix quail, unlike either chickens or ducks, typically nest in high grass or wheat fields (Wetherbee, 1961). The nest are well concealed and the natal plumage provides excellent camouflage. These facts, coupled with the knowledge that the young poults have little temperature regulation and can eat the small seeds at the nest site, suggest that the quail poults do not follow the mother long distances in search of food as do chicks and ducklings. Although Wetherbee (1961) reports that 4 day old coturnix disperse as far a 100 meters from the nest, we could find no indication in the literature that young coturnix extensively follow either parents or sibling. Since these birds probably follow their mother very little in their natural habitat, the response topography in imprinting should differ

from the typically studied following response. The results of the present experiment show that this is the case, thereby further demonstrating the generality of imprinting in precocial birds. The phenomenon can be shown, in the absence of the following response, by measuring other behavioral components of the event.

Results of this experiment also indicate that there is a sensitive period for imprinting in this species that does not coincide with the sensitive period in species heretofore studied. Whereas the early imprinted group  $(E_1)$  shows all of the criteria for concluding it did become imprinted to this stimulus, the late imprinted group  $(E_2)$  exhibited as much total fear behavior as the controls and as many or more distress calls than did the control groups. Wetherbee (1961) points out that coturnix quail have an exceedingly rapid maturational rate compared with most gallinacious birds. The incubation period is 16 days for the coturnix as compared with 21 days for the domestic chick and the coturnix is sexually mature only 30 days after hatching. The apparent relationship between the time at which imprinting can occur and developmental rate suggests that the sensitive period may have morphological and physiological correlates which could predict and explain its onset and termination. However, to discover these correlates, a great deal more comparative data on species exibiting this sensitive period and exact determination of its growth and decline are required. In any event, this experiment indicates

that the sensitive period for imprinting in the coturnix quail has terminated by the time the bird is eleven hours old, measured from the time of hatching.

Since pilot work indicated that a visual stimulus alone was not sufficient to establish imprinting in this species, an auditory component was added. Stettner (1966, personal communication) reveals that with bobwhite quail (Colinus virginianus) it is possible to transfer the imprinted response from one object to another by pairing the auditory component with the second object. The results of the present experiment indicated that there was a diminution of distress calls and total fear behavior over trials. As can be seen from Figures 2, 4 and 5, this effect was most pronounced in the early - imprinted group (E1). The drastic reduction of distress calls and fear behavior in the El group, in the S-OFF condition, suggests that the imprinting attachment in this group may show some generalization or transfer to the alley in which the birds were both imprinted and tested. However since the trials effect is evident in other treatment groups, these data can also be interpreted either as a general fatigue effect or as habituation to the total stimulus situation. Furthermore it should be noted that the trials effect interacted with both stimulus condition and treatment suggesting caution in its interpretation.

Stettner's results also suggest that, in the bobwhite quail, the auditory stimulus is of primary importance in imprinting. No direct tests were made in the present experiment as to the primacy of the audio and visual components of the stimulus.

However, the following facts suggest that the auditory stimulus is of primary importance in maintaining the imprinted attachment. First, the early-imprinted group  $(E_1)$  did not spend any more time with the stimulus in the S-ON than the S-OFF condition. Secondly, this group  $(E_1)$  did not differ from the other groups in time spent in view of the stimulus in either stimulus condition. These results agree with several recent investigations which have shown auditory stimulation to be of primary importance for the establishment and maintainance of the following response in many species, while in other species a visual component is necessary and/or sufficient (Klopfer, 1959; Gottlieb and Klopfer, 1962; Gottlieb, 1965; Gottlieb, 1963; Smith and Bird, 1964; Boyd and Fabricus, 1965; and Fischer, 1966). The most parsimoneous interpretation of these reports and the present results is that the animal is adapted to a rather specific ecological niche and the stimulus modality which will elicit the strongest response in an artificual imprinting experiment is the same as expressed most often in natural parent-young behavior of the species. Since the parent-young behavior of the coturnix quail has not been systematically studied, it is possible only to guess that the young birds are most responsive to the auditory stimuli since much of the time the parents are not in sight because of tall grass or wheat separating the parent from the nest-site.

Two sets of rather unexpected, but interesting results occurred in the present experiment. First, the control groups produced more distress calls in the S-OFF than the S-ON condition

in both tests, and secondly, the  $E_2$  group emitted more distress calls than the other groups during the initial test. These results can be explained by hypothesizing a mutually exclusive scale of fear responses that the young birds of this species can exhibit. That is, the birds can show fear behavior in one of two ways. First, the strongest fear response is escape activity. The activity includes running around the perimeter of the enclosure, pecking at the walls, and jumping at the corners. The second, an less intense type of fear activity is making distress calls. It was observed in the present experiment that the birds never displayed these behaviors simultaneously. The distress call of the young coturnix quail was observed only to occur when the bird was in a particular posture (see appendix B), and never while the bird was running. It is further hypothesized that the respective probabilities of the two responses appearing are dependent upon the amount of novelty in the total stimulus complex of the bird (see Andrew, 1964).

Several points of evidence can be established for interpreting the behavior of the control groups and late-imprinted group with this theoretical model. First, this model would predict that presentation of the imprinting stimulus would elicit increased fear in subjects to whom the stimulus was entirely novel. This, coupled with the experimenter's observation that the control group displayed more escape behavior in the S-ON condition than the S-OFF condition, suggests that the reason the control groups produced fewer distress calls in the S-ON condition is because the intensity of the fear in the S-ON

condition raised the probability of excape behavior, thereby inhibiting distress calling. This interpretation is further supported by the fact that, although distress calls occurred with reliably greater frequency in the S-OFF condition, total fear behavior (escape activity plus distress calls) diminished going from the S-ON to the S-OFF condition (Figure 6); again suggesting that escape behavior was markedly increased in the presence of the stimulus. The behavior of the late-imprinted group  $(E_2)$  is explained by the fact that these subjects had been previously exposed to the imprinting stimulus allowing them to habituate to it to some extent, and therby lessening the probability of escape behavior and raising the probability of distress calling. One point of evidence supports this interpretation. Although this group  $(E_2)$  showed reliably more distress calls than the other groups in the S-ON condition of test 1. these subjects did not exceed other groups in total fear behavior during this test; indicating that the amount of escape behavior must have been under that of the other groups.

The theoretical model presented here has, of course, not been tested, but some support can be obtained from the literature. Ratner (1966) proposes that any threatening stimulus elicits a systematic sequence of responses. The response at any time depends on the proximity of the stimulus, and the degree of prior adaptation to the total stimulus complex. Schaller and Emlen (1962) noted that the development of avoidance behavior in the coturnix quail was very rapid and characterized

by "dashes back and forth along the walls" and jumping against the walls. Kaufman and Hinde (1961) show that slight disturbances such as a decrease in temperature or isolation from "social companion" increases the rate of distress calling and that the rate of distress calling in chicks increases over the first 6 days after hatching. Bateson (1964), on the other hand, demonstrated that the activity of young isolated chicks decreases over the first 5 days after hatching. Thus in chicks there seems to be a reciprocal relationship between activity and distress calling, possibly indicating that the young animals are habituating to their environment.

#### Conclusion

The results indicate that imprinting does occur in the Japanese quail (<u>Coturnix coturnix</u>), and that it occurs during a sensitive period in the young bird's development. The topographical characteristics of the phenomenon differ from the birds previously studied in that following did not occur with coturnix. We suggested that the following response is only one of an array of responses involved in imprinting. Which of these responses manifest themselves in any experiment will depend upon the ecology and natural parent-young behavior of the species in question.

The most stimulating outcome of this experiment is the suggestion of a systematic hierarchy of behavioral responses to novel stimuli. A testable theoretical model was presented which hypothesizes a mutually exclusive set of responses with

probabilities dependent on the amount of novelty in the stimulus complex of the organism. This model is amenable to direct experimental testing since both stimulus parameters, novelty, and response parameters, activity and distress calls can be readily quantified.

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AFFENDICES

APPENDIX A

AFFARATUS



Egg turner. Shown within the incubator, this egg turner rolled the eggs twice every 6 hours.



Diagram of the isolation cages used in this experiment. This cage is shown without the guillotine door which fits into the front.



Imprinting alley. In this apparatus the subjects were given their initial treatment and tested in test 1. The stimulus is shown suspended from above the alley. The motor drives the stimulus.



Testing box. This apparatus which shows the stimulus in one compartment was used for the second test on each subject.



Button panel with which data was recorded and switch selecting stimulus condition.

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APPENDIX B

FOSTURES



Young Coturnix in erect standing position. This posture was assumed when birds gave distress calls.



Young Coturnix in relaxed position. This posture was assumed when the bird appeared undisturbed.

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