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SEXUAL IMPRINTING: THE RELATION OF PREFERENCES
FOR SEX OBJECTS AND SOCIAL REARING CONDITIONS

by

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DISSERTATION

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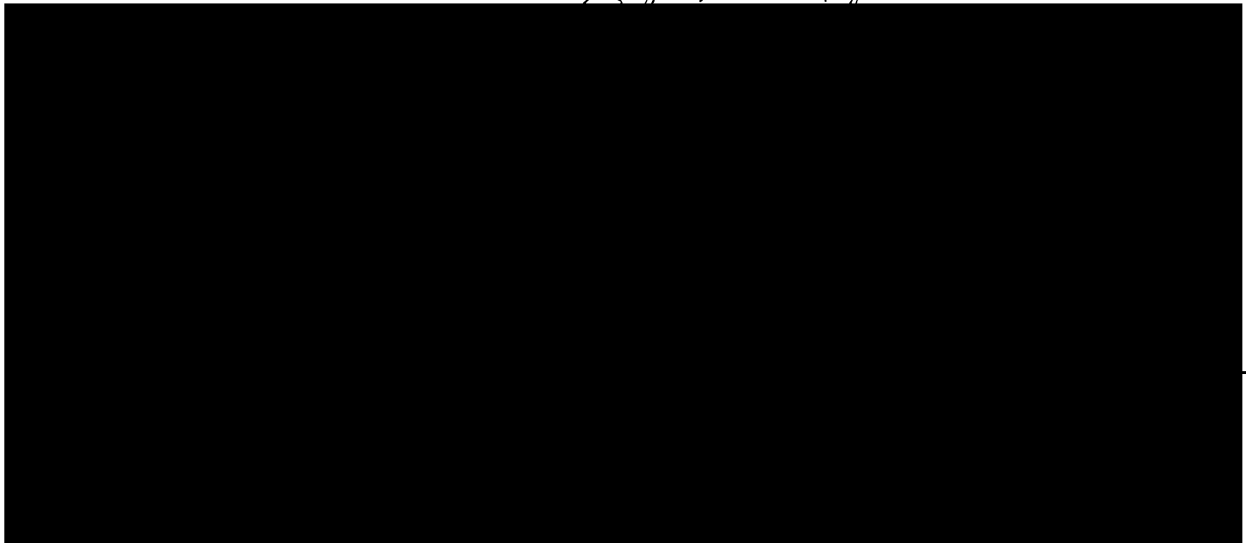
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ABSTRACT

This study examined the influence of early social experience with albino age mates on subsequent sexual behavior in adults. 40 male Japanese quail _Coturnix_ _coturnix_ _japonica_ were reared under various conditions of exposure to albino conspecific age mates. The first group was reared with only normal conspecifics for either the first 5 or 20 days posthatch (NEX). The second group was reared with only albino age mates for the first 5 days posthatch (SEX). The third group was reared with only albino age mates for the first 20 or 25 days (PEX). The fourth group was reared with only normal age mates for the first 15 days and then with only albino age mates from day 16 to 25 (LEX). All subjects were housed individually subsequent to treatment. Observations were made of sexual responses directed toward either an albino or normal female in a choice test. All experimental males mounted. NEX and SEX males all mounted normal females. Nine of the ten PEX males mounted an albino female. Four of the ten LEX males mounted an albino female. In a second observation all males were provided an albino female alone for five minutes. All but the NEX males mounted the albino female. These data are discussed with respect to behavioral processes influencing such response tendencies. It is concluded that an imprinting process best describes the preference for mounting albino females exhibited by the PEX group. And that a habituation process best describes the mounting of the albino female by SEX and LEX males when the albino alone was presented.

Group in Psychology

OUTLINE

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SUMMARY

INTRODUCTION

The primary goal of this investigation is to contribute some observations of the effects of early social experience on subsequent mating habits in precocial fowl. The theoretical issues of concern emerged from the criticisms offered by Konrad Lorenz (1935) regarding the limitations of association learning theory. Lorenz discussed an ontogenetic adaptive process, termed imprinting, that was unlike the conditioning process previously described by Pavlov (1927).

I. Imprinting: A Theoretical Description.

Lorenz's construct of imprinting describes the interaction of innate and learned variables which function to establish the animal's future preferences. The recognition of conspecifics is not innate in many species of fowl (Lorenz, 1935, Klopfer, 1959). Lorenz suggested that the acquisition of species identity resulted from a particular process that involved the attachment of instinctive behavior to the parent during a brief period subsequent to hatching. Lorenz cited the common observation of following behavior in neonate precocial fowl[1] as an example of an instinctive behavior pattern which is directed toward the parent. Hatchling's typically respond to the initial appearance of a parental object by approaching and following. The result of this social interaction is the formation of a bond for the stimulus

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1. Avians can be distinguished on the basis of the degree of independence from parental care which they possess at the time of hatching. The term 'precocial' refers to those avians such as ducks, chickens, etc., that possess early independence. The term 'alticial' refers to species, such as pigeons, that require a greater amount of parental care subsequent to hatching.

characteristics of the parental object, so that the hatchling directs future following behavior to the parent. In addition, this social interaction serves to direct subsequent social behavior toward stimulus objects that possess properties common to the parent object.

Lorenz supported his view by citing examples wherein species of nidifugous fowl had been artificially incubated and deprived of the opportunity to direct their following behavior to conspecifics. Instead these young attached their following behavior to humans or other available social objects. In such cases once the hatchling attached its following response to a specific object it continued to follow the foster-parent, often ignoring the presence of conspecifics. These animals subsequently directed much of their adult social behavior toward members of the foster-species to which they were initially exposed. In addition to these observations, Lorenz noted a number of reports of cases wherein nidicolous fowl that had been hand-reared without exposure to a conspecific also directed their courtship behavior toward humans or other incorrect species with which they had been reared.

II. Differences Between Imprinting and Conditioning.

In his description of imprinting, Lorenz noted that this learning process differed from classical conditioning in a number of ways. For example, he stated that imprinting could only take place during a brief ontogenetic period, and that this period was the result of biological preparation and readiness. Lorenz observed that the critical period was "dependent on a quite definite physiological developmental condition in the young bird" (1935, p. 127). In addition to this difference between imprinting and classical conditioning, Lorenz suggested that once the object of the instinctive behavior is acquired, it cannot be

lost, hence imprinting is an irreversible process. These character-
istics of the imprinting process were cited by Lorenz as being essenti-
ally different from the typical characteristics ascribed to classical
conditioning, e.g., the contingency of the conditioned stimulus to the
unconditioned stimulus and the reinforcing properties associated with
the unconditioned stimulus.

Several subsequent students of imprinting have noted other char-
acteristics attributed to the imprinting process by Lorenz that are
also dissimilar to association learning (Bateson, 1966; Hinde, 1962,
1963; Moltz, 1963 and Thorpe, 1963). Those conditions are that the
imprinted social object acquires the capacity to elicit future instinc-
tive behavior which is not part of the neonate's behavioral repertoire
during the time that the imprinting takes place. This principle indi-
cates that behavior systems that are not yet manifested have become
conditioned to an object with which they have never been associated.
Hence, the principle of contiguity is not a functional part of this
learning process.

The final difference between imprinting and classical condition-
ing alluded to by Lorenz derives from the point that imprinting estab-
lishes a bond for a class of objects rather than a specific member of
a class of objects. Both of these latter characteristics were attrib-
uted to the effect of imprinting by Lorenz. He indicated that imprint-
ing establishes a permanent and exclusive species identity for subse-
quent instinctive social behavior. However, Lorenz also pointed out
that for different species the establishment of the social object for
functionally differing instinctive behavior patterns may occur inde-
pendently of the previous imprinting. So that while certain instinc-

tive patterns may be directed toward one social object, there may be other patterns that are not. Lorenz observed that at least for some species "imprinting of different conspecific-oriented functional systems to the relevant object occurs at different points of time in individual ontogeny" (1935, p. 131). In other words, the conditioning of social objects for independent instinctive systems (separate behavioral activities), such as flying, flocking, etc., may occur at different ontogenetic points.

Lorenz cited the case of the jackdaw imprinted to humans as an example of a bird having differing social objects for functionally different instinctive behavior patterns. In this case the jackdaw was imprinted to humans for all its instinctual behavior except for flying in the company of a flock which was directed toward Hooded Crows, and feeding and care of its young which was directed toward conspecifics. So that although Lorenz did suggest that imprinting possessed other characteristics that were essentially different from the process described by learning theories, it is clear that Lorenz did not rule out the possibility that there may be some variation in terms of the social object to which a particular instinctive pattern is directed.

III. Review of the Literature of Imprinting.

The past twenty years has witnessed an enormous growth in the study of the imprinting process. Numerous reviews of imprinting have appeared. Most studies of imprinting concerned the type of stimuli that would elicit following behavior; the age range in which a hatchling would readily follow a novel stimulus object or the age range in which following would result in subsequent preference for the

previously followed object. Few studies have been directed toward the permanency of an established preference or the direction of subsequently developed social behavior (e.g., sexual behavior) toward conspecifics of the imprint species.

The importance of specific stages of ontogeny in the development of social attachments has often been cited as one of the more intriguing characteristics of imprinting (Immelmann, 1972; Hinde, 1962). The study of critical periods for imprinting has been typically examined in the more limited context of the hatchlings' responsiveness to a wide variety of stimulus objects during the first few days posthatch. Very little research has been addressed to the study of early social experience on subsequent social attachments in adulthood (e.g., long term effects). The following section describes the existing literature that deals with the relationship between early social experience and subsequent sexual behavior. Since there is no established criterion to predetermine whether imprinting has occurred, it is necessary to examine those studies that have the common property of exposing neonate hatchlings to either a surrogate parental object or a foster species, and later examined preference for that object or species.

A. Evidence of Early Social Experience and the Selection of a Mate. Craig (1914), Goodwin (1948, 1958), and Warriner, Lemmon and Ray (1963) have all provided data which point out that selection of a mate is related to species characteristics experienced during their neonatal and juvenile periods. While attempting to cross-breed pigeons, Craig observed that males reared in isolation did not successfully choose a mate. He concluded that it was not possible to cross-breed

pigeons unless they were reared in the presence of the species of the intended mate. Goodwin (1948) suggested that the range of mates that a young pigeon might select was related to his previous experience - that is, the greater the variety of species in his environment, the greater the range of potential mates he may select. In a subsequent paper he reported that there was a high correlation between the coloring of foster parents and the selection of a mate by male pigeons. Nice (1962) reported that a variety of pigeons which she hand-reared all sought domestic pigeons for mating which they had seen and heard during their development. She concluded that unless the hatchling was completely isolated from conspecifics, it was unlikely that such experience would establish an inappropriate sex partner. Perhaps the clearest evidence demonstrating how early experience is related to mate selection in pigeons was provided by Warriner, et al., (1963). These investigators examined the affects of rearing by foster-parents on subsequent mate selection of two similar species of pigeons that were clearly distinct. The eggs of White King and Black King pigeon pairs were exchanged and the foster-parents were allowed to rear the young. When the experimental pigeons were sexually mature they were transferred to a large community cage and allowed to mate. 26 of 32 males chose mates of the same color as their foster parents. Only 14 of 42 females were mated with males that were the same color as their foster parents. As was indicated by both Goodwin and Craig, it appears that females play a less significant role in mate selection in that there was no relation between color of the male and the female's foster parents.

Several investigators have indicated that conspecific experience during a neonatal critical period is not necessary for adult sexual

behavior with conspecifics. Fisher and Hale (1957) reported that conspecific social experience was not necessary for intraspecific copulatory behavior to occur in either New Hampshire or Barred Rock roosters. Wood-Gush (1958) reported similar observations in Brown Leghorn chicks that had been isolated for 6 1/2 months prior to experience with conspecifics.

Androgen hormone treatments have been employed by several investigators in an effort to ascertain parameters associated with the establishment of a preference for a sexual object. Schein and Hale (1959) induced sexual behavior in juvenile turkey cocks with daily injections of 1 mg of testosterone propionate from the 6th to the 35th day. They reported that the development of the pattern of sexual behavior is not dependent upon early social or sexual experience. The hand reared subjects exhibited the same sexual pattern in response to the presentation of a hand, as the control chicks exhibited in response to poult heads, etc.[2] They also reported that the early social experience markedly modified the releasing value of certain stimuli. If the cock had experienced an otherwise neutral object during the neonatal period, it was more apt to engage it sexually. For example, hand-reared turkeycocks (isolates) were responsive to the presentation of a human hand, whereas the groups that were reared with siblings were generally not responsive to the human hand.

B. Relation of Ontogenetic Stages and Subsequent Preferences.

Bambridge (1962) compared the effects of following a particular stimulus

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2. Fisher and Hale (1957) reported that male poults of several species would readily direct courtship behaviors, such as waltzing and pecking, at a variety of stimuli. A taxidermic poult head was one of the more effective stimuli for releasing such behavior.

object on subsequent choice of the familiar object over a novel object
for induced sexual behavior. He exposed three groups differing in ages
to one of two moving objects. All the chicks received a daily injec-
tion of testosterone propionate. In a choice test on days 19-20, the
chicks which responded directed sexual responses to the object they
followed. 18 of the 19 cockerels that responded had been exposed to
the model from the second through the 9th day, whereas only one subject
that had been exposed to the model from day 10 through day 17 directed
sexual responses toward the imprint model.

Guiton (1961) reported that an imprint object, either a triangular
or rectangular box, that was used to elicit following in Brown Leghorn
hatchlings was preferred as a sexual object over the unfamiliar model
in a simultaneous choice test when the cocks were sexually mature.
However, in a subsequent choice test between the imprint object and a
stuffed Brown Leghorn hen, all subjects responded to the stuffed hen,
while only two subjects responded to their imprint object. Thus, the
early following experience did affect the adult's sexual responsivity
toward an object that would have otherwise provided equal attraction,
but such a preference was not sustained when the choice was against a
conspecific model. It should be noted that the isolation treatment
employed in this (Guiton's) study was limited to the first week post-
hatch, from that point on all of the chicks were housed communally.

In a following paper, Guiton (1962) reported that when chicks were
maintained in continued isolation from the imprinting treatment of fol-
lowing either the triangular or rectangular box until the time of test,
the experimental cocks did exhibit a preference for the imprint object
over a stuffed Brown Leghorn hen. This preference was sustained after

four days of communal housing from the 90th to the 94th day posthatch. Thus, when the period of isolation is extended over the first four months, preference for an imprint object is sustained. Guiton observed that these roosters were still sexually responsive to humans in the presence of hens at seven months, so he performed an additional observation when the cocks were eight months old. At this point, he isolated all the experimental roosters for 24 hours. At the end of the 24 hours, he entered the pen of the isolated rooster. All of the roosters that had been isolated for 90 days emitted sexual responses to the experimenter. However, when conspecific hens were introduced to the pen, all subjects immediately directed their sexual responses toward the hens. It appears that biologically appropriate objects were preferred by sexually mature roosters even when they had been isolated during their first 90 days after hatching.

Klinghammer and Hess (1964) presented data suggesting that there is an optimal period for transferring squabs to human care in order to effect a change in the preference for a sexual object in the mature bird. However, these data more convincingly support the view that later experience with conspecifics will usually reverse any attachment to biologically inappropriate objects. These investigators reared Blond Ring Doves (Streplopelia risoria) in a variety of social conditions, and examined the effects of the rearing conditions on the choice of a sexual object when the birds were sexually mature. They reported that regardless of the time that the squab was removed from its parents, if it was communally housed with conspecifics as a juvenile the sexually mature bird responded to a heterosexual conspecific. It was also observed that for subjects that were removed from their parents prior to

weaning and were then visually isolated from all birds until the time
of testing, that there was an optimal period for removing the squabs
from their parents in order to effect a change in the sexually mature
bird's preference for a human over a heterosexual conspecific. Kling-
hammer and Hess argued that the onset of fear occurring during this per-
iod is an important aspect of why a greater percentage of birds trans-
ferred at 7 - 9 days responded to humans than those transferred at ear-
lier or later periods. However, two conditions somewhat weaken the
credibility of this view. First, the manner in which the data have been
presented does not allow the reader to perform a statistical analysis
to determine if there are reliable differences among the age groups.
No statistics are presented by the authors. It seems that there are
reliable differences in the percentage of responses directed toward
conspecifics among subjects transferred after 10 days and those trans-
ferred before. However, a second complication is that both male and
female doves were included as subjects, and it has previously been sug-
gested that females tend to play less of a role in mate selection among
these species (Goodwin, 1958, and Warriner, et al., 1963).

Perhaps the most interesting aspect of these data is derived from
the group that was reared by their parents until weaned and then main-
tained in visual isolation from avians. This group exhibited a symmet-
rical reaction - 2 chose a human, 2 chose a dove, one responded to both
the human and the dove, and one did not react to either. These data
suggest that while the early experience may be important for establish-
ing the basis of species preference, experience during the juvenile
period does have an impact on such sexual preferences. Schutz's (1965)
data have led him to conclude that the critical period for sexual im-

printing occurs at later intervals than the critical period for follow-
ing. He observed that 22 of 34 Mallards raised exclusively with a con-
generic partner for 40 days posthatch paired with a member of the spe-
cies with which they were raised. Pair determinations were based on
consistent proximity to a particular species of female in a field situ-
ation wherein both conspecifics and congenerics were available. Schutz
also noted that early experience with congeneric adults was more effec-
tive for establishing subsequent preferences than was similar experience
with age-mates.

Guiton (1966) extended his study of the permanence of bonds estab-
lished during the neonatal period. He reared Brown Leghorn cockerels
in visual isolation from other fowl for 47 days. During this rearing
treatment, he handled the isolates with yellow gloves. The isolates
were compared to a communally reared group in a simultaneous choice test
between a yellow glove and a stuffed pullet on the 47th day. Both con-
trols and isolates had been treated with testosterone oenanthate in
order to induce sexual responsivity. The isolates emitted fewer sexual
responses toward the pullet than did the controls, while the proportion
of isolates reacting to the yellow gloves was significantly higher (see
Table I). After three days of contact in a communal pen there was no
difference between the proportion of isolates and controls reacting to
the stuffed pullet. The isolate group remained significantly more re-
sponsive to the yellow glove than the communal group. This data sug-
gests that certain stimuli, such as the taxidermic model of a conspeci-
fic hen, requires a minimum of experience in order to effect a prefer-
ence for that object. The data also suggests that the range of objects
to which a male will address sexual responses can be extended as the
result of early experience.

TABLE I

Comparison of Sexual Responsivity to Two Objects
Before and After Three Days of Adult Socialization

| | | Test 1 | | | | Test 2 | |
| | | Sex Object | | | | Sex Object | |
	N	Pullet	Glove	N		Pullet	Glove
Isolates	11	4	10	17		12	15
Controls	6	6	1	9		9	2

Table I: Significantly fewer isolates reacted to the pullet (p < 0.025, Fisher Exact Probability Test) while significantly more isolates responded to the yellow glove (p < 0.005). After 3 days of communal housing (Test 2) there were no differences between the groups in their response to the stuffed pullet, while significantly more isolates responded to the glove (p < 0.01).

Data supporting this view were provided by Gallagher (1965), who demonstrated that if albino Japanese Quail _Coturnix_ _coturnix_ _japonica_ were included in the brood of a normal group of _coturnix_ during the first four days posthatch, then a majority of males would mount and copulate with albino females at sexual maturity when the albino female was presented alone. Males reared without albino chicks in their brood all failed to mount during a ten minute test period in which only the albino female was presented. In other words, it appears that when the hatchling is allowed to experience a novel or foster species, then the likelihood that adult sexual behavior will be directed toward similar objects is increased. The question of whether the foster species will be irrevocably preferred over conspecifics has not been discussed at this point.

C. Permanence of Preference for an Imprinted Foster Species.

Immelmann (1966) observed that when sufficient early experience with a closely related species was provided, the established bond was evident

when the birds were sexually mature. He foster-reared Zebra finches (Taeniopygia guttata castanotis) by Society finches (Lonchura striata f. domestica). As adults all male zebra finches preferred society finches. These males were then confined with female conspecifics until they had successfully reared young and were again observed for their preference between society and zebra female finches. These males still preferred the congeneric females.

The following is a summary of the data pertaining to the establishment of species-bond for social and reproductive behavior:

1. Neonatal social experience is not necessary for sexual behavior in sexually mature roosters.

2. Exclusive neonatal and juvenile social experience with congeneric adults of related species usually results in a preference for a mate from a member of the foster species.

3. In those cases where inappropriate inanimate objects were compared to conspecific models, it appears that a few days of early juvenile experience with conspecifics appeared to be sufficient to establish a preference for the conspecific model. However, when juvenile experience does not occur during the first 3 months posthatch, then the preference for imprint models will persist. These experiments clearly indicate the limits to which sexual attraction can be permanently established.

4. In those cases where objects were comparable, early experience with the object was more effective than later experience in terms of establishing a preferred object.

5. Early neonatal experience was not the only condition in which preferences for inappropriate objects could be established.

6. The likelihood that a stimulus object would release sexual responses

is highly related to its presence during both a neonatal and juvenile
period and the amount of previous experience with any competing stimuli.
7. The degree of experience necessary to establish an object with pri-
mal social attention is affected by the nature of the stimulus.

IV. Critique of Lorenz's Theory of Imprinting.

The following is a critique of Lorenz's theory of how imprinting
establishes a permanent species bond during a brief neonatal period.
According to Lorenz, imprinting occurred to the first stimulus object
that released instinctive behavior, so that imprinting was a rapid pro-
cess, occurring only within specific physiological limits, and was ir-
reversible once it was established. The data described within this
introductory section do indicate certain modifications regarding the
limits in which imprinting can occur. For example, the establishment
of preferred social stimuli does not occur equivocally for all stimuli.
Second, at least for some species, ontogenetic periods at which prefer-
ences are established occur at points other than the neonatal period.
Third, while a preference for a particular species or subspecies may be
established, this does not preclude sexual behavior from occurring with
other species when the animal does not have access to its desired spe-
cies. The problem of assessing the notion of irreversibility is that
in those cases where data were provided as evidence of a reverse in
species preference, the criterion for concluding that either imprinting
or a reverse occurred is subject to criticism. In the case of the
Klinghammer and Hess (1964) observation, for example, the fact that the
squabs were hand-reared by humans from as early as the third day post-
hatch was presumed to be the evidence for the occurrence of imprinting.
In order to convincingly demonstrate a reversal of a preference for a

sexual object, it would be necessary to show a change from the choice of one object to the choice of another.

Guiton's data exhibit change in terms of preferences of stimuli present or absent during development. At earlier periods his cocks selected a yellow glove (a familiar object) over a stuffed pullet (a novel object), whereas at a later point they selected conspecific hens (not familiar during the first 47 days posthatch) over a human (present during the neonatal and juvenile periods). In order to conclude that a reversal of the preference for a sexual object had occurred, a number of assumptions pertaining to such an observation are required. First, it must be presumed that the induced sexual responses addressed to the yellow glove rather than a stuffed pullet is evidence that imprinting to the yellow glove had occurred, and that the yellow glove is the primal object for sexual responsivity. If this were the case, then it must also be assumed that there was an established association between the human and the yellow glove. Perhaps a choice test between a yellow glove and a conspecific hen would have been more appropriate, or at least a comparison should have been made between the yellow glove and a human. In any case, these data do suggest the limits of permanent attachment that is readily established in chickens.

Immelmann's (1966) paradigm seems to be an appropriate procedure in which to make an assessment of the permanence of a preference for a species. He showed that the effect of rearing by foster congeneric parents established a preference for the foster species, and that adult experience with conspecifics did not alter the preference for the foster species.

The question of a critical period for the establishment of racial

or species preferences has not been resolved. It appears certain that a simple notion of a critical period for establishing following behavior is not adequate for describing the process by which the bird attains its species-bond. Rather it would appear that the early experience probably serves to increase the likelihood that the neonate will interact with that species at later periods. It may be that habituation to novel stimuli is prolonged after the onset of fear responsivity, so that the subject is more apt to interact with a familiar object if the remaining object is unfamiliar. It may be that preference for sexual objects is established during a crucial period occurring at some juvenile stage of ontogeny, so that if there is a critical period for establishing a preferential species for mating, then it is likely that this period occurs beyond the first few days posthatch.

The question pertaining to the rapidity in which an animal acquires a perceptual schema for a preferred species is more complicated than the impression originally conveyed by Lorenz. The fact that there may be different perceptual objects for differing behaviors poses the possibility that the time-course for acquiring the various preferential schemata may be different. The development of a perceptual schema of a parental object to follow by precocial fowl must be completed by the second day posthatch. Experimental observations have indicated that as little as ten minutes of following experience is sufficient to allow the hatchling to successfully discriminate a familiar model 24 hours later (Hess, 1959). Since there is less understanding of ontogenetic time-related experience and preference for a particular species for mating, it has not been possible to observe the rapidity of such a process. It does seem that if the sexual imprinting process occurs

at a different time than imprinting of a parental object, then it would be unlikely that the process of sexual imprinting would require as rapid an acquisition of the species characteristics as was the case for following. The hatchling has a more constrained time period in which to learn parental features than a juvenile that would have had comparably greater familiarity with both his siblings and parents. Hence, it would seem unlikely that if these processes are separated that they would entail similar time-courses.

In summary, the data reviewed in this paper require certain modifications pertaining to Lorenz's theory. First, the assumption that the following behavior of precocial fowl is an absolute indicator of the imprinting process should be discarded in that there has been no evidence of such a relationship (Immelmann, 1966; Klinghammer and Hess, 1964; and Schutz, 1965). Second, it is clear that the early experience of exposure to a stimulus object is not a sufficient condition for sexual imprinting. The nature of the stimulus object is a crucial aspect in establishing a preferred object (Bateson, 1966; Gottlieb, 1965; Guiton, 1962). And third, the crucial questions pertaining to a critical period for imprinting would seem to be: 1) at what stage does it occur, neonatal or juvenile? 2) does the period remain constant when imprinting occurs to a foreign species? and 3) what are the conditions that govern the critical period?

The data, however, do not preclude Lorenz's view that the imprinting process establishes a species-social bond during a brief ontogenetic period; that once the preference is established, it will not reverse; and that the establishment of a preferred mate occurs long before the onset of mating behavior.

V. Experimental Proposal.

The preceding review reveals that while early social experience appears to influence mate selection the parameters which govern this effect have not been isolated. One of the major difficulties in conducting a study of the influence of early social experience upon subsequent preference for a mate has to do with the prolonged period from the neonatal treatment stage to sexual maturity. It is necessary that the nature of the animals social experience from the time of hatch to the time of test be precisely known in order to compare effects due to different ontogenetic treatments of social experience (Hinde, 1970). For example, in Schutz's study (1965) the experimental Ss were allowed ad lib social experience with available fowl including conspecifics during an extended period prior to testing. This procedure confounds the interpretation of the effect of early experience in that there may have been an effect of early experience that functioned to prime an interspecific relationship that was subsequently maintained through continuous contact during the adolescent period. The point being that such an interpretation would fit the association learning theory model. The importance of the animals' intervening social experience is evidenced to a certain extent in Guiton's (1966) observation that the adolescent experience of cockerals altered their choice of stimulus objects, at least in the case of a choice between a yellow glove and a conspecific hen (Table I). While the best available evidence suggests that the period for sexual imprinting is a juvenile rather than a neonatal stage, further research is needed in which the experimental subjects received standard social experience when they are not subject to experimental social treatment.

In addition to the problem of the need to control the social experience from hatch day to test day, there exists a difficulty in obtaining a specific behavioral criterion such as copulation that will serve as evidence for a preferred sexual object. In many species of avians, lengthy courtship activities usually precede the behavior of copulation. This problem can be easily avoided by employing the Japanese Quail, Coturnix coturnix japonica, as previously recommended by Gallagher (1965). The coturnix is a suitable species to study the effects of early social experience on mating preferences for two reasons. First, the coturnix becomes sexually mature in approximately 42 days posthatch. In addition to the early sexual maturation, the coturnix is a desirable species to study in that the males are highly active sexually so that drugs are not necessary to induce sexual responsiveness. Several other investigators have described the sexual behavior of the coturnix (Beach & Inman, 1965; Farris, 1967; and Schein, et al., 1972), and have observed that this species is clearly suited for the study of spontaneous mating behavior under standard laboratory conditions. The specific questions addressed in this investigation are as follows. First, is it possible to establish the albino female coturnix as a preferred sexual object over the normal female coturnix as a result of social experience with age-mates? The second question pertains to the issue of whether specific ontogenetic stages exist in which an avian acquires a preference for a sexual object. Coturnix hatchlings were exposed exclusively to albino age-mates at various age levels and for various durations to determine if a preference for an adult albino female coturnix in a simultaneous choice test could be established. A previous study indicated that when albino age-mates were included in the

brood of <u>coturnix</u> hatchlings that such experience increased the readiness of adult males to mount albino females when they were the only females presented to sexually mature male <u>coturnix</u> (Gallagher, 1965). Males that had no previous experience with albinos all failed to mount an albino female under similar conditions. In a simultaneous choice test all males mounted normal <u>coturnix</u> females in preference to an albino female. Thus, <u>coturnix</u> males previously observed preferred normal to albino females in a sex choice test. This observation is compatible with the general view that in order to establish a preference for a foreign or subspecies, some type of exclusive rearing regime with the foster species is a necessary condition (Wallace, 1963).

METHOD

Subjects: The Ss used in this study were 40 virgin male Japanese quail <u>Coturnix</u> <u>coturnix</u> <u>japonica</u> obtained on the day of hatch from the Animal-Husbandry Department of the University of California at Davis. All of the hatchlings were derived from the 908 strain which is maintained by the animal husbandry department as a normal control group. The Ss were immediately transferred to a brooder located on the campus of the University of San Francisco. The albino <u>coturnix</u> that were used as treatment stimuli and test stimuli were also obtained from the University of California at Davis campus. The albinos were also of the 908 strain, and were obtained on either the day they were hatched or as adults. Maintenance of subjects: Ss were maintained on an ad lib schedule of water and food throughout the entire experimental period. Each chamber housing Ss (Figure 1) was provided with a 10" water vessel that was attached to the chamber from the outside and provided sufficient water for at least a twenty-four hour period. Water was changed daily. For the first two weeks posthatch the chicks were provided with poultry starter feed (Woodard, Abplanalp and Wilson, 1965) in two 60 x 15cm pitre dishes. After the second week posthatch, the chicks were transferred to a diet of Purina Startina and kept on this diet until the end of the sixth week when they were put on a diet of Purina Layhenia.

Experimental Brooder: The brooder consisted of small individual chambers (Figure 1) placed in rows and columns within an enclosed room where the temperature was regulated by two electric heaters. The overall size of the brooder room was 12 x 4 x 8'. It was enclosed on one side by 1" pine and by 3 mil polyvinyl on the other side. A mini-max

INDIVIDUAL CHAMBERS

Figure 1. The chambers that were used to house the experimental Ss within the brooder room.

thermometer indicated a thermal variation of $\pm 2°$ F so that a satisfactory temperature could be maintained throughout the brooding period.

There were no lights within the experimental brooder. Continuous lighting was maintained throughout the experiment by three 200 watt lamps, one placed overhead and two facing the transparent polyvinyl wall of the brooder room.

Experimental Test Apparatus: The testing apparatus was a large rectangular box (2' x 4' x 2') constructed of 3/8" plywood on the bottom, top and three sides (Figure 2 and 3). The front of the apparatus was covered with 1/2" hardware cloth which allowed the observer to view behavior anywhere within the apparatus. The roof of the apparatus was hinged so that the Ss could be placed within the apparatus as well as removed. This apparatus was lighted from within by two 60 watt lamps that were permanently mounted one on the two end walls facing each other (see Figure 3) just above the chamber of the stimulus female.
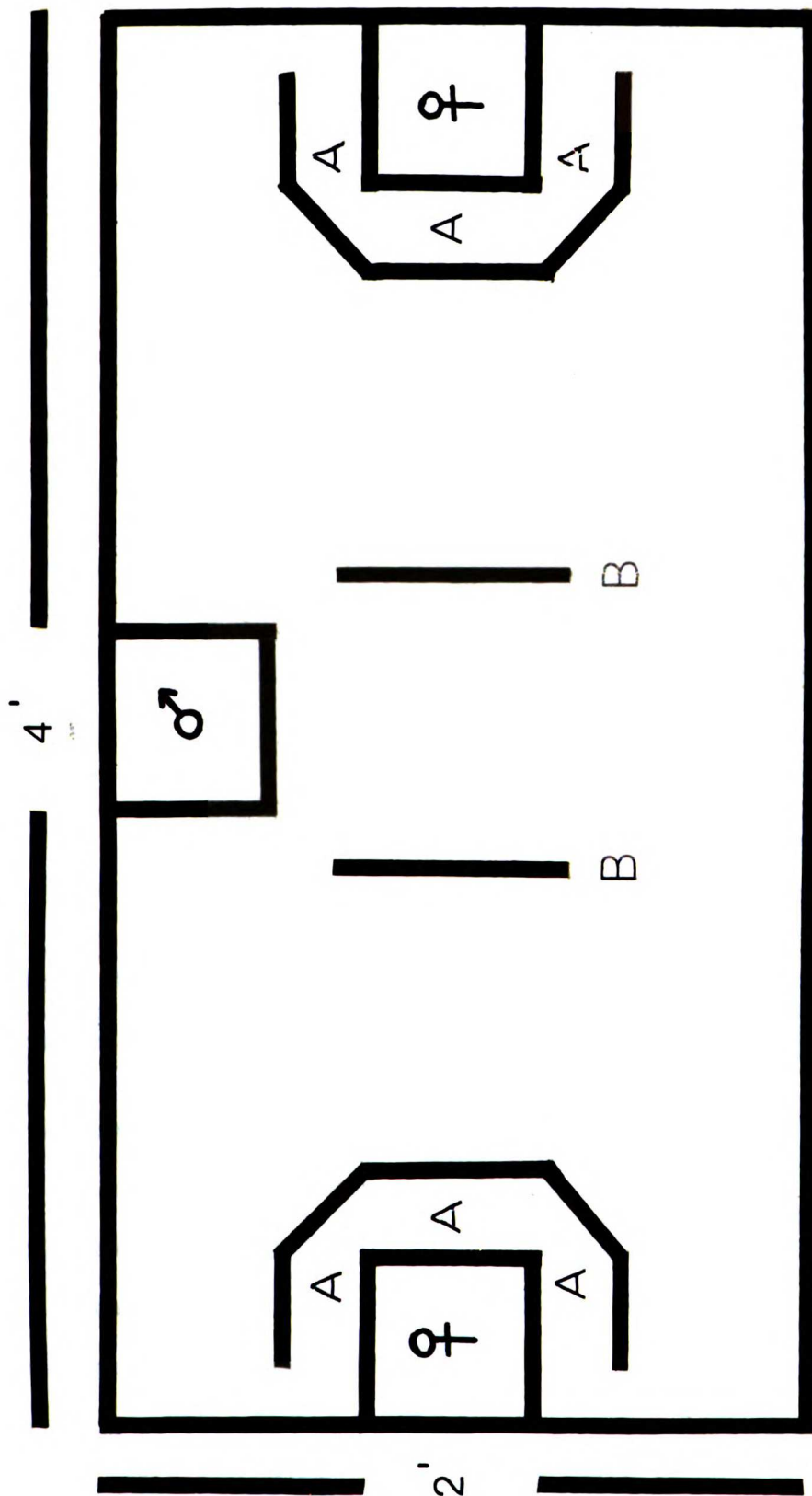
Figure 2. The floor plan of the experimental apparatus. "A" is the approach area. "B" is the boundry line which the S must cross after an approach response in order to qualify for an additional approach. The females were housed in the end chambers and the experimental male was housed in the center chamber.
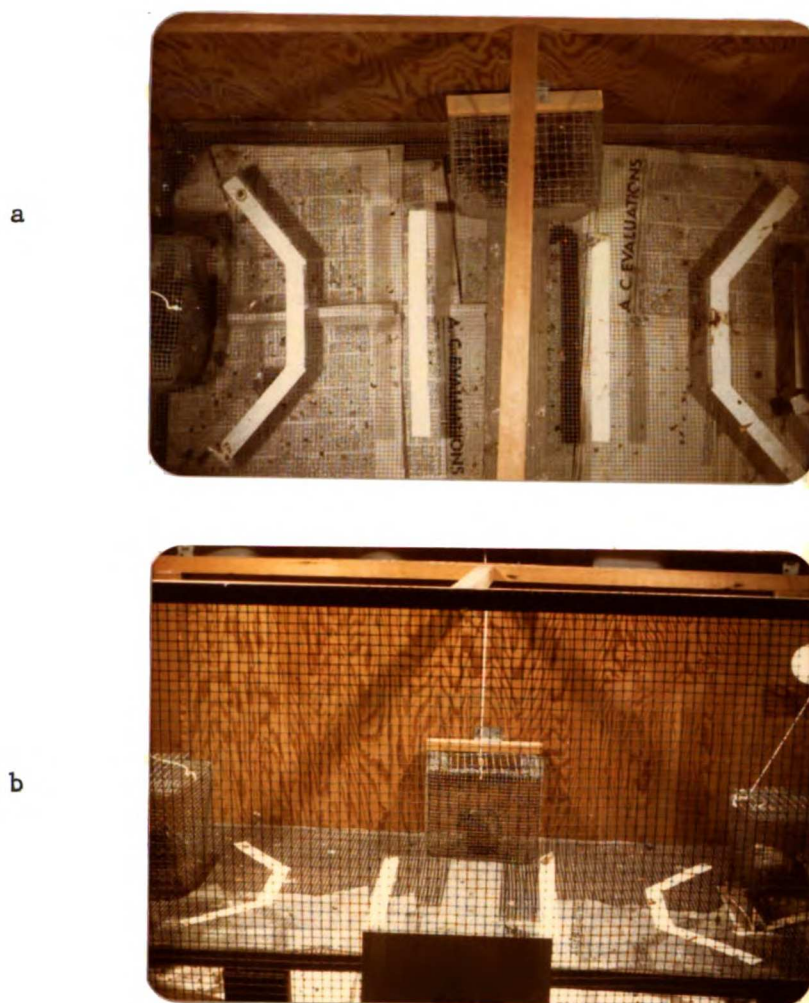
Figure 3. (a) A top view and (b) a front view of the experimental testing apparatus. The experimental S is in the center cubicle and the test animals are in the side cubicles.

The floor of the apparatus was elevated 4" from the bottom of the box in order to allow removal of waste materials. The floor was 2' x 4' and consisted of 1/4" hardware cloth. Two sets of boundaries were pro-vided on the outer floor of the experimental apparatus. The first set was a perimeter border three inches from the edge of each stimulus cage (see Figure 3). This boundary served in the recording of when the ex-perimental S was within sufficient distance of the stimulus object to

be considered in the "approached" status. A second set of boundaries
was provided each of which was 12" from one of the stimulus chambers.
These boundaries served as the basis for determining when an S had left
the area of the stimulus object.

At each end of the apparatus centered against the wall, there was
a small chamber 8" x 8" x 10" constructed of 1/2" hardware cloth that
housed the stimulus females during the experimental observation (test)
period. These chambers were hinged and could be elevated from outside
of the apparatus by pulling a string that was attached to the top of
the chamber. This system allowed the investigator to release the birds
to the outer floor of the test apparatus without opening the hood of
the test apparatus. This procedure produced a minimum amount of extran-
eous input to the experimental observation, and thus reduced the amount
of time required for adaptation to the experimental apparatus. The third
chamber (also 8" x 8" x 10") was located against the middle of the long
solid wall. This chamber will be referred to as the experimental cham-
ber and housed the experimental male prior to its release to the outer
chamber. All three chambers within the test apparatus were rigged in
a similar fashion.

Experimental Treatment: There were four variations in the dura-
tion of exposure of the normal coturnix hatchlings to albino coturnix
age-mates. Table II summarizes each treatment condition in terms of
the number of Ss in each condition, the posthatch age of the S during
exposure to albino age-mates, and the age at which the S was placed in
an individual chamber. The first group received no visual or tactual
experience with albinos during rearing (NEX). After the fifth day post-
hatch half of the group (NEX$_b$) were housed alone in order to control

TABLE II

TREATMENT DESIGN

Treatment Groups	N	0-5	6-10	Days Posthatch 11-15	16-20	21-25	26-
NEX_a	5	N	N	N	N	N	I
NEX_b	5	N	I	I	I	I	I
SEX	10	A	I	I	I	I	I
PEX	10	A	A	A	A	A	I
LEX	10	N	N	N	A	A	I

Note: N = Housed with normal age-mate
       A = Housed with albino age-mate
       I = Housed alone

for effects of visual isolation experienced by the second group. The
remaining half of the group (NEX_a) was housed individually after the
twentieth day posthatch. The second group was housed with albino age-
mates during the first five days posthatch (SEX). After the fifth day
the albinos were removed from the brooding chamber and the remaining
normal coturnix were housed individually. The third group was housed
with albino age-mates during the twenty to twenty-five days posthatch
(PEX). These Ss were also all visually isolated subsequent to the re-
moval of the albinos. The fourth group was communally housed with nor-
mal coturnix age-mates during the first fifteen days posthatch and then
housed with an albino age-mate from the sixteenth to the twenty-fifth
day posthatch (LEX). All members of the NEX and SEX groups were housed
individually after the twentieth day posthatch. All members of the PEX
and LEX groups were housed individually after the twenty-fifth day post-
hatch.

Testing Procedure: The observational procedure was designed to
determine initial preference of the virgin experimental male for either
an albino or normal female coturnix in a simultaneous choice test.
Prior to the experimental observation all Ss were inspected in order to
access the male's state of sexual maturity. A procedure previously em-
ployed and described (Beach & Inman, 1965: Gallagher, 1965; Sachs, 1965,
1967 and 1969) was used to classify each male's sexual maturity. This
procedure involved a visual inspection of the male's cloacal gland
(Figure 4). A sexually mature and active male exhibits an engorged
cloaca. In addition, slight pressure produced by the thumb and index
finger upon the cloacal gland will cause emission of a white foam, a
meringue-like substance that is exuded from the cloaca during copula-
tion (Figure 5). Males not sexually active are characterized by the
absence of both cloacal engorgement and 'meringue' emission. All males
used as experimental Ss in this study were judged to be sexually active
24 hours prior to the initial experimental observation. Males were in-
spected daily for fourteen days after the forty-fifth day posthatch or
until they achieved a "sexually mature" classification. Ss were again
inspected prior to the experimental observation and those which failed
to reach maturity discarded from the study.

The normal and albino female coturnix employed as stimulus objects
in this study were drawn from a colony of females that had been reared
from the day of hatch in the same brooder room as the experimental Ss
or adults obtained from the Animal-Husbandry Department of the Univer-
sity of California at Davis. All of the females were derived from the
908 strain. The females were communally housed in a standard 20" x 12"
x 20" bird cage prior to their use as stimulus objects. Since there

Figure 4. A slightly engorged cloacal gland of a male coturnix.

Figure 5. A slight emission of the meringue substance from the male's cloaca.

were observable differences in the size of females, all females were weighed so that an albino and normal female of approximately the same weight could be paired for each experimental trial. The females ranged in weight from 115 to 160 grams. In pairing females for each experimental observation a 10 gram tolerance was allowed. The ten gram toler-

ance seemed to be a desireable criterion in that there were sufficient females that could be paired using this basis. And in addition, it was observed that the mean weight of the coturnix egg was 10.0 grams. Since all of the females employed in this study were egg layers and egg laying occurred during the experimental hours, it was deemed unnecessary to try to provide a closer control over the weight factor.

While the role of the female coturnix in the selection of a mate has not been fully described, it is clear that the female does vary with respect to the behavior in response to the male's approach and attempt to mount. No specific attempt was made to provide females that were particularly receptive, other than the elimination of females that jumped within the 'stimulus chamber'. After placement of the females within their respective chamber, the females were observed for a two minute period. If a female jumped within the stimulus chamber more than three times within the two minute period the female was replaced and a similar observation was applied to the new female.

All experimental observations were conducted between the hours of 1:00 to 4:00 P.M., and were obtained in the same experimental room which housed the experimental apparatus. This room was 7'x7'x8' and contained a table and two straight back chairs. The experimental apparatus was placed on the floor directly in front of the experimenter. The experimenter used three stop-watches and a prepared data sheet in the recording of the behavior observed during the experiment. The first stopwatch was used to time, first, the initial adaptation period, second, the initial two minute period allowed the male in the outer chamber, and finally, the latency to mount. The second and third stopwatches were employed to record the duration S spent in front of each stimulus chamber

housing the two female test subjects.

Prior to the experimental observation both lamps in the experimental apparatus were lighted, and the electric fan that ventilated the experimental room was activated in order to mask any extraneous noise in the room adjoining the experimental room. The lights in the room were left off during the observation period. This procedure appeared to provide an adequate connubial environment in that neither the experimental or stimulus animals exhibited any unusual interruption of behavior during the observational periods. When disturbed or frightened, the behavior of the coturnix is characterized by a persistent vertical leaping, so that a disturbed coturnix tends to exhibit a rather prominent 'fright response'.

The albino and normal females were always placed in their respective chambers prior to the introduction of the experimental male. This procedure insured that the male would not be affected by longer periods with either the albino or normal female. The females were exchanged after each test so that each experimental male was provided with a fresh pair of females. In addition, the position of the normal and albino females was rotated for each male within an experimental group, so that a counterbalance existed with respect to the position of the stimuli of albino and normal female.

The final step in the preparation was the placement of the experimental male into the test chamber. All experimental males were taken directly from their housing chamber to the experimental chamber. After the placement of the S into the experimental apparatus the Ss were provided two minutes to adapt to the experimental apparatus prior to the initial release of the experimental male. If the experimental male

jumped more than three times during the adaptation period, an additional two to three minutes of adaptation was provided. If the bird continued to jump throughout the extended adaptation period, then he was removed from the experiment.

Upon attaining the adaptation criterion, the experimental S was released to the outer floor of the apparatus and given two minutes to approach the two stimulus females. After the two minute period both females were released simultaneously. The male was given ten minutes to mount one of the two females.

Observational Measures: The initial measure recorded was the approach response, defined as having occurred when the S entered the circular demarked area approximately 3" from the perimeter of the stimulus chamber (See Figure 2). The experimental S was considered to be within the approach area when it had both feet on or within the taped boundary. In addition, the S was required to be oriented toward the stimulus object (See Figure 6). Approach was recorded both in terms of frequency and duration of approach. Duration was measured in terms of the total time spent oriented toward the female within the approach area during the two minute period following the release of the S. An 'approach' was recorded each time the S entered this area and exited out of the area and away from the stimulus chamber to the second set of boundaries that were twelve inches from the face of the stimulus chamber (Figures 2 & 3).

The final two measures were recorded following release of the females to the outer floor of the apparatus and consisted of the S's choice of either the albino or normal female and the latency from time of release to the time of mount. The mounting behavior of the coturnix

Figure 6 shows an experimental male within the approach area and ori-
ented toward an albino female.

is rather dramatic (see Figures 7 & 8) and clear cut. The male grabs

the dorsal neck region of the female with its beak and mounts from the

rear. While mounting, the male flaps its wings to aid in maintaining

balance and leans away dorsally from the female, so that it appears to

be falling off the female's tail (Figure 8). The latency to mount was

recorded when the S 'neck-grabbed' and mounted from the rear.

Figure 7 shows the experimental male grabbing the neck region of an
albino female and mounting from the rear.

Figure 8. An experimental male holding the dorsal neck region of an **albino** female, extending its wings in a flapping movement and falling **off the** tail of the female.

Twenty-four hours after the first trial a second test was performed. This test, referred to as the "Albino Test", was performed to determine if the experimental S would mount an albino female when it was the only accessible female. The procedure of this test similar to the simultaneous choice test with the exception that at the time of release of the female only the albino female was released. The S was given five minutes in which to mount the albino female. If the S failed to mount the albino within the five minute period, then the normal female was released, and the S was given an additional five minutes to mount one of the two females. The presentation of the normal female at the end of the five minute period with the albino female was included to insure that the S was sexually active at the time of this observation.

RESULTS

A complete record of all the individual data is presented in Appendix I. Of the various measures obtained, mounting preferences in the simultaneous choice test, and the incidence of mounting albino females in the albino test appear to be the most interesting observations. Comparisons of treatment groups are presented in terms of: (1) the approach response obtained in the simultaneous choice test prior to the release of the caged females; (2) the choice of a sexual object between albino and normal females when the stimulus females were released (both categorical and latency differences); (3) the incidence of mounting albinos in the albino test; (4) the relationship between approach response prior to the release of the stimulus female and mount response subsequent to the release of the females.

A preliminary examination of the data indicates that there are no differences among treatment groups that are related to differences in the duration of isolation treatment. Four males were eliminated from the data for failing to mount within the allowed ten minute period or failing to adapt to the experimental apparatus. One male was eliminated from both the NEX_a and NEX_b groups and two males from the SEX group were also eliminated. A chi-square test of the differences between Ss isolated from the 6th day posthatch and those Ss not isolated until after the 20th day posthatch was not statistically significant (X^2 = 3.60, p > .05).[1] An examination of Ss approaching a female during the two minute period prior to the release of the test females indicates that

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1. All statistical procedures used in analyzing the data of this study were obtained from Siegel, 1956, unless otherwise indicated. The .05 level of confidence is the criterion that will be employed in this study for acceptance or rejection of the null hypothesis.

there is no difference between Ss isolated subsequent to the 6th day

posthatch and those not isolated until after the 20th day posthatch

(x^2 = 2.16, p > .05). Table III contains a summary of the number of

Ss mounting a female with respect to both treatment groups and isola-

tion duration. Since there were no categorical differences in terms

of a preference for either an albino or normal female between groups

isolated at six days and those isolated at twenty days posthatch, the

data were pooled with respect for the experimental exposure condition

(NEX_a and NEX_b).

TABLE III

RELATION OF ISOLATION DURATION
AND THE N OF Ss MOUNTING A FEMALE

Condition	Isolation From 6th Day Posthatch			Isolation From 20th Day Posthatch			
	NEX_b	SEX	Total	NEX_a	PEX	LEX	Total
Number	6	12	18	6	10	10	26
Approached	5	10	15	5	10	10	25

I. Approach Response.

The data contained in Table IV indicate for each treatment group

whether or not an S approached either or both stimulus females, and a

chi-square test of the response differences within each treatment group.

It can be seen in Table IV that the incidence of approaching normal fe-

males during the two minutes preceding the release of the stimulus fe-

males is greater in all conditions than the incidence of approaching

albino females. The overall observed differences described in Table IV

among treatment groups is statistically significant (x^2 = 19.8, p <

.02). However, the difference in approaching females within treatment

TABLE IV

SUMMARY OF THE APPROACH TO STIMULUS FEMALES

GROUP	N	ALBINO ONLY	NORMAL ONLY	BOTH FEMALES	NEITHER FEMALE	x^2	ρ
NEX	10	0	9	0	1	22.8	<.001
SEX	10	0	4	3	3	3.6	>.05
PEX	10	3	4	0	3	3.6	>.05
LEX	10	1	3	1	5	4.4	>.05

groups is statistically significant only for the NEX group.

The number of Ss that approached and the duration of the approach both in terms of the total time and the median for those Ss that approached are presented for each treatment group in Table V. Data on the frequency of approach are not presented since only on rare occasions did any S have more than one approach response. A Chi-square test (Siegel, 1956) of the observed differences in the number of Ss that approached from each treatment condition was not significant (X^2 = 2.81, ρ = .30). It can be readily observed in Table V that not all Ss approached either of the two stimulus objects presented in the simultan-

TABLE V

SUMMARY OF APPROACH RESPONSE MEASURES

Group	N	Ss Approached	Total Time Approached	Med. Duration Ss That Approached
NEX	10	9	300	(:27)
SEX	10	7	238	(:27)
PEX	10	7	181	(:14)
LEX	10	5	150	(:23)

Note: The time of approach and median times are given in seconds.

eous choice test. This difference in the incidence of approach is re-
flected in the total time spent in the approach area in front of a fe-
male for each group. However, when the average time was calculated for
Ss that approached, the group differences were less apparent. Since
there were no differences among groups in terms of the incidence of ap-
proaching, no further statistical analysis was performed on this data.

II. Mounting Preference for a Female in the Simultaneous Choice Test.

A summary of the data describing the initial mounting choice of a
female by virgin males in the simultaneous choice test is presented in
Table VI. It can be seen in Table VI, first, that all ten Ss that had
no previous experience with albino quail (NEX group) chose to mount nor-
mal female coturnix. Second, all ten Ss that were housed with albinos
during the first five days posthatch (SEX group) mounted normal female
coturnix. Third, nine of the ten Ss that were housed with albino age-
mates during the first twenty to twenty-five days posthatch (PEX)
mounted albino females. In the fourth (LEX) group, which had exposure
to albino age-mates during the sixteenth to twenty-fifth days posthatch,
six of the ten males mounted normal females.

TABLE VI

SIMULTANEOUS CHOICE TEST

Number of Ss Mounting

Exposure Condition	Normal Females	Albino Females
NEX	10	0
SEX	10	0
PEX	1	9
LEX	6	4

The data obtained in the preference test were first examined to determine whether the observed overall differences among groups were statistically reliable. A chi-square test indicated that the observed differences would occur by chance less than one time in a thousand if in fact there were no true differences among groups in terms of a preference for either the normal or albino females (X^2 = 24.85, p = .01, two tail test). The observation of reliable differences among groups permits comparison between pairs of treatment groups to determine which treatments produced reliable response differences. Table VII contains a comparison of the differences among groups in terms of preference for either the albino or normal female based on a Fisher Exact Probability test.

TABLE VII

SUMMARY OF THE TEST FOR SIGNIFICANCE
AMONG TREATMENT GROUPS

	NEX	SEX	PEX	LEX
NEX		N/S	.005	.05
SEX			.005	.05
PEX				.05

The data were examined further to determine if the observed preference for either the albino or normal female within each treatment group was statistically greater than chance. A binomial test was performed for each condition. It can be seen in Table VIII that the observed differences in the preference for a female obtained in NEX and SEX groups are statistically reliable beyond the .002 level of confidence. The observed difference for the PEX group is statistically reliable beyond the .03 level of confidence. Whereas, the observed dif-

TABLE VIII

SUMMARY OF THE BINOMIAL TEST

Group	Z Score	Probability
NEX	2.92	.0018
SEX	2.92	.0018
PEX	1.89	.0294
LEX	.95	.1711

ference for the LEX group was not statistically reliable within the .05 level of confidence. These data indicate that there is a reliable effect of prior social experience in terms of the observed preference for either the albino or normal female for the NEX, SEX and PEX groups but not for the LEX group. The case of experience with albinos only during the first 5 days or no experience with albinos at all produced a male with a preference for a normal female. Whereas, the prolonged rearing condition with only albinos, PEX, produced a male with a preference for albino females. The condition of early experience with normals and later experience with albinos did not result in a clear preference for either albino or normal females. It is concluded that the differences exhibited in terms of preference for either albino or normal females

TABLE IX

MEDIAN MOUNT LATENCIES IN SECONDS

Group	Normal Female	Albino Female	Combined Median
NEX			(99.9)
SEX			(195.9)
PEX	582.6	135.0	(172.2)
LEX	193.2	154.2	(170.4)

observed among the treatment groups result from the experience with albino age-mates which serves to override the typical preference for normal females.

A summary of the median mount latencies is presented for each treatment group in Table IX. The median latency to mount either normal or albino females is described. In addition, the median latency to mount without regard to the female mounted is given. The treatment groups were compared on only the latter measure, since only in the case of the LEX group was there a division in the choice of stimulus females.

A Kruskal-Wallis one-way analysis of variance indicated that the latency data of the difference among the treatment groups is statistically reliable beyond the .001 level of confidence (H = 117.29, $p <$ .001). A further comparison of the latency to mount data was performed in order to determine statistically reliable intergroup differences. Table IX contains a summary of the probabilities that the observed differences are statistically significant as determined by a Sign test. It can be seen in Table X that the latency differences between the NEX group and the PEX and LEX groups is statistically reliable beyond the .001 level of confidence. The observation of a .055 level of probabil-

TABLE X

Confidence Levels of the
Differences in Mount Latencies

	NEX	SEX	PEX	LEX
NEX		.055	.001	.001
SEX			.055	.172
PEX				.377

*One tailed test.

ity that the observed difference between the NEX and SEX groups and the
observed difference between the PEX and SEX groups are on the side of
the stated rejection level. So it is concluded that those Ss reared
without albino age-mates (NEX) mounted sooner than Ss with 20 to 25
days experience with albinos (PEX) and the Ss with experience with al-
binos during the sixteenth to twenty-fifth day posthatch. Further,
there were no statistically significant differences in the observed
latency to mount among any other compared groups.

III. The Analysis of the Data Obtained in the Albino Test.

In the albino test which was administered 24 hours after the sim-
ultaneous choice test, Ss were given five minutes with only the albino
female in the outer cage of the test apparatus. A summary of the data
describing the number of males mounting an albino female in the albino
test is presented in Table XI. Table XI contains the frequency of Ss

TABLE XI

Albino Test

Exposure Condition	Number of Ss Mounting A's in the 1st five Min.	Number of Ss Mounting N's in the 2nd Five Min.
NEX	0	10
SEX	10	0
PEX	10	0
LEX	10	0

for each treatment condition that mounted albino females during the
first five minutes of exposure or mounted normal females during the
second five minutes. It can be seen in Table XI that when the female
albino was the only stimulus object available, all males that had some

previous exposure to albinos mounted the albino female (SEX, PEX and LEX groups). In addition, all Ss that had no previous experience with albinos (other than the initial test exposure to albinos) failed to mount albino females during a five minute exposure period. The observed responses of either mounting or not mounting the albino female within the various treatment groups are all statistically significant beyond the .001 level of confidence (Binomial test; $Z = 2.92$, $p = .0018$).

The only observed differences in the mounting of an albino female, in the albino test, among treatment groups was the case wherein no member of the NEX group mounted an albino female. A Fisher Exact Probability test indicates that the observed differences between the NEX group and the SEX, PEX and LEX groups is statistically reliable beyond the .005 level of confidence. It is concluded that exposure treatments to albino age-mates of either the first five days posthatch or for ten days during the juvenile period increase the readiness of <u>coturnix</u> males to mount albino females as compared to males that have had no prior experience with albino females.

IV. The Relationship Between the Approach and Mount Responses.

The final step in the analysis of the data obtained in this study is the examination of the approach and mount responses obtained in the two separate tests in order to determine if there is a relationship between these two responses. There were eight possible outcomes of the approach and mount responses. First, the S could have approached a normal female and subsequently mounted a normal female; second, the S could have not approached either female and mounted a normal female; third, the S could have approached an albino female and mounted a normal female; and fourth, the S could have approached both the albino

and the normal female and then mounted the normal female. For each of the above conditions a reciprocal case could occur prior to the Ss mounting of an albino female.

Since the primary interest in these data is to determine if there is a reliable relationship between these two responses, the data were divided into two categories for each treatment condition. The first category described the Ss that mounted females which they had previously approached in the two minute period preceding the release of the females in the simultaneous choice test, and the second category described the Ss that mounted females that they had not previously approached. Table XII contains a summary of the organization of these data. A chi-square test indicates that the observed differences among treatment groups is

TABLE XII

Comparison of the Approach and Mount Data

	Ss That Mounted Approached Female	Ss Mounting Female Not Approached
NEX	9	1
SEX	7	3
PEX	3	7
LEX	4	6

statistically significant (X^2 = 9.26, $p < .05$). Thus, the treatment groups are further characterized by a difference in the tendency to mount a female which they had previously approached. The tendency to mount a female that had been previously approached during the preliminary observation period decreased in relation to the tendency to mount albinos increased. For example, in the NEX group nine of the ten Ss mounted the normal female which they had previously approached and none

of these Ss mounted an albino female in either the simultaneous choice test or the albino test. A binomial test of this outcome indicates that this observation is statistically significant ($p < .02$). In the remaining groups, which the increased incidence of mounting an approached bird decreased in relation to the incidence of mounting albino females, these differences were not statistically significant. Thus, it is concluded that for the SEX, PEX and LEX groups there is no relationship between the approach and mount responses. Table XIII contains a summary of the probabilities that the observed differences in the approach/mount response are statistically reliable. These probabilities were all computed with the Fisher Exact Probability Test. It can be seen in Table XIII that the only reliable differences between groups was between the NEX group and the PEX and LEX groups.

TABLE XIII

Summary of Probabilities of
Differences in the Approach/Mount Responses

	NEX	SEX	PEX	LEX
NEX	N/S	N/S	.01	.05
SEX			N/S	N/S
PEX				N/S

DISCUSSION

The data obtained in this investigation demonstrates that it is possible to establish the albino female coturnix as the preferred sexual mate in a simultaneous choice test. This preference for albinos results from prolonged exclusive experience with albino age-mates prior to sexual maturity. The preference for albinos contrasts with the more typical observation that normal females are preferred and hence fits the outcome described by Lorenz of the relationship of early experience with social objects and subsequent sexual preferences. In the discussion I will examine several criticisms that have been put forth to suggest that such adaptation does not result from a special process such as imprinting. Much of the controversy can be described in terms of whether the learning of particular stimulus features of a social object occurred in a special context (Bateson, 1966 and Hinde, 1962) or by a special process such as imprinting (Lorenz, 1935 and Hess, 1964). The identification of ontogenetic periods in which young birds are more susceptible to the effects of their social environment would support Lorenz's description of an imprinting process as opposed to a special context interpretation that suggests that the acquisition of a species social bond is peculiar only to the extent that it describes the animals original acquisition of a class of stimulus objects for social responsivity.

The data obtained will be discussed in terms of their implication for the above theoretical problem, especially as these data reflect on the issue of a possible sensitive period for the establishment of a species social bond. The additional observations obtained in the albino test demonstrates that there is more than one sexual attitude

(the term attitude is used in this paper to describe the various mounting response tendencies observed in simultaneous choice test and the albino test) that is characteristic of the coturnix observed. These latter data will be discussed in terms of their implication for both the imprinting hypothesis and a proposed habituation hypothesis.

I. The Effect of the Social Treatment Conditions on the Choice Response.

A. The Approach Response. The proportion of Ss approaching normal over albino females was greater for all treatment groups. However, only in the case of the group that had no previous experience with albinos (NEX group) was there a statistically significant preference for normal females. These data do not support a critical period interpretation of the acquisition of a social bond. In fact, in both the SEX and PEX groups the experimental males had no previous visual experience with normal coturnix prior to the simultaneous choice test, and in each condition more Ss approached a normal female than approached an albino female. This observation would lead one to believe that the exposure treatments to albino age-mates was limited to providing an equivocal attitude toward adult albino females. In short, the measure of the approach response indicated that the prior experience, whether it occurred during the first 5 days posthatch, the first 20 days posthatch, or for 10 days during a juvenile period, served only to establish the albino female as a somewhat atypical stimulus object.

B. The Mount Response. The data obtained with respect to mounting behavior, in contrast to the approach response, indicate a strong effect of treatment upon the selection of either albino or normal females. While the age groups employed in this study do not allow for

a precise description of a sensitive period for the establishment of a
preference for either an albino or normal female, it will be argued that
such a conclusion is the best interpretation of the data.

II. Treatment Effects on Mounting Behavior.

A. Neonatal Experience. The data presented in Table IV indicate
that exclusive exposure to albino age-mates during the first five days
posthatch (SEX group) was insufficient to establish a preference for
albino females even when the male has had no previous experience with
normal coturnix. This observation points out that if a critical period
for sexual imprinting exists, it does not exist in the coturnix during
the neonatal stage at least in the case where albino age-mates are used
as stimulus objects. The nature of the stimulus object employed in this
study is important, in that the adult female may constitute a perceptu-
ally different stimulus object than the albino hatchling. It may be
the case that the characteristics of the stimulus that are acquired
during the treatment period are quite specific and that the character-
istics of the adult albino coturnix may be sufficiently different from
the albino hatchling. Schutz (1965) has reported that interspecific
sexual imprinting was more readily effected when adults were employed
as imprint objects as opposed to age-mates.

The fact that the exposure to albino age-mates during the first
five days posthatch does not effect a social bond for albinos is import-
ant in that these males had no other previous social experience and yet
they all manifested a clear preference for normal female coturnix. It
would appear that there exists a propensity in male coturnix to mate
with normal females that is not dependent upon previous social experi-
ence with normal coturnix. Wood-Gush (1958) had previously noted that

social experience is not a necessary precondition for sexual behavior

in Brown Leghorn cocks. In addition, Andrew (1966) observed that early

experience with a moving object (a human hand), that could readily elic-

it following behavior and sexual responsiveness in the hatchling, was

not sufficient experience to provide such a stimulus with properties

to subsequently release copulatory responses in the sexually mature

adult. So, there seems to be no direct evidence of the existence of a

critical ontogenetic period for acquiring a permanent species bond dur-

ing the neonatal stage.

The experience of exclusive exposure to albino age-mates during the

first five days posthatch clearly had an effect on the sexually mature

male's readiness to mount albino females (Table XI). When the SEX males

were presented albino females alone in the albino test, they all mounted

the albino within five minutes. This behavior is in contrast to Ss that

had to previous experience with albinos (NEX group). In no case did NEX

males mount an albino female in the albino test. The observation that

early experience with albinos effected an increased readiness to mount

an adult albino female, suggests that significant modification by early

social experience with albino hatchlings governs the mechanism(s) of

the perception of a stimulus object as an acceptable sexual object.

This effect was similar to the earlier observation that mere inclusion

of an albino age-mate in the brooder during the first four days post-

hatch was sufficient to effect an increased readiness to mount an al-

bino female when no other female was present (Gallagher, 1965). The

implication of such modification in the readiness to respond sexually

to an albino female in adult male coturnix is that the mechanism that

mediates this change differs from descriptions of the imprinting proc-

ess in that the albino female is clearly not the primary sexual object for the SEX group. This suggests that the perception of a stimulus as a sexual object may result from at least two mechanisms; one that fosters a stable preferred object and another that designates objects as acceptable mates when access to primary object is denied.

B. Prolonged Early Experience. Perhaps the most interesting observation provided by this study is the preference for albinos exhibited by the group that had prolonged social experience with albino age-mates (PEX group). This group in all but one case mounted the albino female in the simultaneous choice test (Table IV). This particular observation does not provide conclusive evidence to support Lorenz's view of a critical period for sexual imprinting. However, it does demonstrate that prolonged early experience with albino age-mates can produce a stable preference for albino females. This fact also suggests that it is possible to determine if there are particular ontogenetic stages which delimit the acquisition of stable preferences for a stimulus object such as an albino female. The fact that the PEX group did prefer albino females in the simultaneous choice test encourages future study of the coturnix to further compare shorter ontogenetic periods in order to determine if there is in fact a propitious period for the acquisition of a preferred sexual object.

C. No Early Experience with Albinos. The question of what circumstances account for the establishment of the preference for normal females in the simultaneous choice test cannot be logically deduced from the data obtained in this study. That is, it cannot be concluded that the establishment of the normal female coturnix as a primary sexual object in the NEX group is a result of either the social regimen

or an innate system. The fact that SEX males all preferred normal fe-
males demonstrates that social experience with normal coturnix is not
required for the establishment of normal females as a primary sexual
stimulus object. It cannot be concluded that the preference for normal
females is innate in that the social experience with albinos may have
served to prime the chick's readiness to interact socially without es-
tablishing the albino as a primary stimulus object. It is clear from
the stable response preference for normal females exhibited by SEX males
that there is a greater tendency for coturnix males to develop a prefer-
ence for normal over albino females. This conclusion is further sub-
stantiated in that the component of the NEX group that had only five
days experience with normal hatchlings also all selected normal female
coturnix in the simultaneous choice test.

III. Behavioral States Related to Treatment Conditions.

At least three and possibly four behavioral categories describe
the mating responses obtained in the simultaneous choice test and the
albino test. These behavioral categories will be referred to as atti-
tudes in the remainder of this paper. The first attitude is evidenced
in the NEX group that only mounted normal females (Tables IV & VI).
The second attitude is depicted by the SEX group in which all males
mounted normal females in the simultaneous choice test and subsequently
all mounted albino females in the albino test. The third attitude is
witnessed in the PEX group that exhibited a consistent preference for
albino females in the simultaneous choice test. A final attitude may
be evidenced in the absence of a preference for either the albino or
normal female exhibited by the LEX group.

The observation of consistent preference for either an albino or

normal female as observed for the NEX, SEX, and PEX groups suggests that these groups are characterized by a "primary sexual attitude" toward one of the two females. While there is no apparent reason to expect that these "primary sex attitudes" are homogeneous with respect to the mechanisms which mediated their development, such an attitude can be behaviorally differentiated from a "secondary sexual attitude" that is evidenced in the SEX group's response toward albino females in the albino test. In the SEX group, no S preferred albino to normal females, but all Ss mounted albino females when normal females were not accessible. Thus the SEX group is characterized as having both a primary sex attitude toward normal females and a secondary sex attitude toward albino females.

The final condition to be dealt with regarding sex attitudes pertains to the behavior of the LEX group that did not manifest a group preference for either albinos or normal females. This fact may indicate that the LEX animals do not have a primary sex attitude for either normal or albino females, that the two stimuli are equivocal, or it may mean that the treatment affected members of this group differentially and some acquired a primary sexual attitude for normal females and others acquired a primary sexual attitude for albino females.

IV. Mechanisms of the 'Primary Sexual Attitude'.

A. Sensitive Period. The observation of different behavioral attitudes toward normal and albino females opens the question of the nature of the mechanisms that govern the development of different attitudes. In the case of the primary response attitude, this system may be the product of a process that resembles Lorenz's imprinting construct. If the primary response attitude were a product of an imprinting process,

then according to Lorenz's description of this process, the primary response attitude should be established only during a specifiable onto-genetic period.

In the present investigation the precise time-course of a sensitive period could have gone undetected, in that the treatment conditions did not cover all posthatch ages. For example, no group received exposure to albinos only during the period from the sixth day posthatch through the fifteenth day. Immelmann (1972) has recently suggested that sensitive periods for social attachment are far more complex than originally described by Lorenz. For example, he reported that the sensitive period for establishing the following response to a stimulus object occurs during the neonatal period and tends to be of very brief duration, while the sensitive period for sexual imprinting appears to be of much longer duration extending through the juvenile period (see Introduction section III B, pp. 7-12). Also Immelmann notes that there is greater intraspecies variability with respect to sexual imprinting than previously described by Lorenz. The variability in the sensitive period is such that in some cases the effects of social experience during a common sensitive period of the species may not establish a primary sexual attachment. Such an explanation would account for the one male in the PEX group that selected a normal female in the simultaneous choice test.

In addition to the above criticisms of the sensitive period construct, the data obtained in this study point out that the experience with specific social stimuli are not equivocal, in that more exposure is required to establish a preference for the albino than the normal female.

Very sparse data exist regarding sensitive periods for sexual imprinting. Schutz (1965) indicated that the sensitive period in Mallards (Anas platyrhynchos) begins somewhere between the 5th and 19th day posthatch and continues to about the 45th day. It is difficult to be more precise regarding this sensitive period because Schutz varied the length of exposure, age levels of exposure as well as stimulus objects. Each of these variables may modify the specific time-course for various portions of the sensitive period. More recently, Schutz (1970) has described the sensitive period in the Greylag goose (Anser anser) as beginning about 50 days posthatch and terminating at about 140 days. Immelmann (1972) has indicated that sexual imprinting in Zebra finches (Taeniopygia guttata castanotis) must occur between the 13th and 40th day posthatch. The data obtained in this study support the growing generalization that the establishment of sexual preference for other than the conspecific occurs at a juvenile period rather than a neonatal period.

B. Principle of Association. The fact that the PEX group had a stable preference for albino females in contrast to the stable preference for normal females exhibited by the NEX and SEX groups indicates that the visual characteristics of the adult albino female coturnix acquire properties for releasing sexual responsiveness as a result of a particular regimen of previous social experience. Such an observation indicates that a primary sexual object can be established as a result of exogenous variables. This point is significant in that all of the treatments of social experience occurred prior to sexual maturation. Hence the principle of contiguity so often stressed by learning theorists has been abridged.

The construct of "latent learning" as described by Tolman (1948) also seems inappropriate to explain why the SEX group all selected normal females while the LEX group was divided with respect to the selection of either the normal or albino female. The argument will be put forth that the observed difference in mate preference between the SEX and LEX group (Table VI) constitutes evidence that there is an ontogenetic difference in terms of the male's susceptibility to the influence of social stimuli. The existence of a parameter of an ontogenetic sensitive period for the acquisition of a preferred mate would distinguish the acquisition of a primary sex attitude from the type of behavior modification typically described by latent learning. The construct of latent learning does not include a sensitive period component.

It has not been demonstrated that the primary sexual object is the result of an imprinting process such as was originally described by Lorenz (1935). However, it has been demonstrated that the traditional principles of association learning reinforcement, contiguity and latent learning are insufficient to explain the establishment of the primary sexual attitudes as observed in the initial preference for albino females.

V. Modification of Lorenz's Original View of the Imprinting Process.

A number of investigators have put forth modifications of Lorenz's view of the principles by which innate social responses come to be directed toward a primary class of objects (Fabricius, 1964; Hinde, 1961, 1962; Salzen, 1962, 1970; Sluckin, 1965 and Thorpe, 1963). Typically these investigators do not share the view that imprinting occurs only during a precise and very limited ontogenetic period, such as had been described by Hess (1964, Figure 4). Also the principle or irreversi-
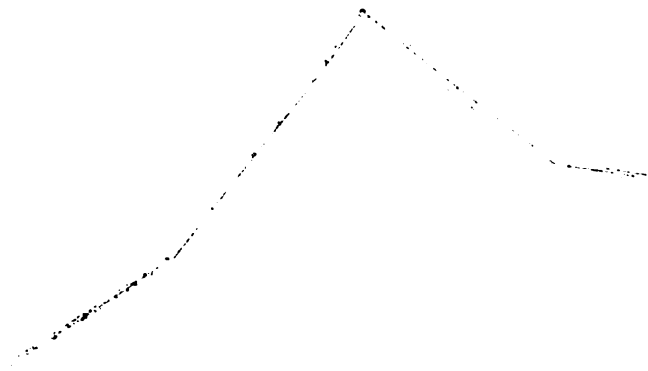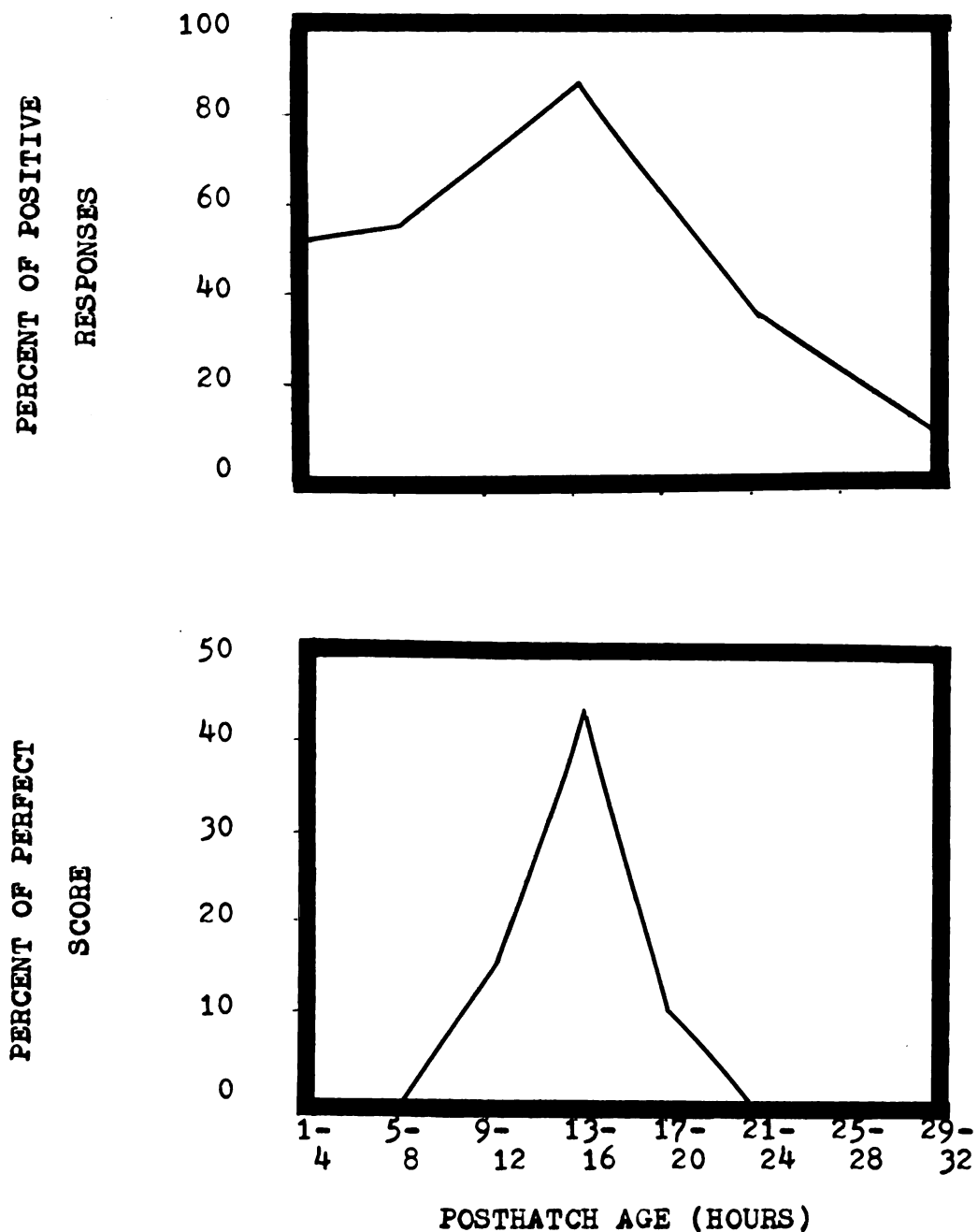
Figure 1. Two ways that Hess (1959a) has organized the results of the simultaneous choice test between the imprint model (a male mallard) and a female mallard. The top graph describes the total percentage of responses directed toward the imprint model. The lower graph describes the percent of ducklings selecting the imprint model on all four test conditions (1. Both models stationary and silent. 2. Stationary but calling models. 3. Both stationary, male silent and female calling, and 4. Male stationary and silent, female moving and calling).

bility is considered to be an overstatement by the above authors. A third criticism offered by the above investigators is that the emphasis of the study of imprinting in the context of the attachment of the following response to a stimulus object is thought to be inappropriate for discerning features of the establishment of a species social bond. Despite the above criticisms these investigators are agreed that imprinting is a process in which an object or goal is acquired and not a process in which a particular set of responses are acquired. This latter view is compatible with Lorenz's purpose of describing imprinting as an interesting example of the attachment of innate systems to a learned stimulus object.

The principles of the critical period for attachment and the permanence of the attachment are less crucial to Lorenz's description of imprinting as a special process of adaptation than the point that the development of a social bond is established in a manner other than the successive acquisition of stimulus-response patterns by some form of conditioning. In other words, Lorenz's view is that the biology of the organism contributes to the organization of the behavior and the learning component is merely the acquisition of a particular class of stimuli which ultimately serves to release the particular behavior pattern.

The data obtained in the simultaneous choice test for NEX, SEX and PEX groups (Table III) support the view that a process such as the modified view of imprinting does serve to establish a specific class of objects as a primary object for future social behavior. However, the precise parameters of this process, with respect to permanence of the attachment and the precise time-course for the establishment of the species bond for different stimulus objects and at age levels are in

need of further investigation both in the field and in the laboratory
(Evans, 1970; Hess, 1972).

VI. Association Theory View of the Acquisition of Sexual Attitudes.

An association theory interpretation of the data of this study
would be supported if a variable, such as the length of exposure to a
specific social object (an albino age-mate), functioned to establish
the status of albinos as a sexual object. The Ss in the NEX group,
0 days exposure to albinos, did not mount albinos in either the simul-
taneous choice test or the albino test. The SEX group, 5 days of ex-
posure to albino age-mates, only mounted albinos when normal females
were not present. The LEX group, exposed to albino age-mates for 10
days, in four cases mounted albino females in the simultaneous choice
test and all mounted the albino in the albino test. Finally, the PEX
group, exposed to albino age-mates for 20 to 25 days all but one se-
lected albino females in the simultaneous choice test. So that in each
of these treatments there was a progressive increment in treatment dur-
ation and in addition there was a corresponding increase in the inci-
dence of sexual responsivity toward albino females.

The observation that the LEX group failed to develop a preference
for just one of the two stimulus objects suggests that there is an
ontogenetic period in which coturnix males are more susceptible to the
influence of albino age-mates in terms of subsequent mount preferences.
This conclusion is based on the fact that five days of exposure treat-
ment to albino age-mates (SEX group) failed to produce a single pref-
erence for an albino female over a normal female in a simultaneous
choice test despite the fact that SEX males had no previous experience
with normal coturnix. In contrast the LEX group was exposed to normals

for the first 15 days posthatch prior to ten days of exposure to al-
binos. Four of the ten LEX males selected albino females in the simul-
taneous choice test. The fact that LEX's had 15 days of exposure to
normals and SEX's did not have any exposure to normals indicates that
the later exposure period is more crucial for establishing albinos as
a preferred sex object.

If the ratio of time spent with albinos and normals during the
treatment period is considered, then a comparison of the treatment con-
ditions received by the SEX and LEX groups and their subsequent mount
preferences provides doubt that an association theory explanation,
such as the length of exposure to albino age-mates, could account for
the observed differences among groups. For example, all Ss in the SEX
group had 5 days experience with albinos and 0 days experience with
normals, a 0-5 ratio, and all SEX Ss mounted normals in the simultan-
eous choice test. The LEX group received 15 days with normals and 10
days with albinos, a 3-2 ratio. LEX's preferred normals 6-4 in the
simultaneous choice mount test. Association theory is hard put to ex-
plain why LEX's that had a 3-2 ratio of experience with normals mounted
normals less frequently than the SEX group that had a 0-5 ratio of ex-
perience with normals. It might be argued in support of contiguity
theory that coturnix require a minimum amount of experience with al-
binos in order to establish the albino as a preferred object. The
treatment of five days received by the SEX group was below the minimum
exposure required to establish a preference for albinos; but ten days
is sufficient time for the establishment of a preferred response. This
interpretation seems highly unlikely, unless it is also presumed that
once the minimum amount of experience occurred, then preferences would

occur equivocally and arbitrarily. Such a rationale is vague, complex and lacking empirical support. Future research can readily deal with this problem by comparing groups receiving ten days exposure at various ontogenetic age levels. If there is no sensitive period for establishing a sexual preference, then all groups would be equivocal with respect to selecting albino females in a simultaneous choice test.

On the basis of the data obtained in this investigation, it should be concluded that developmental change in the stimulus objects, the subjects, or some combination of changes in both is responsible for the observed difference between the LEX group and the SEX group in the number of males that selected albino females in the simultaneous choice test. While it is highly probable that the change in the stimulus object is important (Schutz, 1965) the fact that experience with albino age-mates during the first five days posthatch (SEX) modified adult sexual attitudes as observed in the albino test, indicates that the age level of the individual plays the more important role in establishing a primary sexual attitude toward albino females. Thus it is concluded that the best interpretation of the data of this study is that the primary sex response attitude results from the social experience occurring during a juvenile sensitive period.

One implication of the above interpretation that a sensitive period for acquiring a preferred sexual object occurred during a juvenile period rather than a neonatal period, is that such a sensitive period is characteristically unlike the sensitive period typically described by many students of imprinting (Bateson, 1966; Bjarall, 1967; Gottlieb, 1961; Hess, 1964; Klopfer & Gottlieb, 1962; Jaynes, 1957; Lorenz, 1935 and Moltz, 1963) in which the primary experience with a social object

during a neonatal sensitive period served to establish a preference for that object.

If we presume that the onset of the critical period for the acquisition of a preferred sexual partner in coturnix occurred prior to day 16, then the LEX Ss should have become imprinted to the normal coturnix. Indeed, I have already noted that there appears to be an inherent propensity toward the selection of normal females as observed in the SEX group. Hence, it would have been expected that all of the LEX Ss would have selected normal females in the simultaneous choice test. If the onset of the critical period occurred after the 16th day posthatch, then why is it the case that six Ss mounted normal females?

VII. Implication of the Sexual Attitude of Males Reared with First Normal and Then Albino Age-mates (LEX).

There are at least two possible explanations that would support a sensitive period point of view. First, while the onset of the critical period may generally occur prior to day 16 posthatch, the lack of maturity of the stimulus object may have been an important variable. And second, there may be individual variation in terms of the onset of the sensitive period for imprinting. So, if we presume the onset of the sensitive period at some point prior to day 16 posthatch, then it may be the case that a) for certain Ss there may have been insufficient time for sexual imprinting to occur because of the individual's delay in the onset, and/or b) that the normal age-mate to which the S had been exposed might not sufficiently resemble the mature normal female presented in the simultaneous choice test in those cases wherein the LEX Ss preferred the albino female. The fact that normal females were selected by other members of the LEX group suggests that either these

Ss were advanced in terms of the onset of their sensitive period, that the normal coturnix to which they were exposed sufficiently resembled the adult sexual object, or a combination of these influences.

The conclusion that four Ss in the LEX group were sexually imprinted to albinos may appear to deny the component of primary stimulus object as part of the critical period construct. However, it has been demonstrated that sexually inadequate stimulus objects that previously elicited responsivity in the neonate were no longer attractive when presented to the adult (Andrew, 1966 and Guiton, 1966. See Introduction, page 11). The proposition that stimulus objects are characterized during development by graded levels of approximation to a sexually mature female is considered a possibility and a contributing factor rather than an explanation of the results of the division of preference observed in the LEX group. The condition of individual variation in terms of onset and termination of a sensitive period seems to be at least as an important variable for an explanation of the observed variation in preferences exhibited by the LEX group in the simultaneous choice test.

It has been noted by others (Immelmann, 1972) that there are individual differences in terms of the onset of sensitive periods and that individual differences in terms of chronological age account for the observed variation in sensitive periods for species attachment. This view is supported by the data describing the onset of sensitive periods for the attachment of the following response to a specific object (Bateson, 1966; Gottlieb, 1961; Jaynes, 1957 and Sluckin, 1965). So it is reasonable to conclude that the onset for sexual imprinting began prior to the 16th day posthatch, but that in at least four cases

(in the LEX group) the onset was delayed to the point that insufficient time remained prior to day 16, when the albino age-mate replaced the normal age-mate, in order to establish the normal <u>coturnix</u> as the primary sexual object.

VIII. Mechanisms of Secondary Sexual Attitude.

While it remains reasonable to maintain an imprinting point of view regarding the establishment of the observed primary preference for either normal or albino females, the data clearly indicate that Lorenz's theory of imprinting does not account for all forms by which a stimulus object attains its capacity to evoke sexual responses. This is evident in the apparent modification of the SEX males readiness to mount albino females in the albino test. Even if social experience during a juvenile sensitive period does establish the primary sexual attitude, it would be necessary to explain the manner in which early experience modified sexual attitudes so that albino females would be more readily mounted, as is evidenced in the 100% mounting exhibited by the SEX and LEX groups of albino females in the albino test (Table X).

The most appealing model to explain this behavior is derived from the Groves-Thompson (1970) dual process theory of habituation. This theory postulates that two processes, sensitization and habituation, develop independently as a result of repeated or continued presentation of a stimulus. The development of the two processes are assumed to interact in terms of the final behavior. In support of this theory, neural cells have been described that increase their responsiveness to repeated stimulation (sensitization) while other cells were observed to decrease their responsiveness to repeated stimulation. These two

outcomes are presumed to be processes of the central nervous system that govern the organism's subsequent behavioral response.

It is well known that fear responsivity increases during the first few days posthatch in avians (Bateson, 1964; Collias, 1952; Hess & Schaefer, 1959; Salzen, 1962; and Spalding, 1873). Both Rubel (1970) and Schaller and Emlen (1962) have reported increased fear responsiveness during the first few days posthatch in coturnix. Several investigators have suggested that the onset or incresaed manifestation of fear responsiveness is related to the decreased tendency to approach and follow (Guiton, 1959; Hess, 1959; and Hinde, et al., 1956), and presumably therefore related to the decrease in the tendency to develop an attachment for an unfamiliar social object (Bateson, 1966 and Moltz, 1960).

Thus if a coturnix hatchling is habituated to albinos during a sexually premature period, but not allowed sufficient exposure during a sensitive period, it would be expected that the sexually mature male would more readily approach an adult albino female than a non-habituated male. In this study SEX males and the 6 LEX males that preferred normals in the simultaneous choice test may have habituated avoidance responsiveness to albinos during their earlier exposure period, so that when they were presented with an adult albino female (in the albino test) there was a certain amount of stimulus generalization of the albino age-mate to the adult female. The habituation of avoidance responsivity coupled with the stimulus generalization of sensitization of the readiness to respond to albinos as social objects accounts for the observed difference in mounting albinos in the albino test between the SEX and LEX groups and the PEX group that did not mount albinos

(Table X). The above view that a dual process habituation sensitiza-
tion system serves to establish the secondary sexual attitude is based
on two conclusions. First that fear responsiveness to novel stimuli
increases during the first few days posthatch. And second, that habit-
uation plays a role in the reduction of fear responsiveness in avians.

A. Development of Fear Responsiveness. A number of studies have
described an increase in fear responsiveness in avians to unfamiliar
stimuli or environments as a function of age (Candland, Nagy & Conklyn,
1963; Collias, 1962; Fisher & Campbell, 1964; Hess, 1959c; James &
Binks, 1963; Kruijt, 1964; Schaller & Emlen, 1962). Hebb (1946) sug-
gested fear arises from the animal's sensitivity to discrepancies or
changes in objects in its environment or the environment itself.
Bateson (1966) suggested that the lack of fear responsivity in neonatal
avians is due to the hatchling's lack of experience with its environ-
ment. According to investigators such as Bateson (1971), Salzen (1970),
and Sluckin (1965), observed increases in fear responsivity in juvenile
chicks results from experience with specific aspects of the environ-
ment. Experience with specific stimuli allows the animal to distin-
guish familiar stimuli from unfamiliar stimuli. It is the increase
in the proportion of unfamiliar cues in the juvenile's environment that
produces the observed increase in fear responsiveness. This is in con-
trast to the view that suggests that fear responsiveness in avians in-
creases during development as the result of posthatch development of
neural mechanisms that mediate fear (Hess, 1959b & c and Schaller and
Emlen, 1962). The importance of these divergent views pertains to the
theoretical implication of whether or not innate physiological mechan-
isms are related to changes in the susceptibility of developing an

attachment to a novel social object. If fear responsiveness is tied
to the physical maturation of mediational substrates, then exogenous
variables cannot modify the emergence of fear responses. If exogenous
variables cannot influence the onset of fear responsiveness and novel
social attachment is selectively impeded in a fear responsive animal,
then the behavioral characterization of a critical period would be
supported.

Salzen (1962) demonstrated that experience with stimulus objects
and environments are related to the occurrence of a number of types of
fear responses and that fear responsiveness occurred at all neonatal
stages in Brown Leghorn X Light Sussex chicks. These observations sup-
port Hebb's view that experience with the environment provides the basis
of changes in the incidence of fear responses. Phillips and Siegel
(1966) examined the development of a variety of fear responses in reac-
tion to a two second ringing of an electric doorbell in two strains of
White Plymouth Rock hatchlings (F_6) that had been selected for high and
low body weight. Independent groups of both strains were compared un-
der two conditions of rearing - visual isolation and communal housing.
The latency to peep from onset of the doorbell, percentages of Ss def-
ecating within a twelve minute period from onset of doorbell, latency
to run and distance run all increased from initial low levels as a
function of age during the first week posthatch. There were several
observed differences between treatment groups and strains, so that
there is evidence that both endogeneous and exogenous variables func-
tion to effect particular patterns of fear responsiveness. This con-
clusion is compatible with Denenberg's (1964) general conclusion re-
garding the effects of infantile stimulation upon adult behavior in

rats and mice. Denenberg observed that infantile stimulation reduced
the amount of emotionality exhibited by adults in novel situations; how-
ever, the function of a true critical period for such an effect is some-
what less certain as a generality. Denenberg cautioned that utility
of critical period constructs should be limited to specific contexts.
"...any single 'critical period' is, at least in part, dependent upon
the parameters of stimulus intensity." (1964, p. 337). At this point
it would be premature to conclude that the increase in fear responsive-
ness is not related to the maturation of a neural substrate.

B. The Role of Habituation in the Reduction of Fear Responsivity.
The question that remains is how does experience with an environment or
stimulus object effect the development of the Ss attitude toward its
environment. It was suggested earlier (page 16, Discussion) that when
a hatchling has continued experience with a stimulus object or environ-
ment, then its tendency to avoid that object, or exhibit other 'fear'
responsiveness, is reduced. Thus in an environment to which the S has
habituated, one would expect the S to go about in a normal fashion.
In a novel environment, one would expect that the animal would exhibit
some form of stereotypic response pattern. Indeed, several studies
have indicated that familiarity with the environment (i.e., habitua-
tion of fear responsivity) reduced the amount of following of an im-
printed object. Moltz and Rosenblum (1958) reported that Ss that were
habituated to the experimental apparatus exhibited lower amounts of
following behavior than controls. Moltz, et al., (1959) provided ad-
ditional data to support the view that fear stimuli served to strength-
en the follow response. These investigators administered electric foot-
shock both inside and outside the experimental alley. Ducklings

shocked inside the alley followed more than groups shocked outside the experimental alley and control groups not shocked. Salzen (1966) reported that the removal of tall water vessels from the home cage of chicks increased the amount of distress vocalizations. Hoffman (1968) reported that the amount of distress vocalization in Peking ducklings was proportionately related to the amount of unfamiliarity of the environment subsequent to the removal of an 'imprint stimulus'. The above observations lend support to the view that familiar objects serve to facilitate adaptation to a novel environment by reducing typical fear responsivity.

The fact that the habituation of fear responsivity can be generalized has been demonstrated by Martin & Melvin (1964) and Melvin & Cloar (1969). Martin & Melvin observed a decrement in fear responsivity in bobwhite quail (Colinus virginianus) in response to a live hawk in a group that had previous experience with a hawk silhouette. Melvin & Cloar used an "innate suppression" technique to measure the degree of fear responsiveness upon presentation of a live hawk. Those Ss that were presented with a pigeon in the experimental situation for four days prior to the presentation of the live hawk exhibited significant reduction in their median suppression of key pecking. These observations support the view that habituation to novel stimuli, can genealize to a somewhat varied situation and allow the animal to perform a normal routine, even when the stimuli possess innate capacity to elicit fear. Thus, the early experience with albino age-mates served to habituate the SEX male's avoidance of albino stimuli, thus increasing the probability that these males would view the albino female as a potential sexual object. The sensitization to albinos as social objects served

to release sexual responsiveness to the albino female in those cases
where the albino female is not the preferred object.

IX. Latency to Mount in the Simultaneous Choice Test.

The data describing the latency to mount a female demonstrate
that exposure to albino age-mates serves to increase the amount of
time from the release of the females to mounting a female (Table VIII).
Since the observed differences in mount latencies between the SEX, PEX,
and LEX groups were not significant (Table IX) the variation in laten-
cies among these groups cannot be considered an effect of treatment.
The observed increased latencies imply that the effect of exposure of
albino age-mates is to establish the albino as a somewhat competitive
sexual object to the normal female. In the case of the SEX group, this
effect only momentarily retards the male's advance toward the normal fe-
male. In the PEX group this effect is harder to appreciate in that
there was a consistent selection of the albino female in the simultan-
eous choice test for this group. It may be the case that while the
PEX male holds the albino as its primary sex object, the albino female
itself may not contribute the same sexual invitation as a normal female.
This point is mere conjecture in that there were no apparent behavioral
postures or patterns that differentiated the albino and normal females.
An alternate explanation is that the male in the SEX, PEX and LEX groups
finds the albino female an interesting sexual object but in some cases
not as attractive as the normal female. Thus, the rise in latency is
viewed as resulting from a decision or choice that is being made and
that such a consideration is not being made by the NEX male. An explan-
ation of this order is appealing in that all of the Ss exposed to albi-
nos prior to testing accepted the albino as a sex object in the albino

test, while some males preferred the normal female in the simultaneous choice test. Further, it was demonstrated by the SEX group that prior experience with normal coturnix is not necessary for males to mount normal females. So that, only the NEX group appeared not to attend to the albino female as a potential sexual object. At least, in this study there was no observation of a NEX male that mounted an albino female in any of the test conditions.

X. Comparison of the Approach and Mount Data.

The observation that only the NEX group reliably approached and mounted the same female (normal) raises a question pertaining to the validity of using an approach measure to indicate sexual preferences. A number of students of imprinting have used the "approach response" as a measure of the animal's preference between two objects (Gottlieb, 1965, 1971; Hess, 1964; Klinghammer & Hess, 1964 and Salzen and Meyer, 1967, Salzen et al., 1968). The meaning of such a response must be considered as unclear. In the case of the NEX group the approach response proved to be a valid predictor of the males' subsequent selection between the normal and albino females for mounting. Thus when the coturnix male has had no previous experience with albino age-mates, then its sexual attitude toward normal females is quite robust. This robustness is reflected in both invariant selection of the normal female to approach and mount and the unhesitating manner in which the NEX male executes its mounting. In all other groups there appears to be some evidence of uncertainty and/or hesitation in terms of the approach response. It is clear that in the SEX, PEX and LEX groups the albino female constitutes a sex object, in that all of these males mounted the albino female either in the simultaneous choice test or in

the albino test. Since three of the SEX males approached albino females
it can be presumed that the SEX male is responding to the presence of
an added, although less desirable, sexual object. In the PEX and LEX
groups there was a lower incidence of approaching as well as more cases
of approaching both the normal and albino females. Thus it can be in-
ferred from the approach and mount data (Table XI) that the greater the
amount of experience with albino age-mates the less likely a coturnix
male will be decisive in his choice between normal and albino females.
This condition is further evidenced in the greater latency to mount in
the simultaneous choice test by albino experienced males (Table VIII).
Thus the experience with albino age-mates requires sexually mature males
to engage in some increased evaluation between the normal and albino
females.

The conclusion that experience with albino age-mates serves to in-
crease time related processes of discrimination in the simultaneous
choice test is interesting in that it further suggests that the "sexual
attitudes" that have been described in this paper are varied and that
the mechanisms that produced each of the attitudes may have been inde-
pendent. The fact that the approach-mount data are unrelated except
in the NEX group draws attention to the problem of assuming a relation-
ship between separate behavioral responses. The fact that it is neces-
sary for males to approach a female prior to mounting does not mean
that males that will mount a free and accessible female will stand near
the same female when she is confined.

XI. Conclusion.

It may be the case that the coturnix is genetically programmed to
acquire its species identity in a special manner, such as is described

by the imprinting process. However, this condition does not necessarily preclude the coturnix from acquiring a sex habit with albinos by an alternate means, such as the dual-process mechanism of habituation and sensitization that has been proposed in the discussion. The fact that 'primary sexual attitudes' were observed and that the exposure condition necessary to establish the primary sexual attitude for the normal was different from the albino indicates that the stimulus features of the object acquired are not comparable. The fact that greater exposure duration with albino age-mates ultimately produces a primary preference for albinos indicates that there is a process by which the male's attitude toward a normal can be modified to include albinos. The fact that this can happen even when the male has had previous experience with normal age-mates suggests the importance of social experience during particular ontogenetic periods.

The observation of various sexual attitudes toward albino females indicates that the use of behavioral measures of particular species to infer or criticize psychological principles such as the sensitive period or irreversibility must be considered within the context of the animals nature as well as the independent variables. For example, the coturnix male is highly active sexually (Schein, et al., 1972) and is quite promiscuous (Wallace, 1963). Hence, it would be unreasonable to expect that the coturnix would not adapt sexually outside the limits of a sensitive period. Whereas in the case of the ring dove Streptopilia risoria (Lehrman, 1964) or the Canada goose Branta canadensis (Ramsay, 1951) prolonged courtship patterns occur prior to copulation and monogamous mating patterns exist. In animals that typically manifest monogamous sexual patterns it is reasonable to expect that sexual

imprinting would result in behavior wherein sexual responsivity would be more or less permanently restricted to a conspecific of the imprint object. In promiscuous species, on the other hand, permanency of an imprint effect could only be determined in a simultaneous choice test.

The recognition of variation in species sexual behavior should free investigators from the polemics of the controversy that imprinting is a unique process and allow a more fruitful study of the context in which animals typically acquire their species identity and the extent to which typical behavior is dependent upon endogenous and exogenous variables. It is certain that the imprinting process does not account for all of the observed sexual attitudes of the coturnix. However, it would be premature to rule out the importance of sensitive periods in the development of the 'primary sexual attitude'.

The coturnix is highly suited for further laboratory research pertaining to the amount of social experience necessary to establish the albino as the 'primary sexual object'. The question of a precise time-course of a sensitive period can be investigated without undue hardship of prolonged social isolation. Subsequent description of the precise time-course of a sensitive period will further strengthen the view of how the imprinting process establishes a species identity, but it will not provide evidence that only the imprinting process can produce such an outcome.

SUMMARY

The present investigation has focused on the relationship of so-
cial experience during different developmental stages and subsequent
mating behavior. Japanese quail <u>Coturnix</u> <u>coturnix</u> <u>japonica</u> were em-
ployed as subjects in that these avians become sexually mature as early
as 42 days posthatch and they readily mate in an experimental apparatus.
Four different treatments of exposure to albino Japanese quail were
compared on a number of measures to determine how a particular regimen
of social experience might affect social behavior in sexually mature
males.

The four experimental treatments were: First, exposure to normal
age-mates only for either the first 5 or 20 days posthatch and then
isolation from the 21st day posthatch (NEX). Second, exposure to al-
bino age-mates for the first 5 days posthatch and then isolation (SEX).
Third, exposure to only albino age-mates during the first 20-25 days
posthatch and then isolation (PEX). Fourth, exposure to normal age-
mates during the first 15 days posthatch, exposure to albino age-mates
from day 16 through day 25, and then isolation.

The first measure obtained was the experimental virgin male's ap-
proach to a confined female in a simultaneous choice test between a
normal and albino female. This measure proved to be an unreliable pre-
dictor of mate preference except in the case of the NEX group. Hence,
except for those cases wherein subjects are reared with typical social
objects can one expect that measures such as the approach response be
related to more typical social interaction such as mating.

The second observation was the mount preference for either the
albino or normal female in a simultaneous choice test. Both the NEX

and SEX groups selected normals 100% of the time. The PEX group selected albinos in all but one case. The LEX group was essentially equivocal with respect to a preference, 6 selected normal females and 4 selected albinos. This observation demonstrates that it is possible to establish the albino coturnix female as the preferred sexual object on the basis of a program of social experience. The data are discussed in terms of mechanisms that may serve to produce the observed differences among treatment groups.

The final observation was whether or not coturnix males would mount albino females (within 5 minutes) when they were presented alone. This latter observation served to differentiate the NEX and SEX groups and suggested that sexual responsiveness toward a particular social object may result from more than a single influence. Again, data from the albino test were discussed in terms of the mechanisms that were thought to be responsible for the observed differences among groups.

An imprinting mechanism is thought to be responsible for the selection of albinos in the simultaneous choice test for both the PEX and LEX groups. The rationale for such a conclusion was based on the difference between the SEX and LEX groups in the number of subjects selecting an albino female in the simultaneous choice test. No members of the SEX (early exposure period) group mounted albinos in the simultaneous choice test, whereas 4 LEX's (later exposure period) mounted albinos in the simultaneous choice test. This difference was concluded to have resulted from social experience at a later ontogenetic stage rather than due to the increased duration of exposure in that the LEX group was exposed to normals for 15 days (a greater amount than the 10 day exposure treatment) and the SEX was not exposed to normals at all.

A habituation-sensitization mechanism is thought to be responsible for the difference in mounting albino females in the albino test between the NEX group and the SEX and LEX groups. No NEX mounted an albino female, whereas all SEX and LEX males mounted albino females. This interpretation is based on the observation that avians generally manifest increased fear responsiveness toward novel objects after the first few days posthatch, and that experience with novel objects has been shown to reduce subsequent fear responsivity toward the experienced object. Further, it is assumed that in addition to the generalization of habituation from the earlier exposure to albinos there also was some generalization of sensitization to albinos as social objects.

The _coturnix_ appears to be a highly suitable species for the further study of those parameters effecting preferences for albinos in a simultaneous choice test.

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
APPENDIX I

	Approach		Simultaneous Mount		Albino (1st)	
NEX	N	A	N	A	A	N
2N	:59		1.92			.05
220a	:16		4.39			4.74
220b	1:22		.05			4.05
223	:37		.37			2.00
221	:16		.54			1.09
226	:07		1.16			1.42
301	:34		1.41			2.11
302	:27		2.31			1.57
404	:22		2.10			1.43
606	–		3.04			1.36
SEX						
A9	1.47		.01		.02	
A109	:09	:26	.10		.70	
212	–	–	3.69		4.63	
300	:17	:12	4.71		4.04	
303	:19	:08	2.84		2.12	
502	–	–	4.24		3.78	
608	:23	–	4.07		3.19	
609	:09	–	8.14		4.17	
703	:08		.69		.07	
704	–	–	1.23		.16	

PEX	Approach		Simultaneous Mount		Albino (1st)	
	N	A	N	A	A	N
A103	–	–		2.25	.10	
401	1:17	–		1.02	.04	
403	–	–	9.71		.50	
501		:10		6.30	.17	
600		.28		3.49	.48	
601	:27			4.53	.71	
602	:12			.29	.08	
700	–	–		1.70	.05	
701	:13			9.63	.42	
702		:14		.82	.37	
LEX						
N208	–	–		.14	.17	
N209	–	–		2.58	1.26	
402a	–	:36	9.16		.72	
402b	–	–		7.24	.15	
505a	–	–	3.10		.09	
505b	:19	–	4.68		4.21	
607	:12	:11	2.18		3.09	
611	–	–		2.55	1.17	
NA705	:51		1.61		4.14	
NA706	:21		3.54		3.33	

COPY 1