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# Sociogenesis of species-typical and species-atypical behavior in mallard ducklings

Sexton, Cheryl Ann, Ph.D.

The University of North Carolina at Greensboro, 1994

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# SOCIOGENESIS OF SPECIES-TYPICAL AND SPECIES-ATYPICAL BEHAVIOR IN MALLARD DUCKLINGS

by
Cheryl Ann Sexton

A Dissertation Submitted to
the Faculty of the Graduate School at
The University of North Carolina at Greensboro
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Although social experience has been recognized as important for the development of behavior, little is known about how social experience contributes to behavioral development. This study demonstrated that altering the social experience of young, developing ducklings can induce novel behavioral phenotypes as well as constrain the development of novel behavior, and also investigated the mechanisms by which such phenomena occur.

First, the influence of the social environment for inducing atypical preferences was demonstrated. Previous research has shown that the mallard duckling's naive preference for the mallard maternal call can be altered by providing very specific auditory experiences during prenatal and postnatal development. A species-atypical preference for the chicken maternal call over that of the mallard will result if ducklings are prenatally exposed to the chicken call for 48 hours, but not if they lack this prenatal exposure. This study showed that a non-prenatally exposed duckling reared socially with peers that were exposed prenatally to the chicken call developed the atypical preference, in contrast to a non-exposed duckling that was socially reared with other non-exposed peers.

Second, several hypotheses of possible mechanisms of the social environment that induced the development of the atypical preference for the chicken call were investigated. I assessed whether prenatally exposed ducklings behave differently during social rearing experience than non-prenatally exposed ducklings by comparing their behavior and vocalizations during 48 hours of social rearing. The results showed that prenatally exposed ducklings do not approach the speaker more than non-prenatally exposed ducklings, thus failing to support the hypothesis of imitation. Prenatally exposed ducklings also were not less aroused, thus failing to support the hypothesis of optimal arousal for learning. Vocal behavior was different between the two groups, suggesting that the hypothesis of stimulus enhancement by vocalizations was correct. However, vocalizations were subsequently ruled out as a necessary for atypical behavior to develop because ducklings reared with muted peers learned the preference as well as ducklings reared with vocal peers. Finally, it was shown that specific social enviroments are necessary for the atypical preference to develop in prenatally exposed ducklings as well as non-prenatally exposed ducklings. The results in sum illustrate the truly bi-directional, interactive nature of the developmental system, to which social influences make a critical contribution. The implications of these results for understanding evolutionary change and stasis are discussed.

## APPROVAL PAGE

This dissertation has been approved by the following committee of the Faculty of the Graduate School at the University of North Carolina at Greensboro.

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# CHAPTER I

# INTRODUCTION

The maintenance of species-typical behavior has been a major topic of interest within the fields of animal behavior and development. The argument that characteristics remaining stable across generations are genetic in origin has been replaced by the more sophisticated understanding that an entire developmental complex is inherited by the offspring; it is this complex that ensures inter-generational stability (Gottlieb, 1971; Lickliter & Berry, 1990; Oyama, 1992; West & King, 1987). One aspect of the developmental complex is the social environment in which the offspring are reared. This aspect of the environment, like other environmental components such as sensory stimulation or nutrition, has been suggested as a canalizer for the development of species-typical behavior (Galef, 1976; Gottlieb, 1991b, 1991c; Klopfer, 1961, Stamps, 1991).

In contrast, a variety of experiences has also been shown to alter the development of species-typical behavior. A number of studies have demonstrated the kinds of experiences that can induce atypical development, including auditory experiences (Gottlieb, 1982), visual experiences (Gottlieb, Tomlinson, & Radell, 1989; Lickliter, 1990a; 1990b), and temperature (Matsuda, 1987). Social interaction has also been shown to be an inductive experience for novel behavioral development (reviewed below). The development of atypical or novel behavioral phenotypes is an important first step for producing variation within a species that can lead to evolution (Bonner, 1983; Gottlieb, 1992; Piaget, 1978; Reid, 1985). Only after they have first appeared in development can variations be selected according to the principle of natural selection, as first pointed out by Mivart in 1871 (cited in Gottlieb, 1992).

The purpose of this research was to investigate how the development of both species-atypical and species-typical behavior is affected by the social environment ducklings experience during their early development. In the wild, the precocial duckling is typically reared in the company of other ducklings which, it is argued, is an important component of species-typical development. Usually, the social environment serves to limit the probability that novel behavior will be expressed by supporting the development of species-typical behaviors through transmission of similar patterns of behavior from individual to individual within a population as a consequence of social interaction (Galef, 1976; King, 1968; Klopfer, 1961). Therefore, altering aspects of the social environment may be fundamental for inducing novel phenotypes. The goal of the current research is to investigate some possible mechanisms of the social environment that perturb species-typical development and make behavioral modification possible.

## The Importance of Modifiability for Evolutionary Change

The promotion of atypical behaviors during development is as interesting as the development of species-typical behaviors (Gottlieb, 1987a, 1987b). Atypical behaviors, or changes in behavior, have been suggested by many theoreticians to be the first step toward evolutionary change (Bonner, 1983; Gottlieb, 1992; Johnston & Gottlieb, 1991; Lamarck, 1809/1984; Leonovicova & Novak, 1987; Mayr, 1963; Piaget, 1978; Reid, 1985; Wyles, Kunkel, & Wilson, 1983). Behavioral change is most readily accomplished by overcoming or changing the canalizing influences that are present in the usual course of individual development. Several writers have recognized that altering canalizing factors and the resultant production of novel behavior during development (by other than genetic means) could act as an important mechanism of evolution (Gottlieb, 1992; Gray 1987; Jamieson, 1986; Johnston & Gottlieb, 1991; Matsuda, 1987; Reid, 1985; Stamps, 1991; Tierney, 1986). Therefore, studies of atypical behavioral development deserve much more attention than they have received in the past since such studies provide critical insights for understanding the role of behavior in evolution.

The canalizing influences of development leading to species-typical outcomes are not restricted to genetic influences. Natural selection operates on phenotypes without regard to their developmental history. Thus, natural selection involves a selection for the entire developmental manifold, including both the intrinsic (genetic) and normally occurring extrinsic interactants of ontogeny (Gottlieb, 1971; Lehrman, 1970). These extrinsic features include nutrition, temperature, parent-offspring interactions, habitat, sensory experiences, and social interactions, among others. The development of species-specific characters does not need to be dependent upon features which have become "genetically assimilated" or "innate", so long as the necessary extrinsic features are invariably present during the usual course of ontogeny (Johnston & Gottlieb, 1991). Therefore, variations in species-typical behavior may arise from a change in any one of the interactants in the developmental process, either intrinsic or extrinsic. The aim of these experiments was to demonstrate the influence of one of these interactants, namely, social experience with peers that have or have not had certain prior experiences during development.

## The Significance of the Social Environment for the Induction of Species-Atypical Behavior

The social environment, defined here as interaction of an organism with other members of its own species, is particularly interesting for studying the modifiability of developmental outcomes. The social environment provides a rich array of constantly changing cues available to predict future events. Additionally, social learning has been long recognized as a mechanism for introducing behavioral novelties

(Galef, 1988). Boyd and Richerson state "...social learning is interesting because it mixes aspects of a system of inheritance with aspects of ordinary phenotypic flexibility, creating a system for the inheritance of acquired variation" (1988, p. 32). It has even been suggested by Vygotsky that social experience is the factor which fosters all higher psychological processes in humans (van de Veer & Valsiner, 1988). Thus, understanding the way social experience interacts within the developmental complex of an organism may provide clues to the evolution of the most complex behaviors.

Perhaps the most striking evidence of the impact of social influence on species-atypical development is offered by the song learning literature. Juvenile songbirds interactively tutored by an adult male of a different species will learn the songs of that species, whereas they will not learn those songs if they are merely broadcast by a tape recording (Baptista & Petrinovich, 1984, 1986). Thus, social interaction with the adult tutor induces species-atypical behaviors in the young songbird. The actual mechanism or means by which the social interaction achieves its effect has not been investigated.

Social interaction with similarly aged conspecifics has also been shown to be important in the development of species-typical behavior. The species-typical behavior of "freezing" is observed in ducklings when they hear the maternal alarm call of their species. However, ducklings only show this behavior if the social setting during exposure to the alarm call is the same as the setting in which they were reared (Miller, et al., 1990). In particular, ducklings reared in isolation freeze when they hear the alarm call if they are alone, but not if they are with other ducklings. Likewise, socially reared ducklings freeze to the alarm call only if they are with conspecifics, but not if they are alone. Although the mechanism by which these alternate responses develop has not been investigated, Miller's experiments provide a further demonstration of the importance of social experience to normal development.

## Modifiability of Behavioral Development in Mallard Ducklings

All studies to date with precocious birds have demonstrated the same species-typical behavior. The young hatchlings of these species have a "naive" preference for the maternal call of their own species including chickens (*Gallus gallus domesticus*), domestic and wild mallard ducks (*Anas platyrhynchos*), wood ducks (*Aix sponsa*) (Gottlieb, 1971), willow grouse (*Lagopus lagopus)* (Allen, 1977, 1979), bobwhite quail (*Colinus virginianus*) (Heaton, Miller, & Goodwin, 1978), and Japanese quail (*Coturnix coturnix japonica*) (Park & Balaban, 1991). Historically, this preference for the species-specific call was believed to be an innate ability that functioned in imprinting. Subsequent experiments have revealed this naive preference to be an epigenetic outcome requiring specific, normally occurring experiences during embryonic development. For example, the experience of hearing self-produced vocalizations or conspecific vocalizations is necessary for promoting the species-typical maternal call preference in two species of ducklings (summarized in Gottlieb, 1981).

Experiments with domestic mallard ducklings (Gottlieb, 1991a) have shown that species-typical development can be "derailed" by offering non-typical auditory experiences during embryonic and early post-hatching development. Mallard ducklings which have been exposed to a <u>chicken</u> maternal call for 48 hours before and 48 hours after hatching demonstrate a preference for the chicken maternal call over the mallard maternal call if they are reared socially in small groups of siblings. Ducklings given the same non-typical auditory experience but reared in isolation (without siblings) do not prefer the chicken call but rather display the species-typical preference for the mallard maternal call. Therefore, it appears that the species-typical social experience is a critical component for inducing change into the developmental process.

However, little is known about the specific aspects of socialization that promote atypical behavioral development. Physiological and sensory experiences provided by the social experience obviously must contribute to the modification of the typical developmental process. For example, Gottlieb

(1993) demonstrated the importance of tactile stimulation for inducing atypical behavior. He reared ducklings with the non-typical auditory experience in non-typical rearing situations that deprived the ducklings of specific sensory experiences, either visual, auditory, or tactile. Ducklings reared together but deprived of seeing each other developed the atypical preference for the chicken call, and ducklings reared together but deprived of hearing each other also developed the atypical preference. In contrast, ducklings that were deprived of tactile contact showed the species-typical preference for the mallard maternal call, even though they could see and hear each other through clear plastic barriers during rearing. When ducklings were reared with stuffed ducklings, thereby receiving tactile contact, they also developed the atypical preference. Gottlieb hypothesizes that tactile contact promotes an optimal level of arousal for learning the non-typical maternal call, thus allowing behavioral development to be modified. Ducklings that are appropriately aroused are most able to learn the atypical preference.

To recap, mallard ducklings that experience the chicken maternal call both prenatally and postnatally develop an atypical preference for the chicken call over the mallard call if they are reared socially, but not if they are reared in isolation. It is important to note that the required amount of auditory experience with the chicken call is quite high; it must be provided for 48 hours before and 48 hours after hatching for 30 minutes every hour. If this auditory experience is reduced, the atypical preference does not develop. This has been demonstrated with socially-reared ducklings exposed to the chicken call only postnatally, and with socially reared birds that were exposed to the chicken call only prenatally (Gottlieb, 1991a). The absence of either the prenatal or postnatal exposure to the chicken call allowed the normally canalized behavior of a naive mallard maternal call preference to develop.

### Purpose of the Study

This project had two main purposes. First, to demonstrate how social interactions with ducklings that had prenatal and postnatal exposure to the chicken call would induce a preference for the chicken call in a target duckling that had only postnatal exposure to the chicken call. Second, to discover the mechanism by which this social experience achieves its effect.

To this end, I determined if the absence of prenatal exposure to the chicken call could be compensated for by providing certain social experiences to the developing organism. I determined that a target duckling would develop the atypical preference for the chicken call, even when it did not have the normally required prenatal auditory stimulation, if it was socially reared with other ducklings that <u>did</u> have the prenatal auditory experience, as long as all the ducklings experienced postnatal exposure together. The induction of atypical behavior in the prenatally-deprived target duckling must result from the postnatal social experience it has with broodmates that experienced the chicken call prenatally.

In studying the influence of socialization on behavioral development, I focused on the contribution of the broodmates' activity for inducing the atypical preference behavior in the target duckling. I hypothesized that some process of enhanced social learning must take place during the interactions of the ducklings. The processes by which social learning occurs are a matter of debate (review in Galef, 1988) and poorly understood. Therefore, this study examined three likely ways the social rearing experience could have its effect on the target duckling.

The first hypothesis holds that social learning results from imitation, in which an individual learns a behavior by directly observing another perform that behavior. Since the training and testing conditions are so dissimilar, imitation does not seem likely in the present case; nonetheless, some component of the behavior in the testing situation may be modeled by broodmates in the rearing environment. For example, broodmates that have been exposed to the chicken call prenatally may be attracted to the broadcast of the chicken call during postnatal social rearing and move toward the speaker whenever the call begins. If target ducklings model this behavior during social rearing, they may also move toward the speaker broadcasting the chicken call in the testing arena. Another possibility is that if prenatally-exposed ducklings spend more time under the speaker in social rearing, target ducklings may learn to associate the comfort of their siblings with the broadcast of the chicken call, and thus be attracted to that call in the testing arena. Experimental observations were therefore made to test these possibilities.

The second possible mechanism was optimal-arousal. Gottlieb (1993) showed that although ducklings reared in social groups develop the atypical preference, ducklings that are prevented from touching each other (but can see and hear one another) fail to learn the atypical preference. He demonstrated that ducklings without tactile contact were much more behaviorally aroused, and suggested that ducklings that are overly aroused cannot learn to prefer the chicken call. In the current study, all subjects had complete tactile contact. However, it is possible that ducklings that do not have prenatal experience with the chicken call fail to show the atypical preference (Gottlieb, 1991) because they are overly aroused by the novel auditory stimulation provided after hatching. The socialization effect in the current study may result, therefore, from a calming effect the prenatally stimulated broodmates have on the target duckling, thereby inducing an optimal level of arousal that permits learning to occur.

The third mechanism I explored was stimulus enhancement. Spence (1937) defined stimulus enhancement as "a change in stimulus conditions, the enhancement of the particular limited aspect of the total stimulus situation to which the response is to be made" (p. 821). Stimulus enhancement suggests the behavior of conspecifics draws attention to a previously neutral stimulus in the environment, making it more salient to the individual. The individual then performs the novel behavior because the characteristics of the stimulus promote that action. In the present case, stimulus enhancement might occur if some behavior of the prenatally-exposed broodmates increased the saliency of the auditory experience for the non-exposed target duckling, which otherwise might ignore the broadcast. The most obvious way the broodmates may alert the target duckling to the chicken call broadcast is by vocalizing more often when the call begins, specifically, emitting more "contact" calls.

To investigate the contributory influences of socialization on development, it is necessary to compare animals that have been reared in similar situations, excepting their social interactions with others. However, an experimenter cannot instruct a social group of broodmate ducklings to behave in certain ways toward a target duckling. Therefore, I reared target ducklings with broodmate ducklings that differed in their developmental histories, assuming that different developmental experiences might result in different social interactions with target ducklings. Specifically, I reared target ducklings that had no prenatal exposure to the chicken call in two conditions: (1) either with broodmates that had prenatal exposure to the chicken call and subsequently showed a preference for that call, or (2) with broodmates that did not have prenatal exposure to the chicken call, and subsequently did not prefer the chicken call. In this way, the impact of specific social environments on the development of behavior can be demonstrated.

## Hypotheses and Predictions

Recall that:

a) "POST" ducklings have not been prenatally exposed to the chicken call but do experience the call postnatally in a social group; they typically <u>do not</u> prefer the chicken call over the mallard call in an auditory choice test.

b) "PRE/POST" ducklings have been exposed to the chicken call both prenatally and postnatally in a social group. PRE/POST ducklings typically <u>do</u> prefer the chicken call over the mallard call.

1. Social Induction Hypothesis. If social interactions with broodmates can induce the development of an atypical preference for the chicken maternal call, then a target POST duckling reared with PRE/POST broodmates will prefer the chicken call.

2. Imitation Hypothesis. If the target duckling's atypical preference is learned by imitating the motor behavior of its broodmates, then the PRE/POST broodmates and the target ducklings they are reared with should show a greater affinity for the speaker that broadcasts the chicken stimulus during social rearing than the POST broodmates and their targets. Specifically, PRE/POST broodmates and targets should spend more time under the speaker and should approach the speaker more often when the call is broadcast than POST broodmates and their targets.

3. Arousal Hypothesis. If the target duckling reared with PRE/POST broodmates demonstrates the atypical preference because it is optimally aroused compared to ducklings reared with POST broodmates, then the PRE/POST duckling broods should emit fewer distress calls (a measure of behavioral arousal) than POST duckling broods.

4. Saliency/Vocalization Hypothesis. If the target duckling demonstrates the atypical preference because the broodmates increase the saliency of the chicken call by emitting "contact" vocalizations, then the PRE/POST ducklings should give a greater number of contact calls than the POST ducklings, when the chicken call is being broadcast.

If a greater number of contact calls are given by PRE/POST ducklings than by POST ducklings, that provides evidence that vocalizations could be important for directing the target's attention to the stimulus. However, other behaviors of the broodmates may also increase the saliency of the chicken stimulus even in the absence of vocalizations. This can be tested by rearing target ducklings with muted broodmates. If contact vocalizations are critical for inducing the atypical preference in the target duckling, then target ducklings reared with muted PRE/POST broodmates will not develop the atypical preference for the chicken call, unlike target ducklings reared with vocal PRE/POST broodmates.

5. Social Support Hypothesis. To support the development of species-atypical behavior in a prenatally-exposed duckling, social interaction may need to be provided by ducklings with similar developmental histories in order to be maintained, and may be derailed by social interactions with conspecifics that have different developmental histories. If a social environment consisting of similarly developing ducklings is necessary for atypical behavior to develop, then PRE/POST target ducklings reared with POST ducklings should not develop the atypical preference, unlike ducklings reared with PRE/POST broodmates.

# CHAPTER II

# EXPERIMENT ONE

## Can Social Interaction Induce Atypical Development?

If social interaction induces the development of atypical behavior, then a duckling which normally develops the species-typical preference should develop the atypical preference when reared with other ducklings that show the atypical preference. To test this hypothesis, I reared target ducklings that had no prenatal experience with the chicken call (POST) and then tested their preferences in an auditory choice test with the chicken call and mallard call at 48 hours. In the Control condition, the target animal was reared with a social group of 5 broodmate ducklings which, like the target, had no prenatal experience (POST). In the Experimental condition, the target animal was reared with a social group of 5 broodmate ducklings that did have prenatal experience (PRE/POST) with the chicken call. If social interaction with prenatally-exposed broodmates can induce the development of atypical preference behavior, then target ducklings reared with the Experimental broodmates should develop the atypical preference whereas target ducklings reared in the Control condition should not.

## Method

### *Subjects*

Subjects in all experiments were Peking ducklings, a domesticated form of the mallard duck (Anas platyrhynchos). This breed demonstrates species-typical behaviors similar to the wild form (Gottlieb, 1971; Miller, 1977; Johnston & Gottlieb, 1981). Fertile, unincubated duck eggs were received weekly from a commercial supplier. Duck eggs were incubated at around 38 °C and 65-74% relative humidity in Petersime incubators which turn the eggs automatically every 6 hr for 23 days. The eggs were then transferred to separate hatchers in which the same conditions were maintained. The hatching eggs were checked frequently and the time of hatching of each duckling was recorded to the nearest hour. All ducklings used in these experiments were reared socially; prenatally they were in the hatchers with other hatching eggs, and postnatally they were in communal rearing boxes. To control for the possible influence of between-hatch variation, subjects in each condition came from different batches of eggs on a weekly basis, until 25 subjects were obtained for each condition.

National and institutional guidelines for the care and use of animal subjects were followed in all experiments.

### *Embryonic and postnatal stimulation*

Embryos that received prenatal stimulation were exposed in the hatcher to a tape recording of a chicken maternal call beginning on day 24 of prenatal development, approximately two days before hatching. The embryos were stimulated by sound emanating from eight small (10 cm) Oaktron weatherproof speakers on a tray 8 cm above the tray on which the eggs were kept, so that each egg was quite close to the sound source. After hatching, the ducklings were placed in a communal brooder with a single large (16 cm) speaker (Acoustic Research midrange dome radiator) suspended about 12 cm above the floor.

The sound equipment was on for 30 min/h from day 24, 0800 (around 48 h before hatching) until about 48 h after hatching, at which time the birds were given a preference test. During the 30-min period, the chicken maternal call is actually broadcast for 22.5 min.

### *Testing apparatus*

Standard simultaneous auditory choice preference tests were conducted, as described by Gottlieb (1975). All ducklings in a rearing group were tested individually in the same testing apparatus at around 48 h after hatching (range: 44-52 h). Testing was conducted in a circular arena, 178 cm in diameter, surrounded by an 81-cm high opaque black curtain, which shields the observer from the duckling's view. The subject's behavior was observed by means of an angled mirror placed above the arena. The duckling was placed in the test apparatus equidistant from two hidden loudspeakers. All the birds were given a 5-min simultaneous choice test between the mallard and chicken maternal calls, each of which emanates from one of the loudspeakers. The speaker which emanated the chicken call was randomly chosen, and alternated so that half of the group heard the chicken call from one speaker and half the group heard it from the other speaker. To control for stress levels associated with the experimenter removing animals to the testing arena, the target duckling was always the third duckling to be tested. The sound intensity of the calls peaked at 65 dB (scale B, fast reading) at the point where the duckling was introduced into the test arena.

Exposure to the chicken call in the communal rearing boxes was terminated at the time of the 48-h test; the birds were retested at approximately 65 h (61-69 h) to determine if they retained the preference shown at 48 h without further exposure to the chicken call. The speaker which emanated the chicken call at retest was the opposite speaker used in the test. The testing room was maintained at around 20 °C throughout testing.

A system of foot-operated timeclocks was used to score the latency and duration of each duckling's response to the calls. An atypical preference was scored only if the duration score in the approach area of the chicken call was at least twice that accumulated in the approach area of the mallard call. To analyze whether the birds within a group showed a preference for the atypical call, the binomial test was used (if $p < .05$, then the group demonstrated a preference). As a further measure of preference, the differences between the raw duration scores (in sec) to each call were analyzed using the Wilcoxon test. To preclude the inclusion of transient wanderers in the responding category, birds that accumulated an uninterrupted total of less than 10 sec in the approach area of either call were scored as non-responders and were excluded from the analyses. All $p$ values were one-tailed in the hypothesized direction.

Test Calls: The mallard maternal call used in these experiments is composed of 9 notes which make up a burst. The repetition rate of the notes in the burst is 3.7 notes/sec. The chicken maternal call is composed of 7 notes and occurs at a repetition rate of 2.3 notes per second.

### *Rearing procedure*

Upon hatching, each duckling was marked with a colored pen for individual identification. The duckling was then placed in a large box with opaque walls (62 x 34 x 28 cm) with 5 broodmates that hatched within 3 hr of the target duckling. The rearing compartment was heated by two 75-W bulbs, one at each end, which maintained the temperature at 29-31 °C.

**Results and Discussion**

Since Gottlieb (1991a) showed that social groups of ducklings exposed only to postnatal stimulation fail to develop the chicken call preference, I expected the same result for my Control condition. This finding was confirmed, as shown in Table 1. This table also shows that, as predicted, the Experimental target ducklings exhibit a statistically significant preference for the chicken call over the mallard call at both 48 and 65 hours. Results from Wilcoxon Signed Rank tests on the duration scores support this conclusion. These findings reconfirm results I obtained in a pilot study (see Appendix A).

**Table 1.** Preferences of target ducklings in simultaneous auditory choice test with mallard and chicken maternal calls at 48 and 65 h after hatching in Experiment One.

| | | | | Preference | | |
|---|---|---|---|---|---|---|
| | Age (h) | *N* | Number responded | Mallard | Chicken | Both |
| Control | 48 | 25 | 25 | 17 | 6 | 2 |
| | 65 | 25 | 21 | 9 | 10 | 2 |
| Experimental | 48 | 25 | 25 | 5 | 18* | 2 |
| | 65 | 25 | 24 | 1 | 23** | 0 |

*$p$=.022, **$p$<.001, binomial test

The Control results show that POST ducklings raised in a social context fail to develop the atypical preference, presumably because they lack prenatal experience with the chicken call. This behavioral outcome can be modified simply by rearing a POST duckling with broodmates that have heard the chicken call prenatally. The only factor that differed between the rearing environments of the POST and PRE/POST broodmates was the prenatal experience of broodmates. Therefore, the difference must be due to a difference in the way the two kinds of broodmates behave during the 48 hours of social rearing.

# CHAPTER III

# EXPERIMENT TWO

## Tests of Competing Hypotheses to Explain the Effect of Social Induction

Given that the development of species-atypical behavior was induced by 48 hours of communal living, I investigated three possible psychological mechanisms by which this could occur.

## The Imitation Hypothesis

The explanation usually offered when social learning has been demonstrated is imitative behavior. However, imitation does not seem a likely explanation for the results obtained in this study, for several reasons. First of all, the behavioral response measured in this study (the preference test) is a novel behavior performed by an individual alone in the testing apparatus. Additionally, there is a striking difference in context between the test situation and group rearing; the preference test takes place in a markedly different environment that is much larger and brighter, and offers a choice between two auditory stimuli. An individual's psychological state is also very different during the test: ducklings typically are very aroused during the test and emit a high number of distress calls. In contrast, during social rearing, the ducklings are in a non-threatening environment and are exposed to only one auditory stimulus. However, it is possible that during social rearing the ducklings perform a component of the behavior shown in the preference test. During the broadcast of the chicken call (which occured at regular intervals during rearing), the target duckling's broodmates may demonstrate their own attraction to the call, which subsequently, may be imitated by the target duckling and transferred to the preference test. For example, if PRE/POST broodmate ducklings congregate under the speaker that broadcasts the chicken call during rearing, or approach it more often than POST broodmates, the target duckling may learn to approach the speaker either by imitating their behavior or associating the chicken call with the comfort of their broodmates. To empirically investigate this possibility, I observed the groups in Experiment One and compared their behavior during rearing. The PRE/POST broodmates from the Experimental group and the POST broodmates from the Control group were compared on their proximity to the speaker that broadcast the chicken call, as well as their respective target ducklings. If the imitation hypothesis is correct, then broodmates of the Experimental group should be under the speaker more often and approach the speaker when the call begins, unlike broodmates of the Control group.

*Method*

The subjects consisted of the ducklings described in Experiment One. Seventeen Control groups and sixteen Experimental groups were randomly selected for observation. Each duckling's position relative to the speaker was noted four times during the postnatal social rearing period at 12 ± 3 hour intervals. The 12-hour intervals were at the following times 1) 6 hours after hatching, 2) 18 hours after hatching, 3) 30 hours after hatching, and 4) 42 hours after hatching. These intervals allowed for sampling to occur across the 48 hours of social rearing and were averaged together for all analyses unless otherwise noted. Each group was observed by means of an angled mirror above the rearing box. A circular area (diameter 22 cm) directly under the speaker delineated the "speaker zone." An animal which had more than half of its body within this circle was considered *IN* the speaker zone, otherwise it was *OUT*. In addition, any duckling which was in tactile contact with a broodmate in the approach zone was noted but also scored as *OUT*. During every observation period, a "snapshot" record (Altmann, 1974) of each duckling's position was noted every minute for 5 min. The observation periods occurred at the following times: 1) the last 5 min of the silent period before the call was broadcast, 2) the first 5 min of the 30-min broadcast of the maternal call, 3) the last 5 min of the 30-min call period, and 4) the first 5 min of the silent period when the call was not broadcast. The five snapshot records within an observation period were averaged to provide an estimate of the activity for that period. Sixteen Experimental groups and seventeen Control groups were observed.

I performed two-sample Wilcoxon rank-sum tests (equivalent to the Mann-Whitney *U*) to determine whether a greater percentage of PRE/POST broodmates was in the speaker zone than POST broodmates, for each observation period, averaged across all time periods. The behavior of the target animal was similarly analyzed, using the average number of *IN* scores per observation period as the dependent variable. Additionally, the differences between scores of the first observation period (when the chicken call was silent) and the second (when the chicken call began) were analyzed to determine if subjects approached the speaker when the call began. The latter analyses were also conducted for each individual time period to examine longitudinal changes in behavior using a Repeated Measures Analysis of Variance.

### *Results and Discussion*

As shown in Figure 1, the percentage of PRE/POST broodmates under the speaker in the Experimental group was not statistically significantly different from the percentage of Control POST broodmates, for any observation period (all $p > .1$; actual $p$ values are provided in Appendix B, Table I). Even though the PRE/POST broodmates had prenatal experience

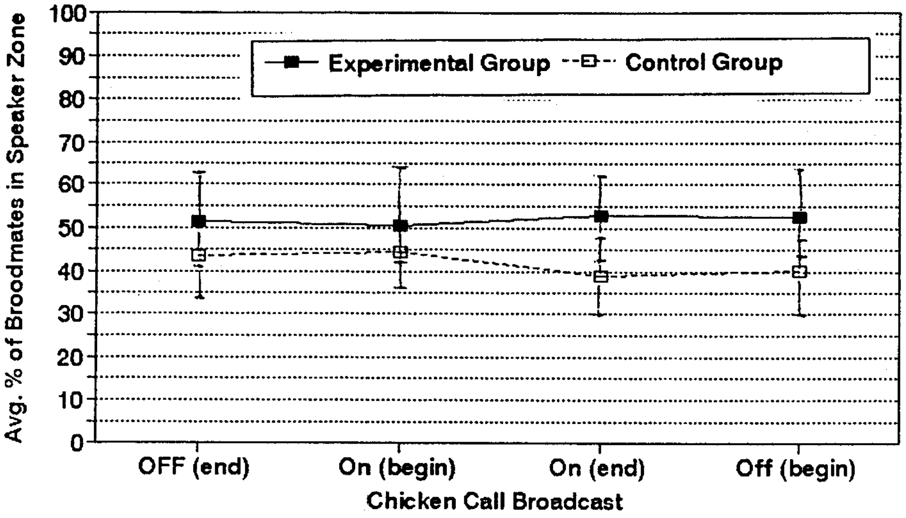

*Figure 1 Broodmates' presence in speaker zone (and 95% Confidence Interval bars)*

with the chicken call, they were not more likely to be clumped under the sound source of the call than the broodmates that had no prenatal experience with the call. Similarly, Figure 2 shows that target animals reared with PRE/POST broodmates were no more likely to be in the speaker zone than target animals reared with POST broodmates, for any observation period (all $p > .1$). This is additional evidence that the proximity to the speaker of both target animals and broodmates appear to be similar across conditions.

It may be argued that the important behavior is not time spent under the speaker but rather actually moving toward the speaker when the call begins. To address this issue, the measure obtained during the observation period taken during the last 5 min of the 30-min silent period was subtracted from the measure obtained during the first 5 min after the call began. The percentage of PRE/POST broodmates under the

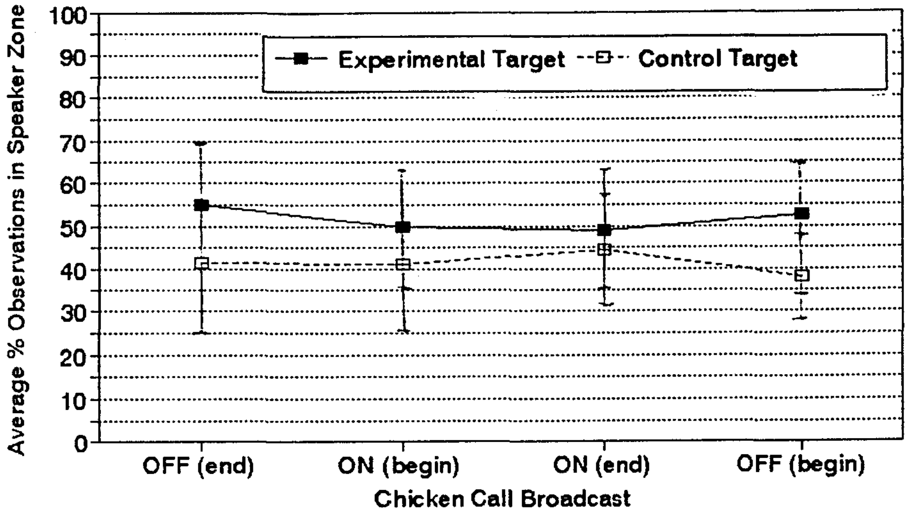

*Figure 2.* *Targets' presence in the speaker zone (and 95% C.I. bars)*

speaker when the broadcast began actually decreased (mean = -.88%) and was not statistically different from the POST broodmates of the Control group (mean = .70%; *p* = .69). This pattern of results was similar for the target ducklings; the target ducklings' percentage of observations under the speaker was not statistically different in the two groups (*p* = .91).

These results suggest that the attractiveness of the chicken call for the Experimental target ducklings does not result from closer proximity to the chicken call during rearing, associating the call with the comfort of siblings, or observing broodmates approach the speaker when it is broadcast.

Thus far, all of the results analyzed the behavior of the subjects averaged across all four time periods (6 hr, 18 hr, 30 hr, and 42 hr after hatching). To examine whether

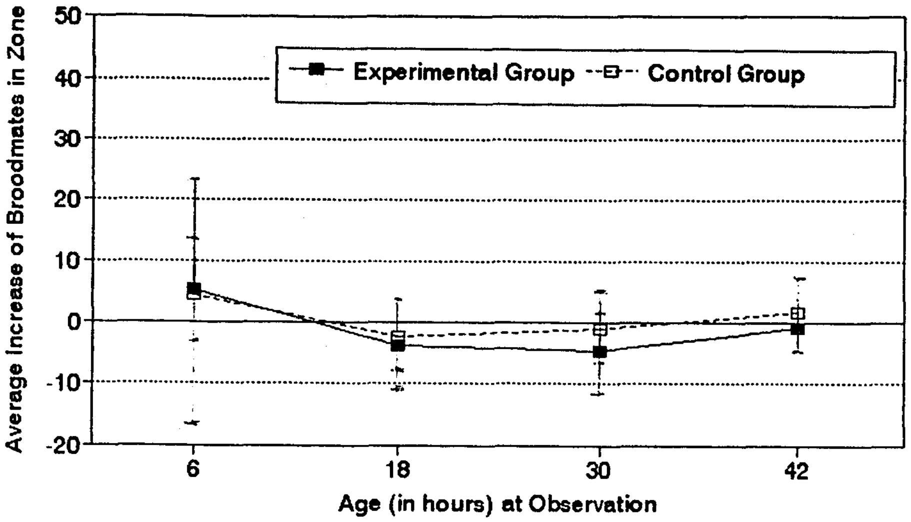

*Figure 3. Mean increase (95% C.I.) of broodmates observed under the speaker when call began*

longitudinal changes in orientation to the chicken call occurred, the percentage of ducklings under the speaker during the 5-min period before the call began was subtracted from the first 5-min period after the call began, and these differences were compared for each age observed. As Figures 3 and 4 illustrate, behavior of the target and broodmate ducklings do not appear to change across ages. The repeated measures analysis of variance confirms this impression (ANOVA tables in Appendix B, Table II).

Thus, it appears that the modification of the Experimental target ducklings cannot be explained simply by suggesting that the target ducklings learn to approach a speaker broadcasting the chicken call by imitating their PRE/POST broodmates.

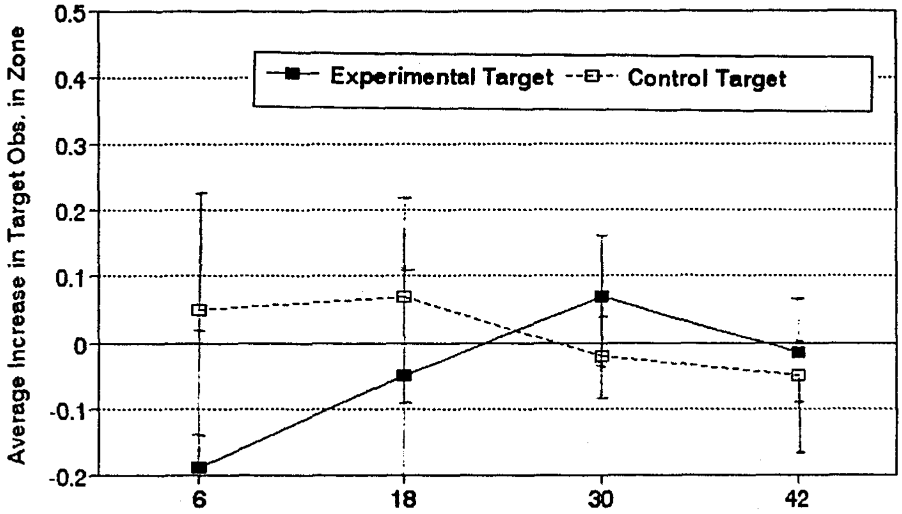

*Figure 4.* *Mean increase (95% C.I.) in observations of target under speaker when call began*

**The Optimal-Arousal Hypothesis**

Another explanation for the difference in developmental outcomes of the two groups is that POST ducklings fail to develop the species-atypical preference because they are simply too aroused to learn the novel call. Hebb (1955) first suggested that an optimal arousal level may be necessary for learning, and his hypothesis has been supported a number of times. Gray (1990) showed that highly aroused chicks, as indicated by a high rate of distress peeping, had the poorest performance on an auditory discrimination task. Gottlieb (1993) demonstrated that ducklings reared in tactile isolation but with constant auditory and visual contact preferred the species-specific mallard call and displayed much higher rates of distress calling during rearing and behavioral testing. In contrast, ducklings reared socially with tactile contact prefer the chicken call and emit lower rates of distress calling. The overly aroused ducklings failed to show the atypical developmental outcome (preference for the chicken call). It may be argued that in Experiment One of the present study, ducklings not exposed to the chicken call prenatally are more aroused by the postnatal stimulation than ducklings that have been prenatally exposed to the chicken call because the call is unfamiliar to the former and its broadcast disturbs them. If this is true, then the socially reared POST broodmates should be more aroused during exposure to the chicken call since they have not had the prenatal exposure of the PRE/POST broodmates. Since high numbers of distress vocalizations have been shown to been positively correlated with non-optimal high arousal levels and non-modifiability in ducklings (Gottlieb, 1993), I used distress vocalizations as a measure of arousal.

### *Method*

As described above, I monitored the Experimental and Control groups during social rearing. All vocalizations emitted were noted for each of four, 5 min observation periods that were performed at 12 hour intervals. Vocalizations were classified as either 1) unambiguous distress calls (high-pitched, long, slow notes, Scoville & Gottlieb, 1980), 2) unambiguous contact calls (low-pitched, short, fast notes, Scoville & Gottlieb, 1980) or 3) other. Because vocalizations of particular individuals are very difficult to discriminate during social rearing, the values reported refer to the entire group of 6 ducklings, with the vocalizations of the target and five broodmates combined. Calls were compared between the two groups using one-tailed Wilcoxon Rank-Sum tests, predicting that ducklings in the Control group would emit more distress calls.

### *Results and Discussion*

The average number of distress calls per 5-min observation period across all 4 time periods is given in Table Two. The number of distress calls per 5-min observation period given by the Control group was not statistically greater than the number emitted by the Experimental group (*p* = .89). It is apparent that in both conditions, ducklings were not aroused enough to emit a notable number of distress calls.

**Table 2.** Overall mean (S.E.) vocalizations.

| Call Type | Condition | N | Mean | Std Error |
|---|---|---|---|---|
| Distress | Control | 17 | .02 | .009 |
| | Experimental | 16 | .07 | .034 |
| Contact | Control | 17 | 6.99 | 1.89 |
| | Experimental | 16 | 10.36 | 2.57 |
| Other | Control | 17 | 158.94 | 15.28 |
| | Experimental | 16 | 134.46 | 9.98 |

The average number of contact vocalizations and vocalizations classified as other are also given in Table 2.

A higher frequency of either contact or other vocalizations might suggest a higher level of general arousal in a group. As Figure 5 illustrates, no statistical differences were observed between conditions for contact vocalizations ($p$ = .83) or other vocalizations ($p$ = .12).

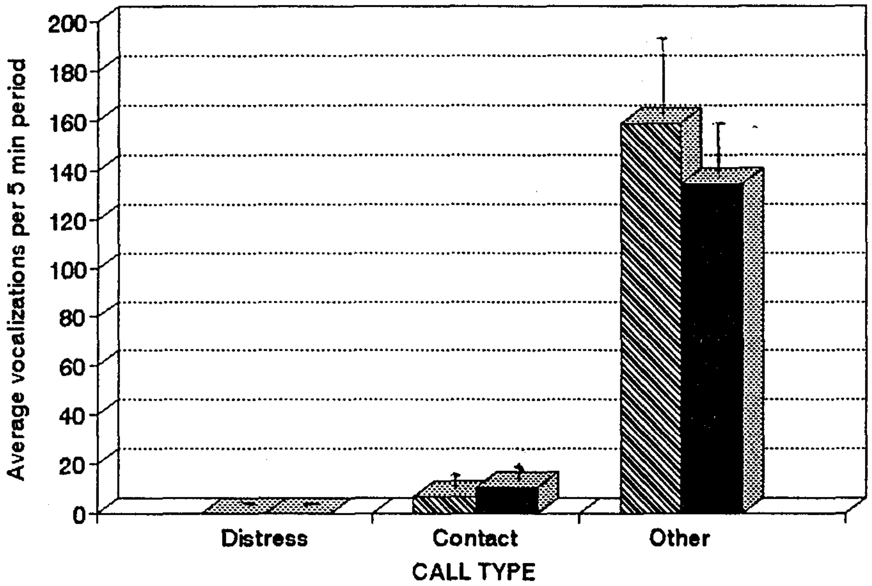

*Figure 5.* *Mean vocalizations (and 95% C.I.) during social rearing.*

Based on this information, I conclude that the control ducklings were not excessively aroused; the failure for target ducklings reared with POST broodmates to develop the atypical call preference does not result from being reared with overly aroused siblings.

## The Saliency/Vocalizations Hypothesis

The previous results failed to support the hypotheses of imitation or optimal-arousal as explanations for the induction of species-atypical behavior by social interaction. A third way the induction may occur is by a process of stimulus enhancement. Specifically, the target POST duckling may develop the atypical preference because the vocalizations of its PRE/POST broodmates direct the attention of the target duckling to the chicken call, making the call more salient to the target duckling. It has been shown that embryos deprived of prenatal exposure to their own or siblings' contact calls have a reduced sensitivity to certain components of the mallard maternal call; in particular, the higher frequencies (Gottlieb, 1976) and the repetition rate specificity (Gottlieb, 1979) incorporated within the maternal call. It seems likely, therefore, that prenatal exposure to the chicken maternal call would facilitate the development of sensitivity to certain auditory components of the call. Ducklings which have prenatal exposure to the chicken maternal call may find the call more salient because of an increased auditory sensitivity, and are thus more likely to learn to prefer the novel call during postnatal exposure than ducklings without prenatal exposure.

The saliency hypothesis suggests that the behavior of the broodmates of the target POST duckling directs its attention to stimuli in its environment that might otherwise be ignored. For this study, the saliency hypothesis proposes that some behavior of the PRE/POST broodmates directs the attention of the target duckling to the chicken call, making the call more salient to the target duckling and promoting the development of its auditory preference for the call. What behavior of the PRE/POST ducklings might play this role is not known; however, prior research has demonstrated the critical importance of contact vocalizations for the development of the species-typical preference for the mallard call (Gottlieb, 1979, 1980a, 1982). Additionally, Gottlieb (1993) observed that socially reared ducklings that developed the atypical preference for the chicken call gave more contact calls during rearing than tactually-isolated ducklings which failed to develop the atypical preference. Therefore, one way in which the chicken call may become more salient to the target duckling is by association of the chicken call with the contact vocalizations of its broodmates. The previous results showed that the absolute number of contact vocalizations did not vary across groups, but the analysis did not reveal <u>when</u> vocalizations were given. If the contact calls serve as attention-getting signals, then PRE/POST broodmates should call more when the stimulus begins than POST broodmates.

### *Method*

The frequency of contact vocalizations given during social rearing was collected for the two conditions in the manner described above. The difference between the number of contact vocalizations given during the last five min of the silent period and the first five min of the broadcast period was compared across conditions using one-tailed Wilcoxon tests on the paired differences. Vocalizations classified as "other" were also compared because they may in fact be a variant of the contact call or serve some communicative function that is still unknown. Additionally, I analyzed the differences between the last 5 min of the stimulus period and the first 5 min of the silent period, to be sure that changes in call frequency are a function of the stimulus itself, and not just a change in the sensory environment.

### *Results and Discussion*

As shown in Table 3, the increase in contact vocalizations given during the first 5 min of the chicken call's broadcast in the Experimental groups was statistically greater than the Control groups ($p = .002$). The same was true for the vocalizations classified as other ($p = .0009$).

**Table 3.** Average change in ducklings' vocalization frequencies when the chicken call began (averaged across all 4 time periods).

| Call Type | Condition | N | Mean | Std Error |
|---|---|---|---|---|
| Contact | Control | 17 | - 1.53 | 1.69 |
| | Experimental | 16 | 11.89 | 5.15 |
| Other | Control | 17 | 32.19 | 19.51 |
| | Experimental | 16 | 122.77 | 14.89 |

One-tailed Wilcoxon Signed-Rank tests were also performed to determine whether the observed differences were significantly greater than 0. The differences were statistically greater for the Experimental groups (contact calls: *N* = 16, *p* = .0008; other calls: *N* = 16, *p* = .00005) but not for the control groups (contact calls: *N* = 17, *p* = .79; other calls: *N* = 17, *p* = .08). The analysis of the differences between the last 5 minutes of the stimulus period and the first 5 min of the quiet period did not yield any significant differences, showing that the effect is specific to the onset of the chicken call, not simply a response to a change in the environment.

A repeated-measures analysis of variance was performed on the differences between the silent period and when the chicken call came on to examine if the increase in vocalizations varied as a function of age. The average change in contact calls is shown in Figure 6. Not surprisingly, the effect of

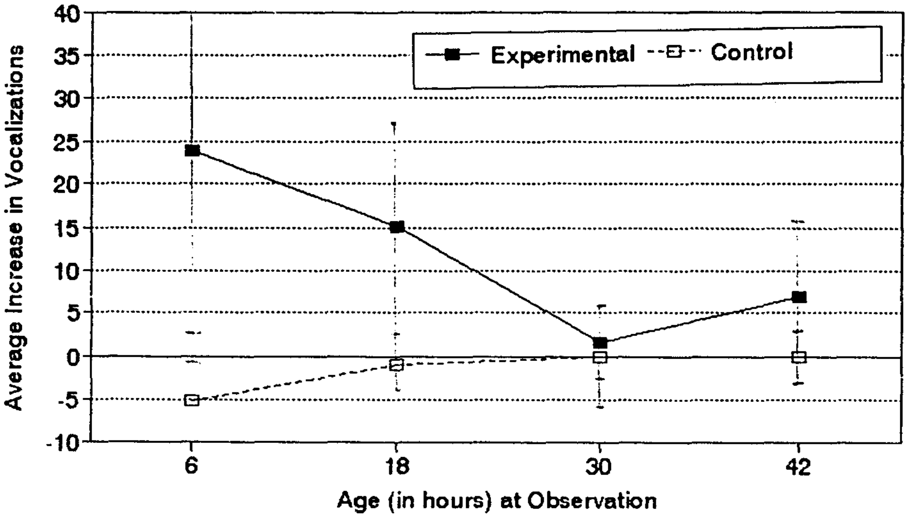

*Figure 6.* *Mean increase (95% C.I.) in contact calls in the 5 min following onset of the chicken call.*

rearing groups was significant ($F_{(1,31\ df)}$ = 6.45, $p$ = .02). The effect of age was not significant ($F_{(1,3\ df)}$ = 1.08, $p$ = .3604) but a significant interaction exists ($F_{(1,3\ df)}$ = 2.99, $p$ = .0351). This interaction results from a diminishing effect of the call on vocalizations given by the PRE/POST group over their first day of life, compared to the effect on the POST group, which stays about zero across the two days. The analysis of the unclassified other vocalizations (shown in Figure 7) also shows the significant effect of group ($F_{(1,31\ df)}$ = 13.37, $p$ = .0009). The trend for increasing vocalizing across ages is not significant ($F_{(1,3\ df)}$ = 2.20, $p$ = .09), and neither is the age by group interaction ($F_{(1,3\ df)}$= .66, $p$ = .57).

These longitudinal analyses indicate that the PRE/POST ducklings' vocal response to the chicken call changes over

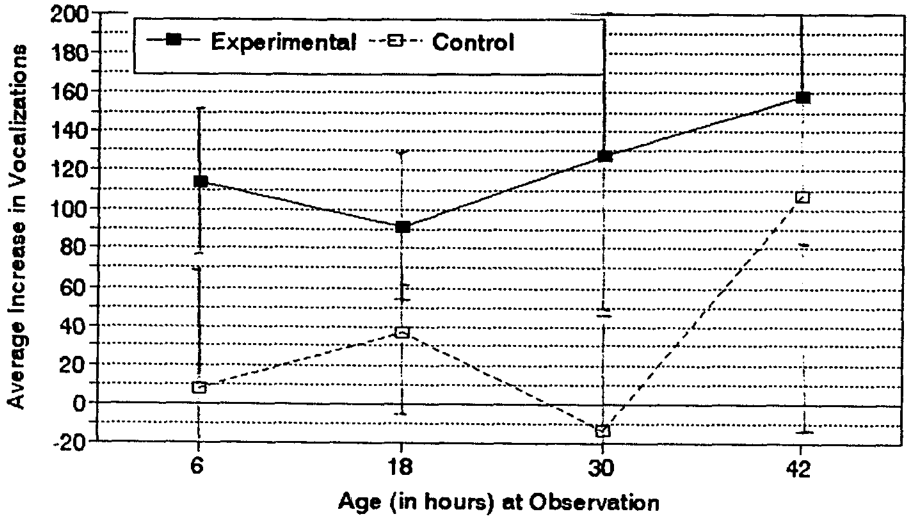

*Figure 7 Mean increase (95% C.I.) in other vocalizations in the 5 min following onset of the chicken call.*

time. At six hours after hatching, PRE/POST ducklings dramatically increase the frequency of contact calling when the chicken call is broadcast, unlike the POST ducklings. This effect also occurs at 18 hours, but not as strongly. By the second day, PRE/POST ducklings are less responsive to the broadcast. The change of the unclassified other calls in response to the chicken call broadcast is more variable across time in both groups, but it is clear that PRE/POST ducklings give many more vocalizations to the broadcast than POST ducklings do. Thus, these results indicate that the onset of the call has different effects on the vocal behavior of the Experimental and Control groups. Although it is unknown what the increased frequency of vocalizations of the PRE/POST broodmates indicate to the target duckling, it is not unreasonable to speculate that calling in response to the onset of the chicken call broadcast at the very least makes the call more noticeable, as suggested by the Saliency/Vocalizations Hypothesis.

# CHAPTER IV

## EXPERIMENT THREE

### Influence of Vocalizations on Modifying Behavioral Outcomes

The finding that more contact calls were given by PRE/POST broodmates when the call began suggests that an association between the chicken call and the contact vocalizations exists for the broodmates, but does not specifically address whether the contact calls are necessary for inducing the atypical preference in the target duckling. To further investigate the importance of vocalizations for inducing malleability, I reared target POST ducklings each with 5 muted PRE/POST broodmates. If the target duckling does not prefer the chicken call, then that supports the hypothesis that the vocalizations of the broodmates play a role in the induction of the atypical preference. If, however, the target duckling still develops a preference for the chicken call in this situation, it indicates that the vocalizations of the broodmates are not necessary to influence the development of the target duckling. Some other, more subtle behavior of the broodmates would be implicated by that result.

#### *Method*

The methodology for rearing and testing ducklings was the same as described for the Experimental group in Experiment One with the exception that all 5 PRE/POST broodmates in the social group were muted before hatching. The POST target duckling did not undergo the muting procedure, thereby retaining its voice. Thirteen groups of muted ducklings were tested.

Muting procedure: Ducklings that are muted undergo the following operation. On day 24 of incubation (about 2 days before hatching), eggs are candled and embryos which are "tenting" are selected for the muting procedure. A small hole is cut in the shell over the airspace, then the embryo's head and neck are extracted. A topical anesthetic is injected under the skin directly above the syrinx. A small incision is then made to expose the internal tympaniform membranes of the syrinx. Collodion, a non-toxic surgical glue, is applied directly to these membranes which then forms a rigid sheath and prevents the membranes from vibrating and producing sound (Gottlieb, 1975). The incision is closed with surgical glue and the embryo is replaced in the hatcher until it hatches. This procedure does not cause permanent damage (the duckling recovers its voice after the experiment), nor significant mortality as compared to unoperated controls (Gottlieb, 1975).

### *Results and Discussion*

As shown in Table 4, target ducklings reared with muted PRE/POST broodmates developed the atypical preference for the chicken call over the mallard call just as target ducklings reared with normal PRE/POST broodmates. This surprising result is evidence against the hypothesis that the calls of broodmates are required for inducing the development of the atypical preference for the chicken call.

**Table 4.** Preferences of target ducklings in simultaneous auditory choice test with mallard and chicken maternal calls at 48 and 65 h after hatching in Experiment Three.

|  | Age (h) | *N* | Number responded | Preference |  |  |
|---|---|---|---|---|---|---|
|  |  |  |  | Mallard | Chicken | Both |
| Muted | 48 | 13 | 13 | 1 | $10^{*}$ | 570 2 |
| Broodmates | 65 | 13 | 12 | 1 | $10^{**}$ | 1 |

$^{*}p = .046$, $^{**}p = .011$, binomial test

It is important to note that the average percent of muted broodmates per group that demonstrated the atypical preference for the chicken (76%) was similar to the average percent of Experimental (non-muted) broodmates that demonstrated the atypical preference (77%). Thus, the muting procedure and subsequent social rearing with drastically reduced exposure to sibling vocalizations (recall that the target subject retained its voice) did not affect the development of a species-atypical preference in these broodmates.

# CHAPTER V

# EXPERIMENT FOUR

## Is Specific Broodmate Behavior Necessary?

The previous experiments investigated three possible mechanisms by which the broodmates could be influencing the target duckling, but none of these appear to explain the effect. However, specific social interactions of prenatally-exposed broodmates must be provided in order to induce change in a non-exposed target duckling. Given that prenatally-exposed ducklings do not develop atypical preferences when reared in isolation, but do so when reared socially, the question arises: Is it merely being reared socially that suffices or are social interactions peculiar to PRE/POST ducklings required? To investigate this question, I compared the preferences of PRE/POST target ducklings each reared with 5 POST broodmates to the preferences of POST target ducklings each reared with 5 PRE/POST broodmates. If specific interactions peculiar to PRE/POST broodmates are necessary above and beyond mere stimulation of the social environment, then a PRE/POST duckling reared with POST broodmates should not develop a preference for the atypical call. Since there is reason to believe from the foregoing experimental results that PRE/POST ducklings do offer some subtle cues to their POST target duckling, it was predicted that in this instance, the PRE/POST target duckling would not develop the atypical preference for the chicken call because the social cues provided by fully exposed, PRE/POST broodmates are absent.

### *Method*

The methodology and testing of the subjects were the same as described for Experiment One with the following exception. The prenatal experiences of target and broodmate ducklings was reversed, so that in this experiment the target duckling had pre- and postnatal experience with the call, and the 5 broodmate ducklings had only postnatal experience. In other words, this group was a reversed version of the original Experimental group.

### *Results and Discussion*

The preferences of the target ducklings in this Reverse Experimental group are given in Table 5, along with the results of Experiment One for comparison. The target ducklings in the Reverse Experimental group do not behave the same as the ducklings in the Experimental group; when tested at 48 hours, Reverse Experimental target ducklings do not manifest a preference for the chicken call whereas Experimental target ducklings do. Even though these target ducklings had prenatal exposure to the chicken call that the Experimental targets did not have, it would appear that their social environment failed to support the development of the atypical preference. However, these target ducklings did not behave the same as the Control target ducklings either.

**Table 5.** Preferences of target ducklings in simultaneous auditory choice test with mallard and chicken maternal calls at 48 and 65 h after hatching in Experiment Four.

|  | Age (h) | *N* | Number responded | Preference |  |  |
|---|---|---|---|---|---|---|
|  |  |  |  | Mallard | Chicken | Both |
| Reverse Experimental | 48 | 26 | 25 | 11 | 14 | 1 |
|  | 65 | 26 | 24 | 5 | 19* | 0 |
| Control | 48 | 25 | 25 | 17 | 6 | 2 |
|  | 65 | 25 | 21 | 9 | 10 | 2 |
| Experimental | 48 | 25 | 25 | 5 | 18 | 2 |
|  | 65 | 25 | 24 | 1 | 23 | 0 |

*$p$ =.005, binomial test

Reverse Experimental target ducklings do show a preference for the chicken call at 65 hours, which the Control ducklings do not. To understand this result, recall that the first preference test is given after 48 hours of the chicken call broadcast, then the broadcast is turned off and the ducklings are retested after about 17 hours of silence at 65 hours. The latent preference of Reverse Experimental target ducklings for the chicken call at 65 hours may reflect some sort of disinhibition from "suppressive" cues given by POST broodmates during the first 48 hours when the chicken call was broadcast. These results indicate that in order for the atypical preference to develop, it is not enough for a PRE/POST duckling to interact socially with just any conspecifics; rather, specific interactions with PRE/POST conspecifics are necessary. This further supports the idea that some specific behavior of the broodmates supports the atypical development, beyond just the sensory stimulation provided by the presence of ducklings.

The social influence is hardly unidirectional. The behavior of the target duckling also affected the development of the POST broodmates. To demonstrate this effect, the mean percentage of broodmates that preferred the atypical call was calculated for each group and then compared to the percentage of targets that displayed the atypical preference[a]. Figure 8 shows these values for the test at 48 hours. Although the broodmates of the Control group and Reverse Experimental group had the same prenatal experience (i.e. no exposure to the chicken call), the average percentage of Reverse Experimental broodmates demonstrating a preference for the chicken call does not fall within the 95% confidence interval of the Control broodmates percentage. Apparently having just one PRE/POST duckling among the group affected its development.

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[a] Direct comparisons between broodmates and targets are not made because the five broodmates within a group are not independent, therefore the percentage of broodmates that display the atypical preference is calculated *per group* as opposed to using the total *N* of 125 ducklings. Using the per-group calculation decreases the degrees of freedom rendering more conservative estimates of the parameters.

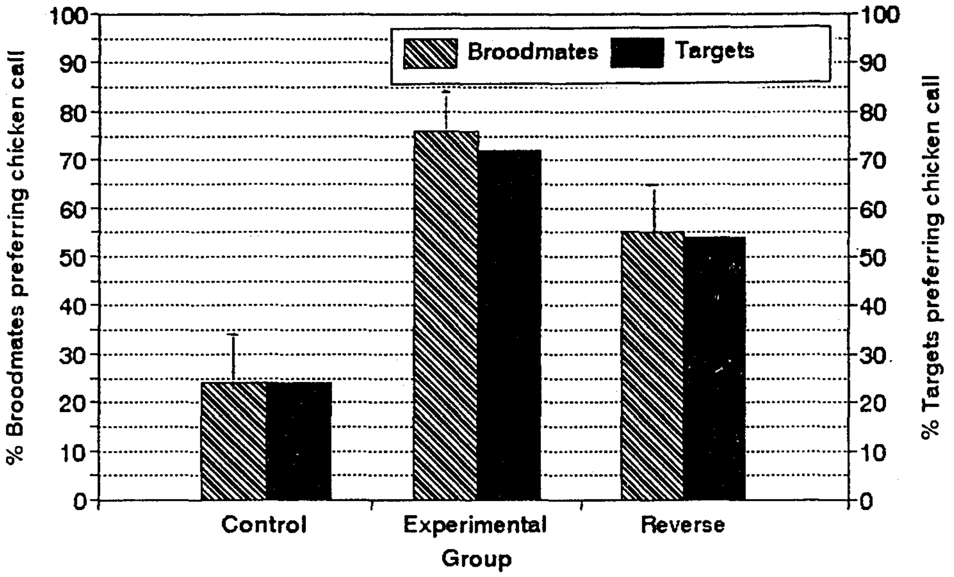

*Figure 8.* *Average percentage (and 95% C.I.) of ducklings preferring the chicken call at 48 hours.*

The same was true for the retest at 65 hours (Figure 9). Of particular interest is the comparison of the Reverse target

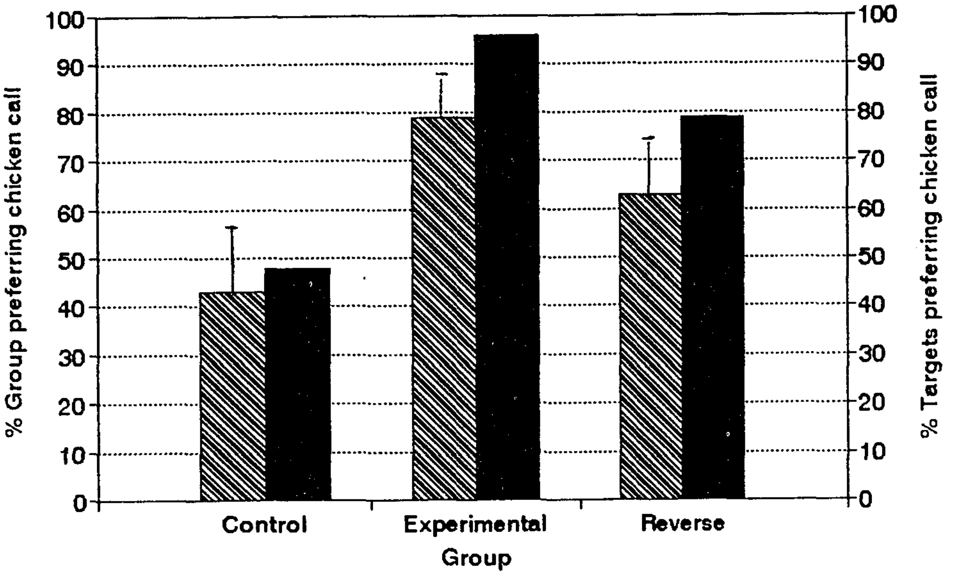

*Figure 9.* *Average percent (and 95% C. I.) of ducklings preferring the chicken call at 65 hours.*

ducklings, which had prenatal experience, to Experimental broodmates, which also had prenatal experience. If the postnatal social environment had no effect, then these percentages should be the same. But the Reverse targets do not lie within the 95% confidence interval of the Experimental broodmates, indicating that rearing with POST broodmates affects the development of the preference for the chicken call, at least at the 48 hour test. After the silent period from 48-65 h however, the Reverse target ducklings do show preference behavior similar to that shown by Experimental broodmates. Perhaps there are cues supplied by POST broodmates ducklings which inhibit the development of the atypical preference and are removed when the call is no longer broadcast.

In general, these results clearly indicate the bi-directional interactive nature of the social environment; a difference in many members can affect a single member and a difference in only one member can affect the whole group.

# CHAPTER VI

# GENERAL DISCUSSION

The purpose of this study was to investigate how the social environment affects behavioral development. The results show that POST target ducklings reared in a social environment of PRE/POST ducklings overcome their prenatal deficit and share the atypical preference their broodmates demonstrate, whereas POST target ducklings reared with other POST ducklings do not. These findings suggest that the behavior of conspecifics provides some subtle cue during the broadcast of the chicken call that influences the developing organism, thereby inducing a novel behavioral outcome.

In addition to demonstrating that social interaction can induce a novel phenotype, this study investigated several possible means or mechanisms of the social induction. Obviously, a likely explanation for such results is imitation. In this study, it could be argued that target ducklings chose the chicken call over the mallard call in the test situation because they learned to approach the speaker broadcasting the chicken call in the rearing box by observing their broodmates doing so. However, differences in approach behavior during social rearing were not observed; the prenatally exposed broodmates were not more likely to approach the speaker broadcasting the chicken call than prenatally deprived animals, nor did they spend more time under the speaker than the others.

Previous research suggested the second hypothesized mechanism. Gottlieb (1991a) demonstrated that an optimal level of behavioral arousal may be necessary for learning to occur, and that over-arousal can prevent the development of a preference for a species-atypical call. However, this mechanism does not explain the results observed here. When Gottlieb compared tactually isolated ducklings to physically interacting ducklings, he found that isolated ducklings were very aroused, emitting an average of 19.9 distress calls per 5-min observation period, and failed to develop a preference for the atypical call. In contrast, ducklings that were able to physically interact emitted only 2.3 distress calls on average, and developed the atypical preference. Like the latter group, all the ducklings in the present study were reared in social groups that allowed them to touch each other. This rearing situation apparently prevented them from becoming overly aroused, for the overall mean of distress calls was less than 1.0 per 5-min observation period in both the Control and Experimental groups.

The third hypothesis, stimulus enhancement, is still a possible mechanism, but its effector remains unclear. Previous research showed that socially reared ducklings, which develop the atypical preference for the chicken call, gave more contact calls than tactually isolated ducklings, which do not show the preference for the chicken call (Gottlieb, 1993). Accordingly, it was hypothesized that PRE/POST broodmates might vocalize more when the chicken call broadcast begins than POST broodmates, thereby enhancing the saliency of the call for the target duckling. Although PRE/POST ducklings in this study did not give more contact calls than POST ducklings, they did increase their contact call production when the chicken call was broadcast, which suggested that indeed vocalizations were an agent of saliency provided by the social environment. To test this idea, the original Experiment One was repeated using PRE/POST broodmates that could not vocalize. If contact calls are essential for the induction of change, deleting them from the social setting should result in target ducklings that fail to develop the atypical call preference. This was not the case, however: targets reared with muted broodmates showed the atypical preference, indicating that contact vocalizations are not necessary to induce species-atypical development. Of course, muted broodmates may still react to the broadcast of the chicken call in a variety of ways: for example, postural changes, startles, head movements, or bill movements (without producing sounds). Any of these behaviors could increase the saliency of the chicken call to the target duckling.

The first three experiments investigated how an atypical preference could be induced in a duckling that had no prenatal exposure to the chicken call by rearing it with ducklings that had prenatal experience. An additional question remained as to whether ducklings with the prenatal exposure also require specific interactions with (other) prenatally exposed ducklings for their atypical call preference to develop. The results of the final experiment addressed that issue; it appears that particular features or aspects of social environments are necessary even for ducklings that have benefitted from prenatal exposure to the chicken call. When five PRE/POST ducklings were reared together, they demonstrated a preference for the atypical call at 48 hours. When a single PRE/POST duckling was reared among POST ducklings however, the atypical preference was not demonstrated until 65 hours. Thus, it appears that the experience of socially interacting with PRE/POST ducklings has two roles in development (Gottlieb, 1976); for non-prenatally-exposed ducklings the social experience induces species-atypical development, and for prenatally-exposed ducklings it maintains species-atypical development induced by their prenatal exposure to the chicken call.

However, there is another way to interpret the findings of the current study. Instead of interpreting experience with PRE/POST broodmates as actively inducing change in the Experimental target ducklings, perhaps experience with POST broodmates should be considered as actively inhibiting species-atypical development in the Control target ducklings. In these terms, it is suggested that a duckling will develop the atypical preference without prenatal exposure to the call in a variety of social contexts, excepting social interaction with other non-prenatally-exposed birds. As long as the duckling is not overly aroused, as probably occurs in isolation rearing, 48 hours of postnatal experience is enough to induce an atypical preference, unless the duckling is reared socially with conspecifics that suppress the atypical development. The results of the Reverse Experimental group support this Social Suppression hypothesis. Even though the target ducklings were prenatally exposed to the chicken call, when they were reared with POST broodmates, they did not manifest the atypical preference at 48 hours, unlike similar ducklings reared with other PRE/POST broodmates, suggesting that the POST broodmates interfered with the development of the atypical preference. The results of this experiment are even more revealing when contrasted with previous research that showed PRE/POST target ducklings reared in groups of stuffed ducklings do develop the atypical preference at 48 hours (Gottlieb, 1993). Ducklings which experienced the call prenatally and postnatally did not require "active" social cues, as suggested by the Social Induction hypothesis, merely tactile contact with the stuffed ducklings.

Although mechanisms of Social Suppression were not addressed in this study, several possibilities can be ruled out. For example, the observational data indicate that Control ducklings were not less likely to be under the speaker during the broadcast, nor did they move away from it when the broadcast began. A deficit in contact calls is also not a likely explanation; even though Control groups emitted fewer contact calls than Experimental groups, the Muted groups had presumably insignificant numbers of contact calls and yet their targets showed the atypical preference.

Thus, an unanswered question that remains from this study is whether the atypical development demonstrated by target ducklings in the Experimental group was induced through some specific interaction with broodmates, or whether target ducklings in the Control group failed to develop the atypical preference because they were suppressed by their interactions with broodmates that failed to develop the atypical preference. An experiment that would address this important issue would be to rear a POST target duckling with stuffed ducklings. If non-prenatally-exposed ducklings reared with stuffed ducklings fail to develop the atypical preference, then that would suggest socially interacting with "knowledgeable" prenatally-exposed broodmates is necessary for the atypical preference to develop. If, however, the target ducklings did develop the atypical preference, then that would suggest that failure of POST ducklings in the Control group to develop the atypical preference results from social suppression, and not simply a lack of prenatal exposure to the chicken call.

## Implications for the Study of Development

In studies of behavioral development, the role of conspecifics has often been overlooked as an integral factor of the developing system (Lickliter et al., 1993). But as this work demonstrates, it is an important component of the developmental manifold, deserving as much attention as the more often studied components such as nutrition or sensory stimulation. However, the purpose of this work is not to demonstrate yet another "environmental" perturbation that affects development. Rather, its goal is to emphasize the truly bi-directional interactive nature of the developmental system. By adopting a systems view of development, the interactive nature of all levels of the developing system is recognized, from the basic biological components of genetic expression to the highest levels of community and culture. The current research contributes to a series of experiments investigating development of a species-atypical preference for a novel call, which has shown how perturbations at many levels affects development of this behavior. The variety of inputs that has been shown to affect this behavioral outcome include: extensively stimulating the ducklings with atypical sensory input (Gottlieb, 1991b), removing self-produced canalizing vocalizations (Gottlieb, 1991a), or socially rearing with atypical conspecifics (current study). The number of ways by which the atypical preference can occur is indicative of a point of vulnerability in the system (Cairns et al., 1990). Only by adopting a multiple-entry, multipathway systems approach to the organism can we understand the interrelated dependencies of its development.

Additionally, these experiments demonstrate the critical importance of maintaining species-typical social environments for studying the development of species-typical behaviors. As Lickliter has cautioned, typical experiential stimulation must be present during the normal course of development if investigators are to successfully design experiments to understand normal development (Lickliter et al., 1993). This was most clearly illustrated by noting the effect that even one prenatally exposed duckling had on the five non-exposed broodmates. The behavior of these broodmates was distinctly different from broodmates that were reared with a non--prenatally-exposed target duckling.

## Implications for the Study of Evolution

This study investigated the development of a behavioral neo-phenotype, specifically, the development of a preference for a species-atypical call. As discussed earlier, many evolutionary theorists now hypothesize that the development of novel phenotypes, particularly behavioral ones, may be the first step in evolution. But in order for evolution to occur, phenotypic changes must persist across generations. The trans-generational persistence of phenotypic changes over evolutionary time, or neophenogenesis (Johnston & Gottlieb, 1990), offers a mechanism of evolution that does not require a change in genetic frequencies. Rather, the persistence of all the interactants that constitute the developmental manifold is necessary. The developmental interactant I offer in this study as a mechanism of both developmental and evolutionary change is social interaction. Although this study did not address trans-generational effects, it has demonstrated that an individual that socially interacts with conspecifics possessing different developmental histories will show a different developmental outcome, without requiring a change in genotype. As long as the altered social environment persists across generations, the novel developmental outcome will also persist. Of course, the same can be said of any change in the interactants of the development manifold. For example, a persistent change in food resources, temperature, or other ecological factor could also have the same impact on evolution. Changes like this, however, are rare compared to the inherent flexibility of social interactions among organisms.

Nonetheless, I would argue that the social environment has a more powerful effect on constraining evolution. The focus of evolutionary investigations has most frequently focused on the origins of change. The gradual incorporation of the developmental approach into evolutionary thinking has led to experimental demonstrations of the trans-generational effects of extra-genetic developmental changes (for reviews see Gottlieb, 1992 and Johnston & Gottlieb, 1990). However, an overlooked question is: given the ease with which developmental modifications can be created in experimental situations, why has this not occurred in nature? In other words, what accounts for the strong tendency for evolutionary conservation? Again, the answer lies with the understanding that the entire developmental manifold is transmitted across generations, and not just genetic material. Thus, even mutations of the DNA will not affect the evolution of a species if the developmental resources that contribute to novel genetic expression resulting in neophenotypes, including social interactions, are not present in future generations. I propose that the results of this study illustrate how the social environment is a powerful conservative force for this effect. The fourth experiment demonstrates "social conservation" by showing that even if one animal, through mutation or other developmental accident, should be different from other members of its species, the social environment will serve to restore the species-typical outcome. Thus, if evolution is to occur, the neo-behavioral phenotype will have to evolve in a system that supports its existence, which includes the social environment.

This interpretation leads to an interesting speculation about one possible mechanism of stasis in evolution. As highlighted by Eldrege & Gould (1972; Gould & Eldrege,1993), the static nature of evolutionary history of a species

"...must be viewed as an active phenomenon, not a passive response to unaltered environments" (1993, p. 223), and "maintenance of stability within species must be considered as a major evolutionary problem" (1993, p.224). The process of social conservation that I propose may be one of the ways in which evolutionary equilibrium is maintained. Given the infrequency with which successful neophenotypes develop in an individual, the likelihood that such changes would occur simultaneously in a social group, or in a social group that supports the change, is even more rare, which obviously would contribute to the conservation observed in evolutionary history.

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# APPENDIX A

## PILOT RESULTS

Preferences of subjects collected in a pilot study conducted during July - November, 1992.

| | | | BROODMATES | | | TARGET | | |
|---|---|---|---|---|---|---|---|---|
| Age | N | n resp | ML | CH | Both | ML | CH | Both |
| Experimental | | | | | | | | |
| 48 | 82 | 67 | 15 | 33 | 7 | 3 | 8 | 1 |
| 65 | 82 | 61 | 6 | 42 | 3 | 0 | 8 | 2 |
| Control[b] | | | | | | | | |
| 48 | 18 | 15 | 11 | 2 | 2 | | | |
| 65 | 18 | 16 | 6 | 9 | 1 | | | |

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[b] No target animal was specified in this group; both broodmates and targets do not experience prenatal exposure to the chicken call.

# APPENDIX B

## STATISTICAL TABLES

Table 1. Actual *p* values from two-sample Wilcoxon rank-sum tests comparing Experimental (n=16) and Control (n=17) groups.

| Subject | Obs. Period | Off(end) | On(begin) | On(end) | Off(begin) |
|---|---|---|---|---|---|
| Broodmates | Total | .49 | .35 | .16 | .33 |
| Targets | Total | .12 | .20 | .34 | .19 |
| | 6 | .27 | .17 | .26 | .11 |
| | 18 | .08 | .18 | .33 | .47 |
| | 30 | .17 | .02 | .06 | .08 |
| | 42 | .45 | .45 | .45 | .07 |

Table 2. Repeated measures analysis of variance table for broodmates in Experiment Two.

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| Group | 1 | 82.3975 | .26 | .61 |
| Error | 31 | 9741.1176 | | |
| Age | 3 | 1360.0000 | 1.21 | .31 |
| Age * Group | 3 | 94.1800 | .08 | .977 |
| Error | 93 | 34961.8235 | | |

Table 3. Repeated measures analysis of variance table for target ducklings in Experiment Two.

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| Group | 1 | .1080 | .97 | .33 |
| Error | 28 | 3.1040 | | |
| Age | 3 | .1413 | .56 | .64 |
| Age * Group | 3 | .7000 | 2.76 | .047[a] |
| Error | 84 | 7.0987 | | |

[a] This significant interaction likely results from the marked decrease in approach behavior observed at 6 hours. The Wilcoxon Sign Rank Test indicates that this value may be statistically different than 0 (*p* = .08), unlike all the other values. Since there is no theoretical reason to believe that the target ducklings in the two groups should differ at 6 hours of age, the observed difference probably does not reflect an effect of different social rearing experiences.