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Early Social Responses in Gallus: A Functional Analysis

Abstract. *Early socialization leads to the establishment of species awareness, or imprinting, in many birds and mammals.* Gallus *chicks normally develop species-specific preferences prior to exposure to a parent, but early exposure is necessary to maintain these preferences. Descriptive rather than functional analyses have led to apparent disagreement about early socialization behavior; from an ecological viewpoint, such behavior is both adaptive and predictable.*

The process of early social bonding between parent and precocial offspring during an early sensitive period was termed "imprinting" by Lorenz (*1*) and remains a central feature of ethology. Imprinting per se is usually not studied, but approach, following, stay-near tendencies, and vocalizations are used to infer that socialization with the stimulus object is taking place. Contradictory results of such studies are the rule rather than the exception (*2*), and Klopfer (*3*) has compared imprinting with a Cheshire cat. Domestic chicks are often said to be especially poor subjects for imprinting studies because of their great response variability.

Laboratory and field studies conducted within an ecological framework demonstrate that early socialization processes in domestic chicks are highly consistent, highly adaptive, and very similar to those observed in wild jungle fowl. I show that *Gallus* chicks do not imprint to a parent in the sense of establishing a preference, but early exposure to key features of the parent is necessary to maintain preferences developed prior to exposure. To be effective, such exposure must be within the "sensitive period" that lasts for about 4 days in *Gallus* chicks (*4*). Chicks respond selectively to the parent at hatching, but early deprivation or exposure to inappropriate stimuli impairs subsequent responsiveness to parental stimuli. These results are consistent with the hypothesis that selective early experience can have behavioral as well as anatomical and physiological consequences (*5*). Lorenz (*1*) envisioned imprinting as a process by which "a sort of consciousness of species" is established in offspring that do not have "innate perceptory patterns," or preferences; I extend imprinting to include maintenance or consolidation of preferences developed prior to exposure to an imprinting stimulus.

In the first study, domestic chicks were individually placed in a circular apparatus 120 cm in diameter with a central core that housed a kymograph motor with a revolving arm. Objects suspended from the arm revolved between inner and outer walls about 38 to 40 times during each 20-minute session and were visible to subjects; an implanted speaker could provide auditory stimuli from the object. A speaker suspended from the arm outside the outer cloth wall could furnish auditory stimuli independent of visual cues. The number of revolutions (each 3 m) followed during training, the predominant type of vocalization, and postural changes were recorded. In addition, each chick was classified into a functional category (*6*) of contact-seek, contact-maintain, or contact-avoid on the basis of overall performance during an exposure session.

Chicks were individually exposed to a continuous tape recording of the clucking of a broody hen (A), to a multicolored ball 20 cm in diameter (V), or to the ball with the recorded clucking (AV) for 20 minutes per day on days 1 to 5 after hatching (first exposure at 24 ± 6 hours). In order to determine if exposure led to relatively stable preferences, chicks were individually given both simultaneous and sequential choice tests on day 12 (most investigators test for "stable" preferences after only 24 hours of isolation). Between exposure sessions, they were housed in 30-cm^3 heated wooden boxes and furnished with food and water.

Results were clear and consistent. All chicks exposed to clucking from an unseen speaker followed the sound almost constantly during days 1 to 5 after hatching (Fig. 1). They constantly uttered localization (or "distress") calls and maintained the head-up posture associated with contact-seeking. Naturalistic studies on jungle and domestic fowl (*7*) show that chicks separated visually, but not auditorily, from their mother exhibit the same "lost chick" phenotype seen in the A birds of this study. Such conditions cause both parent and offspring to contact-seek. On day 12, after a week of isolation, 38 of the 39 survivors exhibited clear positive responses toward the cluck, but not if the recording was played at faster or slower than normal speed. They responded negatively toward silent objects.

Chicks exposed to the clucking model (AV) followed less strongly than did those exposed to clucking alone (Fig. 1). Their general posture and vocalizations suggested little distress (the social unit of hen and chick is intact). Again, the parallel between chicks in the AV situation in the laboratory and naturalistic behavior of undisturbed jungle fowl or domestic chicks foraging near the parent was striking. In the circular apparatus, a chick could learn that it maintained auditory and visual contact most of the time without constantly following. Many of the chicks would follow the model for part of a revolution, stop and peck at the floor or walls, then orient toward or approach the model, uttering "pleasure peeps" as the model approached from the other direction. From a functional point of view, AV chicks behaved as if they were with the mother. Chicks with the mother normally feed, preen, explore, and exhibit other behaviors that are usually inhibited when the social unit is disrupted. Tests on day 12 showed that 65 of 80 survivors responded posi-

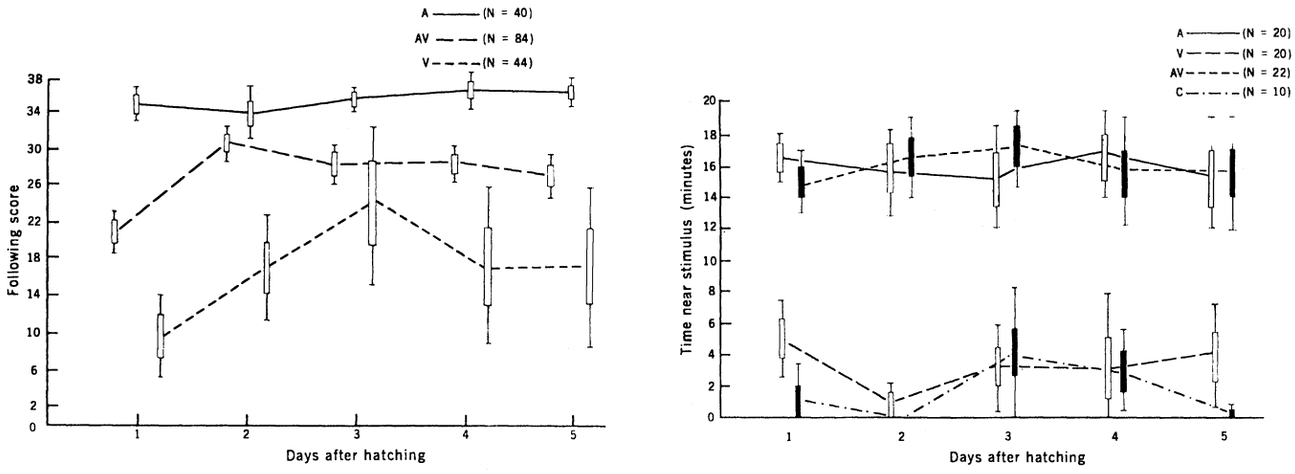

Fig. 1 (left). Amount of following (number of revolutions) by chicks exposed to broody hen clucking (A), to a model emitting clucking (AV), or to a silent model (V) for 20 minutes per day on days 1 to 5. End points of vertical lines are 95 percent confidence limits; end points of vertical bars are means ± standard errors. Fig. 2 (right). Time (per 20-minute test) spent near a hidden speaker emitting clucking of a broody hen (A), near an adult hen plus a hidden speaker emitting clucking (AV), near a silent hen (V), and near an empty enclosure (C). Means ± standard errors are represented by vertical bars; end points of vertical lines are 95 percent confidence limits.

tively to the clucking multicolored model or to a red ball emitting the familiar sound; responses to the silent model were difficult to categorize, but fewer than half of the chicks exhibited positive responses to it.

Behavior of chicks exposed to the silent model (V) was quite variable; they followed less than A or AV chicks (Fig. 1) and did not attend to the object consistently. That is, they often exhibited "searching" behavior even when following. Tests on day 12 verified the low effectiveness of the silent objects; 13 of 14 V chicks responded positively to the silent model, but none responded positively to the clucking stimulus. Apparently, early exposure to clucking is necessary to maintain responsiveness to the maternal call.

I suggest that chicks develop rather specific auditory-visual "perceptory patterns" (*1*), "neuronal models" (*8*), or "schemas" (*9*) for the parent prior to hatching and that objects that do not match releasers normally associated with the parent are poor substitutes for the natural parental type. These hypotheses were examined further in a second study.

The test compartment in this experiment was a 75 by 170 cm alleyway; the exposure and testing schedule was as in the first study. Chicks placed at one end of the runway could approach to within 30 cm of stimuli presented at the opposite end; a wire screen prevented actual contact. Time spent within 15 cm of the screen, activity, posture, vocalizations, and functional category of behavior during testing were recorded for each chick. Groups were exposed to clucking (A); to a nonbroody, silent adult domestic hen (V); to the hen plus clucking from a hidden speaker (AV); or to an empty apparatus (C).

Tendencies of all A and AV chicks to seek contact with the stimulus during training were high (Fig. 2); each chick went to the wire enclosure preventing access to the stimulus and attempted to gain entry. Tendencies of chicks exposed to the empty apparatus (C) and to the silent hen (V) were similar; their behavior was variable but can be best described as irregular cycles of contact-seeking (localization or distress calls and searching). That is, all chicks (A, AV, V, and C) were in a "social unit disrupted" context and exhibited contact-seeking behavior; in A and AV chicks the behavior was directed and canalized by the auditory-visual stimuli, whereas no such effect obtained for C or V chicks.

On day 12, after a week of social isolation, 86 percent of the A and AV chicks responded positively to clucking but only if it was presented at normal tape speed; percentage responses to the silent hen were 0, 35, 42, and 6 for C, V, AV, and A, respectively.

These results offer a framework within which many apparently conflicting reports on imprinting may be resolved. Silent objects that are not associated with species-specific releasers (clucking, food-calling, and so forth) and models emitting extraspecific sounds do not match chick schemas for social stimuli; behavioral responses to such stimuli are variable, and stable preferences for the stimuli are difficult to establish. Clucking alone matches one part of the parent schema; however, without visual access to the parent the chick is "lost," a situation that has been dangerous over evolutionary time and for which a stereotyped response is observed (emit localization calls and search, or contact-seek). Direct access to a clucking model represents a "social unit intact" status; contact-seeking is inhibited and functional behavior of lower priorities may occur. High variability often associated with chick responses in "imprinting" studies is due largely to the use of descriptive, not functional, classification and to the fact that the context of many such studies is that of "social unit disrupted." Exposure to the species-specific maternal call maintains preference developed prior to exposure and leads to greater specificity of attachment. Failure to validate such preferences by early exposure leads to their regression (*10*).

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Social Rank in House Mice: Differentiation Revealed by Ultraviolet Visualization of Urinary Marking Patterns

Abstract. *Ultraviolet light has been used to examine urine marks deposited by adult male house mice on filter paper on the floors of their cages during overnight tests. Both the urination frequency and the pattern in which urine was deposited on the filter paper depended upon social rank. Dominant males vigorously marked their entire cage floor, whereas subordinate males typically voided urine in only two to four pools in the corners of their cages.*

In many mammalian species excretory products such as urine, feces, and glandular exudates constitute an important source of chemical communicants (pheromones). Such cues often serve to modify specific behavioral and physiological functions among recipient members of the same population (*1*). Many investigators have documented the importance of urinary pheromones and olfactory reception in both aggressive and sexual behavior in mice (*2*). Physiologically, urinary priming pheromones produced by adult mice have been implicated in both the enhancement and suppression of ovulation in immature and mature females and even in the prevention of implantation in recently inseminated females (*3*).

In the course of an investigation of the relationships between social rank and testicular function in house mice, we noticed that the bladders of subordinate males consistently contained more urine than those of their dominant counterparts killed at the same time of day. This differential accumulation of urine prompted a series of studies. The results that we report here document urinary marking behavior in adult male house mice and demonstrate that the frequency and pattern of urinary marking is strongly dependent upon dominance status. Moreover, our studies illustrate the utility of ultraviolet light as a way of evaluating urinary marking patterns, an approach that will undoubtedly prove useful in elucidating some of the behavioral and physiological consequences of sociality in this and other species.

Laboratory-raised descendants of a wild stock of house mice (*Mus musculus*) were reared in a room maintained at 23°C with a light:dark cycle of 14:10 (lights on at 5 a.m.). Excess food (Wayne mouse breeder diet) and water were provided at all times. Mice were weaned at 21 to 23 days of age and then each animal was isolated in a cage (30 by 30 by 15 cm) where it remained until reaching maturity at 55 to 60 days of age, at which time it was used in one of three experiments.

In the first experiment the relationship between social rank and the volume of bladder urine was examined after 10 hours of pairing (7 p.m. to 5 a.m.). Eleven pairs of dominant (unwounded) and subordinate (wounds on rump or tail) mice were killed by cervical dislocation. We took care to minimize spontaneous urination by killing the animals within 15 seconds after first handling the cage. Urine that was voided during handling and killing was pooled with urine that was aspirated from the bladder with a syringe. The total volume of urine in the syringe was considered as bladder urine.

Table 1. Percentage of total radioactivity recovered from urine deposited on filter paper after dominant and subordinate male mice received a single intravenous injection of [^{3}H]inulin. Each value represents the mean ± the standard error of the mean of the results for three mice.

Hours after injection	Percentage of total radioactivity recovered	
	Subordinate	Dominant
1	30.0 ± 5.4	64.8 ± 1.1
2	6.8 ± 4.3	12.4 ± 2.4
4	32.4 ± 6.8	8.4 ± 1.2
8	18.2 ± 3.1	6.8 ± 0.7
18	9.6 ± 3.7	3.8 ± 0.5
Total	97.0 ± 1.3	96.2 ± 1.2

No urine could be detected in the bladders of eight out of the 11 dominant males. The volume of urine in the bladders of the other three dominant males ranged from 0.06 to 0.14 ml and averaged 0.03 ± 0.01 ml for all 11 dominant males. Urine volume among the subordinate males averaged 0.63 ± 0.08 ml and ranged from undetectable in one animal to 1.02 ml at the extreme. Thus the bladders of the subordinate males typically contained, on the average, at least 20 times as much urine as those of the dominant males.

In the second experiment we used ultraviolet light to examine the frequency and pattern of urinary marking as a function of social status. We obtained urinary marking patterns of ten isolated adult males by placing each male in one compartment of a cage (30 by 30 by 15 cm) that was divided in half by a 0.2-cm wire partition. The bottom of the cage was covered with wood shavings during the day and with Whatman No. 3 MM filter paper between 8 p.m. and 8 a.m. Urinary marks on the filter paper were made visible with the aid of an ultraviolet lamp equipped with a 15-watt tube emitting light at 3666 Å (*4*). Urinary marking patterns of the same males were obtained on the following night after they had been placed in similar cages (cleaned beforehand) as pairs but separated from each other by the wire partition. After urinary marking patterns had been obtained from pairs of mice in each other's presence, the partions were removed for 30 minutes per day for 5 days to permit the establishment of dominance-subordination relationships. Urinary marking patterns were obtained on five consecutive nights. Spontaneous fighting occurred among all pairs immediately after the wire barrier was raised (*5*). A clear dominance-subordination relationship was established in four of the five pairs after the first 30-minute encounter.

Urinary marking patterns presented in Fig. 1 illustrate a typical set of results obtained in these studies. Isolated males deposited urine in 30 to 80 pools or drops over the filter paper as revealed under ultraviolet light (Fig. 1, A and B). A striking change was noted