

SOCIAL CONTEXT AFFECTS BEHAVIORAL RESPONSIVENESS TO
MATERNAL ALARM CALLS IN BOBWHITE QUAIL CHICKS

by

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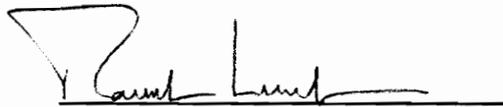
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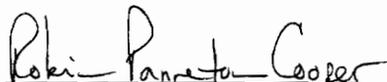
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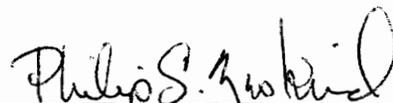
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Michael Bernard Casey

Committee Chairman: Robert Lickliter

Psychology

(Abstract)

These studies examined the effects of altered developmental experience (rearing history) and altered behavioral context (testing environment) on the alarm call responsiveness of maternally naive, incubator reared bobwhite quail chicks. Experiment 1 assessed alarm call responsiveness in socially-reared, socially-tested hatchlings across the first 96 hours following hatch. No significant age effects were revealed. Hatchlings tested at 24 hours did not differ significantly from birds tested at 48, 72, or 96 hours on the two principle behavioral measures (number of grid crossings and vocalizations per one minute trials).

Experiment 2 assessed whether hatchlings' alarm call responsiveness is at least partially dependent on the availability of cover (i.e., hiding sites) in the testing situation. No significant differences in responding were found in comparisons between hiding sites and social (non-hiding sites) testing conditions. However, behavioral observations did indicate that hatchlings in

the hiding site condition utilized the hiding site as an attractor, in that chicks typically huddled and froze around the hiding site structure.

Experiment 3 examined the relative effects of individual testing on socially-reared bobwhite quail hatchlings. Results revealed that individually tested hatchlings increased their locomotor activity following initial exposure to the maternal alarm call when compared to socially tested chicks. Vocalizations were significantly reduced in post-alarm call testing from pre-alarm call levels. However, hatchlings tested individually had higher levels of vocal activity when compared to socially tested chicks. In comparison with socially-reared/socially-tested subjects, socially-reared/individually-tested subjects were more active following exposure to the maternal alarm call than they were prior to exposure to the call.

Results from the three experiments are discussed in terms of species-typical experience and development. It is maintained that species-typical responding to the bobwhite maternal alarm call is partially influenced by social context. An argument for continued polythetic research on behavioral development in avian communication is also made.

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Two of the most prevalent and important acoustic signals for the young of a variety of animal species are the maternal assembly and alarm vocalizations. A number of studies have examined the acoustic signals that allow young animals to recognize their mother and maintain close proximity to her (Evans, 1973; Impekoven and Gold, 1973; Impekoven, 1975). Species-specific acoustic preferences for the maternal assembly call have been demonstrated in wood ducklings (Gottlieb, 1974), mallard ducklings (Gottlieb, 1971; Miller and Gottlieb, 1978), bobwhite quail (Heaton, Miller, and Goodwin, 1978; Lickliter and Virkar, 1989), laughing gull chicks (Impekoven, 1975), ring-billed and herring gulls (Evens, 1973), and domestic chickens (Gottlieb, 1971).

In addition to species-specific responsiveness to maternal assembly calls, the young of a variety of species also respond to parental warning or alarm signals. Offspring may, for instance, freeze, run for cover, dive into the surf, burst into the air, or dig underground following exposure to an alarm call or signal (Busnel, 1977). For example, young bear cubs respond to alarm signals emitted by their mother by climbing into any nearby tree and hiding in the forks of branches (Busnel, 1977). In contrast, domestic chicks typically huddle together under their mother following her vocalization of a warning or alarm call (Busnel, 1977). Interestingly, individuals of a number of animal species respond to alarm signals by running to cover and/or "freezing." Freezing as it is used here is defined as the cessation of vocal and locomotor activity.

Studies of alarm calls, and the various behavioral responses they can evoke, can be traced back to the work of Spalding (1873). More recent work has been done by Sherman (1981, 1985), detailing the role of the alarm call in Belding's ground squirrel nepotism, Tenaga and Tilson's (1977) work on the evolution and development of long distance alarm calls in Kloss' gibbon, Owens and Goss-Custar's (1976) concern with the adaptive significance of alarm calling in shore birds, Shalter's (1979) examination of nesting passerines alarm signal responsivity, Gyger, Karakashian, and Marler (1986) and Gyger, Karakashian, Dufty, and Marler's (1988) work on alarm calling in domestic fowl.

Klump and Shalter (1984) provided an exhaustive review of the acoustic behavior of birds and mammals as it occurs in the predator-prey context. Their review details the various factors that affect the structure of alarm signals as well as the functional significance and evolution of such alarm signals. However, despite a large literature concerned with alarm signal characteristics, Harvey and Greenwood (1978) argued that the evolution and function of alarm call behavior is an area that has attracted more theories, but produced fewer data, than any other issue in anti-predator behavior studies.

While many species have some sort of alarm signal, whether it is acoustic, chemical, or visual, and some sort of "typical" behavioral response to it, it is in avian species that behavioral inhibition or a "freezing" response to an alarm call is most pronounced. The "freezing" response has been demonstrated in a variety of avian species, including the domestic fowl (Gallus gallus) (Ficklen, 1991; Gray and Jahrsdoerfer, 1986; Karakasian,

Gyger, and Marler, 1988; Thompson and Liebreich, 1987), chaffinches (Fringilla coelebs L.) (Zucchi and Bergman, 1975), laughing gull chicks (Larus atricilla) (Impekoven, 1975), pheasant chicks (Phasianus calchicus) (Heinz, 1973), and bobwhite quail (Colinus virginianus) (Borchelt, 1970; Borchelt and Ratner, 1973; Eyer and Ratner, 1975). However, the most detailed and systematic research concerned with alarm call responsivity has been conducted with mallard ducklings (Anas platyrhynchos) by Miller and his colleagues.

Miller and his associates have, over the past decade, investigated numerous aspects of the alarm call response in mallard (Peking) ducklings. Initial field observations of wild mallard hens and their broods (Miller and Gottlieb, 1978) revealed that duckling's vocal behavior is maintained and facilitated by the maternal assembly call, whereas the maternal alarm call significantly reduces and inhibits duckling vocalizations. Miller (1980) subsequently demonstrated through acoustic analysis of the mallard hen's maternal assembly and reconnaissance (alarm) calls that these two maternal vocalizations differ with regard to repetition rate, frequency modulation, dominant frequency, and note duration.

To assess the role of these various acoustic features, Miller (1980) exposed incubator reared, maternally naive mallard ducklings to normal and altered-rate assembly and alarm calls. Results of these exposures revealed that slow repetition rates (normal alarm and slowed assembly calls) served to inhibit all duckling vocalizations. Ducklings froze upon hearing the slow rate calls, whereas faster repetition rates (normal assembly and quickened

alarm calls) served to increase the ducklings vocal behavior and facilitated their approach to the sound source.

Miller (1983b) went on to investigate the range of repetition rates that can affect behavioral inhibition in mallard ducklings. Hatchlings were tested in groups of 30 to repetition rates ranging from 0.2 to 3.0 notes/sec in 2/10 second increments. Utilizing various behavioral measures (incidence of inhibition, latency and duration of inhibition), Miller found that the optimal range of repetition rates affecting inhibition extends from 0.8 to 1.8 notes/sec. Within this acoustic range, Miller found that 1.0 and 1.6 notes/sec were most effective in inducing behavioral inhibition. Unexpectedly, very slow repetition rates (0.2 and 0.4 notes/sec respectively) were not as effective as faster notes in promoting inhibition. Thus, Miller concluded that the inhibitory response exhibited by ducklings upon hearing the maternal alarm call reflects an auditory perceptual specificity to a range of moderately slow repetition rates that are characteristic of normally occurring acoustic signals in the perinatal environment.

Miller and Blaich (1986) continued this line of research by assessing the effect of varying the acoustic features of the mallard alarm call on behavioral inhibition or the "freezing" response. Ducklings were tested individually (but reared socially) to alarm calls varied in either note duration, frequency modulation, dominant frequency repetition rate, or repetition rate. They demonstrated that ducklings show a high degree of behavioral specificity to repetition rate. Specifically, it was shown that dominant frequency and frequency modulation play only a minor role in affecting

behavioral inhibition. They thus concluded that the behavioral specificity of mallard ducklings to slow repetition rates typical of maternal alarm calls provides the basis for the development of alarm call responsivity.

In two related experiments, age related changes in alarm call responsivity were also assessed. Results revealed that, although a significant reduction in vocalizations occurred upon exposure to the alarm call at all ages tested (12, 24, 36, 48, 60, and 72 hours post-hatch), birds older than 48 hours exhibited lower levels of freezing than younger birds. Additionally, 12-hr-old ducklings exhibited the greatest level of freezing among the younger groups (Miller and Blaich, 1986).

Blaich and Miller (1988) have also investigated the relative importance of two different sources of normally occurring auditory stimulation: sibling and self-produced vocalizations. In a series of related experiments, they demonstrated that auditory experience of broodmates is a significant factor in the development of behavioral inhibition on exposure to alarm calls. Mallard ducklings that were raised in auditory isolation were found to be less responsive to the alarm call than ducklings that experienced sibling vocalizations (20 out of 30, 67%, of ducklings reared in isolation froze as opposed to 27 out of 30, or 90% of socially reared ducklings).

It appears that development of alarm call responsivity differs from that of responsivity to the mallard assembly call (Gottlieb, 1971). That is, ducklings require only self-stimulation to maintain a species-typical preference for the maternal assembly call, but self-stimulation alone is not sufficient to facilitate a high degree of responsiveness to the species-typical alarm call. However, subsequent work has suggested that although social

auditory experience is important for the development of alarm call responsivity, self stimulation is also an important experiential feature in the development of behavioral inhibition (Blaich and Miller, 1988). Devocalized ducklings were found to be less responsive as a group than vocal ducklings that were reared in auditory isolation. Also, ducklings that received only self stimulation respond like devocalized ducklings that received only sibling stimulation.

Blaich and Miller (1986) also examined the effects of social experience in mallard duckling alarm call responsivity. They determined that rearing birds socially in a 12-bird brood without a hen results in a significant reduction in alarm call responsivity. Results demonstrated that 24 out of 30 ducklings (80%) reared in the vocal-communal condition froze when tested to the mallard alarm call. However, only 8 out of 30 ducklings (27%) reared in the social condition froze. Rearing ducklings socially thus appeared to result in a dramatic reduction in alarm call responding. Miller (1984) originally attributed this reduction to social rearing and the resulting decrease in the level of vocal activity of each broodmate.

These findings were later contested by Blaich, Miller, and Hicinbothom (1989) however, when an interaction between developmental history and behavioral context (i.e., testing situation) was revealed. In the Blaich and Miller (1986) study, ducklings were reared socially, but tested individually. Ducklings that are reared and tested with the maternal alarm call in small social groups respond by significantly inhibiting their vocal behavior. However, if individual socially reared ducklings were tested with the alarm call in an open field, responsivity declined dramatically. Also, individually

reared ducklings responded at a greater level to the alarm call when individually tested than when tested in groups. As such, there appears to be significant interaction between rearing conditions and the test environment/context, such that the same rearing history leads to different behavioral outcomes depending on the context in which the ducklings are tested with the alarm call.

What Miller and his associates have not determined is what aspects of the social testing environment are important for maintaining the freezing response of socially reared ducklings. Future experiments could focus on whether the increased levels of behavioral inhibition displayed by socially reared, socially tested ducklings can be attributed to the ducklings being tested socially, or to the actual physical structure of the social testing environment, or possibly to both factors in some degree. In this light, it is important to keep in mind that an organism's behavior is not simply a function of its developmental history. The same developmental history can lead to different behaviors when an organism is placed in differing contexts. As Kuo (1967) has argued, an organism's behavior is determined by at least five different and interacting factors: morphological factors, biophysical and biochemical factors, stimulating objects, developmental history, and environmental context.

In this light, Miller and Blaich have demonstrated that mallard ducklings freeze upon initial exposure to the maternal alarm call (Miller, 1980). The development of this naive species-typical response thus appears to be based on prenatal auditory experience, and is supported by the observation that devocalized embryos exhibit reduced freezing responsivity (Miller and Blaich,

1986). Further, altering the developmental and behavioral contexts of devocalized ducklings reinstates the freezing response that would decrease significantly without auditory experience of species-typical vocalizations (Miller and Blaich, 1988). Thus, while auditory experience is sufficient in some rearing and testing contexts to promote freezing, it is not necessary in other social contexts. Taken as a whole, this work supports the concept of multiple pathways in behavioral development. In other words, different developmental trajectories can lead to similar or even identical behavioral outcomes (Miller, Blaich, and Hicinbothom, 1990).

A related body of work has begun to examine the development of behavioral responsivity to the maternal assembly call of bobwhite quail (Colinus virginianus) (Lickliter, 1989, 1990; Lickliter & Stombous, 1991, 1992; Lickliter & Virkar, 1989). However, empirical concern with the development of alarm call responsivity in bobwhite quail has been neglected. Anecdotal observations of bobwhite quail vocal behavior can be found in Stoddard (1931) and Stokes (1967), but neither provides an empirical focus. Each of these reports attempts to verbally describe the bobwhites' species typical responses to maternal alarm calls, but neither report provides a detailed empirical account of the development of the behavioral inhibition to the alarm call.

According to Stoddard (1931), the bobwhite brood will scatter to hide at the hen's first alarm call. He maintains that the alarm call is fairly common, and suggests that it is used a great deal during the period of nesting and rearing of the young. When the brood is disturbed, the alarm call is emitted immediately after the termination of the "decoy ruse call,"

and as soon as the chicks have scattered and hidden, or if the parents have failed to decoy an intruder or predator away. Stoddard states that "the alarm call is uttered with machine-like regularity for a time, or as long as danger appears imminent."

Stoddard (1931) notes that young bobwhite "do not remain concealed so long as the parents may desire, for a few may start to move about after a quarter of an hour or so even though the alarm call is still being sounded." He reports that "no one who has watched bobwhites...can fail to be impressed with the frequency with which at some alarm, real or fancied, they freeze and remain motionless for periods varying from a few seconds to several minutes at a time." This may happen several times a day and Stoddard argues it may have significant importance for the survival of the species.

Stokes (1967) provides additional field observations and states unequivocally that, "(m)any birds and mammals freeze but no creatures known to us have it more highly developed or use it more effectively than do the bobwhites." Stokes argues that when chicks are frozen, their color makes them practically invisible. However, under certain conditions, as in very open or burned over cover, or during heavy rainfall, quail will sometimes run until adequate cover is reached before freezing. Stokes thus proposes that weather and other environmental conditions can directly impact the anti-predator behavior of bobwhites.

Empirical studies examining the freezing response of bobwhite quail are few and far between. One such study is an unpublished thesis (Borchelt, 1970), which provides an account of the development of "fear" displays in

bobwhite quail chicks. In Borchelt's study, four different age groups of chicks were tested for incidence and duration of freezing and immobility. Borchelt operationally defined freezing as "both the lack of locomotion and the absence of distress calling." He defines immobility as "the response elicited by rapid inversion and restraint of the animal usually lasting 15 seconds." Borchelt conducted testing in an open field apparatus. For individual birds, freezing was tested first and immobility was tested 24 hours later. Test-retest trials were conducted at additional 24 hour periods to assess reliability. The testing ages ranged from 4 days through 32 days post-hatch. A statistically significant increase was demonstrated in the duration of freezing between days 9 and 29. A significant increase in the duration of immobility occurred between days 10 and 20 and days 10 and 30. At days 4 and 5, the percentage of birds (12.5%) that responded on both tests was relatively low. However, freezing increased to 44.4% at 9 days, while immobility increased to 22.2% at 10 days. The last two age groups showed a high incidence of birds responding on both tests. The number of distress calls and amount of locomotion was found to decrease with both age and defensive distance. Fewer distress calls and less locomotion occurred after immobility rather than after freezing. Borchelt concluded that as the bobwhite develops it first shows the freezing component and only later displays the immobility component.

While Borchelt's work detailed the development of the freezing response in terms of predator avoidance and defensive distance, it did not incorporate the maternal alarm call into the study. Thus, whereas several investigators have examined alarm call responsivity in precocial birds (Heinz,

1973; Miller, et al, 1990), the bobwhite quail's responsivity has not been systematically examined. Thus, the present study was undertaken to begin to examine some of the critical elements that influence and constrain maternal alarm call responsiveness in bobwhite quail hatchlings.

In approaching this topic, it seems likely that many experiential components potentially contribute to the bobwhite quail alarm call response. No one variable will likely hold preeminence, although repetition rate of the call has been found to be a critical acoustic component for mallard ducklings (Miller and Blaich, 1986, 1988). For example, while extra-organismic variables (rearing conditions, testing context, etc.) are obvious factors, intra-organismic variables (such as developmental age) are also likely important features in the development of alarm call responsiveness.

In this study, I examined the effects of altered developmental (rearing history) and contextual components (testing environment) on the alarm call responsiveness of maternally naive, incubator reared bobwhite quail chicks. The first experiment assessed alarm call responsiveness, in socially-reared, socially-tested hatchlings across the first 96 hours following hatching. The second experiment assessed whether hatchlings' alarm call responsiveness is at least partially dependent on the availability of cover (i.e., hiding sites) in the testing situation. The third experiment examined the relative effects of isolation testing on socially reared birds.

The experiments described here represent a first step in assessing which contextual elements, in accord with particular organismic variables (i.e, alarm call, developmental age) might contribute to alarm call responsiveness in bobwhite quail chicks. This study was in keeping with

other recent lines of research which have attempted to reach a more complete understanding of the contributions of normally occurring experience to the development of species-typical behavior in precocial birds (Gottlieb, 1971, 1985; Lickliter, 1989; Lickliter and Gottlieb, 1988; Lickliter and Stombous, 1991; Lickliter and Virkar, 1989).

General Methods

Subjects

Incubator-reared bobwhite quail chicks (Colinus virginianus) were used as subjects. Fertile, unincubated quail eggs were obtained weekly from a commercial supplier and were refrigerated at 10-13 C for 2 days prior to incubation to reduce errors in calculating the developmental age of the embryos (Gottlieb, 1963). A Petersime Model 1, automatic turning, forced-draft incubator was used to incubate the eggs. Temperature and relative humidity in the incubator was maintained at 37.6 C and 80-85% respectively and checked at least twice daily.

Eggs were candled once a week to detect and dispose of embryos which failed to develop. In addition, eggs were checked regularly near the time of hatching to determine when (within the nearest hour) each chick hatched. In an effort to control for possible effects of variations in developmental age, only chicks that hatched during Day 23 of incubation were used in the experiments. Subjects were drawn from multiple batches of eggs to control for possible influences of between-hatch variations in behavior. Following hatching, subjects were individually identified with small colored dots placed on the top of their heads and reared in large

plastic tubs (45x25x15 cm) with 3 same aged chicks to mimic naturally occurring brood conditions.

Testing Procedure

All subjects were tested in the same testing tub and with the same basic procedure. The testing apparatus consisted of a plastic rearing tub (45x25x15 cm) placed within a 24 cm high arena to shield the observer from the subject's view. A grid pattern of black string was overlaid on the top of the testing tub (see Figure 1). This pattern divided the tub into 6 equal areas measuring 15 cm x 12 cm. A plastic rearing tub was used in testing in order to provide the subjects with equivalent rearing and testing conditions. This helped to prevent any possible confound resulting from differences between the physical structure and properties of the testing and rearing conditions.

A midrange dome-radiator speaker was positioned outside the testing tub as part of the larger arena structure. The speaker was connected to a Tascam model 122-B cassette tape recorder located on a control table. Sound levels were maintained at 65 dB throughout all testing sessions. An observer sat at the control table and observed each subject or group of subjects' activities through a large mirror positioned above the arena. Each test began with a one-minute period of silence to allow the subjects to become acclimatized to the physical shift from rearing room to testing room. This was followed by a 30 second burst of the bobwhite maternal alarm call (acoustical details of the call are provided by Heaton, Miller, & Goodwin,

1978). A one-minute post alarm call test period (silence) completed the total evaluation session.

Data Collection

During the pre- and post-alarm call test periods several behavioral measures were recorded. In both social conditions, a measure of grid crossing (total number of grids crossed by each subject), vocalizations (total number of notes made by the 4 subjects in each testing group), and huddle duration (total time spent by all 4 subjects within the same grid space) were made. Grid size was determined in pilot testing by the space occupied by 4 bobwhite hatchlings at the same time. In the individual testing condition, each subject was scored on total grid crossings and total vocalizations during the pre- and post testing sessions. Huddle duration could not be assessed due to the nature of the individual testing situation.

It should be noted that huddle duration and number of grid crossings are not entirely independent of each other. Huddle duration is defined as the total time spent by all 4 subjects within the same grid space. Thus, subjects cannot cross any grids while in a huddle. However, taking a measure of the time subjects huddle together provides an important qualitative character in the phenomena of behavioral inhibition. Subjects may inhibit their behavior, but not necessarily within the same grid. Subjects appear to seek out each other when they huddle together in response to the maternal alarm call. In this light, huddle duration is a significant measure of social activity in the testing situation.

All testing sessions were video-taped with a Panasonic WV-3230 NewVicon color video-camera to facilitate accurate recording of dependent measures. Video-tapes were initially coded by one research assistant using a TEAC MV-510 video-tape player. The research assistant reviewed the tapes three times per testing situation, first recording the number of grid crossings per individual subject. A second review of each test session was done to assess a total number of vocalizations made by all subjects as a group (except in the individual test condition where a total score for each subject was obtained). The third video-tape review was made to measure total huddle times in social test conditions. A second research assistant recoded 10% of all test trials using the same equipment and procedures. Inter-rater reliability between the independent coders was assessed for all three dependent measures and found to be .998 using a Pearson product correlation procedure.

Data Analysis

Kurtosis for the three independent measures indicated that they were not normally distributed. Therefore, in all testing conditions pre- and post-test data for the three dependent measures were initially evaluated with a Wilcoxin signed rank test. Any possible main effects for age, condition, and age x condition interaction were assessed using a repeated measures ANOVA. Pairwise comparisons were examined using Neuman-Keuls post-hoc procedure. As data collected in this study violate the assumption of normality, any parametric analyses of these data must be prefaced with this warning.

A group score for individually tested subjects was created for comparison with social conditions in number of vocalizations. This was done by combining the individual scores of chicks that were raised together (in groups of 4) but tested individually. Thus, this comparison may be interpreted with some reservations.

Experiment 1: Influence of Developmental Age on Alarm Call Responsivity.

As there are no empirical studies specifically assessing the development of alarm call responsivity in bobwhite quail, a basic description and examination of possible age related changes was required to set the stage for further work. Miller (1987, 1980) and Miller and Gottlieb (1978) have provided such a description for mallard ducklings. In particular, the purpose of this experiment was to assess alarm call responsivity of bobwhite quail in a social context across the first four days following hatching (24, 48, 72, 96 hours of age).

Method

Eighty bobwhite quail were tested at either 24, 48, 72, or 96 hours following hatch. Chicks were tested socially in groups of 4. A 1 minute pre-test of silence allowed the chicks to acclimatize to the arena situation. A 30-sec burst of the alarm call was followed by a 1 minute post-test period (see General Methods section). Birds were video taped throughout the course of the 2.5 minute trial. Scores for grid crossing, vocalizations, and huddle duration were obtained from the video-tapes, as described in the General Methods section (see Appendix A).

Results

As shown in Table 1, subjects significantly reduced their locomotor activity (as measured by total number of grid crossings) following exposure to the maternal alarm call at all ages tested ($p < .0001$). In addition, Table 2 shows that subjects significantly reduced their total number of vocalizations following alarm call exposure in all 4 age groups tested ($p < .0001$). Table 3 illustrates that subjects also significantly increased their time spent huddling with broodmates following exposure to the maternal alarm call ($p < .0001$).

Consistent with findings from other avian species, this experiment demonstrates that socially reared and socially tested, maternally naive bobwhite quail hatchlings inhibit their vocal and locomotor behavior following exposure to a bobwhite maternal alarm call. This pattern of behavioral inhibition was seen across the first four days following hatch. ANOVA procedures did not reveal any significant age effects, in that chicks did not differ in their inhibition of behavior following exposure to the maternal alarm call at any of the ages tested. This finding stands in contrast to work with mallard ducklings (Miller, 1987), in which alarm call responsivity was found to significantly decline by 48 hours following hatching.

Experiment 2: Effects of Hiding Sites on Alarm Call Responsivity.

Previous studies have demonstrated the importance of environmental context on species typical behavioral responding in several species, including domestic goat kids (Lickliter, 1984), and mallard ducklings (Miller,

Hicinbothom, Blaich, 1990). However, the role the physical testing context plays in directing or constraining behavioral performance has not received adequate study in the domain of animal behavior (Timberlake, 1989). Anecdotal reports (Stoddard, 1931; Stokes, 1967) from the field suggest that bobwhite quail hatchlings first run to cover and then freeze when they hear the maternal alarm call. Pilot observations for this study also indicated that bobwhite chicks seek out some form of cover on initial exposure to the maternal alarm call. In this light, the present experiment examined alarm call responsiveness of chicks that were reared and tested with available hiding sites.

Method

Eighty subjects were tested once at either 24, 48, 72, or 96 hours following hatch. As in Experiment 1, chicks in this experiment were tested in groups of 4. Unlike the chicks in Experiment 1 however, subjects in this experiment were reared from hatching to testing with two hiding sites present in their rearing tub. These hiding sites consisted of two black plastic containers (7x5x5 cm) provided at opposite ends of the rearing and testing tub (see Figure 2). Subjects were observed to enter (and remain) in these hiding sites during the rearing period prior to testing. As in the previous experiment, individual scores for grid crossing were obtained from review of the video tapes. Group scores for vocalizations and huddle duration were likewise obtained from video tapes.

Results

As expected, subjects significantly reduced their locomotor (Table 4) and vocal behavior (Table 5), and increased their total huddle duration (Table 6) following exposure to the maternal alarm call at all ages tested ($p < .0001$). These results replicate the results obtained in Experiment 1. Analysis of variance procedures revealed no main effects for age or condition (social vs. hiding sites) in grid crossing or vocalization measures. However, ANOVA results indicated a main effect for age $F(3,32) = 3.51$, $p < .02$ in huddle duration. Post-hoc analysis with the Neumann-Keuls procedure revealed a significant increase in huddle duration at 24 and 96 hours of age as compared with 48 and 72 hours. No significant condition by age interaction effects were found.

While subjects in this experiment did inhibit their locomotor and vocal behavior and sought increased proximity to conspecifics, they did not make consistent use of the hiding sites provided. Video-taped sessions indicated that while subjects huddled in proximity to the hiding site structures, they did not typically enter the available hiding site during the testing trial. These results suggest that bobwhite hatchlings may prefer to hide in a huddle with conspecifics rather than be separated from each other in the narrow confines of a hiding site. In other words, subjects appeared to use each other as hiding sites rather than the physical structure provided in the testing situation.

Experiment 3: Effects of Individual Testing on Alarm Call Responsivity

Several studies have examined the effects of conspecifics on species-typical behavior in precocial avian species (Johnston & Gottlieb, 1985; Lickliter, 1989; Lickliter & Gottlieb, 1985, 1988). For example, Blaich and Miller (1986) and Blaich, Miller, and Hicinbothom (1989) found that socially reared, individually tested mallard ducklings are less responsive to the mallard maternal alarm call than are socially reared, socially tested ducklings. Pilot data for the present study likewise suggested that a similar phenomena occurs with bobwhite quail. That is, bobwhite quail alarm call responsivity appeared to be influenced by the presence or absence of conspecifics. To further assess this relationship, this experiment specifically examined the effects of individual (isolation) testing on alarm call responsiveness of socially reared chicks at 24, 48, 72, 96 hours following hatching.

Method

Eighty bobwhite quail hatchlings were tested at either 24, 48, 72, 96 hours following hatching. Subjects were tested once and all subjects were tested individually. As in the previous experiment, individual scores for total number of grid crossings and total number of vocalizations were obtained from video tapes made during testing. However, because of the nature of isolation testing, huddle durations could not be obtained.

Results

As seen in Table 7, subjects tested in social isolation demonstrated a significant increase in locomotor activity following exposure to the maternal alarm call at 24, 48, and 96 hours ($p < .0001$). In addition, ANOVA comparisons of grid crossings between conditions were significant, $F(2,237) = 6.73$, $p < .0014$. Neumann-Keuls post-hoc tests revealed that individually tested hatchlings increased locomotor activity following initial exposure to the maternal alarm call when compared with socially tested birds. Vocalizations were, however, significantly reduced in post-alarm call testing (Table 8, $p < .0001$). ANOVA comparisons of vocalizations between social/hiding sites and isolation testing conditions were significant, $F(2,57) = 25.86$, $p < .00001$. Neumann-Keuls post-hoc procedures revealed that hatchlings tested in isolation had increased vocalizations when compared to chicks tested in social conditions. No significant age effects were indicated by ANOVA procedures, nor were there any significant condition by age interaction effects.

These data indicate the importance of social context to the alarm call responsiveness of bobwhite quail hatchlings. When compared to socially tested chicks, chicks tested individually were found to increase their locomotor activity and inhibit their vocalizations following exposure to the maternal alarm call. In other words, in comparison with socially reared, socially tested subjects, socially reared, individually tested subjects were more active following exposure to the maternal alarm call than they were prior to exposure to the call. This finding stands in contrast to anecdotal

reports (Stokes, 1967, Stoddard, 1931) of bobwhite chick behavior, as well as empirical findings obtained from other precocial avian species. For example, whereas Blaich and Miller (1986) demonstrated that socially reared mallard ducklings tested individually do not freeze as reliably as those tested in social groups, he did not report that individual testing resulted in increased behavioral activity.

One possible explanation for the findings of the present experiment is that bobwhite quail chicks are generally more precocial at hatching than are mallard ducklings. The bobwhite quails' more mature locomotor abilities may account, at least in part, for their increase in behavioral activity during testing. Another possible explanation might be that given the absence of conspecifics, chicks had no available place to hide. When tested in social conditions, bobwhite chicks will huddle together, often digging beneath one another and "unfreezing" other chicks. Another bobwhite chick might fill the need for cover or hiding site in the social testing situation. This explanation would seem to be supported, at least in part, by the results of Experiment 2. In any case, further research is needed to assess these possibilities.

General Discussion

By way of review, the results of this study demonstrated that maternally-naive, socially-reared bobwhite quail chicks alter their vocal and locomotor behavior following initial exposure to the bobwhite maternal alarm call. In all testing conditions (i.e., social, isolation, and hiding sites), significant changes in chicks' behavior were observed following exposure to

the alarm call. On the one hand, chicks tested in social conditions (social and hiding sites) inhibited their vocal and locomotor activity following exposure to the maternal alarm call. In contrast, bobwhite quail chicks tested individually were found to significantly increase their locomotor activity following exposure to the alarm call.

Zing-Yang Kuo, a pioneer developmental psychobiologist, proposed that the "ultimate goal of the behavioral epigenetist is detailed, qualitative and quantitative analysis of the variations of the environmental context and their effects on behavior (1967, p.163)." The experiments presented here provide a first step toward this goal in the domain of early auditory responsiveness in bobwhite quail. Whereas, results revealed no significant age effects across testing conditions, significant contextual effects on responsiveness were found in social vs. individual testing conditions.

What conclusions can be drawn from the present study? Kuo (1967) offered a taxonomy of five primary determinants of behavior (morphological, biochemical, stimulus array, developmental history, and environmental context). Kuo argued that "the effectiveness of stimuli depends on...the interwoven effects of many determining factors." This study focused on alterations in the environmental context during rearing and testing. Of course, the environmental context is only one of a number of contributors to behavioral responsiveness. Nonetheless, this study did demonstrate that the social context is important in the nature of alarm call responsiveness, at least during the days immediately following hatching. The finding that subjects tested individually actually increase their behavioral activity following exposure to the call suggests that in order for the maternal alarm

call to be effective (i.e., inhibit the hatchling's activity), the presence of conspecifics is required.

The increase in locomotor activity of individually tested birds is an example of the subject response variability in this study. In all age groups and testing conditions, large standard deviations were reported (refer to Tables 1-8). For example, the standard deviation for grid crossing across all age groups and testing conditions was 6.02 in pretests and 7.28 in posttests. This was particularly evident in the individual testing condition where standard deviations for grid crossing collapsed across age groups was 7.32 pretest and 10.64 posttest. Such variability may be attributed to a number of possible factors. One possible explanation is derived from arguments presented by Gottlieb (1991), who proposed that normally occurring (i.e., species-typical) experience serves to canalize or constrain the behavioral development of young organisms. Since the subjects used in these experiments did not receive species-typical experience (i.e., they were maternally-naive and incubator hatched), it may be that their behavior was not constrained or canalized to the degree found under typical conditions. In the wild, bobwhite hatchlings would likely have numerous exposures to the maternal alarm call, both pre- and postnatally (Stoddard, 1931; Stokes, 1967). The physical environment they are reared in would also be more complex than that afforded in this study. For example, hatchlings would likely have many more hiding sites in their natural situation. The absence of these contextual influences may leave the laboratory reared bobwhite hatchling's behavior less constrained and thus potentially more variable than normally reared birds.

Additionally, as Gottlieb and others have pointed out, many non-obvious experiential factors might be absent under laboratory reared conditions. It is known, for example, that bobwhite quail synchronize their hatching in the wild (Vince, 1972). However, incubator reared bobwhite embryos do not appear to synchronize their hatch, at least in our laboratory. This lack of hatching synchrony may be attributed to embryos not being able to hear each other vocalize prior to hatching. While this may or may not have any impact on alarm call responsiveness, it does demonstrate that in the absence of specific species-typical experience, the hatchlings behavior can be more variable (demonstrate more degrees of freedom).

In this light, the nature of the measures that define the phenomena of interest in this study also need comment. Grid crossings and number of vocalizations appeared useful ways to quantify the amount of behavioral activity of each subject before and after exposure to the maternal alarm call. Huddle duration, while not entirely independent of the grid crossing measure, also provided a useful measure of the sociability of subjects, as well as a measure of the quality of their behavioral inhibition. However, while these measures are effective in assessing behavioral inhibition, they are not without need for refinement. For example, total grid crossings are a function not only of the organism's behavior, but also the nature of the grid pattern. Smaller grid spaces would have yielded higher grid crossing totals, and alternatively larger grid spaces would have yielded lower totals. As a case in point, even when subjects were not crossing the grid patterns, they were in some instances still moving about. This behavioral activity (for

example, the jostling about of subjects in the huddle) was not sufficiently captured by the behavioral measures employed in this study.

The scoring of vocalizations was also dependent on several factors, most notably the presence of conspecifics. Subjects tested individually were given individual vocalization totals. However, subjects tested socially were given a group vocalization total. Thus, while some subjects in the social conditions may have vocalized many times, others may have made relatively few vocalizations. It might be possible to mitigate this factor to some degree with the use of more sophisticated technology. However, such technology was not available for this study. In this light, future work should focus on the refinement of vocalization measures for socially tested subjects.

In this light, this study represents a beginning step in the analysis of alarm call responsiveness in bobwhite quail chicks. Future work should have several goals. Miller (1988) states that laboratory work must be anchored in field studies. This is true for his work on the alarm call responding of mallard ducklings and is also true for future work with bobwhite quail. A comprehensive description of the range of species-typical responding found in the wild would do much to illuminate the patterns of alarm call responding seen in this study. In addition to field work, more extensive acoustic analysis of the alarm call itself is needed. As Miller and Blaich (1986, 1987) have demonstrated in mallard ducklings, acoustic analysis is necessary to reveal what particular acoustic components (i.e., repetition rate, fundamental frequency, etc.) are most effective in inducing behavioral inhibition in bobwhite chicks. In this light, the present study

attempted to obtain normative, baseline data detailing the responsivity of maternally naive, socially-reared bobwhite quail chicks to the species-typical maternal alarm call. This study demonstrates the potential range of behavioral responding and possible developmental outcomes that are characteristic of the organism-contextual transaction found in this particular species under specific rearing and testing conditions.

Future work should begin to detail not only the range of behavioral responding (degree of behavioral plasticity, see Miller, 1981), but also should employ experiential modification and experimental manipulation to uncover the conditions, experiences, and events necessary and sufficient for alarm call responsivity to emerge. That is, a developmental analysis of bobwhite quail hatchlings alarm call responsivity must include both a normative assessment of behaviors, and then be followed by controlled experimentation to examine the parameters that both define and constrain the development of alarm call responsiveness. This study focused on the first step, the description of the phenomena.

While aspects of future studies will of necessity parallel work previously done by Miller and his associates with mallard ducklings, examining alarm call responding in bobwhite quail will provide an analysis of a different kind of precocial avian species (i.e., mallard ducklings are water fowl, bobwhite quail are a gallanationous species). As such, future work will provide the means to continue an extended polythetic analysis in determining the generality of such behavioral concepts as the development of species-typical perception and communication (Jensen, 1967; Cairns, 1979).

Investigating two distinct species in parallel provides an excellent opportunity to employ polythetic criteria in comparative research.

"Polythetic criteria demand that we have detailed information about the interchanges in both species before we can judge their relatedness with regard to a particular characteristic (Cairns, 1979)." Jensen (1967) argues that polythetic generalizations should be based on a "matrix" of differences and similarities when attempting to apply the same behavioral concept to two different species or developmental phenomena. It is insufficient to focus on a single "critical" feature to justify commonality. Indeed, this is the very essence of comparative developmental psychology. Studying only one avian species and extrapolating to all other avian species is insufficient to capture the rich diversity inherent in developmental studies. As Cairns (1979) points out, "premature extrapolation (between species) makes for poor science because it results in (1) an incomplete analysis of the phenomena, and (2) a failure to examine directly the mechanisms that control the behavior in the individuals about which the generalization is made."

In this light, future experiments should examine whether repetition rate is indeed the dominant acoustic characteristic in the bobwhite maternal alarm call. Repetition rate has been demonstrated to be the critical acoustic feature for mallard ducklings' assembly and alarm call responding (Miller, 1983), as well as bobwhite quail assembly call responding (Lickliter and Stombous, 1992). Thus, it is hypothesized that repetition rate is also the critical acoustic feature for bobwhite alarm call responding.

Additionally, future work must investigate if there are any critical prenatal auditory experiences that facilitate the development of bobwhite behavioral inhibition as the species-typical alarm call response. The present study demonstrates that bobwhite quail hatchlings respond to the maternal alarm call by inhibiting their vocal and locomotor activity essentially from hatching. Thus, the search for critical acoustic experiences that support the development of this behavior should begin in the prenatal period.

Bobwhite embryos are typically exposed to three sources of prenatal auditory experience: self-produced, sibling produced, and maternally produced. Miller and Blaich (1988) have demonstrated that auditory experience with broodmates is a significant influence in the development of mallard duckling alarm call responding. They have also demonstrated that self-stimulation alone is not sufficient to maintain a high degree of behavioral inhibition in response to the mallard maternal alarm call (Miller and Blaich, 1988). In this light and in keeping with the previously stated rationale to continue a polythetic based research program, a series of related experiments should investigate whether self-produced, sibling produced, and/or maternally produced vocalizations are necessary and sufficient to facilitate and maintain auditory responsiveness to the bobwhite maternal alarm call.

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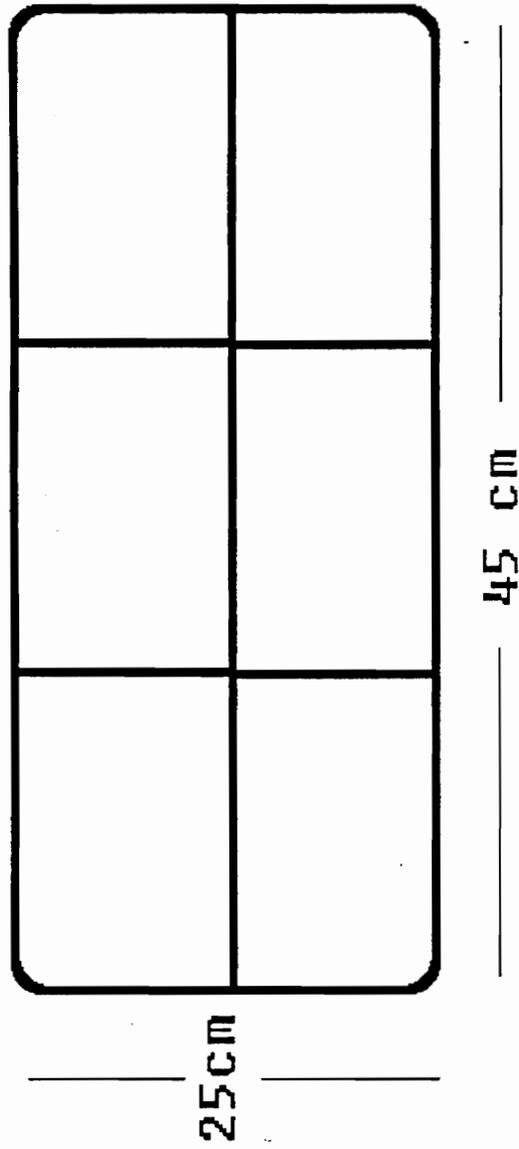


Figure 1
Testing Tub Grid Pattern

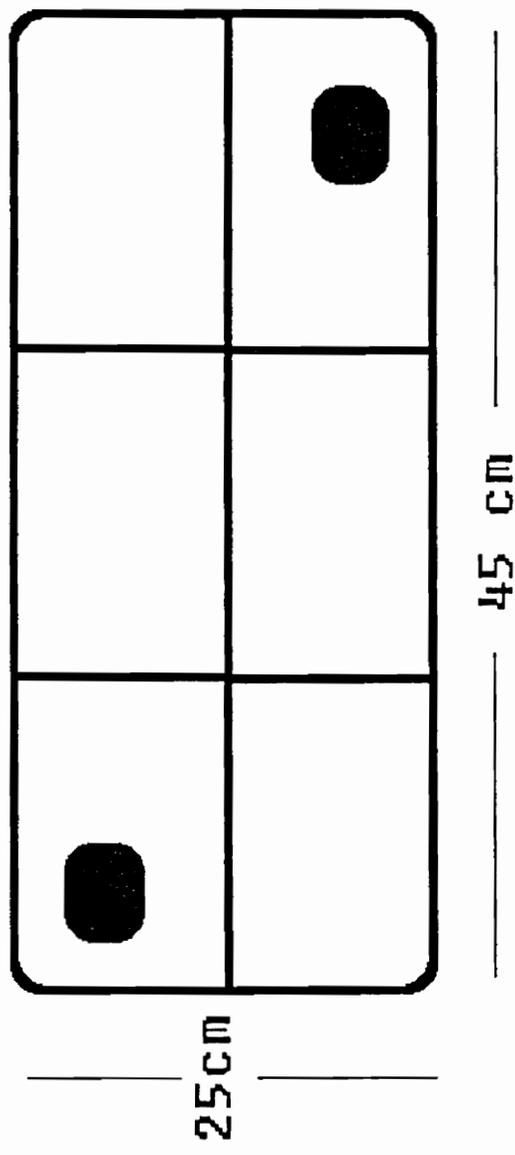


Figure 2
Testing Tub Grid Pattern
with Hiding Sites

Table 1

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of grid crossings in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Social	24	20	8.05 (5.61)	2.35** (3.60)
Social	48	20	4.50 (2.50)	0.75** (1.48)
Social	72	20	5.70 (5.69)	1.10** (2.57)
Social	96	20	4.85 (3.05)	0.20** (0.62)

Standard deviations are listed in parentheses.

* All subjects reared and tested in groups of 4.

** ($p < .0001$)

Table 2

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of vocalizations (per group) in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Social	24	5	106.40 (61.21)	78.60** (46.51)
Social	48	5	103.40 (53.33)	88.20** (65.34)
Social	72	5	72.20 (43.96)	55.00** (30.22)
Social	96	5	96.00 (57.20)	37.40** (56.43)

Standard deviations are listed in parentheses.

*All groups consisted of 4 subjects each.

**($p < .0001$)

Table 3

**Alarm call responsivity of bobwhite quail hatchlings:
Mean total huddle duration (per group) in seconds**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Social	24	5	18.00 (4.95)	39.80** (12.40)
Social	48	5	30.80 (13.59)	39.80** (28.11)
Social	72	5	31.80 (14.18)	38.80** (23.66)
Social	96	5	38.20 (19.33)	58.60** (3.13)

Standard deviations are listed in parentheses.

* All groups consisted of 4 subjects each.

**($p < .0001$)

Table 4

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of grid crossings in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Hiding Site	24	20	2.65 (2.03)	1.40** (2.08)
Hiding Site	48	20	7.60 (8.45)	3.10** (7.25)
Hiding Site	72	20	8.10 (5.51)	1.25** (2.43)
Hiding Site	96	20	5.60 (4.51)	0.20** (0.62)

Standard deviations are listed in parentheses.

* All subjects reared and tested in groups of 4.

** (p < .0001)

Table 5

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of vocalizations (per group) in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Hiding Site	24	5	68.80 (42.30)	61.60** (45.83)
Hiding Site	48	5	62.20 (61.15)	32.00** (56.63)
Hiding Site	72	5	89.00 (45.37)	24.40** (40.75)
Hiding Site	96	5	123.60 (22.81)	20.20** (37.83)

Standard deviations are listed in parentheses.

*All groups consisted of 4 subjects each.

**($p < .0001$)

Table 6

**Alarm call responsivity of bobwhite quail hatchlings:
Mean total huddle duration (per group) in seconds**

Testing Condition	Age (hrs)	N	Pre-test	Post-test
Hiding Site	24	5	35.00 (21.95)	37.40** (27.51)
Hiding Site	48	5	8.20 (14.53)	31.80** (29.14)
Hiding Site	72	5	10.00 (17.48)	23.40** (26.02)
Hiding Site	96	5	27.60 (10.64)	57.60** (5.37)

Standard deviations are listed in parentheses.

* All groups consisted of 4 subjects each.

**($p < .0001$)

Table 7

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of grid crossings in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Isolation	24	20	5.90 (7.00)	8.15** (10.19)
Isolation	48	20	3.10 (5.24)	4.50** (10.01)
Isolation	72	20	8.70 (9.66)	8.35*** (10.74)
Isolation	96	20	3.95 (5.79)	8.40** (11.82)

Standard deviations are listed in parentheses.

* All subjects reared in groups of 4, but tested individually.

**($p < .0001$)

***N.S.

Table 8

**Alarm call responsivity of bobwhite quail hatchlings:
Mean number of vocalizations (per group) in one minute trials**

Testing Condition	Age (hrs)	N*	Pre-test	Post-test
Isolation	24	5	191.00 (139.01)	171.60** (98.55)
Isolation	48	5	188.20 (59.21)	167.20** (57.67)
Isolation	72	5	192.60 (62.91)	146.60** (57.67)
Isolation	96	5	178.40 (88.57)	158.80** (70.19)

Standard deviations are listed in parentheses.

*All groups consisted of 4 subjects that were tested individually.

**($p < .0001$)

Appendix A

Alarm Call Response Data Collection Sheet

Group: _____ **Week:** _____ **Subject:** _____

Day 23: _____ **Hatched:** _____ **Coder:** _____

Date: _____ **Time:** _____ **Age:** _____

Pretest (1 min): **Silence**

Activity Measures:

Grid Crossing: _____

Vocalization: _____ (Dt / Ct)

Huddle: Y / N

Duration: _____

Hidden: Y / N

Test (30 sec): **Alarm Call**

Activity Measures:

Grid Crossing: _____

Vocalization: _____ (Dt / Ct)

Huddle: Y / N

Duration: _____

Hidden: Y / N

Post Test (1 min): **Silence**

Activity Measures:

Grid Crossing: _____

Vocalization: _____ (Dt / Ct)

Huddle: Y / N

Duration: _____

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