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RESPONSES TO DISTRESS SIGNALS IN BOBWHITE QUAIL
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RESPONSES TO DISTRESS SIGNALS IN BOBWHITE QUAIL
(Colinus virginianus)

By

Mary Lee Nitschke

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ABSTRACT

RESPONSES TO DISTRESS SIGNALS IN BOBWHITE QUAIL (*Colinus virginianus*)

By

Mary Lee Nitschke

Two studies examined three main hypotheses regarding responses to Bobwhite quail in a laboratory situation to recorded distress vocalizations of conspecifics and of members of other species. The first prediction was that recorded distress calls would elicit defensive responses and suppress nondefensive responses in Bobwhite quail. Second, conspecific distress calls were expected to be the most effective, especially in eliciting the defensive response of freezing. For distress calls of other species, the closer the evolutionary relationship between the species, the more effective the distress calls should be in eliciting freezing. Finally, because results of earlier studies of habituation (or decrement of response) to repetitions of distress vocalizations have been equivocal, the prediction regarding habituation was made in the form of the null hypothesis, that no habituation would be observed in any signal condition.

Because Bobwhite quail are highly social animals, triads of birds (two males, one female) housed together were also tested together. The general procedure was the same in both studies. A triad of birds

first underwent habituation to the experimental chamber, a sound-proofed box equipped with speakers for auditory stimulus presentation and that permitted behavioral observation. All triads were then observed for a six-minute behavioral baseline period. Following the baseline, all triads first heard one trial of a recording of Bobwhite quail food call, after which three trials of the auditory stimulus appropriate for the triad's experimental group were presented. A trial consisted of two five-second presentations of a call with a ten second intersignal interval. Intertrial intervals were at least two minutes.

In Study 1, independent groups of six triads of birds each heard either Bobwhite quail distress call or taped silence following the food call. In Study 2, independent groups of five triads of birds each heard one of six auditory signals following the food call: Bobwhite quail distress call, chicken distress call, blue jay distress call, rabbit distress call, reversed Bobwhite quail distress call control, and Bobwhite quail food call control. Because Bobwhite quail in groups tend to act in concert, average frequencies of response for each triad of birds constituted the basic unit of analysis. Spectrographic analyses of the stimulus calls were also prepared.

Results of both studies generally supported the first hypothesis. All distress calls did elicit defensive responses, and some non-defensive responses (such as vocalization) were suppressed although others (such as preening) were not. Hypothesis Two was partially supported. Among avian species, Bobwhite quail distress calls were

most effective in altering responding, with chicken distress calls next most effective and blue jay distress calls least effective--a decrease in order of degree of evolutionary relatedness, as predicted. However, rabbit distress calls were as effective as conspecific distress calls in affecting the behavior of Bobwhite quail. This result may reflect different temporal attributes of the rabbit distress call as revealed by spectrographic analyses of all of the calls. A very different explanation may be that the rabbit, though further removed phylogenetically from Bobwhite quail than other avian species, nonetheless shares the same ecological niche as Bobwhite quail, and so rabbit distress calls have strong signal value for these animals. Finally, responses to these auditory signals clearly showed habituation over trials in this laboratory setting.

A primary question motivating this research was whether distress calls communicate universally: Is a scream a scream in any language? The results of these studies show that the responses elicited by a "scream" are constrained by several contingencies, including phylogenetic relationships, environmental contingencies, and what the animal is doing when it first hears the scream.

DEDICATION

To "E"

who loved
who cared
who helped
who believed

in memory of

CorriAnne and Rusty and Stan

whose interactions brought it all together for me.

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INTRODUCTION

The Present Study

Behaviors that are typically called communicating range over all the classes of consummatory behavior (Denny & Ratner, 1970). In birds, these behaviors generally involve postural displays and vocalizations. Of particular interest here is the issue of how birds respond to the category of communications known as distress signals when heard in a laboratory situation. Three main questions are asked.

The first question concerns how bobwhite quail respond upon hearing the distress vocalization of a member of its own species (conspecific vocalization). Within the constraints of the laboratory, the present study takes a look at the question, "What does the animal do when presented with a recorded distress call of a bobwhite quail as an isolated auditory stimulus?"

Some theorists (e.g., Lieberman, 1977) have suggested that one of the universals in communication among different species (interspecific communication) is the distress signal. Put in a more general way, one might ask whether a scream is a scream in any language. Background information obtained from animal breeders, and also from human mothers, support the notion that humans readily respond to the distress vocalization of other species of animals. The second question of interest for the present study, then, is to observe how the

bobwhite quail responded to the distress vocalizations of species at different degrees of evolutionary relatedness to themselves.

Habituation, the waning of a response with repeated stimulation, is one of the most basic learning phenomena. The circumstances under which habituation of defensive, survival, and fear responses might occur is an unresolved issue (Hinde, 1970). Habituation of fear responses to visual stimuli and to some auditory stimuli is readily observed in the laboratory and in situations in which artificial predators are used (Leibrecht, 1974). However, in situations using auditory stimuli (Zeiner & Peeke, 1970) and in those using live predators as stimuli (Curio, 1975), habituation is not consistently observed. In the present study, then, the third question of interest was whether habituation would be observed to auditory distress stimuli over three repetitions of the stimuli in a laboratory situation.

Birds have natural defensive responses to alerting signals. The defensive distance model proposed by Ratner (1967) suggests that when an animal's survival is threatened from a very short distance, one of the highly probable responses will be freezing, or immediate cessation of all movement. The present study examines both defensive responses such as freezing and nondefensive responses such as pecking and preening made in response to auditory distress signals and to nondistress comparison signals.

To clarify and elaborate on the rationale for considering these questions, the remainder of this introductory chapter covers

the following topics: (1) Distress signals, the responses which they elicit, and the available data regarding interspecific communication of distress; (2) Freezing as a defensive response; (3) Habituation and its implications in the case of defensive responses; and (4) The attributes of bobwhite quail which make them a good choice as experimental animals for this study. Finally, some pilot work is described which served as a basis for a number of procedural decisions made for this study.

Distress Calls

Description of Distress Calls

A distress call refers to the call or vocalization given by a captive bird (or other animal) when seized by a predator or held by a human. Distress calls are different from alarm calls, which are the calls given by a bird (or other animal) that is itself free when it sights some potential danger. This distinction, made by Frings and Frings (1968) and accepted by most investigators, is used throughout this paper.

A distress call typically has the characteristic of being a loud, repetitive burst of sound that includes a wide range of frequencies, with the fundamental frequencies generally slurred and downward sloping when examined spectrographically. Kok (1971) notes that the distress call has a piercing, harsh, squealing quality in the grackle, and many writers mention this aspect of this call in a variety of species. Johnsgard (1975) says that the typical quail distress call is loud and piercing, with a broad frequency range,

and has other characteristics such as sudden onset and repetitiveness that made the signal easy to localize (Erulkar, 1972). Cink (1971) has studied spectrograms for several species of quail and notes that the distress call is nearly identical even among rather distantly related quails. These descriptions agree with the signal characteristics specified by Marler (1957) as the ideal sound needed for a bird to localize its source: A high pitch for location by intensity difference, a low pitch for location by phase difference, and a sharply broken and repetitive sound for location by time difference. The distress calls of adults in several of the galliformes look quite similar spectrographically. Collias and Joos (1953) discuss such attributes in the distress signal of the domestic fowl, and Williams (1969) shows that for the California quail, although there is some variation between individuals, the configuration of the call is the same regardless of sex of bird or individual bird making the call. Williams also shows that the call is very similar for both the California quail and the bobwhite quail. Ellis and Stokes (1966) note that the distress call of the chukar partridge, the gambel quail, the California quail and the domestic fowl are pictorially analogous.

Since the universality of effect of distress calls is one issue of concern for this research, it is interesting that the distress call of other animals and some mammals share some of the characteristics discussed above. Smith, Smith, Oppenheimer and Devilla (1977) note that the scream of the black-tailed prairie dog is elicited when this wild dog is caught in a leg trap or when it is

handled by a human (a standard procedure for eliciting distress calls in many species). Waring (1970) shows the typical signal characteristics for prairie dogs, which is a clear, high-pitched, variable (or complex) signal with a sudden onset. Smith et al. (1977) state that the prairie dog scream appears to encode a message of "escape if feasible," but this team did not specifically test responsiveness of the prairie dogs to this signal. Brand (1976) mentions that chipmunks, when attacked, emit a squeal, a high-pitched (up to 14KHz) complex sound. This is especially true if they are bitten. His spectrogram for the chipmunk appears similar to other recordings of distress signals.

Scott (1968) and Compton and Scott (1971) have shown that the distress cry of a domestic canine puppy is characterized by a number of different kinds of sounds, highly variable in form and pitch. It is a mixture of yelps and squeals in no particular order which serve as distress signals that are easily localized. They suggest that the function of this form of the signal is to prevent habituation in the listener.

For experimental purposes, the most common method of eliciting a distress signal from birds and small animals is to capture and hold the animal by the feet. Investigators disagree as to whether or not it is necessary to allow the wings of birds to remain free to flap, but the necessary condition appears to be holding the bird by the feet. Numerous investigators, including most mentioned herein, state that this hand-elicited distress call is the same call that is given when a bird is captured by a predator. Stefanski and

Falls (1972a) have made spectrographical comparisons of a distress call from a hand-held bird with that given by a bird captured by a hawk. They found no significant differences between the two signals. Frings and Frings (1958) report a similar finding. Accordingly, the feet-holding method was used to elicit the bobwhite quail distress calls in this study.

Responses Elicited by Conspecific Distress Signals

Eibl-Eibesfeldt (1970) suggests that the death cry or the distress cry of many animals may function as warning signals to conspecifics. Several of the investigators mentioned above suggest that since distress calls are easily localized, they could serve to provide information to conspecifics about the location of a predator. Tinbergen (1968) further implies that distress signals may have some universality across species in that they function to turn off attack in the primate species. Similarly, Frings and Frings (1964) suggest that a human may escape attack from a great ape by screaming (screaming is considered to be the primate distress signal). They suggest that screaming will turn the attack behavior into a rescue or solicitation behavior pattern. They fail to mention what the consequences of being rescued by a great ape might be for the human.

Responses to distress signals of conspecifics vary with the conditions present. Generally, a distress signal from a young animal elicits parental approach. There is an excellent review of this aspect of distress signaling by Noirot (1972) which focuses on

maternal behavior. However, we are primarily concerned with this question in adult members of a species, and so such signalling by immatures or young members of a species will not be discussed further.

Frings and Frings (1964) suggest that responses to distress signals vary with the social organization of the species. Solitary species show little or no reaction to distress signals, whereas species that are moderately dispersed are attracted by the distress signal of a conspecific, which often elicits mobbing. In compact flock birds, e.g., starlings, the distress signal is a strong repellent and will disperse an entire flock, danger to one member implies danger to the others.

Approach Toward Distress Signals

Let us first examine some instances in which the response to a conspecific distress signal is a positive phonotaxis, that is, approaching the source of the sound. (It must be remembered that it is not clear in all of these cases that it is only the auditory component of the signal that may be the effective stimulus.) Fretwell (1973) notes that a bluebird caught in a mist net screams when handled, and that this elicits mobbing by conspecifics. Generally other passerines are also attracted to a bird emitting distress signals in the net. Stefanski and Falls (1972a), using a playback paradigm, found that conspecifics (sparrows) approached the speaker and produced alarm calls and threat displays. A further observation, reported by Falls in the above-mentioned report, describes a blue jay being attacked by a sharp-shinned hawk. The screaming jay elicited

approach by the other jays with the result that the hawk released the screaming jay and flew off. Kok (1971), investigating the grackle, and Chamberlain and Cornwell (1971) playing crow distress cries, both report that conspecifics were attracted to the source of the sound, approached, and showed alarm behaviors. Eibl-Eibesfeldt (1970) reports that many apes and monkeys will attack blindly if a conspecific gives a distress call upon being handled by the keeper or caretaker, even though their keeper is a familiar stimulus. Forsythe (1970) reporting on the behavior of a passerine, the long billed curlew, observes that this species' response to hearing a conspecific distress signal is to crouch and freeze.

In quail, a social species, both Stokes (1967) and Johnsgard (1975) report that distress calls from other quail attract conspecifics and may result in attempted assistance and the elicitation of alarm calling. Stokes mentions several instances of being attacked by males if he elicited a distress cry from a bird he captured from the same pen occupied by the attackers.

Avoidance of Distress Signals

Conspecific distress signals can also produce negative phonotaxis, or fleeing from the source of the sound, a phenomenon which fruit growers and others have found useful for its practical applications in controlling birds' behavior. Frings and Frings (1968) give an excellent review of the practical uses of bioacoustic methods to control problem species of birds and insects. Frings and Jumbar (1954) report that a starling distress call played at

night in a starling roost will clear large areas of starlings if played consecutively for several nights. Frings, Frings, Jumbur, Busnel, Bigan, and Gramet (1958) report the results of several studies involving crows. The distress call of crows living in France (*C. monedula*) played to mixed flocks of birds feeding in the fields served to disperse the flocks in about 75% of the cases tested. They also ran tests (played distress calls) at night in roosts of mixed members of the Corvid family. The birds would disperse and stay away from 3 to 30 days before returning. When the distress signal of the French crow was played to crow populations in the United States, the U. S. birds showed no response. And when crow vocalizations taped in the U. S. were played to the French crows, they were only minimally responsive. Although most writers concur with Smith's (1978) suggestion that it is not likely that there would be regional dialects in bird calls (as opposed to bird songs which do show differential dialects), the France-United States study suggests that the possibility of dialects in calls would bear investigating, at least for these species.

Whether they represent approach or avoidance, the responses to conspecific distress signals can be categorized as defensive responses. On the basis of the findings reviewed, it is predicted that the presentation of conspecific distress calls to bobwhite quail will result in the elicitation of defensive responses and in the suppression of nondefensive responses.

Interspecific Communication of Distress

Alcock (1975) argues that, as a result of convergent evolution, interspecific communication of danger readily occurs. For example, totally unrelated species might exhibit behavior patterns that are remarkably alike because such patterns are effective. Their effectiveness reflects the evolution of similar responses because of similar selection pressures, i.e., convergent evolution. Hinde (1970), commenting on the adaptiveness of behavior, also notes that signal movements have been subject to selection for their efficiency. In fact, Marler (1957) has found that signals are transmitted by simple sounds which may be shared by several species. The alarm calls given by passerines when a hawk flies over are almost identical for the reed bunting, the blackbird, the great titmouse, the blue titmouse and the chaffinch. Similarly, mobbing calls of birds from several families show convergence (Marler, 1959). The form of calls varies with their function. This is illustrated by the alarm calls for all of the species mentioned above, which sound like a high thin whistle. These calls share the characteristics of long duration, no sudden changes in pitch, and of beginning and ending gradually, all of which are elements which do not convey information about the position of the calling bird.

There is considerable support in the literature for interspecific similarity of alarm and warning calls among birds that share a habitat. Since we will not be dealing specifically with alarm calls in this dissertation, the reader is referred to Hinde's

Bird Vocalizations (1969) which covers the alarm signals in detail.

Frings and Frings (1964) state that almost all birds have distress signals, generally raucous shrieks, which they emit upon being captured, and that the distress calls of the higher vertebrates sound much alike. Stefanski and Falls (1972b) agree that a casual survey of the distress calls of many genera suggests that congeneric species frequently have similar distress calls.

Marler (1957) in discussing the specific distinctiveness of communication signals in birds, suggests that all danger signals should be in the same category as alarm calls in which interspecific communication is common in birds, mammals, and orthopteran insects. Hinde (1970) suggests that convergence occurs in many displays associated with predators because the prey species living in a given area are better protected if they respond to each others' alerting and danger signals. It would appear then that the distress signal should have inter-specific communication value.

Boudreau (1968) reports that even crude imitations of rabbit distress sounds will lure hawks, owls, and mammalian predators within rifle range, and that other birds will approach to investigate. Indeed, the whole idea of "predator calling" as a hunting technique is built on the fact that predators do respond to distress signals of various other species, the rabbit having one of the most general ones. In fact, there are at least two business firms that specialize in producing distress signals of a variety of species, to be used in

the field to attract animals to the source of the sound. Hand "kissing," which produces a squeaking sound, is a common field technique employed by naturalists and ornithologists to lure birds within visible range. Andre, reported in Hartley (1950), states that the plumage hunters in Trinidad imitate the hooting of an owl to attract hummingbirds and other species, since this sound elicits mobbing behavior. Reports of this type are common in the general bird literature. The possibility must be kept in mind, however, that any novel sound may elicit approach and exploratory behavior in many of these species.

Burt (1967) reports an observation common to many naturalists that the blue jay is the sentry of the woods. That is, when a blue jay screams, most of the members of the habitat hide or freeze in response. To my knowledge there are no experimental investigations or verifications of this event. Another aspect of inter-specific communication that should be mentioned here is that it may not be the vocalization per se that is the stimulus for alerting behavior to danger signals. Riney (1951) gives a charming account of the relationship between birds and deer in a forest habitat. He notes that deer react to two main types of environmental disturbance involving birds: (1) bird sounds which indicate a sudden change in the birds' activities, such as the sudden whirr of wings and the scolding of jays, etc.; and (2) the "zones of silence" that often surround intruders as they penetrate previously undisturbed areas. He suggests the silence results from alarmed birds fleeing into the

canopy or freezing. The best evidence Riney offers for these observations is that he has been able to induce deer to resume their normal behavior or "break their freeze" by imitating "conversational" bird calls.

Experimental Studies of Interspecific Communication of Distress

Chamberlain and Cornwell (1971) played the distress calls of three sympatric species to the common crow species in a field study. When the blue jay distress call was played, crows gathered to the speaker in five out of ten tests. For the calls of the common grackle and the starling, they reported, respectively, no response in five of six tests and on "unpredictable" response.

The most thorough study of interspecific communication involving distress signals has been done by Stefanski and Falls (1972a & 1972b), studying members of the Fringillidae (the song sparrow, the swamp sparrow, and the white-throated sparrow). Using distress calls recorded from birds captured in mist nets or captured and held by the feet, they investigated both intra- and inter-specific responses in these species. The calls were played to territorial pairs in successive stages of the breeding cycle. Responses measured were approach, movement about the speaker, alarm calls, and displays, latency of response, closeness of approach, number of movements, and number of calls elicited. Both males and females showed peak periods of responsiveness in all categories in the nest-building, egg laying, late nestling, and fledgling stages of the

breeding cycle. In the inter-specific study, the song and swamp sparrows responded strongly to each other's calls, which are alike in length, carrier frequency, and frequency range and which overlap broadly in the rate of frequency modulation. The white-throated sparrow, whose calls differ in these properties, responded only weakly to the distress calls of the other species. As might be expected, the white-throated distress signal elicited only weak responses from the song and swamp sparrows. Stetanski and Falls also found considerable variability in different dependent variables; intra-specific responding was stronger in the calling rate and movements measures but not in the closeness of approach or latency to respond.

Two other manipulations in this study are of specific interest. One of these manipulations consisted of playing artificial calls that simulated the natural distress calls in length, carrier frequency, and frequency range to song and swamp sparrows. There were no significant differences found in any of the response measures between the natural calls and the artificial calls. Song sparrows were then tested on mechanically produced calls which varied in carrier frequency, rate of frequency modulation, and length of the call. With respect to each property, the birds responded strongly if the value of that property fell within the range found in the natural calls, but they responded weakly if the value fell outside this range. Stefanski and Falls conclude that all three of these properties are used in call recognition.

The other interesting manipulation in this study consisted of placing a live predator in the vicinity of the speaker when playing distress calls. Briefly, there was no significant change in most of the measured dependent variables when a live predator was present. There was one major difference, however. Once the predator was in view, the responding bird directed its displays to the predator rather than to the speaker. The sparrows' displays to the predators consisted mainly of threat displays and diving attacks.

The behavior of the predators used in this manipulation is also of some interest. The squirrel approached the speaker when the distress signals were presented, while the blue jay remained motionless or froze during the distress signal until the sparrows arrived on the scene.

Stefanski and Falls suggest three functions served by interspecific responses to distress calls: (1) the predator may be startled by the other birds' responding and allow the prey to escape; (2) the responding bird receives information about the predator and its location; and (3) the harassment and distraction provided may enable the young to hide or escape. Distress calls may also function to teach the young about predators.

Other observations suggest that the distress signal itself may have a defensive function in addition to recruiting help and spreading alarm. Stokes (1967) suggests that the onset of this sudden loud call may so alarm the predator that it momentarily releases its grip on the prey. He reports that Nygren observed a

Cooper's hawk catch a chukar partridge, which at once gave a loud piercing scream. In reaction, the hawk momentarily released its grip and the captured chukar escaped. Summner (1935) and Bremond (1963) report similar observations.

The conspecific distress cry is a salient stimulus that may function to elicit fear or defensive responses to various species. Bolles (1970) suggests that a salient stimulus such as a distress signal elicits species-specific defense responses such as freezing and suppresses other behaviors such as grooming and exploring. Fentress (1968), studying the grooming responses of voles, found that following the presentation of a frightening stimulus such as a pain cry voles flee and/or freeze. Increasing the strength of the stimulus increased the duration of freezing and also the duration of suppressed grooming.

Since the results of several studies indicate that distress signals can be effective interspecifically, and further suggests that degree of effectiveness of signals vary directly with phylogenetic relatedness, it is predicted that the effectiveness of distress signals of other species in eliciting defensive responses in bobwhite quail will decline in the order of increased distance between the two species along a phylogenetic scale. For signals to be used in this study, effectiveness of signal is predicted to decline from the conspecific in the order; chicken distress signal, blue jay distress signal, rabbit distress signal.

Freezing

That freezing is a prepotent defensive response is shown by its generality across species. Robinson (1969) in classifying animal defensive systems lists freezing as the most prevalent behavioral correlate of crypsis (protective coloration). Hinde (1961, 1970) lists freezing as a fear response and one of the postural adaptations promoting safety from predators. Carthy (1958) suggests that cessation of movement has the double advantage of making invertebrates less conspicuous to enemies and less attractive to the predator. Eibl-Eibesfeldt (1961), investigating the prey killing behavior of polecats that had been fed rodents and chickens, notes that none of the experimental animals attacked either the rat or the chicken as long as the prey animal remained motionless on the spot. In both cases, once the animal started to move, the polecat pursued it.

Bolles (1970), in discussing species-specific defense responses, gives a review of freezing as it pertains to the rat literature in avoidance learning. He notes that freezing is always near threshold, that it is seen whenever any novel stimulus event occurs, and that freezing effectively competes with other behaviors such as exploring and grooming.

Freezing is also common in the passerine or song bird species. Curio (1975) notes that freezing is seen in response to a hunting sparrowhawk, as long as the hawk is far enough away that its presence does not elicit fleeing into the canopy. In veeries, Dilger (1956) describes the freezing crouch which is adopted instantly upon sight of a flying predator. The bird crouches close to the substrate,

the plumage is tightly compressed and the head may be retracted between the shoulders. The bird remains in this posture for two to three minutes without making any visible movement. Power (1966) describes a similar response in parakeets. If the flock is confronted with the sudden approach of a predator, the individuals crouch in a completely rigid, immobile state with the eyes open wide and the plumage compressed, and they may remain in this state for 15 minutes or more. Forsythe (1970) describes a similar postural pattern that occurs in response to distress calls of conspecific chicks of the long-billed curlew.

In gallinaceous birds, freezing is a well known response in the nondomestic species. Stoddard (1931) says that a salient behavioral characteristic of the bobwhite is freezing to aerial predators. During freezing in aves, the bird's posture is characterized by a complete lack of movement, the plumage appears compressed, the eyes are wide open and the bird remains in the posture for a variable period of time. Stokes (1967) notes that the bobwhite chicks may freeze, or run for cover and then freeze for an hour or more, in response to either the appearance of a predator or to high pitched squeaks that resemble their distress signal. These descriptions are also found in works on closely related species. Freezing is similar in the California quail (Williams, 1969), the Gambel quail (Ellis & Stokes, 1966) and the chukar partridge (Stokes, 1961). Wood-Gush (1971) notes that freezing in the domestic fowl develops on day one in chicks to auditory stimuli and somewhat later to visual stimuli. Kruijt (1964) describes freezing of chicks of

the Burmese red junglefowl as developing out of the squatting posture in the first few days after hatching, and concurs with Wood-Gush that the bird freezes in the posture it happens to adopt at the moment of alarm.

Freezing as a postural behavior pattern within aves appears to have common characteristics, to be involved in predator defense or survival responses of aves, and to be elicited by alerting or danger signals significant to the species involved. Accordingly, although a number of behaviors were examined in this dissertation research, the defensive response of freezing is of special interest.

Habituation Studies

Given the signal function of distress cries for conspecifics and also for members of other species, one might wonder whether habituation--response decrement with repeated presentations of a stimulus--would be observed in response to distress signals to the degree it is for responses to other types of signals.

Habituation to distress cries in the rat was investigated by Zeiner and Peeke (1969, 1970) using a suppression technique for an innate response. Suppression of the drinking response to recordings of rat distress cries habituated over days, with the major decrement occurring over the first day. In six days of testing, habituation did not reach zero, primarily because the rats continued to orient to the distress stimulus. Freezing was the initial response to any novel stimulus. This tended to be followed by exploratory behavior such as rearing, which habituated over days. Using a pure tone of a

frequency approximating the dominant frequency of the distress cry stimulus produced more rapid and more complete habituation than that seen to the natural distress cry stimulus. Previous habituation to a pure tone had little effect on initial responsiveness to the distress cry, but experience with the natural distress cry depressed subsequent response to the tone. Zeiner and Peeke suggest that a naturally occurring auditory stimulus presumably carries with it some additional information regarding aversiveness.

For a review of habituation as a general psychological process, see Denny and Ratner (1970). Leibrecht (1972, 1974) provides a comprehensive bibliography of habituation studies, including auditory studies. Hinde (1970) mentions that fear responses such as freezing typically are followed by avoidance behavior. If avoidance of the fear-producing stimulus is prevented, habituation occurs and the previously fear-producing stimulus loses its initial strength. Freezing and other defensive responses are replaced by exploration. Martin and Melvin (1964) investigated the fear responses of bobwhite quail to a silhouette model of a predator and to a live red-tailed hawk by flying these stimuli over a pen containing a single bobwhite. They ran two trials daily with a 3 minute ITI. Their total fear response consisted of: (1) a short run of less than 5 seconds, (2) stop and crouch and compress plumage, and (3) freezing or "immobility" for 10 to 13 minutes.

As might be anticipated, the live hawk elicited the strongest responses, both in terms of freezing duration and of frequency of

crouch and escape behavior. On trial 1 of a live hawk presentation, seven of the nine birds exhibited a total fear response pattern, while only one bird in the silhouette condition showed this strong a response. Martin and Melvin found habituation occurring to both stimuli as well as faster habituation to the stimulus presented second. If the live hawk was presented first, it appeared to have a sensitizing effect similar to that noted in the Zeiner and Peeke studies just mentioned. That is, if the hawk were presented first, the response took about four days to habituate, whereas if the silhouette were presented first, habituation took only one or two days. Martin and Melvin's (1964) description of the short run part of the fear response sounds very much like the protean defensive display, which is a highly erratic, zigzagging flight in response to attack (Humphries and Driver, 1970). Bobwhites in the research reported in this paper exhibited similar behavior at the onset of an auditory distress signal.

As Nice (1962) points out and as pilot work in the present study showed, an isolated bobwhite in an experimental apparatus is often an inactive animal. It would be interesting to see if the presence of conspecifics would lead to shorter or longer durations of inactivity, since Zajonc (1965) postulates that presence of conspecifics facilitates only the dominant response the individual makes in a situation.

Melvin and Cloar (1969) presented a view of a live hawk in a chamber adjacent to a bobwhite quail key pecking for food. Initially, the view of the perched hawk elicited strong freezing and

suppressed key pecking, but habituation to the hawk was rapid and showed no recovery after 18 days without presentation of the hawk stimulus. This study "unfairly" pitted freezing against key pecking. These birds were at 65% of their free feeding weight and had not eaten for 24 hours. While this may be a fine model for rat studies, it is not an appropriate procedure for work with quail. These subjects were severely food deprived and 24 hours is a long hungry spell for an animal with the rapid metabolism of a quail. This same deprivation paradigm was also employed by Gardner and Melvin (1971) who presented a live hawk flapping its wings to quail feeding in an adjacent chamber. Using widely spaced trials (one daily), they found that the freezing response to the sight of the hawk habituated rapidly and by day 4 had reached zero responding.

The results of these studies are in contrast to those of Curio (1975) in a study of organization of anti-predator behavior in the pied flycatcher. He found a lack of habituation when a live predator was presented under natural conditions, though mobbing habituated with stuffed dummies of a predator. However, it is difficult to compare laboratory and field studies of this nature. It is possible that habituation to a predator in the laboratory may involve some stimulus-specific response decrement to the "circumstances" of the encounter. Whereas the constantly changing conditions of the encounters with a predator in the natural setting may dishabituate the response. Hinde (1961) comments that responses to novel stimuli, such as startle and orienting responses, are subject to rapid habituation if not reinforced by further stimuli indicative of danger. The

rat literature on habituation of startle responses to auditory stimuli (see Davis, 1974, for review) certainly shows this phenomenon clearly. Hinde further suggests that responses to specific predators or danger signals such as the aerial alarm call of the chicken, are less likely to habituate than the general responses just mentioned.

Frings and Frings (1968), in discussing the advantages of using alarm and distress signals for bioacoustic control purposes, also point out that natural signals have advantages over the use of synthetic noises. Two of the advantages they mention are that natural signals are effective at low intensities (as low as 3 dB above ambient level) and that habituation is much slower because these communication signals are part of the social structure of the bird populations. Boudreau (1968) also notes that sounds with a sharp onset or just general "alert" noises that primarily elicit startle and orienting responses habituate rapidly and are ineffective if used alone in a bioacoustic control procedure.

Many attempts at bioacoustic control of birds' behavior have failed. One possible reason for this was suggested to me by Johnny Stewart (personal communication). He speculated that one of the primary reasons novices had difficulty in calling predators with his distress signal recordings was that they jacked up the volume too high which renders the communication value of the signal ineffective. This high volume may produce enough distortion in the signal that it is experienced as a novel stimulus. Since novel stimuli habituate rapidly unless reinforced by other stimuli indicative of

danger (Hinde, 1961) such high volume calls should also result in rapid habituation. Frings and Frings (1964) also emphasize that natural signals should not be presented at high volume levels or they lose their effectiveness in eliciting the appropriate responses.

For this dissertation research, the question of interest is whether any habituation would be detected in a laboratory situation over three repetitions of an auditory signal to groups each of which heard a different type of signal.

Bobwhite Quail (*Colinus virginianus*)
as a Preparation

Natural history and observational reports on the bobwhite quail (*Colinus virginianus*) recommend it as an excellent preparation for the study of many of the major classes of consummatory behaviors. In addition to being one of the most popular of the upland game birds of widespread distribution throughout the United States, its varied and distinctive repertoire of social behaviors offers a challenge to our understanding of the behavior of a nondomestic member of the galliformes. It is also a useful laboratory preparation for the study of defensive responses to predators in a social species that exhibits a wide repertoire of behaviors under confinement conditions.

Colinus virginianus is a small variegated brown, black, and buff colored precocial galliforme, native to the United States, which shows cryptic coloration in its habitat. One of the striking aspects of a quail family or a quail covey (a collection of quail larger than a family) is their highly integrated group behavior

(Nice, 1962). The group appears to act in concert as a unit, particularly with regard to daily activities such as preening, dusting, feeding, resting, and predator defense patterns. A typical observation by Stoddard (1931) illustrated predator defense.

. . . alarm causes every bird to freeze and remain absolutely motionless for periods of seconds or minutes, when suddenly, as if at a given signal . . . all relax and go about their business (p. 18).

The primary sources of general information on the bobwhite are Stoddard's (1931) classic text on the habits and preservation of the bobwhite, Johnsgard's (1973) Grouse and Quails of North America, and Stokes' (1967) three-year study of the behavior of this bird. These sources agree that one of the outstanding and prepotent responses in the repertoire of the bobwhite is the freezing response to an alerting stimulus, particularly a source of alarm.

Another attribute of this species that should be pointed out is that it is continually subject to significant predation from aerial predators whose visual search for prey is often dependent on prey movement of a cryptically-colored species. Denny and Ratner (1970) list freezing as one of the most obvious examples of predator defense. Alcock (1975) also points out that hiding from enemies is generally achieved through cryptic coloration and behavior such as freezing. The behavioral aspects of camouflage include more than the ability to remain motionless, although the effectiveness of camouflage is dependent on freezing. An animal will blend into the background only if it has chosen the proper substrate. There is also an appropriate time to freeze and this may be dependent upon the distance

between the predator and the prey animal as suggested by Ratner's (1967) defensive distance model. Many camouflaged animals remain motionless until the last possible moment and then suddenly dash away, exhibiting the protean or variable defensive behavior pattern described earlier (Humphreis & Driver, 1970). This is a highly erratic, zigzagging response to any attack, a behavior pattern which is common in quail before the defensive distance is reduced to zero. Robinson (1969) reminds us that freezing following locomotion is probably of great importance, since movement may have concentrated the attention of the predator on the area in which the animal has come to rest and subsequent movement might be fatal. In addition to the effect of predator prey-distance, the nature of the defensive response may be dependent upon the nature of the alerting stimulus. Worden and Galambos (1970) note that the operation of feature detectors differs for different sensory systems, suggesting that a visual stimulus may be responded to differently than an auditory stimulus.

Bobwhite quail thus have a number of attributes which make them well suited as experimental animals for the present study. They have a rich and readily observed behavioral repertoire, including in particular a readily elicited defensive freezing response. They have the further advantage over the more common laboratory animals in not having undergone generations of domestication as laboratory animals, so their behaviors may more closely resemble those of animals in the wild.

Pilot Work

Because there was no model or paradigm for the planned research available in the literature, considerable pilot work was carried out to test the feasibility of the main study. Pilot work first suggested the necessity of exposing the subjects to the experimental apparatus prior to running test trials. Without prior exposure to familiarize them with the chamber, birds sometimes remained immobile for periods as long as hours, making it impossible to observe any responses to test stimuli. Accordingly, a chamber habituation procedure was instituted for all groups of birds.

In the pilot study, nine independent groups of bobwhite quail, in triads of one female and two males who were housed together, were observed for their repertoire of responses under the following stimulus signal conditions: Bobwhite quail distress signal, chicken distress signal, blue jay distress signal, rabbit distress signal, a goshawk vocalization, reversed bobwhite quail distress signal, bobwhite quail food call, 4 Kz pure tone signal and a taped silence (tape hiss) condition in which no other specific signal was presented. The procedure followed was first to provide habituation sessions as described in Chapter Two. Briefly, subjects were placed in the experimental chamber until they met a predetermined activity criterion (see page 58 for full description of this procedure). Following habituation sessions, all groups first experienced a 6 minute baseline period in the chamber with no signals presented. If they met an activity criterion (defined full in Chapter Two, Method) they were

run through one set of stimulus signals consisting of three presentations of the signal with a 2-minute intertrial interval.

The data of interest were the changes in behavior patterns going from the baseline to the call-signal situation. The important differences and changes found can be summarized as follows: (1) Freezing was minimal to nonexistent during all 6-minute baseline periods. Following this baseline period, freezing duration in seconds decreased in the following order: Bobwhite quail distress call (48 sec.), chicken (24 sec.), blue jay (21 sec.), pure tones (15 sec.), reversed bobwhite quail distress call (8 sec.), and goshawk vocalization (2 sec.). Taped silence, bobwhite quail food call, and rabbit distress call all elicited zero freezing. These results suggested that the distress signals were having differential effects on the experimental birds and that freezing was an appropriate measure of defensive responding. (2) Duration of dusting behavior increased in magnitude from baseline to test signal period for most groups. Exceptions were the bobwhite quail distress groups and the pure tone signal groups, where dusting durations remained low and stable. A decrease in dusting among groups hearing the chicken and blue jay distress calls suggested that the signal had a suppressive effect on this response. Dusting seemed to me an especially useful baseline indicator that these birds had become somewhat comfortable in the test apparatus during habituation to it. All of the birds had experienced dusting as chicks, and as adults all of the subjects were exposed to dusting in the chamber, but they

did not have dust available in their home cages. When they discovered the dust box in the chamber, it was a powerful elicitor. Many of the birds began dusting within a few minutes after entering the chamber and continued to dust intermittently for an hour or more if left in the chamber undisturbed. The birds would often return to dusting immediately following a disturbance--a noteworthy effect, for anything that interrupts or suppresses dusting has to be a fairly powerful stimulus for dust-deprived birds.

Other pilot study results are cited in later sections as relevant to the definition of response measures and scoring categories.

Aims and Purposes of This Study

The present study was designed to provide information relevant to the issues stated below:

1. Birds have natural defensive responses to alerting signals. One emphasis of the project is to assess the effect of auditory distress signals in the bobwhite quail. (a) What are the responses to a distress call in this species? (b) Does a distress call signal elicit defensive responses and suppress nondefensive responses in this species.

Experimental Hypothesis 1: Distress calls elicit defensive responses and inhibit nondefensive responses in bobwhite quail.

2. It is conceivable that distress vocalizations are not necessarily species-specific, e.g., that a scream is a scream in any language. Does the species-specific distress vocalization

function to elicit defensive responses only in conspecifics, or are these signals also effective for other members of the habitat, closely related species, and distantly related species?

Experimental Hypothesis 2a: The conspecific distress vocalization is the most effective stimulus; in particular it will elicit a defensive response, freezing, in greater magnitude than distress vocalizations from other species.

Experimental Hypothesis 2b: The closer the evolutionary relationship between the species, the more effective the distress signal as an elicitor of freezing. The magnitude of freezing in the experimental groups decreases roughly in the following species order: Bobwhite quail, chicken, blue jay, rabbit.

3. A general psychological phenomenon, habituation, typically shows up as the decrement of a response after repeated presentations of a stimulus. Do natural defensive responses (such as freezing) to efficient elicitors (such as distress signals) also habituate? Since available data on this issue are equivocal, we will make a null hypothesis.

Experimental Hypothesis 3: No significant habituation is observed in any signal condition.

4. Distress calls of different species have not been compared spectrographically. Measurements from a spectrographic analysis of the distress signals employed as stimuli in the present study will be made and described.

METHOD

To test the experimental hypotheses, two studies were conducted as outlined in Table 1. In both studies, triads of bobwhite quail were first habituated to the experimental chamber, then placed in the chamber for a six-minute behavioral baseline period following which they were exposed to the experimental stimuli. In Study 1, which was designed to examine responses to the conspecific distress call (Hypothesis 1), independent groups of six triads of birds each heard either bobwhite quail distress calls or a taped silence control. In Study 2, which was designed to compare responses to distress calls of different species (Hypotheses 2a and 2b) independent groups of five triads of birds each heard either one of the four distress calls or one of two control stimuli. Habituation (Hypothesis 3) was examined by comparing responses across the three stimulus presentations in Phase 3 of Study 2 (see Table 1).

Since method and procedure were much the same for both Studies 1 and 2, the following discussion applies to both studies unless one of the studies is specifically designated.

Subjects

Bobwhite quail (Colinus virginianus) was the species chosen for study, for the reasons outlined in Chapter 1. Bobwhite quail eggs were secured from the Michigan State University Poultry Science

TABLE 1.--Experimental Design Summary: Study 1 and 2

		Study 1	Study 2
Phase 1.	Habituation to chamber	Both groups	All groups
Phase 2.	Baseline pretest: Six-minute silent baseline followed by presentation of Bobwhite quail food call	Both groups	All groups
Phase 3.	Experimental test: Three presentations of signal independent groups of triads for each signal type	Independent groups of six triads of birds assigned to one of two signal conditions: Group 1. Bobwhite Quail distress Group 2. Taped silence	Independent groups of five triads of birds each assigned to one of six signal conditions: Bobwhite quail distress call or Chicken distress call or Blue Jay distress call or Rabbit distress call or Bobwhite quail distress call reversed or Bobwhite quail food call Six independent groups of five triads of BWQ each
Subjects		Two independent groups of six triads of BWQ each	
Dependent Variables		(Both studies) Freezing, freezing with head movement, dusting, pecking, preening, proximity, locomotion, gular quivering, vocalization, cautious posture, locomotion to contact; (Study 1 only) pause, rest, explore, orient	

Department breeding flock, which has been in captivity for several generations. All birds were hatched at the Poultry Science facilities and transferred to the Avian Psychology Laboratory at one day of age. Here they were reared in small groups (10-15) in chick cages; they were exposed to dust during this period. Following transfer from the chick cages at approximately 30 days of age, all birds were initially housed in the laboratory in modified brooder cages. These rearing cages met space and housing requirements for this species. Subsequently, all birds were transferred to modified Wehymen pigeon rack cages where they were housed by triads consisting of 2 males and 1 female. These were their home cages during the time that experimental sessions were conducted. Subjects did not have dust available in their home cages.

The sex distribution of 2 males, 1 female in each experimental triad agrees with field data of the composition of the population of this species in its natural habitat (Stoddard, 1931; Rosene, 1969). The birds were tested in these triad units for the following reasons. This is a social species that is only rarely found alone, that is, out of visual and auditory contact with conspecifics in its natural habitat. Previous research has shown (Nitschke, 1971) that when this species is visually isolated from conspecifics, the behavior of a bird alone becomes fragmented and much of the natural repertoire of behavior patterns is suppressed. One aim of testing birds with familiar conspecifics was to maximize the likelihood that a reasonably rich and typical array of behaviors might be observed in the experimental situation.

In addition to this, preliminary pilot testing had indicated that placing one bird in the chamber led to the suppression of all behavior categories except freezing for hours at a time, making testing impossible. When tested together, however, initial freezing to the experimental chamber was much less persistent. Typically, though not always, all three birds would become active within a reasonable period of time, as defined below.

All birds were housed in one room equipped with cool, white fluorescent lamps on a 12L-12D cycle. Each cage was provided ad libitum water and food (MSU Quail Breeder from King Milling Co., and Jolly Wild Bird Seed mix from John A. VandenBosch Co., Zeeland, Mich.). All birds were sexually mature as evidenced by age and plumage. Sixty triads (180 birds) were involved in the two studies. Of these, 12 triads were tested in Study 1 and 30 triads were tested in Study 2. Of the remainder, some were groups of birds who failed to meet experimental criteria as described below and some were extra groups which might have served as replacement subjects, but did not.

Each triad or cage was assigned a number and these numbers were used to enter a random number table to assign cages to groups. Approximately 140 of the birds were 22 months of age and 40 birds were 11 months of age. The younger birds were distributed proportionately across all experimental groups. As far as the author can determine, all subjects were naive with respect to the auditory stimuli employed in this study, with the obvious exception of conspecific vocalizations.

Apparatus

Testing Chamber

Triads of birds were tested and observed in a large acoustic chamber with a viewing window on one side. The chamber was lighted, ventilated, and wired for sound and recording.

The exterior chamber was constructed of 20mm plywood 134cm long x 74cm wide x 61cm high. This shell completely enclosed an interior chamber constructed of 20mm acoustic particle board 95cm long x 59cm wide x 45cm high, which rested on foam rubber corner forms to isolate the interior chamber from the shell. Between the two structures the space was filled with 15cm of fiberglass insulating material. The interior chamber contained speakers mounted in the middle of each end piece, connected to a common input source so that the monaural signal arrived simultaneously. The floor of the interior chamber was covered with laboratory cob meal and contains a plywood dusting tray (2370 sq. cm x 2.5cm high). The ceiling of this chamber contained a plastic light panel and a suspended microphoen connected to the videorecorder. The front of this chamber housed a double paneled observation window 81cm x 40cm. The chamber temperature was 22.5 - 25.5 degrees C, and interior illumination of sufficient intensity to allow videorecording was provided. The ambient noise level reading was between 60 and 65 dB.

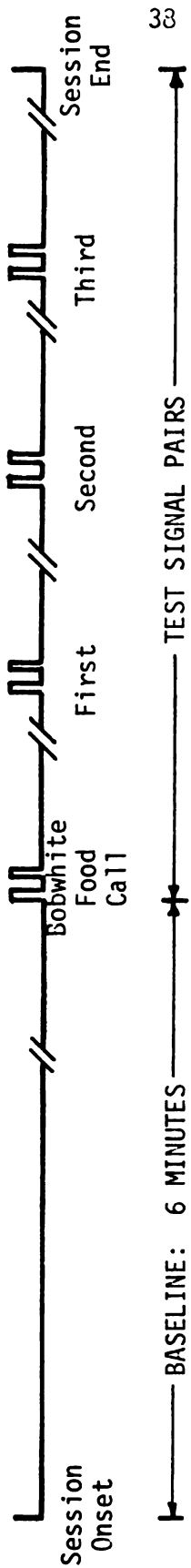
The chamber rested on a large metal rack which was cushioned from the floor by rubber rollers. This apparatus was housed in a room used only for this study. The chamber was large enough to allow

subjects to fly or "pop" freely ("popping" is a sudden flying leap characteristic of these birds, Nitschke, 1971), and to traverse approximately 5700 sq. cm of floor space. When the chamber was set up for testing with all doors in place, the ventilation fan in operation, and the lights on, a sound meter placed inside showed no needle deflection in response to standard laboratory noises. The only reasonable event that deflected the needle under these conditions was slamming, not closing, of the door to the experimental room.

Stimulus Materials

In both studies, the auditory stimuli were presented on prerecorded tapes prepared by the author. All tapes, except taped silence, followed the same format (see Fig. 1). A 6-minute taped silence baseline was followed by one trial of bobwhite quail food-call. For silence, no further signals followed the food call. On all other stimulus tapes, after a minimum of two minutes, three trials of test signal were presented. A trial consisted of two 5-second presentations of a signal separated by a 10 sec. intersignal interval. Each trial was followed by a minimum of two minutes of taped silence. The initial bobwhite quail food call was included so that any startle or other responses to a first stimulus presented in the chamber would not be confounded with responses to the first test stimulus. The rationale for the selected time intervals is discussed under Procedure.

Figure 1. Temporal sequence of signals on all signal stimulus tapes. Each signal lasts five seconds; ISI is ten seconds; ITI is 2 minutes minimum. For taped silence, no signal follows the Bobwhite quail food call.



The stimuli recorded onto different tapes included the following. Taped silence, used in Study 1 only, was used as a control for mechanical tape noises which would be present on all tapes. The bobwhite quail distress call, used in both studies, is the conspecific distress call. All remaining tapes were used in Study 2 only. The chicken, blue jay, and rabbit distress calls represented interspecific distress calls from species having different evolutionary relationships to bobwhite quail, the chicken being closest and the blue jay most distant. The two remaining signals were controls; bobwhite quail food call represents a familiar call from conspecifics which do not have distress signal value, while the bobwhite quail distress call reversed represented a signal which preserves many of the acoustic properties of the distress call such as intensity and frequencies but which, because of the reversal, differed in onset and timing properties.

All stimulus tapes were recorded on a Tandberg 3300X by the author at appropriate levels to minimize distortion. Each tape will be described briefly regarding its source and available recording details. The identification of bobwhite vocalizations were checked to correspond to a tape of bobwhite quail vocalizations provided by A. W. Stokes (personal communication). Details for the tapes made from commercial recordings were provided by Dr. James L. Gullledge of the Cornell Laboratory of Recorded Sounds and Mr. Johnny Stewart of Johnny Stewart Game Calls (personal communications). Appendix F contains spectrogram samples of the signal stimuli used in the dissertation research.

Bobwhite Quail Vocalizations

Food Call. The food call was elicited from quail living in an outdoor pen by placing earthworms on their standard feeding board. These birds ranged in age from 1 to 4 years of age and were from the same source as the subjects in the present study. An AKG-D-190ES directional microphone was pointed at the bird making a clear call in response to the earthworms. The call was recorded at 19cm per s on equipment described in the next section. The tape was then edited to provide a clear five-second segment of the bobwhite food call. This segment was then duplicated to provide the food call stimulus for all other instances so the food call is standard across all tapes.

Distress call. A pilot bird from the present subject population was transported to an isolated room in the laboratory. A male was taken from the carrying cage and held by the feet with the wings left free to flap until the subject gave several distress calls. The calls were recorded by the same method used for food calls. The tape was then edited as before to provide a standard sample for the distress call stimulus. Holding a bird by the feet with the wings free is the standard laboratory procedure for eliciting a distress call (Frings & Jumbar, 1954; Cowan, 1973; Fretwell, 1973; and Cinu, 1971). Stefanski and Falls (1972) believe calls elicited in this manner are indistinguishable to other birds from the distress calls normally given when a bird is seized by a predator.

Reverse distress call. By running the standard bobwhite distress call tape backwards and switching channels utilizing a TEAC 3340-4 channel Simul-sync Recorder this signal was reversed and recorded directly at the same speed onto the recorder used in this study. A backward presentation or reverse signal preserves the temporal periodicity and the spectral distribution except for a sign reversal of the angle as demonstrated by Capranica (1965, p. 85). Since phase difference is primarily important in locating low pitched sounds (Gatehouse & Shelton, 1978), phase difference does not present a problem for the present purpose. This standard reversed 5 second segment was then used to make the reversed bobwhite distress call tape.

Vocalization from Other Species

These tapes were made by direct line recording from a recording played on a Garrard Stereo Record Player at appropriate recording levels. The procedure of making a 5 second standard segment and then duplicating it was followed throughout.

Goshawk Vocalization Tape. An adult goshawk (Accipiter gentilis) was recorded vocalizing near its nest by the Cornell Laboratory of Recorded Sounds. This vocalization is one of the only major vocalizations of this species but Dr. J. L. Gullledge (personal communication) was not able to provide a functional classification for this vocalization. A literature search on the goshawk also provided no information to identify this vocalization. According to Bent (1963) goshawks do very little vocalizing and have an

extremely limited vocal repertoire. The recording used is commercially available from the Houghton Mifflin Company of Boston (Peterson Field Guide Series, 1971).

The next three records are available from Johnny Stewart Game Calls, Waco, Texas.

Jack Rabbit (*Lepus californicus*) Distress Vocalization.

Record No. GC101-C. A "half-grown" blacktail jack-rabbit was trapped and held by the hind legs while the distress scream was recorded on a Nagra 3 recorder.

Domestic Chicken Distress Vocalization. Record No. GC112.

An adult, pen reared, "barnyard hen," domestic chicken (*Gallus, gallus*) was held by the legs while the distress cries were recorded on an Ampex 601 recorder.

Blue Jay Distress Cries. Record No. GC117. An adult, wild caught, blue jay (*Cyanocitta cristata*) was held by the wings while the distress cries were recorded on a Nagra 3 recorder.

Spectrographic Analysis Tape. Each stimulus signal from each of the above tapes were played on the Tandberg recorder at 19cm per S and recorded directly on a Revox A700 1/2 track recorder on Maxell US35-7 Hi Output Hi Energy-Extended Range Tape. This tape was delivered to Professor Oscar Tosi of the MSU Audiology and Speech Sciences Department to use in making spectrograms.

After obtaining standard 5 second segments for each of the stimulus conditions outlined above, stimulus tapes were constructed as follows. The segment was played on one recorder and fed directly

into the left channel of the other recorder with the recording machine running. This was done to prevent "tape squeak" so that there would not be a "prestimulus" noise immediately preceding the stimulus signal. In addition, during the silent periods and the intersignal intervals, the recording machine was operated in the Record mode with no signal input, producing the "taped silence" effect. This allows the normal tape hiss plus whatever internal noise may be produced by the machine itself to be continuous throughout the tape, so that when a new stimulus signal appears, the signal itself should be the only new acoustic information on the tape.

The taped silence tape was produced as described above with only the record mode buttons deflected at the appropriate timing intervals to control for whatever effect this may have produced on the tape.

On each tape, all of the stimulus material was recorded on the left channel of the recorder and this was fed to both speakers in the chamber simultaneously. On the right channel, which was only available to the experimenter, a sequence of timed signals appeared that provided information on time since last call presented and when to stop the recorder if the behavioral criterion (discussed under Procedure) was not met in the two minutes allotted.

Stimulus Delivery Apparatus

All recording tape (BASF LH-LP35) used in this experiment was purchased from the same batch and should, therefore, have similar emulsion characteristics. The taped signal was produced on one

channel of a Tandberg 3300X tape recorder, fed through a Sansui AU101 Integrated amplifier and into mid-range University Sound (5965-978-3535) speakers in the interior chamber. Speaker efficiency tests were run by feeding white noise into the system and recording this under operating conditions in the chamber with an omnidirectional microphone placed at quail height. In addition, a reference signal was provided by running the generated white noise directly onto the tape. This tape was then analyzed by the Michigan State University Audiology and Speech Sciences Department. Briefly, these tests showed that these speakers were suitable for the present purposes and that there were no "dead" spots within the chamber that would prevent the bird from receiving the signals.

Each stimulus tape was run under standard operating conditions with a sound meter inside the chamber to determine appropriate volume level settings. A Bruel and Kjaer Precision Sound Level Meter Type 2203/1613 with a B & K Condenser cartridge type microphone (type 4131) with the slow scale A in operation was used to determine that each signal was not less than 5 dB and not more than 10 dB above ambient noise level in the chamber.

Data Collection Apparatus

Each testing session was recorded by a Sony AV3600 Video-corder through a Cosmocar VCL-08 wide angle lens onto videotape. This set up allowed the observer to tape the subjects at any position in the chamber except the extreme front corners. In the infrequent event that this situation occurred the observer switched to audio

dub and recorded verbally until the subject(s) came back into camera view.

Habituation to the Apparatus

The Pilot Study with bobwhite quail had indicated that a habituation procedure to the chamber was a necessary precursor to experimental procedures, since on first exposure to the chamber birds were likely to freeze and to remain immobile for hours. The habituation procedure consisted of removing a triad of birds from the colony room in their living cages and transporting them to the experimental room, tagging them and releasing them into the experimental chamber. No stimulus signals were provided to the subjects in these sessions. These sessions were not videorecorded but were scored by an observer using a hand tally (see Appendix A). The following scoring procedure was used: At the end of each minute an observer scanned the behavior of the triad and noted what behavior each individual bird was performing at that moment. If at the end of 15 minutes there was a total score for the triad of 33 entries summed over the categories of pecking, preening, dusting, locomoting, and orient/exploring, the habituation session was terminated. The only restriction here was that one bird could not contribute the total activity score. If the score did not total 33 activity points at the end of 15 minutes, the session was extended an additional 15 minutes.

If at the end of 30 minutes, the members of the triad still had not contributed 33 activity points, they were removed from the chamber, weighed, and returned to the colony room. These triads were

subsequently run through the habituation procedure repeatedly, with intervals of a minimum of 24 hours between runs, until the triad met the 33 point activity criterion or until these subjects had been run through 4 complete 30 minute sessions. Only six out of the tested triads of birds failed to meet the activity criterion within four runs.

Procedure

Basic Testing Procedure

Testing orders were randomly predetermined to insure that there was no confounding of any given signal condition with sequence of testing (i.e., early or late in the experiment). The triad of birds which had been randomly assigned to the condition about to be run were tagged individually with masking tape symbols applied to the dorsal feathers between the wings. The birds remained in the colony room while the experimental chamber was prepared for operation by placing approximately 100 grams of sandy topsoil and 15 grams of food in the dust tray, checking the videorecorder, and videotaping the session identification information. All overhead lights were then turned off in the experimental room. The triad of birds was slowly transported into the experimental room in their home cage which was placed at the entrance of the lighted chamber, so that the birds were allowed to walk out of the cage into the experimental chamber by themselves. The birds were not handled by the experimenter at this point; early in pilot work it became clear that such

handling was so disruptive to the birds that there was no point in attempting to work with them further the same day.

Once in the chamber, it was necessary to have some initial assurance that the birds were no longer responding to the chamber as something strange or dangerous, so that any behaviors observed could be attributed to the stimuli of interest. Likewise, following a test stimulus it was necessary to have some assurance that fear (or other) responses to that particular stimulus had dissipated before a new stimulus was presented. Accordingly, the following behavioral criteria were defined:

1. No member of the triad remained in the freezing posture. Freezing here was defined as cessation of all observable movement; the bird remained motionless in whatever posture characterized termination of the behavior ongoing at the onset of the freeze posture (Nitschke, 1971). See Response Measures for full definition.

2. At least one bird had actively engaged in some other class of behaviors such as, for example, pecking, preening, locomoting, exploring, or vocalizing.

If the birds had not met these behavioral criteria within five minutes of entering the experimental chamber, they were allowed additional 5 minute periods to a maximum of 30 minutes before they were removed and the session rescheduled for 24 hours later. Similarly, if a triad of birds did not meet these behavioral criteria within two minutes following presentation of a signal, the signal was postponed for an additional two minutes, and this procedure was

repeated until either the behavioral criterion was met or a maximum session length of 30 minutes was reached. Given this procedure, a session with a given triad of birds contained a minimum of 15 minutes 20 seconds of data collection and had a maximum possible length of 45 minutes. If a triad failed to meet the behavioral criteria within the time limit following a signal, they were rescheduled for another session 24 hours later. If they failed to meet the criteria within the second session, they were dropped from the subject pool. Three triads were dropped for such failure.

At the end of all sessions (whether data collection had been completed or not), the birds were removed from the chamber, weighed, checked for auditory responsiveness, and returned to the colony room. The check for auditory responsiveness consisted of an experimenter placing the bird on a table in a quiet hallway, then snapping the fingers lightly but audibly to one side of the bird (out of the bird's line of vision). Three trials were administered about 30 seconds apart, with the position of the finger snap alternated. All birds but two (from different triads) clearly responded to the finger snap stimulus. However, it was not clear that these two birds were hearing impaired. In both cases their experimental videorecords could be interpreted as showing that they heard at least some of the test stimuli but that they were relatively inactive animals. Therefore, their data were retained.

Response Measures

This section describes the response measures or behavioral patterns as they were defined for scoring the video tapes. All behavioral definitions were used in both Studies 1 and 2 except where specifically stated otherwise.

Activities

Pecking. Any directed movement involving the bird's bringing its beak into contact with an exterior surface in a pecking-type motion.

Preening. The act of a bird's nibbling, mandibulating feathers, or pecking at the body surface. No distinction was made here with regard to the form of the preening, e.g., simple vs. sophisticated. Any preening movement that was reasonably within the care of the body surface category, including oiling and scratching, is scored as preening.

Dusting. Scraping with the bill, scratching, dust tosses, dust rolls, head rubs, side rubs, and the ruffle-shake components of dustbathing, after Borchelt (1975).

Locomotion. Any set of behaviors that served to move the bird from one location in the cage to another, including walking, crawling, running, jumping, flying, flit-popping (Nitschke, 1971), or frolicking (Ratner, 1965).

Locomotion to contact. Locomotion that had as its end result bringing one bird into tactual contact or proximity with another bird. This was only the approaching behavior. Once the birds established tactual contact, the response was scored as proximity.

Gular quivering. The mandibles were open and the gular pouches can be observed to flutter rapidly. The behavior could be performed during resting, locomoting, dusting, cautious posturing, huddling or proximity. It was likely to continue intermittently in one bird for several minutes once it was initiated.

Vocalizing. Any audible vocal signal originating from a bird under observation. When possible, the specific vocalization and the source was identified and classified. A bird might vocalize without distinctive postural or mandible changes and it was not always possible to identify the vocalizer. When postural changes do occur, vocalization was clearly distinct from gular quivering because of the lack of fluttering of the gular pouches.

Postural Patterns

Freezing is a classic postural behavior for the bobwhite and one of the behavioral patterns that it is famous for exhibiting to a variety of stimuli (Stoddard, 1931; Stokes, 1967). It is clearly discriminable to the experienced observer by its characteristic topography of rigidity of the whole animal.

Freezing. A bird ceased all observable movement for a minimum of 3 seconds and remained motionless in whatever posture

characterized termination of the previously ongoing behavior. At the onset of the freeze posture, the plumage appeared compressed, the eyes remained wide open, and the muscle tonus appeared rigid. Birds may remain in a freeze posture from several seconds to several minutes. Birds that freeze in an off-balance posture usually break the freeze or at least make postural adjustments sooner than birds that freeze standing or crouching. A crouching freeze is often preceded by erratic and rapid zigzagging running typical of a protean defensive display. This display often occurs at the first onset of a distress stimulus and is immediately followed by the freezing response.

Freezing with head movements. The classic freeze, with the intense muscle tonus and maintenance of the body posture typical of that pattern, but with minimal and very slow head movements. This appeared to allow the bird to contact the environment without making gross postural changes. The pattern followed freezing and typically was a transition from freezing to another posture. It was included to refine the freezing measure further because often following the onset of a freeze, a bird made a slight head movement while the rest of the body remained rigid.

Proximity. This was scored when one bird was very near another bird and as far as was observable was in tactual contact with another bird. This could occur along with any of the other postural behaviors and was not restricted to instances when the head was withdrawn.

Cautious posturing. The bird stands upright with the legs straight beneath the body, the tail lowered, with the head and neck extended forward, giving the bird a stretched-out appearance. Walking might or might not accompany this posture. It was typically seen when a bird was approaching a novel object and was quite discriminable from orienting.

Orienting (Study 1 only). The bird was observed to directly focus, turn toward, or visually fixate on some point in space with one eye at a time. Typically head movements accompanied this posture as the bird appeared to "scan" the source of the stimulation. Orienting might be accompanied by locomoting, cautions posturing, pausing or proximity.

Exploring (Study 1 only). When it was impossible to identify or specify any of the above behavior patterns with certainty and the observer had reason to believe that the bird was contacting the environment (Denny & Ratner, 1970) or exhibiting investigatory behavior (Scott, 1958), the behavior was categorized as exploring. This category was dropped in later work.

Pausing (Study 1 only). When a bird ceased movement for less than 3 seconds, with the eyes open, for example from dusting, and was not exhibiting other postural responses or activities; that is, the muscle tonus and overall postural topography clearly did not indicate freezing or resting or orienting; and the antecedent conditions indicate no basis for these behaviors, e.g., another bird

flying/popping; the response measure scored was pausing. Basically, this was a category of behavior where the animal just momentarily became still, which occurred frequently as a transition between dusting postures or preening bouts.

Resting (Study 1 only). The bird remained essentially motionless with relaxed muscle tonus, usually with the eyes closed, in one of three postures: (a) lying on one side with the head and/or feet extended; (b) squatting with the undersides touching the substrate with the head withdrawn; or (c) standing upright, often on one foot, with the head withdrawn and (typically) closed eyes.

Scoring

Three trained observers viewed each session tape, with one observer assigned to each bird in the triad. The observer made an entry on the data sheet at the end of or during each elapsed 15 seconds, noting for each behavior whether or not that behavior had occurred during that 15 second period. (A sample data sheet is contained in Appendix A.) This method is a modification of Altmann's (1974) continuous events, one-zero behavior sampling on a focal animal. It does not yield a frequency measure as typically defined in some of the psychological literature, as for example in the operant literature. This procedure arbitrarily fragments frequency by the temporal imposition of 15 second bins. It has the advantage of freeing the observer from forcing complex decisions on the data during tape scoring. The observer sees an instance of that behavior pattern or doesn't see it each 15 seconds and scores accordingly.

When this modified continuous one-zero sampling technique is used, absolute frequency and absolute duration are not obtained. For example, if an observer's bird pecked 10 individual pecks within one 15 second bin, that bin would contain one entry for pecking. In the case of a rapidly occurring, highly discrete behavior like pecking, pilot work indicated that it was possible to achieve highly reliable agreement on whether or not the pecking behavior occurred within each 15 second bin. However, attempts to record the absolute frequency, that is, individual pecks within one 15 second bin, were a disaster.

In contrast, in the case of a highly complex, long duration, multi-componented behavior pattern such as dusting, one 15-second sample reveals only a portion of the total pattern. Absolute frequency and duration are sacrificed for event sampling because to obtain reliable frequency one would need to have discrete parameters for each pattern specified and would wind up analyzing each pattern by first defining its components. For example, in the case of dusting, a decision would have to be made as to which components of dusting, alone or in combination, count as an instance of dusting. Is one dust toss an instance of dusting? Or must it occur in a series of tosses, or be preceded or followed by identifiable behaviors, to qualify as an instance? Even where a behavior pattern has been analyzed into its component parts, as dusting has been (Borchelt, 1975), an observer would still have to make arbitrary decisions about the initiation and termination of the behavior pattern.

However, such fine-grained analysis is not essential to the aims of the present study, which is an exploratory study more concerned with the question of which behavior patterns are elicited or suppressed by different types of signals than with the absolute number of times that one component of any given behavior pattern is displayed by an individual bird.

Reliability

Since reliability can be a transient phenomenon (Reid, 1970), reliability checks were run throughout data collection and observer training. Recall that in scoring videotapes, each of three observers watched a different bird in the triad. Reliability could be checked, first, by repeating a videotape with the same observers so that intraindividual reliability could be checked; and second, by including a fourth observer whose results provided a cross-check against one of the primary observers, so that interrater reliabilities could be computed. In Study 1, interrater reliability expressed as percent agreement between two observers never fell below 80 percent for any behavior category except vocalization.

Table 2 presents a sampling of interrater reliability checks between pairs of scorers during Study 2. All of these comparisons were made during the same week. The observer pairs were chosen so that each of the four individuals who participated in scoring the tapes was paired with at least two other individuals. As Table 2 shows, percent agreement between pairs of observers was again high, with median percent agreement at 96.70 percent and with no case of

agreement less than 73 percent. In fact, only for the categories of proximity, locomote/contact, and vocalization did three or more of the five comparisons fall below 90 percent agreement. These are categories for which lower agreement might be expected. In the case of proximity, contact between birds was difficult to judge on videotape. In the case of locomote/contact, a moving bird's "intention" to contact another bird had to be judged rapidly. Consequently, observers were trained to be conservative in using this category. In the case of vocalization, the problem was in agreeing as to which bird was the source of a vocalization. Vocalizations of uncertain origin might either be omitted inappropriately or attributed to the wrong bird, thus inflating vocalization frequencies. It was difficult to tell that a quail was vocalizing unless it was giving an advertising display. Further, it should be noted that the only instances where agreement fell below 80 percent both involved individual W, who was at that time a recently-trained newcomer to the study.

Data Analysis

The score to use as the basic unit of analysis had to be determined before data analysis could proceed. Recall from the Introduction that the behavior of bobwhite quail in groups is highly integrated; groups of birds tend to act in concert. Consequently, the behaviors of individual birds within triads cannot be assumed to be independent. For this reason, it was decided to use the mean score for the cage, or triad of birds, as the unit of analysis rather than

TABLE 2.--Percent Agreement Across Nine Behavior Categories that a Behavior Did or Did Not Occur for Five Pairings of Four Individuals (R, M, L, and W) who Participated as Observers in Study 2

Behavior Category	Observer Pair				
	R-M	L-M	L-R	L-W	M-W
Pecking	92.86	91.07	91.07	82.14	83.93
Preen	100	96.43	100	100	100
Dust	100	83.93	100	85.71	91.07
Freeze/Head	80.36	98.21	96.43	100	96.43
Freeze	96.43	98.21	100	100	98.21
Proximity	89.28	89.28	87.5	73.21	73.21
Cautious Posture	98.21	100	100	100	94.64
Locomote	87.5	80.36	100	89.29	85.71
Vocalize	100	96.43	89.29	80.36	82.14

the scores of individual birds. These scores were obtained as follows: Each observer observed one bird in a session. The scores for the three observers were then summed, and an average score for that triad (not an average for each bird) was obtained by dividing that sum of three scores by the number of minutes elapsed during that signal period. This time control was necessary in order to be able to compare data across independent groups, since the time required to meet the behavior criterion for progression to the next phase of the study, or for termination of a session, differed over groups. (See Table 1, p. 43; Fig. 1, p. 49; and discussion of procedure, pp. 47 and 48.) Thus the basic unit of analysis was an average frequency per minute obtained for each triad under each dependent measure.

In obtaining this average frequency per minute, the time in minutes used as divisor for baseline sessions included the time from the beginning of the run through the 6 minutes of baseline observation. The time in minutes used as the divisor for the signal period included the time from the beginning of the signal run, which began with a food call signal for all groups in both studies (Fig. 1), through the three trials of experimental signals. These time bases apply for all of the statistical analyses except the habituation data, which compared the first, second, and third test signal pairs (see Fig. 1), and the comparisons of responding on Trial 1 with responding following the food call.

Thus, the basic data unit was an average frequency per minute for each triad of birds on each dependent variable. To obtain mean

scores in Study 1, the means for each of the six triads of birds in each of the two independent signal conditions were summed and divided by six for each dependent variable. The same procedure was used to obtain overall means for Study 2, except that there were only five triads of birds tested in each signal condition and there were six independent signal conditions. These overall means are the data plotted in Figs. 2 through 14.

Data were analyzed in a series of analyses of variance. Significance level was set at $p = .05$, although trends toward significance at $p = .10$ and even $p = .20$ are discussed for hypothesis-generating purposes.

RESULTS

Studies 1 and 2

Overall, Studies 1 and 2 generated the following major findings. Distress calls did indeed elicit defensive responses, and particularly freezing, in both studies; and some nondefensive responses (such as vocalization) were suppressed following distress calls whereas others (such as preening) were not. Thus, the data provide more support for Prediction 1 (p. 29) than not. As for the question of the differential effectiveness of different distress calls (Prediction 2, p. 29), all distress signals studied--as well as the comparison signals--were effective elicitors of defensive responding. Among avian distress calls, bobwhite quail calls did elicit the most defensive responding and blue jay distress calls the least, as predicted; but rabbit distress signals were as effective as conspecific distress signals in eliciting defensive responding, which was not predicted. These results must be viewed as suggestive, however, since signal conditions did not differ significantly from one another. In a less conservative analysis comparing responding only to the first auditory food call stimulus with responding to only the first experimental stimulus, the predicted order was also seen.

As for habituation (Prediction 3, p. 30), defensive responses to the auditory signals used in Study 2 did show significant habituation, with declines in response rate especially evident between the

first and second trials. Evidently auditory signals show the same characteristics as visual signals in laboratory studies such as this one, so far as eliciting defensive responses is concerned.

The remainder of the results section will examine each of these general experimental findings in more detail. Before turning to such detailed quantitative analysis of the data, however, the spectrographic measurements of the distress and control signals will be presented to familiarize the reader with the descriptive characteristics of these signals. Sample spectrograms are available in Appendix F.

Stimulus signal tape samples were spectrographically analyzed by Professor Oscar Tosi, Director Speech and Hearing Sciences Research, Laboratory and Institute of Voice Identification at Michigan State University. One five-second sample of each stimulus signal was used to prepare one of the spectrograms described below.

Broad band spectrograms were prepared to provide a measurement of the acoustic power density bands from each of the signals. This allows inspection of the areas within each call containing the greatest amount of energy and is referred to as acoustical power density.

Narrow band spectrograms were prepared to measure the average fundamental frequency, F_0 , for each call and to detect the frequency range of each call.

Table 3 summarizes the measurements made from these spectrograms by Professor Tosi. The additional measures of interest here

TABLE 3.--A Summary of Measurements Taken from Spectrographic Analysis of Stimulus Signals. (All are distress signals except the control signal, Bobwhite food call. All frequency figures in the table are given in Hz.)

Measure Hz	Stimulus Signal				
	Bobwhite	Chicken	Blue Jay	Rabbit	Food Call
<u>Range</u>					
Lo	800	900	2400	1000	500
High	16000	16000	16000	16000	16000
<u>Average</u>					
<u>Fundamental</u>					
	815	900	3100	1100	520
<u>Frequency</u>					
<u>Acoustical</u>					
<u>Power</u> Lo	1500	1800	3000	1800	500
<u>Density</u> Hi	4300	5000	4000	4500	3000
<u>Duration</u>					
msec.	400	400	400	1000	50
<u>Repetition</u>					
msec	500	250	380	400	130

are temporal characteristics of the signals. Duration is the time (given in milliseconds) of one particular component, labelled the signature of the call. This signature unit refers to the harmonic sound that had a distinct energy spike and appears as one unit on the spectrograph. This unit repeats several times during any one call sample. The time between each unit is referred to as the Repetition in milliseconds in Table 3.

The bobwhite distress signal-reverse is not shown in this table as its measured acoustical characteristics are the same as those reported for the bobwhite distress signal.

The first reported measure in Table 3 is the frequency range of the stimulus signals. The Voiceprint Analyzer used to print the spectrograms did not print above 16,000 Hz. However, in all cases, there was very little energy at these high frequencies and the measures of interest were well within the capacities of the machine. It appears unlikely that an analysis of the frequencies above 16,000 Hz would yield significant new information regarding characterization of these calls.

In Table 3, the bobwhite and chicken distress calls appear to be the most similar of all the calls analyzed across all measures. Other than being a call of higher frequency, the blue jay distress call shares many features of the other avian calls. The rabbit distress call differs from the avian calls most noticeably in its duration, which is more than twice that of the other distress calls. Given the evolutionary relationships among these animals it is not surprising that the avian distress calls are more similar to each other

than they are to the mammalian (rabbit) call. It is also clear that despite the noted similarities, there is variation among all the distress calls, thus satisfying the experimental criteria for differences in the calls used as stimuli in this study.

The bobwhite food call, considered a control call in this study, is considerably different from the others. It is a very short (50 msec.), staccato-like (130 msec. repetition rate) call of lower frequency on all measures than the distress calls. The food call also shows the lowest average fundamental frequency.

Study 1

If Prediction 1 (p. 29) is correct, phase of testing (Baseline v. Signal period) should interact with signal condition (Bobwhite distress call v. taped silence). In the case of defensive responses, and especially freezing, frequencies should increase during the signal period in the distress call condition but not the taped silence condition. In the case of other nondefensive responses, such as pecking, frequencies should decrease in the distress signal condition but not the taped silence condition. To see whether such interactions did appear, a series of 2 (conspecific distress call v. taped silence) x 2 (responding during baseline v. responding following test signals) mixed design analyses of variance with repeated measures on the test phase factor were conducted (Bruning and Kintz, 1968). There were two signal conditions; two test phases in each signal condition; and six triads of birds observed in each signal condition.

Test signal period scores include responses to all signals including the initial food call common to all signal condition tapes (see Fig. 1, p. 49). These data should be conservative as a basis for testing the hypothesis for two reasons. First, in order for an experimental signal to have a differential effect, it had to elicit behaviors over and above what might result from the novelty or startle effect of exposure to the onset of the first auditory signal (the food call). Second, since all three trials of the experimental signal were included, any habituation effects could also work to attenuate the finding.

The ANOVA for freezing responses is presented in Table 4. As Table 4 and Fig. 2 illustrate, the bobwhite quail distress signal is eliciting significantly more freezing than the taped silence signal ($F = 15.96$, $df = 1, 10$, $p < .005$). As Fig. 2 shows, the significant main effect for tests was almost entirely due to the increase in freezing in the bobwhite distress call condition.

Table 5 summarizes the remaining ANOVA results on all the remaining dependent variables measures in this study, which as the reader will recall were scored from videotapes in the same way as was freezing. (Full individual ANOVAs are reported in Appendix B for each behavior category.) Scanning Table 5, one can see that not every behavior category measured was significantly influenced by the experimental conditions. Those behavior categories that showed at least one statistically significant effect or showed an interesting trend, e.g., $p < .10$ are graphically displayed in Figs. 2 and 3.

TABLE 4.--Analysis of Variance of Freezing Responses in Two Independent Groups of Bobwhite Quail, One Exposed to Taped Silence and the Other Exposed to Bobwhite Quail Distress Calls, Tested During a Baseline Period and During Signal Presentation Periods in Study 1

Source	SS	df	MS	F
Total	39.32	23		
Between cages	15.06	11		
Signal conditions	9.26	1	9.26	15.96*
Error (b)	5.80	10	.58	
Within cages	24.26	12		
Pre-Post Tests	9.56	1	9.56	17.12*
Signal x pre- post Tests	9.11	1	9.11	16.31*
Error (w)	5.58	10	.56	

*p < .005

Figure 2. Mean responses in five behavior categories made by two independent groups of Bobwhite quail, one group exposed to Bobwhite quail distress signals and one exposed to taped silence and both tested during pre-signal baseline and post-signal phase presentation periods. All test period differences shown were significant. Freeze and Freeze/head differences were significant both for signal condition and for the signal x test interaction.

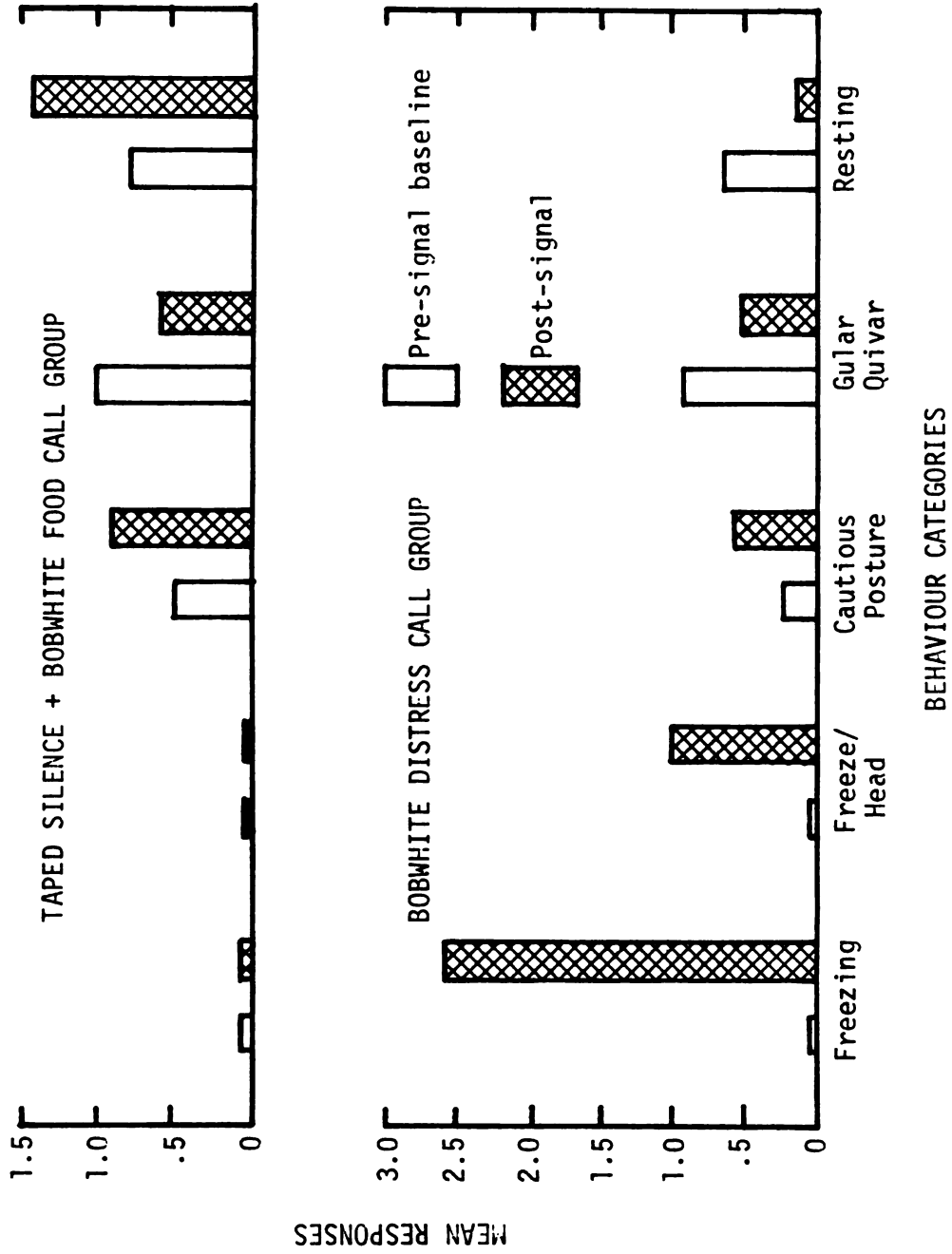


TABLE 5.--Summary of Results of Analyses of Variance for Frequencies of 15 Different Behavior Categories Exhibited by Two Independent Groups of Bobwhite Quail, One Exposed to Taped Silence and the Other Exposed to Bobwhite Quail Distress Calls, which Were Tested During a Baseline Period and During Signal Presentation Periods in Study 1

Behavior Category	Signal Condition	Pre-Post Test	Signal x Test
Pecking	.20	.025	ns
Preening	ns	ns	ns
Dusting	.20	ns	ns
Freezing	.005	.005	.005
Freeze/Head	.05	.025	.05
Proximity	ns	.025	ns
Resting	ns	.20	.05
Cautious Posture	ns	.10	ns
Pausing	ns	ns	ns
Locomotion	ns	.05	.05
Locomote/Contact	ns	ns	ns
Orient	ns	ns	ns
Explore	ns	ns	ns
Vocalization	ns	ns	.10
Gular Guiver	ns	.20	ns

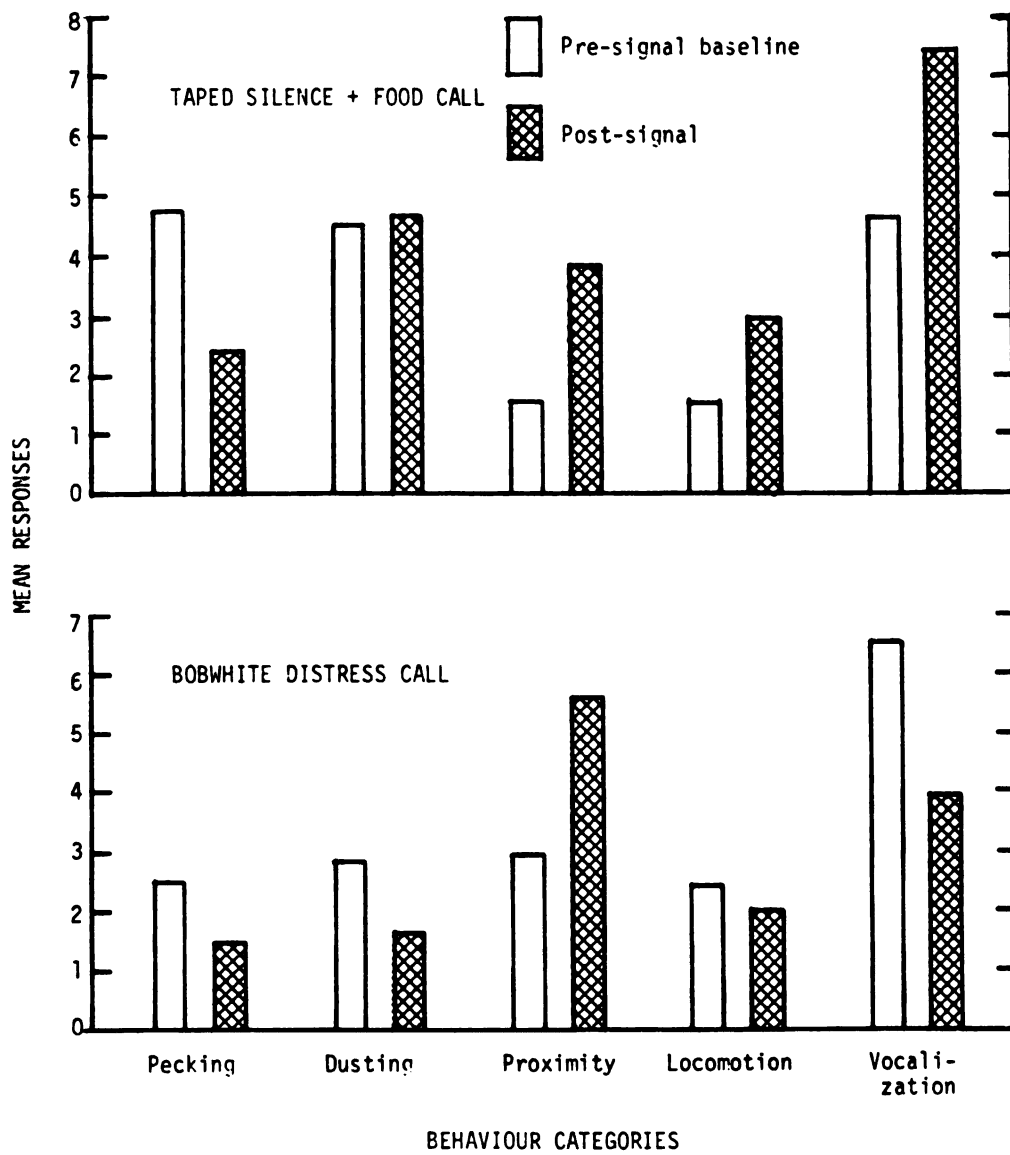
Figure 2 illustrates the direction of the behavior change from baseline to signal period in the behavior categories of freezing, freeze/head, cautious posture, and gular quiver during data collection. As illustrated, the bobwhite distress call clearly elicits freezing behaviors; it may also elicit cautious postures, though this effect is less clear. Gular quiver, which is a response often observed when a bird is stressed, was suppressed during the post baseline period. This result may reflect response competition in these circumstances; that is, responses higher in the response hierarchy array are more probable in this situation than gular quivering.

Figure 3 displays the changes in behavior in each of the two signal conditions during the baseline and signal period tests for the remaining behavior categories that showed trends or significant effects.

Pecking and dusting are slightly suppressed by the distress signal treatment, although the f value for the signal condition effect only reached $p < .20$. Promixity showed a significant increase from baseline to signal period for both signal conditions, and may be reflecting change over time in the chamber for this behavior category for various reasons.

Both locomotion and vocalization show reversals from baseline to signal periods for the two conditions (interaction significant for locomotion, $F = 6.19$, $df = 1, 10$, $p < .10$). Locomotion increases for the taped silence subjects and decreases or is suppressed for the

Figure 3. Mean responses in five categories of nondefensive behaviors made by two independent groups of Bobwhite quail, one group exposed to Bobwhite quail distress calls and one group exposed to taped silence, with both tested during pre-signal baseline and post-signal presentation periods or phases. Pecking and dusting differed significantly over signal conditions. Pecking, proximity, and locomotion differed significantly from pre-signal to post-signal test phase periods. Locomotion and vocalization differed significantly in the signal condition x test phase interaction.



bobwhite distress signal subjects. This same pattern is observed for vocalization. This possibly reflects the influence of the food call signal which often elicits approach and other socially facilitated behaviors such as vocalization. This may also account for the increase in the proximity mentioned above.

It is not possible to draw a clear conclusion about this in the present study.

Study 2

Study 2 was designed to test two experimental predictions:

1. The conspecific distress vocalization is the most effective response stimulus; in particular, this signal elicits a defensive response, freezing, in greater magnitude than distress vocalizations from other species.

2. The closer the phylogenetic relationship between the species, the more effective the distress signal is as an elicitor of freezing.

Thus, it was predicted that the magnitude of freezing in the experimental groups decreases roughly in the following order: bobwhite quail, chicken, blue jay, rabbit. The reversed bobwhite distress call and the bobwhite quail food call were considered control conditions.

The ANOVA test paradigm and data procedure for Study 2 are the same as for Study 1. In Study 2 we have six signal conditions; 5 cages or triads of subjects in each signal condition, and 2 observations (baseline and signal period) on each cage of birds. Thus, the baseline-signal period functions here also as the repeated

measures test in this analysis. This analysis gives a conservative test for the same reasons as in Study 1, namely inclusion of the food call signal common to all experimental groups and inclusion of any habituation effects which might have occurred over the three trials of signal presentation (and, as we shall see, there was significant habituation of some response categories).

Since the freezing response pattern is again of major interest here, the full ANOVA summary table for freezing follows (Table 6).

Table 6 shows that while freezing is not differentially elicited by the different signal conditions (main effect $F < 1$) the signal period is clearly different from the baseline period ($F = 76.04$, $df = 1, 24$, $p < .001$). The predicted signal \times test period interaction was not statistically significant in this analysis. The ANOVA for freeze/Head is almost identical to that shown in Table 6. Full ANOVA tables for each dependent variable are available in Appendix B.

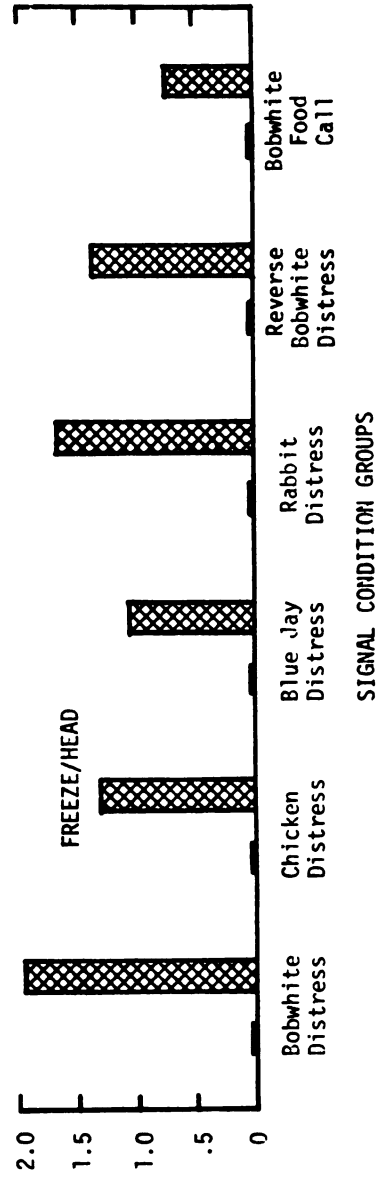
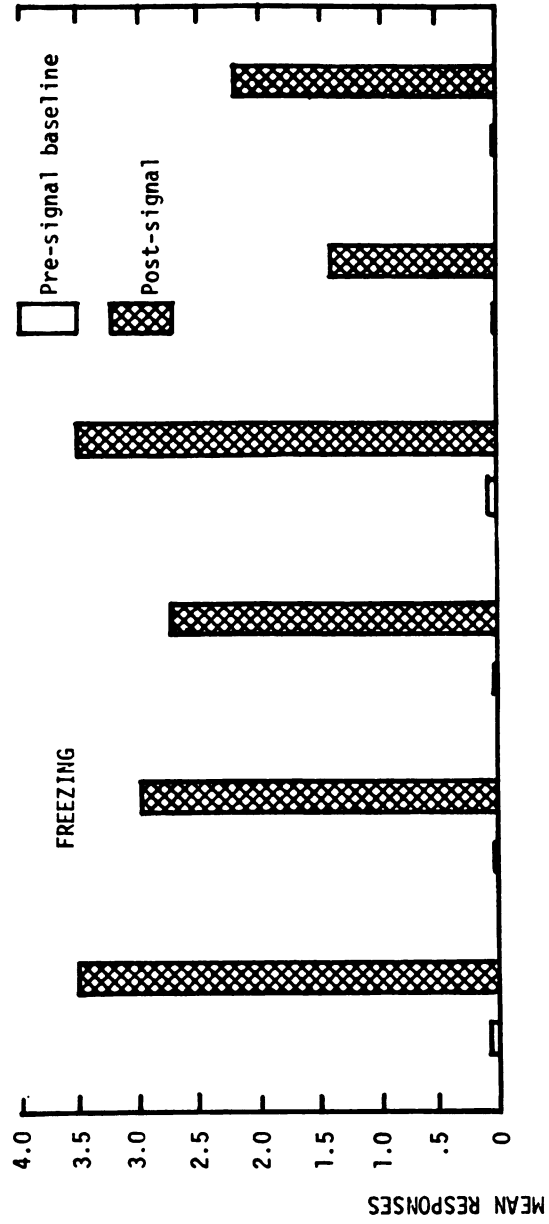
The significant test effect showing distress signals to be efficient elicitors of the defensive pattern of freezing is dramatically illustrated in Figure 4. This figure shows data on the freezing and freeze/Head behavior categories across all six signal conditions for both the baseline and signal period. The clear elicitation of freezing above baseline during the signal period follows the predicted magnitude order within aves. The conspecific distress signal elicits the greatest amount of freezing, followed by chicken and blue jay respectively. This order also follows for the

TABLE 6.--Analysis of Variance of the Freezing Response in Bobwhite Quail During Baseline and Signal Test Periods with Independent Groups Assigned to One of Six Signal Conditions: Bobwhite Quail Distress Call, Bluejay Distress Call, Rabbit Distress Call, Chicken Distress Call, Reversed Bobwhite Quail Distress Call, and Bobwhite Quail Food Call

Source	SS	df	MS	F
Total	228.86	59		
Between Cages	79.56	29		
Signal Conditions	8.46	5	1.69	< 1
Error (b)	70.69	24	2.94	
Within cages	149.70	30		
Test periods	107.68	1	107.68	76.04*
Signals x tests	8.03	5	1.61	1.13
Error (w)	33.99	24	1.42	

*p < .001

Figure 4. Mean freezing responses of Bobwhite quail during pre-signal baseline and post-signal presentation periods for six groups of birds each of which heard a different auditory stimulus. The upper graph shows incidence of full freezing, the criterion for which is full immobility. The lower graph illustrates incidence of freezing with head movements, where the bird's body is immobile but there are detectable head movements. Both behavior categories differed significantly from baseline to signal condition, $p < .001$.



freeze/Head category. In the two control conditions, reverse distress and food call, the subjects show freezing but less than that shown in the experimental signal conditions during the signal period.

The result illustrated in Fig. 4 that was not predicted was the amount of defensive responding elicited by the rabbit distress call: this call was as effective as the conspecific distress call in eliciting both freezing and freeze/Head. Several comments could be made about this finding, but briefly, recall that the spectrographic analysis (Table 3) showed the rabbit call to be the most dissimilar of the distress calls and that it showed the longest duration by two and a half times (1000 msec compared to 400 msec. for the other distress calls).

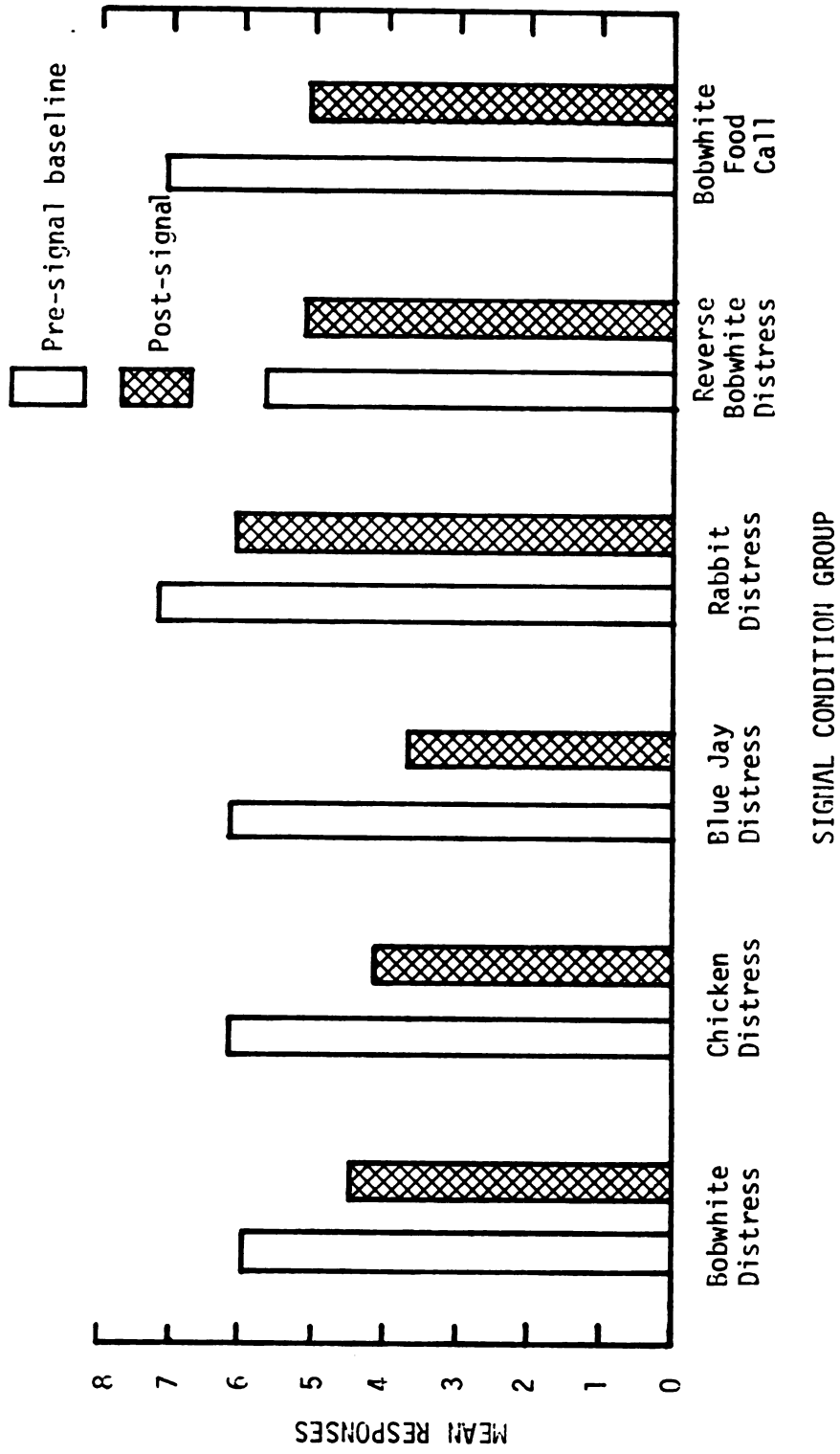
Table 7 summarizes the ANOVA results on all the dependent measures in Study 2, giving the tabled p value for each effect for each behavior category. Only those behavior categories containing at least one statistically significant effect (or showing at least one trend toward significance) are illustrated in the figures following.

Pecking. The first behavior category to show a significant effect in Table 7 is illustrated in Fig. 5. There is clearly a decrease in the pecking response from the baseline to signal period and this decrease is significant, $F = 29.53$, $df = 1, 24$, $p < .001$. There was not a differential suppression of pecking as a function of signal condition and the figure shows no predicted pattern except the decrease from baseline to signal period. This finding is

TABLE 7.--Summary of Significance Levels of Results of Analyses of Variance on Frequencies of 11 Behavior Categories Measured in Study 2, Across Six Independent Signal Conditions and From Baseline to Signal Presentation Periods within Each Signal Condition

Behavior Category	Signal Condition	Pre-Post Test	Signal x Test
Pecking	ns	.001	ns
Preening	ns	ns	ns
Dusting	.20	ns	ns
Freezing	ns	.001	ns
Freeze/Head	ns	.001	ns
Proximity	ns	.001	ns
Cautious Posture	ns	ns	ns
Locomotion	ns	.01	ns
Locomote/Contact	ns	.20	.10
Vocalization	.20	.001	.05
Guler Quiver	ns	.10	.20

Figure 5. Mean pecking responses of Bobwhite quail during pre-signal baseline (open bars) and post-signal periods (hatched bars) to each of six auditory signal conditions. Pecking declined significantly ($p < .001$) from baseline to signal periods.



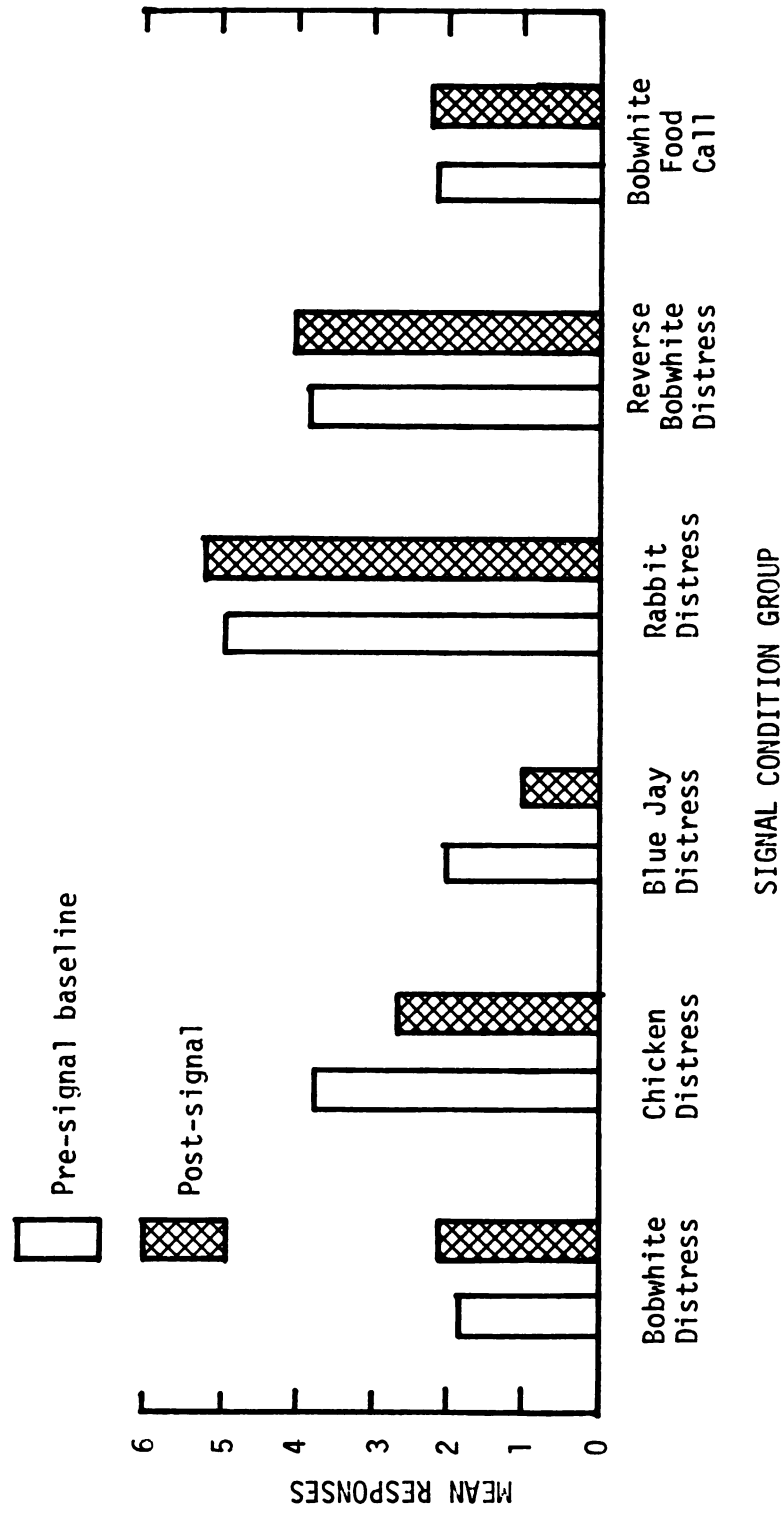
essentially similar to the data obtained in Study 1: a distress call suppresses pecking responses. However, Study 2 suggests that this particular suppression is not unique to distress calls, but occurs for other auditory calls as well.

Preening and dusting. The next two measures shown in Table 7 are considered maintenance or care of the body surface behaviors. Preening shows no significant effects in the ANOVA. This is a behavior that occurs infrequently in this situation; all twelve signal condition means for pecking are less than 0.77 with the exception that pecking was 1.67 in the baseline test of the reverse signal group.

In Study 1 there was a clear trend for dusting to be suppressed by the distress call. In Study 2, although the signal condition F approaches significance, both of the other F s are less than 1. Fig. 6 illustrates the type of variability of responding seen in this response measure. From inspection of this figure, it appears that the birds in the avian distress signal groups dusted less during both baseline and signal conditions. Dusting decreased following the chicken and blue jay signals and increased slightly during the other four signal conditions. Given the variability between groups ($p < .20$) any significant effects due to signal may be measured.

Proximity, a response measure dealing with birds making contact with one another, is also often referred to as huddling and in a social species is observed frequently. It was expected that a

Figure 6. Mean dusting responses of Bobwhite quail during pre-signal baseline (open bars) and post-signal periods (hatched bars) to each of six auditory conditions. Dusting tended ($p < .20$) to differ across signal conditions.



stressful situation might increase contacting responses in this species in the experimental chamber. As shown in Table 7 and illustrated in Fig. 7, the signal conditions elicited proximity responses significantly above baseline levels, $F = 21.43$, $df = 1, 13$, $p < .001$. This repeats the finding in Study 1 that proximity responses increased significantly from baseline to signal test and that it is a frequently observed behavior pattern in the test chamber under all conditions. Proximity responses might be expected to be high during food call signals because of the approach response and social facilitation properties of this stimulus, as previously discussed.

Locomotion reflects basically the amount of motor activity in the chamber in ways that serve to move the bird from one location to another, typically by walking. Since there was no cover or place of concealment offered within the chamber, and locomotion is mutually exclusive of freezing, it was expected that this behavior pattern would be suppressed by the signals. Fig. 8 illustrates the significant decrease from baseline to signal period across the signal conditions, $F = 7.96$, $df = 1, 24$, $p < .01$.

The pattern here is generally one of less locomotion following the baseline period with the exception of the blue jay signal condition which showed no change. In this behavior category, both the reverse and food call suppress this behavior more than the blue jay distress call.

Locomote/Contact, scored only when a bird made a definite approach to another bird, did not mimic the locomotion pattern of

Figure 7. Mean proximity responses of Bobwhite quail during pre-signal baseline (open bars) and post-signal (hatched bars) periods to each of six auditory signal conditions. Proximity was significantly greater ($p < .001$) during post-signal than baseline periods.

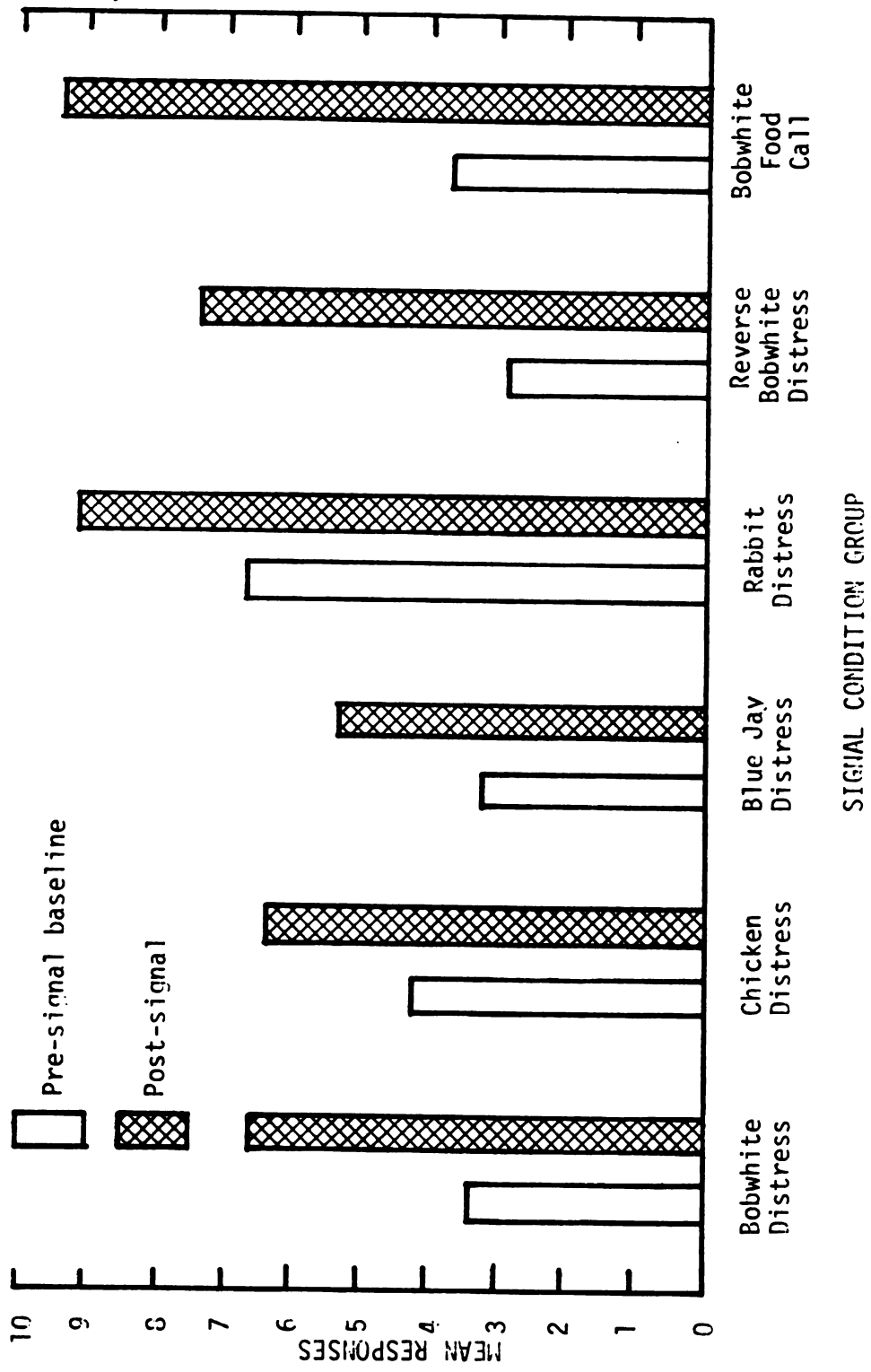
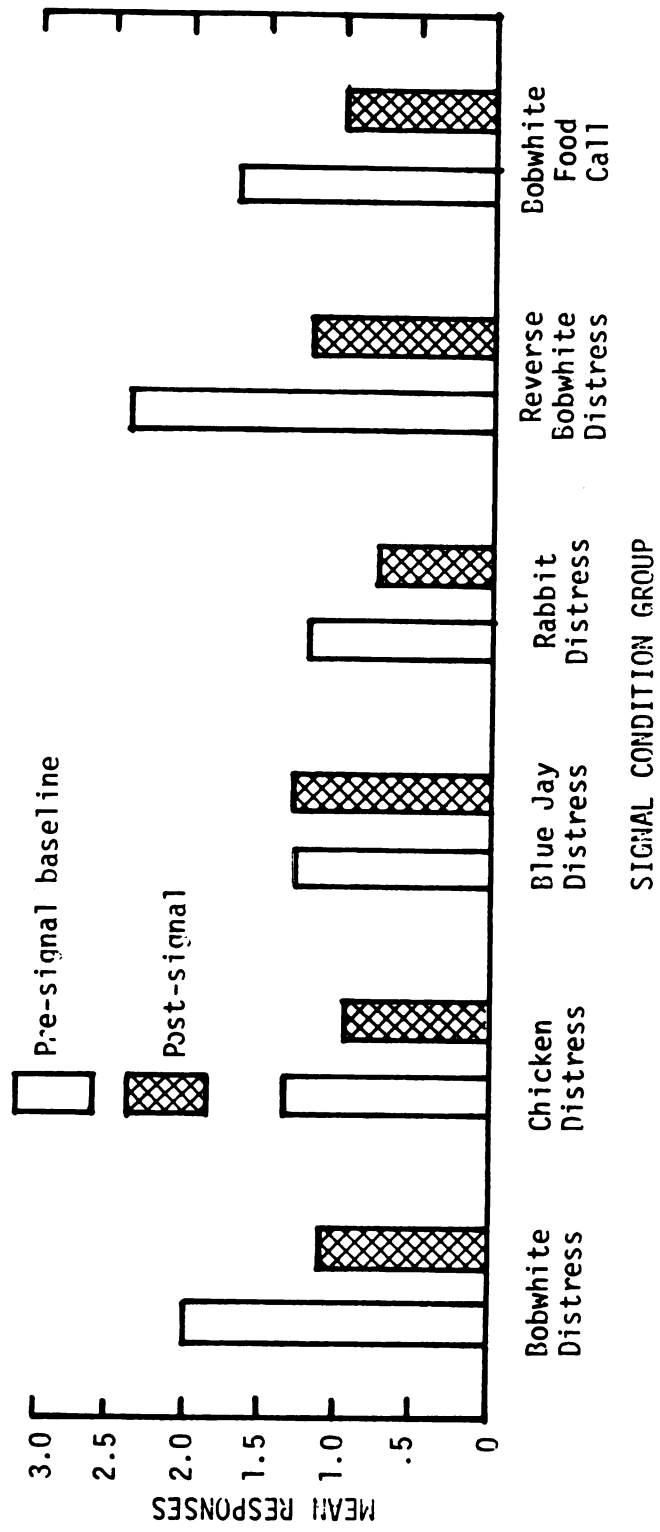


Figure 8. Mean locomotion responses of Bobwhite quail during pre-signal baseline (open bars) and post-signal (hatched bars) periods to each of six auditory signal conditions. Locomotion was significantly greater ($p < .01$) during baseline than signal periods.

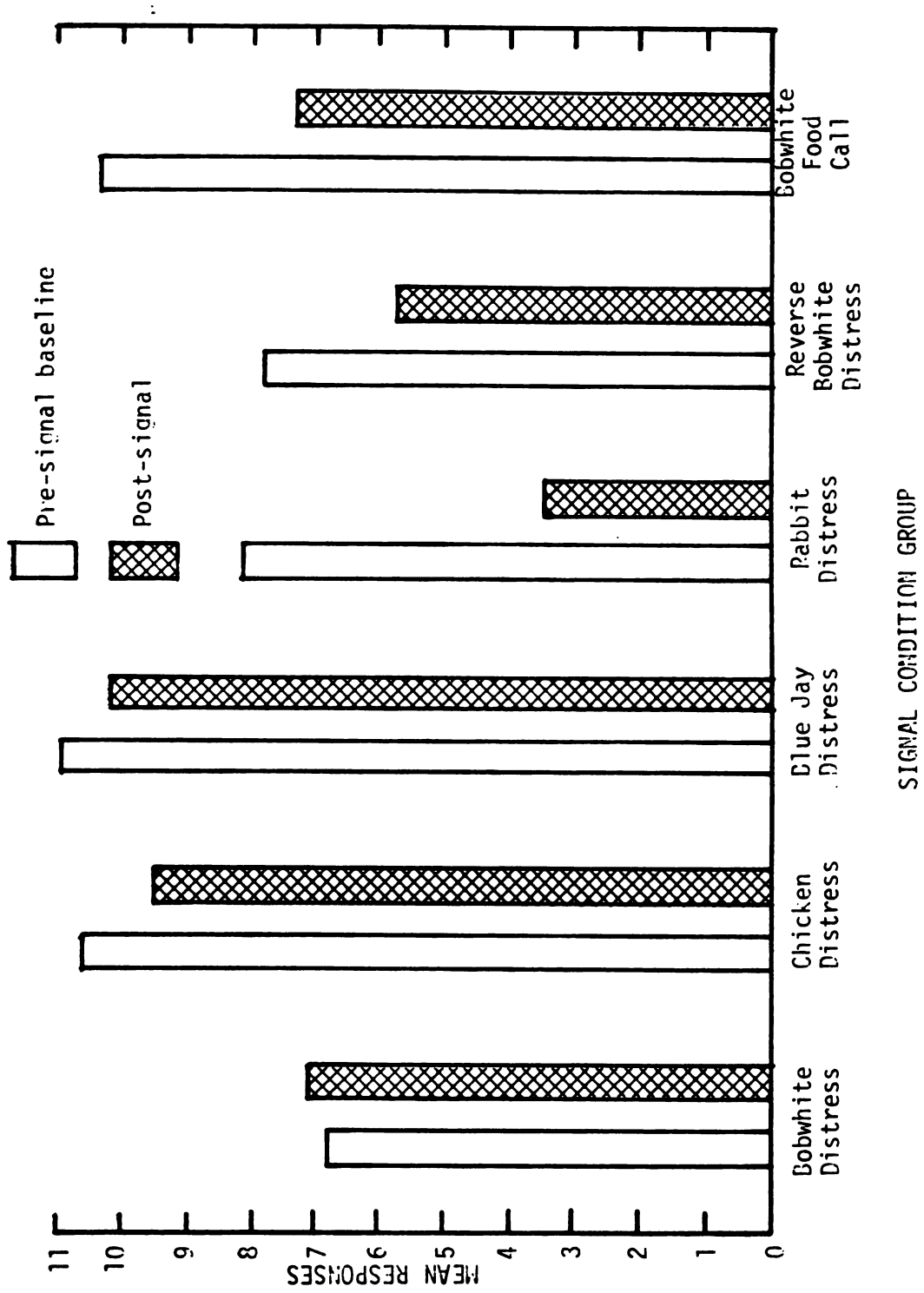


responding. It was for this reason that it was initially designated as a separate behavior category. Consistent with the finding in Study 1, locomote/contact showed no significant effect in Study 2. As can be seen in Table 7, however, both the baseline to signal and the interaction effect approached significance with the pattern of results more closely resembling those for proximity than those for locomotion without contact.

Vocalization included any audible signal given by a bird during testing. Frequently, it was impossible to determine which bird produced the sound, with the result that frequently more than one observer scored a response in this category when only one bird was actually vocalizing. This may in part account for the apparent high frequency of this behavior category relative to the other measured behavior patterns. However, bobwhite do vocalize frequently when they are together in a unit. As Fig. 9 displays, there was a significant decrease in vocalization from baseline to signal period, $F = 19.17$, $df = 1, 24$, $p < .001$. This was in the predicted direction for all the signal conditions except the conspecific distress call. During presentation of the bobwhite distress call signal vocalization responses increased slightly from baseline. As shown in Table 7, the interaction, signal \times test, was a significant effect, $F = 2.78$, $df = 5, 24$, $p < .05$.

Cautious Posture is a pattern most often seen when a bird is approaching something novel. It is also sometimes observed briefly in a group of bobwhite when they first break from a freeze. The

Figure 9.--Mean vocalization responses of Bobwhite quail during pre-signal baseline (open bars) and post-signal (hatched bars) periods to each of six auditory signal conditions. Vocalization was significantly less during signal than baseline periods ($p < .001$), and test period interacted significantly with type of signal ($p < .05$).



present data suggest that it is an infrequent behavior pattern when no visual novelty elicits it. In Study 1, this behavior increased from baseline to signal, but the data only approached significance, $p < .10$. In Study 2, an increase from baseline to signal was observed again in the bobwhite distress call signal group condition; the mean response rose from .4 to .9. The means for the other groups are also of this general magnitude and show no consistent pattern of directional change. Given the low frequency and small variation of the behavior pattern in this test significant effects would not be expected and were not obtained, as shown in Table 7. The same comments regarding low frequency and behavioral variation obtain for the gular quiver category. The twelve means there range from .03 to .73, though the differences are not significant. Gular quivers decreased from baseline for all the signal groups except the bobwhite reverse distress signal, which increased.

Study 2 Habituation

The third experimental hypothesis: No habituation occurs in any signal condition, was tested using the same two factored repeated measures ANOVA used in the previous studies. To examine the data for habituation, however, each trial presentation of the stimulus signal was examined separately. For this analysis we have again six signal conditions, five cages or triads in each condition, and three observations or trials on each cage of subjects. These trials are referred to as 1, 2, and 3 successively in the figures. In this analysis the responding during the food call period, common

across all signal conditions, was not included; only responding to each presentation of the experimental stimulus was examined. Behavior during food call presentation will be treated subsequently in a separate analysis. Only those behavior categories that produced a significant effect in a previous analysis were analyzed here.

The primary question of interest is whether a response decrement is observed over repeated presentations of the stimulus signal. The available data in previous literature on natural defense responses (such as freezing) habituating to efficient elicitors (such as distress signals) are equivocal. It has been demonstrated in the present studies that distress signals do indeed function as powerful elicitors of the freezing response pattern in these animals even under laboratory conditions.

Since freezing has consistently shown up to be significantly influenced by the present experimental manipulations, we will begin the analysis of habituation with this response pattern. The ANOVA table for the freeze response follows as Table 8.

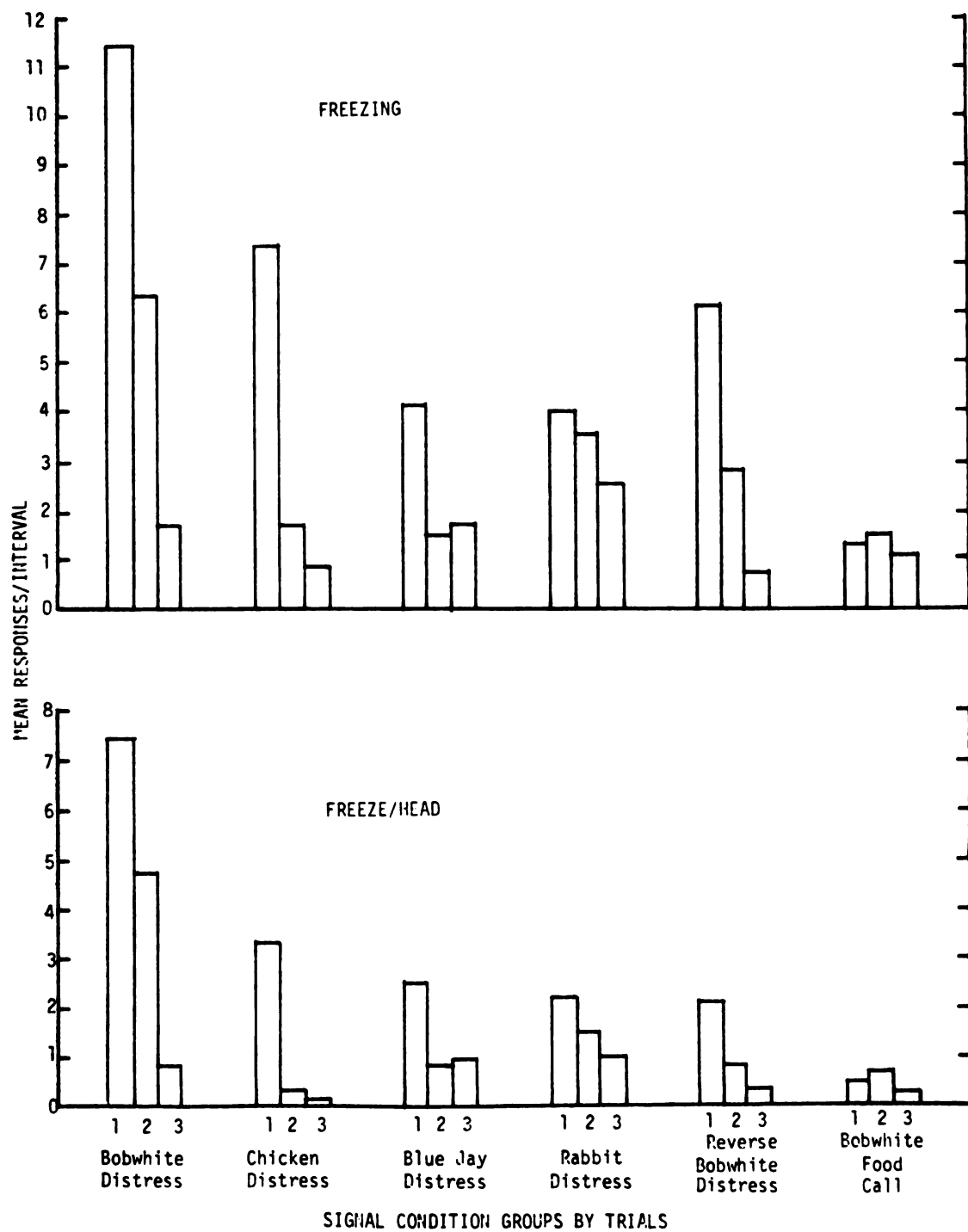
As shown in Table 8, the null hypothesis of no habituation can be firmly rejected since the trials effect was significant. Figure 10 illustrates this effect for both the freeze and the freeze/Head responses, over all six signal conditions. The largest drop in responding clearly occurs from trial 1 to trial 2 in all the distress signal conditions. The only signal condition not showing a response decrement across trials is the food call condition. This is to be expected if the food call is serving as a control condition which elicits little defensive responding in the first place.

TABLE 8.--Analysis of Variance of Incidence of Habituation of Freezing Responses over Three Signal Repetitions for Six Independent Groups of Bobwhite Quail Assigned to One of the Following Stimulus Signal Conditions; Bobwhite quail Distress Call, Chicken Distress Call, Blue Jay Distress Call, Rabbit Distress Call, Reversed Bobwhite Quail Distress Call, and Food Signal Control Call

Source	SS	df	MS	F
Total	28119.29	89		
Between cages	15973.29	29		
Signal conditions	2029.55	5	405.91	< 1
Error (b)	13943.73	24	580.99	
Within cages	12146.00	60		
Trials	2669.49	2	1334.74	8.17*
Signals x Trials	1633.04	10	163.30	< 1
Error (w)	7843.47	48	163.40	

*p < .005

Figure 10. Habituation analysis: Mean defensive freezing responses per interval over three repeated experimental auditory signals (trials 1, 2, 3) showing significant habituation ($p < .005$, both analyses).



Another interesting feature of Fig. 10 is that the extent of trial 1 responding follows the order of decreasing magnitude of freezing predicted in experimental prediction 2b. That is, the closer the phylogenetic relationship between the species, the more effective the distress signal will be as an elicitor of freezing. Also, the mean total responses over the 6 minutes follows the hypothesis for the avian species; the rabbit call (which seems to show less habituation) falls in the middle, as does the bobwhite reverse call.

This confirms the similar observation made in Fig. 4. The present data, Fig. 10, demonstrate that the obtained change in freezing can be attributed to the behavior of the birds during the actual distress signal presentation period. That is, the effect is more striking when responding to the common food call section of the stimulus tape is subtracted out of the data.

Table 9 summarizes the ANOVA results on the dependent measures analyzed for habituation in the present study. The tabled p value for each effect for each behavior category is shown. The complete ANOVA tables for this analysis are available in Appendix D. Only those behavior categories showing significant effects or strong trends in this analysis will be graphed in the following figures.

Fig. 11 illustrates the mean pecking and dusting responses to repeated presentations of the auditory stimulus over all the signal conditions in Study 2. As shown in Table 9, none of these effects were statistically significant though there were several interesting trends.

Figure 11. Habituation analysis: Mean pecking and dusting responses (responses per interval) of Bobwhite quail over three repetitions of auditory signals (trials 1, 2, 3). Differences showed a trend in the predicted direction ($p < .20$, all effects, dusting, $p < .20$, trials, pecking). See Table 9.

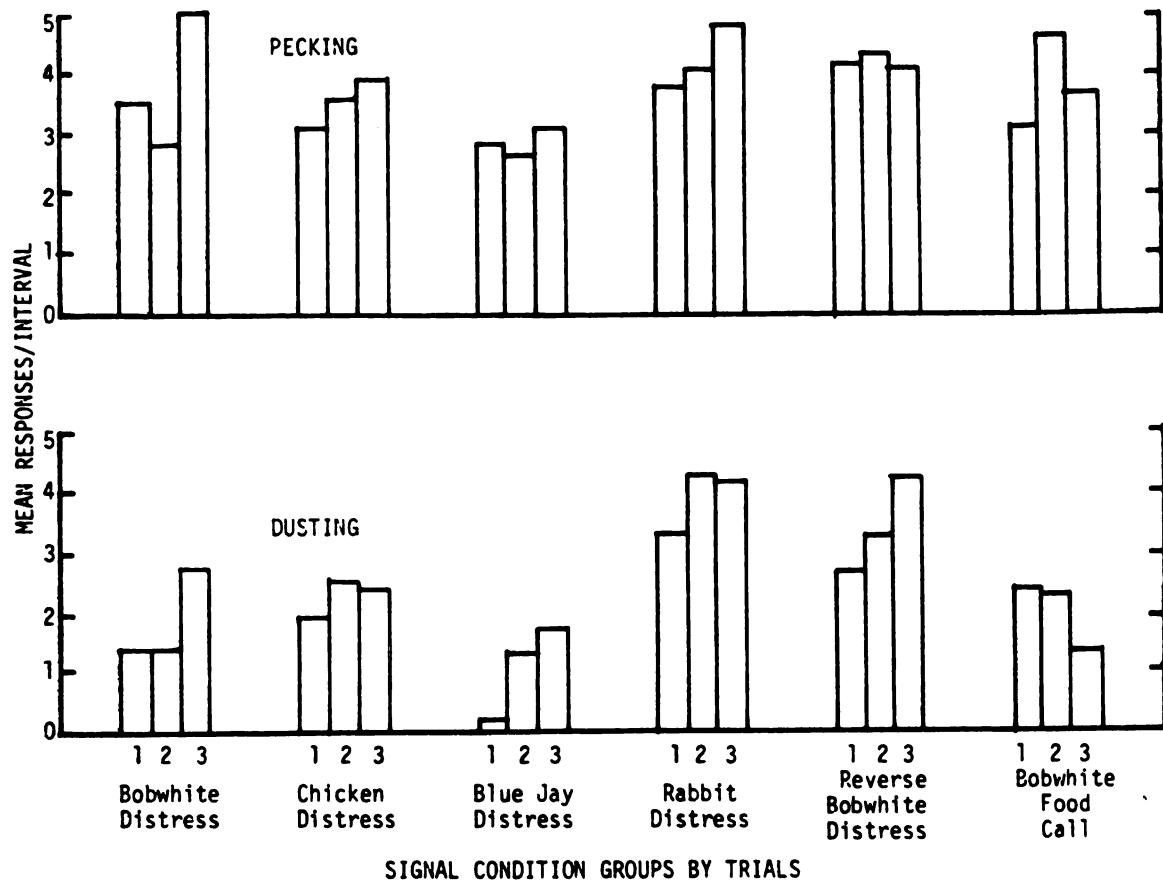


TABLE 9.--Analysis of Variance Results Summarized for Those Behavior Categories that were Statistically Significant in Study 2. Data are Presented from Six Signal Conditions over Three Trials of Signal Presentations of Each Signal Condition

Behavior Category	Signal Condition	Trials	Signal x Trial
Pecking	ns	.20	ns
Dusting	.20	.20	.20
Freeze	ns	.005	ns
Freeze/Head	ns	.005	ns
Proximity	ns	ns	ns
Cautious Posture	.20	.025	ns
Locomotion	ns	ns	ns
Vocalization	.20	.10	ns

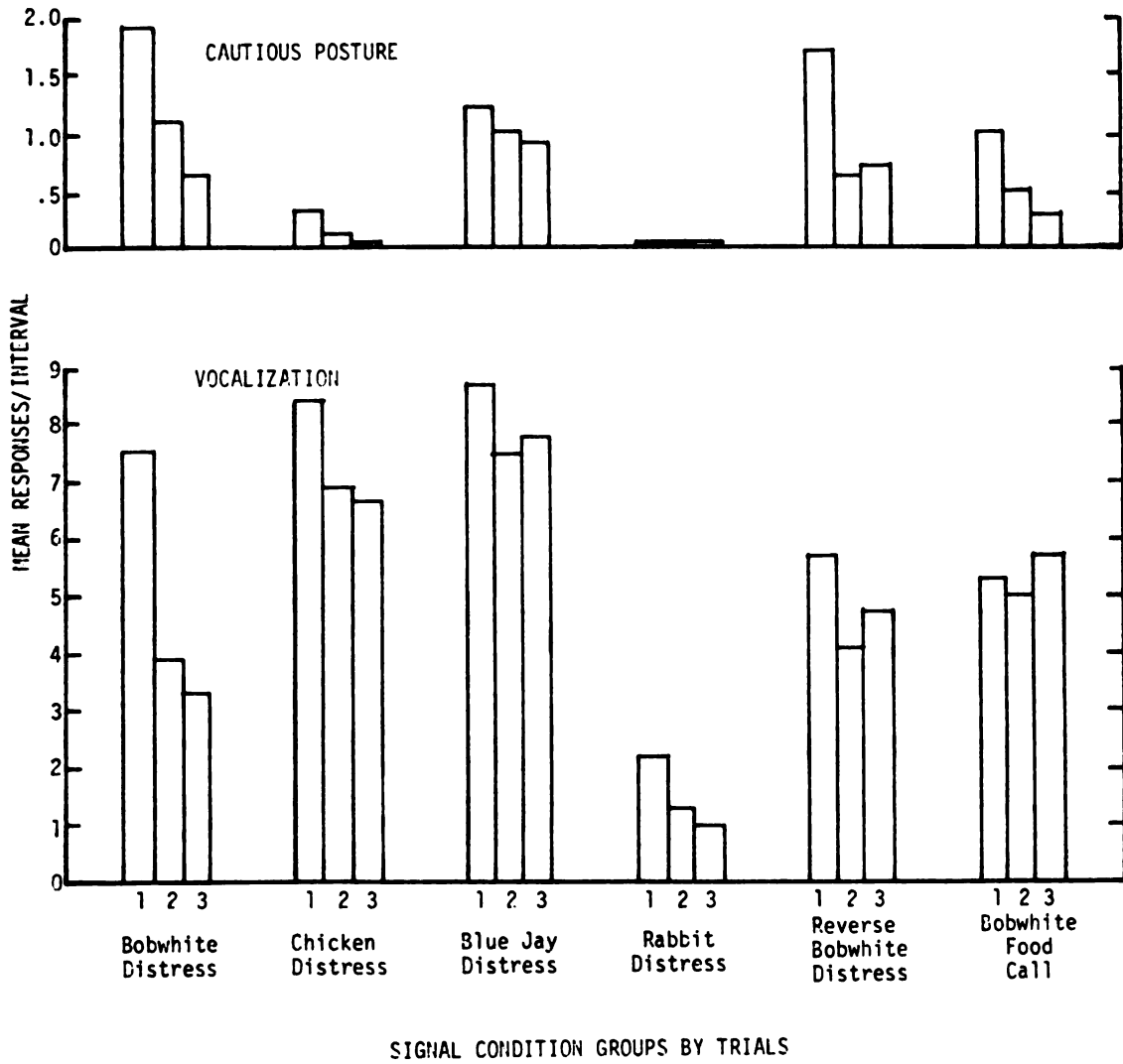
In contrast to the defensive behaviors, pecking and dusting behaviors do not show response decrement over three trials for any of the distress signal conditions. Competing, mutually exclusive patterns hardly could show this decrement if freezing was significant. The real question, then, is, was there a significant increase over trials? The food call signal group shows a slight decrement across trials for the category of dusting, as might be expected of a control condition.

This is not to say that habituation as a process is not illustrated in these data. For both pecking and dusting, several of the signal conditions show an increase over trials in the distress signal conditions. This appears to reflect that the birds are increasingly engaging in these behaviors following the effect of the first signal. That is, this is the reverse of the freezing data in Fig. 10.

This confirms the effect found in the previous analysis of pecking, illustrated in Fig. 5, that pecking is suppressed by the signal presentation. The present analysis points up how the distress signals were suppressing pecking, especially on the first trial of hearing the distress signal. Following this initial suppression, in most instances, the response increases at least by the third trial. The behavior category of dusting shows a similar pattern to pecking over most of the distress signal conditions.

Fig. 12 displays the same analysis for the behavior categories of cautious posture and vocalization. The cautious posture

Figure 12. Habituation analysis: Mean cautious posture responses and vocalization responses (responses per interval) of Bobwhite quail over three repeated auditory signals (trials 1, 2, 3). Habituation was present in both response measures ($p < .025$, cautious posture; $p < .10$, vocalization).



behavior category clearly shows a significant response decrement across trials ($F = 4.59$, $df = 2, 48$, $p < .025$). The rabbit distress call did not contribute to this effect; there is an unmistakable floor effect. The difference between signal groups only approaches significance, $F = 1.79$, $df = 5, 24$, $p < .20$.

Vocalization, the bottom section of Fig. 12, generally shows response decrement over trials for all the distress signal conditions. The food call condition shows only minimal change over the three trials, as might be anticipated for the control condition. This elaborates on the finding in Study 1 that vocalization decreases under the bobwhite distress signal condition. It also confirms the finding in the earlier analysis of Study 2 that vocalization is high under both baseline and signal tests for the bobwhite distress signal condition, shows a significant change from baseline to signal condition, and is differentially affected by the signal conditions (interaction, signal \times test, $p < .05$). Vocalization is generally high in the aves signal groups, and shows a decrement following the first trial. Again, we notice the pattern shown earlier that responding to the rabbit distress signal condition differs from the avian signal conditions.

Study 2 Food Call vs. Trial 1 of Test Signal

Each signal condition stimulus tape initially presented one trial of the bobwhite food call vocalization immediately following the baseline period and preceding the signal condition stimulus.

(See Fig. 1, p. 49.) Thus, all the birds had one trial of a non-experimental auditory stimulus onset in the chamber before the test signal was presented. The results analyzed prior to the habituation analysis always included this common food call period as part of the data during the signal period as a conservative test of the experimental predictions. In addition, habituation was clearly shown to many of the tested signals, suggesting that Trial 1 responses provide the clearest test of any effects of signal conditions.

It is of some interest then to examine separately changes in responding on Trial 1 only in comparison with this common food call period. An ANOVA was prepared for each behavior category that had shown a significant result in previous analysis. In this analysis we again have six signal conditions, two tests (food call vs. trial one) and five cages in each observation. The full ANOVA summary table for freezing follows.

The results shown in Table 10 for the freezing response ANOVA are essentially duplicated in the freeze/Head behavior category ANOVA. All ANOVA tables for this analysis are available in Appendix E.

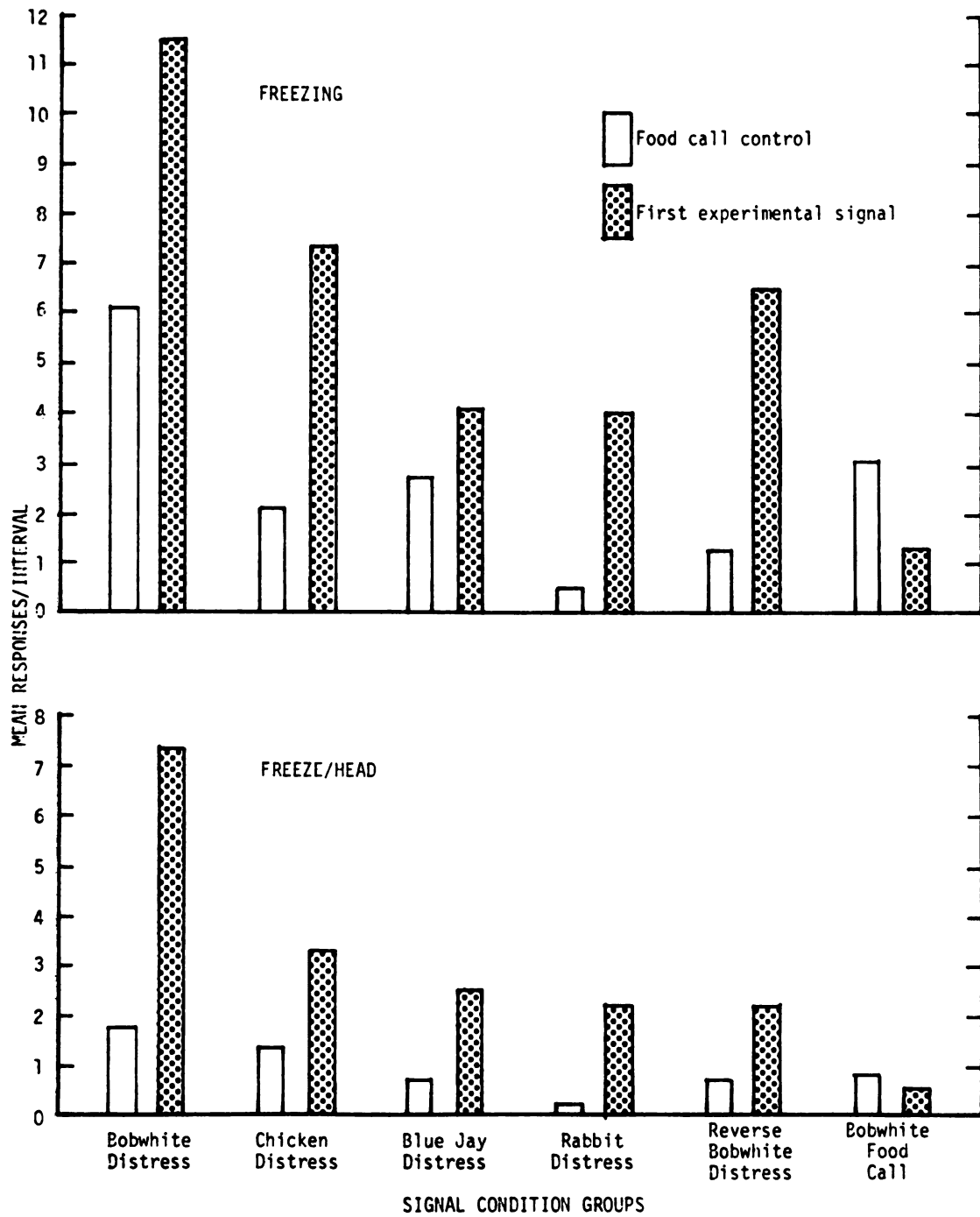
Figure 13 illustrates the pattern of responding for both the freeze and freeze/Head behavior categories over the six signal conditions. In examining this figure, it is immediately apparent that the onset of an auditory stimulus does elicit some freezing behavior in these birds in the chamber. It is also clear that the particular stimulus signal in each distress signal condition elicits freezing

TABLE 10.--Analysis of Variance of the Freezing Response in the Bobwhite Quail under Six Signal Conditions Testing Responding to the Common Bobwhite Food Call versus Responding to Trial One of the Experimental Stimulus Signal. Each Triad Score Constitutes One Unit for Analysis

Source	SS	df	ms	f
Total	24926.50	59		
Between cages	19517.50	29		
Signal condition	2755.70	5	551.14	< 1
Error (b)	16761.80	24	698.41	
Within cages	5409.00	30		
Test (FC vs. T1)	1480.17	1	1480.17	11.42*
Signal x Test	819.43	5	163.89	1.26
Error (w)	3109.40	24	129.56	

*p < .005

Figure 13. Mean defensive freezing responses for a food call signal (open bars) to the first experimental signal, Trial 1 (dotted bars). Defensive responding was significantly greater to the experimental signal in both analyses ($p < .005$, freeze; $p < .01$, freeze/head).



behaviors in greater magnitude than the food call signal. The difference between the food call and trial one responding for both freezing measures was significant. Freezing showed a significant test effect ($F = 11.42$, $df = 1, 24$, $p < .005$) as did the freeze/head category $F = 7.98$, $df = 1, 24$, $p < .01$.

It can also be pointed out in this figure that the magnitude of defensive responding on trial one decreases generally in the species order predicted in the experimental hypothesis: that is, conspecific, chicken, blue jay, rabbit. As seen in several previous figures, the reverse signal is functioning much like a conspecific or at least closely related species distress signal. The reverse signal used here is a conspecific distress signal that has been garbled as to the sequence of occurrence components. Consequently, this signal is novel in one respect, but familiar in another. It would require a component analysis of the signal paradigm to examine what features of this stimulus have signal value for these birds.

The pattern of low magnitude of freezing behaviors observed to the food call signal condition in Fig. 13 also illustrates that this is an appropriate control condition for this study. These results make the point nicely that there is some feature unique to these distress signals that elicit freezing responses in these birds. These quail do show differential responses to these stimuli which are consistent across similar measures (such as freeze or freeze/head). While the differences do not reach statistical significance, probably due to the variability which is high overall, and especially high on

Trial 1 (see Appendix E, Table of means and standard deviations) this consistency suggests that the predicted ordering does in fact occur.

Table 11 summarizes the ANOVA results on the dependent variables analyzed for a difference between the food call and trial one responding over the six signal conditions analyzed in the present analysis. Complete ANOVA tables are available in Appendix E. Only those categories showing significant effects will be illustrated in the following figures.

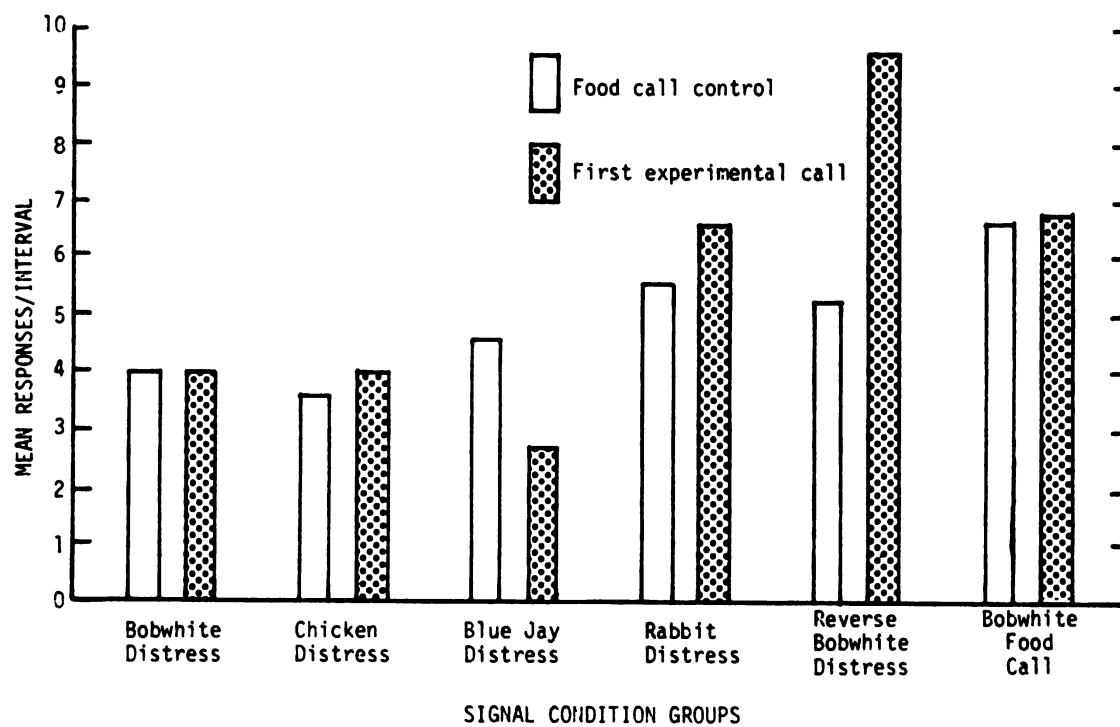
The other significant difference obtained in the present analysis, as shown in Table 11, was in the behavior category of proximity, making contact with another bird. The test effect ($F = 5.28$, $df = 1, 24$, $p < .05$) shows that there was clearly a difference in the number of proximity responses elicited by the food call and responses elicited by the signal conditions in trial one. The signal \times test interaction effect obtained ($F = 7.37$, $df = 5, 24$, $p < .025$) points out that the pattern of this difference is not all in one direction. Fig. 14 illustrates the mean proximity responses across all the signal conditions, showing the difference in responding to the food call and the test stimulus signal in trial one.

In the prior analyses for both Studies 1 and 2, there was a significant increase from baseline to signal period in proximity responses. In the habituation analysis for this behavior category, there was no significant effect. In examining the lack of a directional pattern of responding to the different signals in Fig. 14, this doesn't fit with the other data at first glance.

TABLE 11.--Summaries of Analyses of Variance of Frequencies of Occurrence for Eight Behavior Categories in Response to an Initial Auditory Food Call Stimulus and the First Trial of Experimental Auditory Stimulus for Independent Groups of Bobwhite Quail Each Exposed to One of Six Auditory Distress Signal Stimuli

Behavior Category	Signal Condition	Pre-Post Test	Signal x Test
Pecking	ns	.20	ns
Dusting	ns	ns	ns
Freeze	ns	.005	ns
Freeze/Head	ns	.01	ns
Proximity	ns	.05	.025
Posture	ns	ns	.20
Locomotion	ns	ns	ns
Vocalization	ns	ns	ns

Figure 14. Mean proximity responses to food call and to first experimental signal (trial 1). Proximity responses were greater following experimental signals ($p < .05$), though this effect interacted with signal type ($p < .025$ for signal \times test term).



In examining the raw data means across trials for the habituation analysis (see Appendix D) there is a trend for proximity responses to increase across trials for the following signal conditions: bobwhite, chicken, blue jay, rabbit and food call. Proximity responses in the reverse condition decrease slightly across trials. Given that there was a lot of freezing shown in trial one, and that freezing responses habituated quickly (Fig. 12), this present picture is not contradictory to the earlier results. It is interesting that proximity generally increases across trials 1, 2, and 3, while freezing responses decrease. This may reflect a competing response phenomenon, that is, unless the birds are already near each other on signal trial one, they can't be scored for proximity until they begin moving about following a freeze. These data could also suggest that following their initial experience with the test signal, the birds are making more approach responses to each other as a result of their habituating to the distress signals. An alternative suggestion is to assume that the test signals elicit fear responses and following this experience they tend to huddle or "close ranks."

The present experimental paradigm and results do not allow us to distinguish between these various suggestions from a firm data base. We can say at this point that the data confirm what casual observations of this highly social species suggests, that being near another conspecific is a frequent response in their repertoire.

It is interesting that in Fig. 14, the reversed bobwhite quail distress signal condition shows the greatest increase in

proximity responses from the food call to trial one. It might be that this is a novel signal that has defensive response eliciting features. If we assume this is eliciting fear or antipredator behaviors, then we may be seeing a protean defensive display in trial one in response to a novel and threatening stimulus situation. This protean defensive display, common in quail, is a hectic rushing about zigzagging run (Humphries & Driver, 1970) that occurs before the defensive distance is reduced to zero. This brief display sometimes precedes freezing in these birds and was occasionally observed in this experimental situation. Since it was not scored as a behavior category obviously no conclusions can be drawn at this point. It would be interesting in future research to see if the response pattern of this display occurred more frequently to novel, fear-eliciting or threatening stimuli than to fear-producing stimuli that were familiar.

Summing up the food call versus trial one analysis in Study 2, which is a somewhat less conservative test than the previous analyses, the distress signal stimuli clearly elicit significant freezing behaviors in these birds tending to be in the predicted order, under the present experimental conditions.

The suppression of responding in other behavior categories observed in Study 1 is not shown clearly in the present analysis. It should be pointed out, though, that this present analysis is taking only a partial sample (two trials) of responses that occurred in the total experiment, and that variability was especially high on trial 1 (see Appendix D) making it difficult for effects to reach statistical

significance. However, differences where observed were in the predicted directions.

DISCUSSION

Stimulus Properties of Distress Calls

If a scream is a scream in any language, do all screams have similar features? The stimulus measurements presented in Table 3 do suggest some striking similarities among the distress calls of the gallinaceous birds. As Greenwalt (1968) points out, similar morphology may produce similar sounds. Even though frequency measures for the blue jay differ from those for the gallinaceous birds, the signature duration (400 msec.) is identical across these three species. If duration of the signature were a "universal" aspect of a distress call, one might expect it to be the same across all distress calls. The duration of the rabbit's distress call, and the data in the present study, make this appear unlikely.

It would be of interest for someone to do a study in which the individual component properties of the calls were the focus of the study. Such a focus was, however, beyond the aims and purposes of the present study.

Summary of Expected Findings

The first experimental prediction, that distress calls elicit defensive responses in the bobwhite quail, is clearly supported in both Study 1 and 2. In Study 1, where the conspecific distress call was the only distress call used, all the tested differences for

freezing categories, or defensive responses, were significant and in the expected direction. This was true in spite of the conservative nature of the data analysis performed.

The second part of prediction 1, that distress calls would suppress nondefensive responses such as maintenance activities, was also supported clearly for the pecking response measure. Since pecking is a high frequency behavior for these animals, particularly in the presence of strong pecking elicitors like dust and food, it is difficult to suppress this response. The fact that it did show a significant decrease under these conditions from baseline to signal period ($p < .025$) is, therefore, a strong finding in Study I, and was observed similarly in Study 2 ($p < .001$). Several of the other behavior patterns were also suppressed though the suppression did not reach statistical significance and none of these trends were in the wrong direction.

The next prediction, 2a, that the conspecific distress call would elicit more freezing than the other distress calls, was supported with one exception. The rabbit distress call elicited freezing behaviors as effectively as the conspecific distress call. In examining prediction 2b, that the magnitude of defensive responses would decrease in the following species order: bobwhite, blue jay, rabbit, food call, we see a similar picture (Figure 10). This prediction is supported except for the rabbit signal condition and is further confirmed in the habituation analysis shown in Fig. 10, and in the trial one data shown in Fig. 13.

Thus, both the most and least conservative tests of this prediction agree that the phylogenetic relationship of the species involved is a variable that must be considered in studying communication behavior. The pattern of responding elicited by the rabbit distress signal will be discussed in the next section.

The third major prediction, that no habituation would be observed in any signal condition, was clearly rejected when behavior was examined over the course of three trials. Freezing behaviors decreased significantly over trials in all signal conditions, with the greatest decrease generally seen between trials one and two. There were trends toward significant increases over trials for both pecking and dusting, lending additional support to experimental prediction 1. This suggests that these activities were most strongly suppressed on trial one: that is, freezing behaviors were effectively competing with maintenance activities, and as freezing decreases, pecking and dusting increase. This is similar to the finding reported by Bolles (1970) that freezing competes with exploring and grooming in rats. This further supports Denny's competing response analysis, which stems from elicitation theory (Denny & Ratner, 1970).

That habituation to distress calls is clearly observed in these studies is not to say that it settles the question of whether or not defensive or anti-predator responses habituate to "survival" signals. As pointed out in Chapter 1, experiments in which significant habituation was not observed involved testing in the animal's natural habitat with live predators present. Evidently, in the

laboratory situation these auditory signals function much like other experimental stimuli and the responses undergo habituation. It should also be pointed out that these subjects received no visual confirmation of the presence of a predator or other signals which might indicate danger.

Habituation of freezing responses was not observed in the food call stimulus signal condition. This supports the choice of using the food call as a control condition in these studies. In contrast to the other signal conditions, this points out more clearly that the distress signal is a salient stimulus.

In comparison to the food signal, the reversed bobwhite distress signal elicited the patterns of responses seen for other distress signals--elicitation of freezing, suppression of nondefensive behaviors, and habituation over trials. It may be that sequential ordering of components is less crucial to "distress signal-ness" than is the presence of other attributes as harmonic complexity or fundamental frequency, so that this signal was perceived as a distress signal like the others. It could also have been that the birds responded to the strangeness of familiar components presented in a novel or unfamiliar way, so that the alarm shown to this signal was less a matter of response to distress than to novelty. This issue, unresolvable here, deserves further study.

Further analysis of the magnitude of responding observed at different points during a session illustrates another interesting aspect of bobwhite quail behavior and habituation in this study.

Trial one of the distress signal was maximally behaviorally disruptive, compared to trials two and three. Observing the birds, one was left with the impression that the first trial of a distress signal elicited frantic or panic behaviors in these animals. In contrast, the triad of birds seemed to act more as a unit in trials two and three. One way of looking at this is to examine the changes in the variability measure over trials, given in Appendix D. For example, the standard deviations for incidence of freezing to the signal conditions over trials 1, 2, and 3 show the following:

Trial	Bobwhite	Reverse	Chicken	Blue Jay	Rabbit
1	43	27	29	8	6
2	37	13	4	4	7
3	6	2	2	11	5

This trial one effect is also illustrated by making a similar comparison of the standard deviations for freezing observed to the initial auditory (food call) stimulus and to the first trial of the experimental signal (see Appendix E). In spite of reducing the data base in this analysis (looking at only 2 stimulus presentations/trials) the variability increased from food call to distress signal 1, instead of decreasing as one would expect from habituation. The standard deviations for freezing on these two trials (first distress signal s.d. in parentheses) on the food call trial were: bobwhite 33 (43), reverse 4 (27), chicken 7 (29), blue jay 9 (8), and

rabbit 2 (6). With the exception of blue jay, there is an obvious increase of variability on distress trial one compared to the food call trial. Combining these data with the habituation data, and the variability across trials presented above, suggests that indeed the first time these birds hear a distress signal, particularly a conspecific or closely related species distress call, they respond strongly and, as individuals, quite differently. For a social species known for their synchronous behavior, these data point out in a somewhat different way the effectiveness of the distress call as a salient stimulus.

Unexpected Results

With regard to prediction 2 that the bobwhite distress signal would elicit freezing in a decreasing order that would correspond to the relative phylogenetic relationship (bobwhite, chicken, blue jay, rabbit), the defensive responses elicited by the rabbit distress call were surprising. Recall that Figs. 4 and 10 illustrated that the rabbit distress call was a powerful elicitor of freezing responses in the bobwhite quail, and that freezing following second and third rabbit distress calls showed some habituation, although not as rapidly or as fully as the other distress signal conditions. There are two different points that may be mentioned about the rabbit:

1. The rabbit shares habitat with the quail, and
2. The rabbit distress sound or even crude imitations (Boudreau, 1968) is the most commonly employed sound used in the field for "predator calling."

These were two of the considerations in choosing the rabbit call as a stimulus signal condition for the present study. The current data suggest that interspecific communication regarding danger or survival signals may also be influenced by having similar living conditions. Both the rabbit and the bobwhite quail are ground dwellers having similar habitat preferences and similar predators (Stoddard, 1931). That the rabbit distress signal is so commonly employed in "predator calling" is further evidence of its interspecific communication generality.

The data in the present study raises several interesting questions in regard to interspecific communication and its relationship to phylogenetic status, shared habitat constraints, and effective stimulus components of this signal. The rabbit distress cry had a longer signal duration (more than twice that of the other distress calls). It would require a stimulus components analysis to assess the influence of this duration variable compared to the other signals. From the present study no firm conclusions can be drawn about this issue.

It doesn't appear to be wise to dismiss the effectiveness of the rabbit distress signal on the basis of its being novel to these subjects. Hinde (1961) and others point out that responses to novel stimuli habituate fairly rapidly if not reinforced by further stimuli indicative of danger. As shown in Fig. 10, the rabbit condition resulted in slower and somewhat less habituation than did the other distress signal conditions.

Another somewhat unexpected result in the present study was the extremely high variability shown across all the measures (see Appendices B-E, Tables of means and stand deviations). Given that we were working with a nondomestic species in a laboratory, exploring many different types of behaviors as measures and dealing with defensive or anti-predator responses, high variability was anticipated (Ratner, 1967). However, we thought this might be attenuated somewhat by testing three animals together of a species that is known for acting in concert as a unit (Stoddard, 1931; Nitschke, 1973). However, despite the increased stability resulting from using triads of birds as the unit for analysis, behavior were still highly variable.

During data collection all the observers were convinced that proximity and locomote to make contact with another bird would be significantly different following different distress signal presentations. Proximity showed significant increases from baseline to signal in both Studies 1 and 2, no significant habituation effects, and significant test and interaction effects when comparing responding on trial one to the food call trial (Fig. 14).

Looking over all the Study 2 analyses for proximity, two things stand out. Proximity responses to the rabbit and the reverse calls show a different pattern than do proximity responses to the other calls. As shown in Appendix D, the rabbit and reverse means are relatively higher and more consistent across trials. The stand-are deviations are stable over trials for all the conditions except

rabbit and reverse which show a consistently slight decrease in variability across trials. Again, we note that response to the rabbit signal differs from the other patterns in the data. In the proximity measure, however, rabbit and reverse are producing patterns similar to each other and different from the others. Could this be due to the novelty aspect of these stimuli? Is this what is making them maximally behaviorally disruptive on trial one of the distress signal?

In the bobwhite quail, it is typical for the members of a covey to reconvene and make contact with the covey members following a disturbance. This is usually accompanied by almost continuous conversational chattering as the covey reconvenes (Stoddard, 1931). This is one of the primary reasons we expected to see proximity and locomote/contact show similar patterns in the data. It is quite possible that the two minute ITI employed in the present study was too short to allow these behavior patterns full expression. In the field these reconvening behaviors may take place over long periods of time (Rosene, 1969) depending of course of how widely dispersed the birds are by the disturbance.

One other aspect of the locomote/contact category results that should be pointed out is that scoring this pattern involved the observer inferring intention on the part of a bird. Observers were instructed to be very conservative about this and only score locomote/contact when they felt sure it involved direct approach to another bird. This may have influenced the low frequency with which this category was scored.

Implications for Theory or Research and Generalizability

The results of the present study clearly support the view that various distress calls are strong elicitors of freezing responses in bobwhite quail. This is strikingly true for the conspecific distress signal. A natural, species-typical, readily obtainable stimulus such as this should prove useful in many experimental paradigms. Other workers (Best, 1978; Worden & Galambos, 1970) point out that pure tone stimuli lead to confusing results when working with species-specific response patterns and with sensory systems analysis. Work with other species (Capranica, 1965; Fentress, 1968; and Worden & Galambos, 1970) has illustrated that a distress stimulus can also be usefully varied in intensity and is particularly useful in the analysis of sensory systems. Another spin-off from the present data is the possibility of using this paradigm to do a stimulus components analysis of these signals. It may be that the species-specific distress signal is a whole unit and all the components are necessary to elicit maximum responsiveness.

The study also suggests that distress signals have sufficient generality to be useful for making phylogenetic comparisons in interspecific communication work. It may also be that cross species comparisons of this sort take into account environmental variables such as common habitat and common predators.

These present data are constrained by several factors including relatively small Ns for the number and variability of the questions pursued. Any laboratory study with a nondomestic species is

somewhat difficult to interpret with respect to the narrowing of the response repertoire typically imposed by confinement in a small artificial situation. In a study of the present type it would have been instructive to have provided some visual stimuli indicative of the source of these distress signals, for comparison with the simple auditory condition.

If the study were to be repeated, the first major change that should be made would be much longer minimum ITIs, for reasons previously discussed. In addition, more trials should be run to allow for a fuller analysis of habituation. In this case there should be more attention paid to the sequence of behavior across all the useful behavior categories. Given the patterns of variability and the high variability seen on trial one of a distress signal presentation, it would be interesting to see how the flow or sequence of behavior categories change over longer periods of time.

In summary, the question of whether a scream is a scream in any language can be answered in the typically scientific fashion, "Yes, no, and it all depends." The pattern of responding elicited by a scream will be constrained by phylogenetic relationships, environmental contingencies, and what the animal is doing when it first hears the scream.

APPENDICES

APPENDIX A

SAMPLES OF RAW DATA SCORING SHEETS

CAGE _____

HABITUATION TO BOX

Date _____ E _____

Time Start _____ Time Ended _____

Band
Color Weigh

I		
X		
-		

COMMENTS:

Minutes	Pecking	Preening Self- Allo	Dusting	Resting in Dust Tray	Standing/ Sitting Outside tray	Huddled	LC Locomotion	Orients/ Exploring	Other
1									
2									
3									
4									
5									
6									
7									
8									
9									
10									
11									
12									
13									
14									
15									
16									
17									
18									
19									
20									
21									
22									
23									
24									
25									
26									
27									
28									
29									
30									
			Dust			HUD	LOCO	O/E	

BASELINE PERIOD BEHAVIOR RECORD, STUDY 1

Group _____ E _____ Cage _____

Date _____ Tape _____ Bird _____

DATA: Baseline Order _____

	F=Feed	O=oil Code-allo		H=head	Give Code	R=rest cp=cautious S=stand/sit POSTURE	C=contact	O or E	V=vac QM M OTHER
BASE	PECK	PREEN	DUST	FREEZE	PROXIMITY		LOCOMOTE	Orient/ Explore	
15									
30									
45									
1									
15									
30									
45									
2									
15									
30									
45									
3									
15									
30									
45									
4									
15									
30									
45									
5									
15									
30									
45									
6									
Food Call									
OL									
LSI									
b									
15									
30									
45									
1									
15									
30									
45									
2									
				FREEZE			LOCOM		

SIGNAL PERIOD BEHAVIOR RECORD, STUDY I

Group _____ E _____ Bird _____
 Date _____ Tape _____ Order _____
 DATA _____

Signals	F=Feed	O=oil Code-allo		H=head mut	Give Code	R=nest Cp=cautious S=standing/sit POSTURE	C	O/E	V GQ M	Cop
	PECK	PREEN	DUST	FREEZE	PROXIMITY		LOCOMOTE	ORIENT/ EXPLORES	OTHER	
D1 a										
s										s
b										
15										
30										
45										
1										1
15										
30										
45										
2										2
D2 a										
s										s
b										
15										
30										
45										
1										1
15										
30										
45										
2										2
a										
s										s
b										
15										
30										
45										
1										1
15										
30										
45										
2										
			DUST	FREEZE	PROXIMITY	POS	LOC			

OVERRUN TIME BEHAVIOR RECORD, STUDIES I AND II

Group _____ E _____ Cage _____

Date _____ Bird _____

	F	O=allo		H=head	Code	R Ep	C	O/E	V, GQ, M, Cop ek	
	PECK	PREEN	DUST	FREEZE	HUDDLE	POSTURE	LOCOMOTE	ORIENT EXPLORES	OTHER	
15										15
30										30
45										45
1										1
15										15
30										30
45										45
2										2
15										15
30										30
45										45
15										15
30										30
45										45
15										15
30										30
45										45
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30										30
45										45
15										15
30										30
45										45
15										15
30										30
45										45
15										15
30										30
45										45
	PECK	PREEN	DUST	FREEZE	HUDDLE	POSTURE	LOCOM	O/E	OTHER	

HEARING TEST DATA SHEET, STUDIES I AND II

BWQ Study II--999--Hearing Test Data

CAGE _____ Condition _____

DATE _____ Time _____ E: _____

R to Finger Snap

Bird ID

 T_1 T_2 T_3

_____	_____	_____	_____
_____	_____	_____	_____
_____	_____	_____	_____

Comments:

REQUEST FOR INFORMATION REGARDING RECORDINGS
OF VOCALIZATIONS

M. L. Nitschke, Department of Psychology, Michigan State University,
East Lansing, MI 48824

Record _____

Number _____ side _____

Species and/or subspecies _____

Number of animals involved? _____

Age of the animal(s) _____

Date recording was made: _____

Geographic location of recording _____

History of the animal:

_____ wild caught _____ pen reared

If captive, how long was it held in captivity? _____

Any other comments? _____

Conditions under which the vocalization was recorded: Please be as specific as possible. For instance, what stimulation was responsible for the animal making this vocalization at this time? Was another animal involved, if so how, etc.

Recorder manufacturer: _____

Model # and/or year: _____

Microphone: _____

Other comments: _____

BASELINE PERIOD BEHAVIOR RECORD, STUDY II

Group _____ E _____ Cage _____

Date _____ Tape _____ Bird _____

Data _____ Order _____

Base	PECK	PREEN	DUST	H FREEZE	PROXIMITY	POSTURE	C LOCOMOTE	VOCAL	OTHER
15									
30									
45									
1									
15									
30									
45									
2									
15									
30									
45									
3									
15									
30									
45									
4									
15									
30									
45									
5									
15									
30									
45									
6									
Food Call									
a									
151									
b									
15									
30									
45									
1									
15									
30									
45									
2									
	PECK		DUST	FREEZE	PROX			VOCAL	

SIGNAL PERIOD BEHAVIOR RECORD, STUDY II

Group _____ E _____ Bird _____

Date _____ Tape _____ Other _____

Data _____

SIGNALS	F=feed PECK	O=oil Code-allo PREEN		H=head mud FREEZE	Give Code PROXIMITY	R=rest Cp=cautious S=stand/sit POSTURE	LC=contact LOCOMOTE	O/E ORIENT/ EXPLORES	V GQ M OTHER	Cop
D1	a									
	151									151
	b									
	15									
	30									
	45									
	1									1
	15									
	30									
	45									
	2									2
D2	a									
	151									151
	b									
	15									
	30									
	45									
	1									1
	15									
	30									
	45									
	2									2
D3	a									
	151									151
	b									
	15									
	30									
	45									
	1									1
	15									
	30									
	45									
	2									2
			DUST	FREEZE	PROXIMITY	POST	LOC			

APPENDIX B

DATA ANALYSIS FOR STUDY I

TAPED SILENCE VS. BOBWHITE DISTRESS SIGNAL

TABLE B-1.--Study I. Table of Means and Standard Deviations (σ) for Taped Silence and Bobwhite Distress Signal Conditions During Baseline (pre) and Signal Period (Post) Tests

	Taped Silence		Bobwhite Distress Signal	
	Baseline \bar{X} (σ)	Signal \bar{X} (σ)	Baseline \bar{X} (σ)	Signal \bar{X} (σ)
Pecking	4.58 (2.18)	2.29 (2.23)	2.41 (1.40)	1.46 (.58)
Preening	.77 (.58)	.71 (.66)	.30 (.51)	.34 (.42)
Dusting	4.58 (3.28)	4.66 (4.12)	2.86 (1.91)	1.62 (.94)
Freeze	.03 (.06)	.05 (.07)	.03 (.06)	2.53 (1.49)
Freeze/Head	0 (0)	.07 (.17)	0 (0)	1.04 (.97)
Proximity	1.64 (1.25)	3.83 (1.54)	2.99 (4.24)	5.62 (3.71)
Resting	.72 (1.34)	1.38 (2.03)	.30 (.30)	.14 (.31)
Cautious Posture	.38 (.45)	.86 (.66)	.13 (.12)	.57 (.79)
Pausing	9.50 (2.59)	10.29 (2.47)	10.51 (1.31)	10.60 (.51)
Locomotion	1.49 (1.52)	3.14 (1.51)	2.04 (2.09)	2.06 (1.65)
Locomote/Contact	.83 (.99)	.45 (.54)	.61 (.83)	.45 (.40)
Orient	6.75 (2.13)	6.43 (2.75)	7.78 (1.65)	7.48 (2.11)
Explore	.69 (.20)	.83 (1.03)	.86 (1.02)	.43 (.45)
Vocalization	4.50 (2.37)	7.40 (5.95)	6.63 (4.62)	4.17 (5.17)
Gular Quiver	1.02 (.71)	.55 (.63)	.91 (1.47)	.25 (.16)

TABLE B-2.--Analysis of Variance for Study I

Source	SS	df	MS	f	p
Pecking I					
Total	92.08	23			
Between cage	52.55	11			
Signal condition	13.67	1	13.67	2.06	< .20
Error (b)	66.22	10	6.62		
Within	39.53	12			
Pre-post	15.79	1	15.79	7.41	< .025
Signal x Test	2.44	1	2.43	1.14	ns
Error (w)	21.30	10	2.13		
Preening I					
Total	7.14	23			
Between cage	4.58	11			
Signal condition	1.07	1	1.08	< 1	ns
Error (b)	66.22	10	6.62		
Within	2.56	12		< 1	
Pre-post	.00	1	.00		ns
Signal x Test	.01	1	.01	< 1	ns
Error (w)	2.56	10	.25		
Dusting I					
Total	200.17	23			
Between cage	171.69	11			
Signal condition	34.13	1	34.13	2.48	< .20
Error (b)	137.56	10	13.75		
Within	28.49	12		< 1	
Pre-post	1.99	1	1.99		ns
Signal x Test	2.61	1	2.61	1.09	ns
Error (w)	23.86	10	2.30		

TABLE B-2.--Continued

Source	SS	df	MS	f	p
Freezing I					
Total	39.32	23			
Between cage	15.06	11			
Signal condition	9.26	1	9.26	15.96	< .005
Error (b)	5.80	10	.58		
Within	24.26	12			
Pre-post	9.56	1	9.56	17.12	< .005
Signal x Test	9.11	1	9.11	16.31	< .005
Error (w)	5.58	10	.56		
Freeze/Head I					
Total	9.5639	23			
Between cage	3.8523	11			
Signal condition	1.4113	1	1.41	5.7816	< .05
Error (b)	2.4410	10	.24		
Within	5.7116	12			
Pre-post	1.8692	1	1.86	7.6165	< .025
Signal x Test	1.4114	1	1.41	5.7820	< .05
Error (w)	2.441	10	.24		
Proximity I					
Total	228.47	23			
Between cage	155.64	11			
Signal condition	14.89	1	14.89	1.06	ns
Error (b)	140.74	10	14.07		
Within	72.83	12			
Pre-post	34.87	1	34.87	9.2542	< .025
Signal x Test	.27	1	.27	.0728	ns
Error (w)	37.68	10	3.77		

TABLE B-2.--Continued

Source	SS	df	MS	f	p
Rest I					
Total	35.98	23			
Between cage	32.72	11			
Signal condition	4.12	1	4.12	1.44	ns
Error (b)	28.59	10	2.86		
Within	3.26	12			
Pre-post	.36	1	.36	1.95	< .20
Signal x Test	1.01	1	1.01	5.38	< .05
Error (w)	1.88	10	.18		
Cautious Past time I					
Total	8.09	23			
Between cage	3.67	11			
Signal condition	.43	1	.43	1.34	ns
Error (b)	3.24	10	.32		
Within	4.41	12			
Pre-post	1.24	1	1.24	3.90	< .10
Signal x Test	.00	1	.00	< 1	
Error (w)	3.17	10	.31		
Pausing I					
Total	78.34	23			
Between cage	67.06	11			
Signal condition	2.64	1	2.64	< 1	
Error (b)	64.42	10	6.44		
Within	11.28	12			
Pre-post	1.15	1	1.15	1.23	ns
Signal x Test	.75	1	.75	< 1	
Error (w)	9.37	10	.94		

TABLE B-2.--Continued

Source	SS	df	MS	f	p
Locomotion I					
Total	66.99	23			
Between cage	52.34	11			
Signal condition	.41	1	.41	< 1	ns
Error (b)	51.93	10	5.19		
Within	14.64	12			
Pre-post	4.24	1	4.24	6.60	< .05
Signal x Test	3.98	1	3.98	6.18	< .05
Error (w)	6.43	10	.64		
Locomote/Contact I					
Total	11.19	23			
Between cage	7.71	11			
Signal condition	.07	1	.07	< 1	ns
Error (b)	7.64	10	.76		
Within	3.47	12			
Pre-post	.43	1	.43	1.46	ns
Signal x Test	.07	1	.07	< 1	ns
Error (w)	2.97	10	.29		
Orient I					
Total	103.47	23			
Between cage	90.75	11			
Signal condition	6.53	1	6.53	< 1	ns
Error (b)	84.21	10	8.42		
Within	12.72	12			
Pre-post	.58	1	.58	< 1	
Signal x Test	.00	1	.00	< 1	ns
Error (w)	12.14	10	1.21		

TABLE B-2.--Continued

Source	SS	df	MS	f	p
Explore I					
Total	12.40	23			
Between cage	8.04	11			
Signal condition	.08	1	.08	< 1	ns
Error (b)	7.96	10	.79		
Within	4.35	12			
Pre-post	.13	1	.13	< 1	ns
Signal x Test	.49	1	.49	1.30	ns
Error (w)	3.74	10	.37		
Vocalization I					
Total	520.72	23			
Between cage	357.17	11			
Signal condition	1.80	1	1.80	< 1	ns
Error (b)	355.37	10	35.53		
Within	163.55	12			
Pre-post	.29	1	.29	< 1	ns
Signal x Test	43.17	1	43.17	3.59	< .10
Error (w)	120.09	10	12.00		
Gular Quiver I					
Total	17.66	23			
Between cage	8.85	11			
Signal condition	.24	1	.24	< 1	ns
Error (b)	8.61	10	.86		
Within	8.80	12			
Pre-post	1.95	1	1.95	2.88	< .20
Signal x Test	.06	1	.06	< 1	ns
Error (w)	6.78	10	.68		

APPENDIX C

DATA ANALYSES FOR STUDY II

SIX SIGNAL CONDITIONS--BASELINE VS. SIGNAL TEST PERIOD

TABLE C-1.--Table of Means and Standard Deviations (σ) for Six Signal Conditions During Baseline (B) and Signal Period (S) Tests--Study II

Measure	Bobwhite		Chicken		Blue Jay		Rabbit		Reverse		Food Call				
	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)			
Pecking	B	5.97 (2.18)	6.23 (2.96)	6.20 (1.92)	7.33 (2.90)	5.66 (1.15)	7.17 (1.42)	Preening	B	.27 (.22)	.47 (.52)	.27 (.28)	.27 (.51)	1.67 (2.44)	.50 (.52)
	S	4.38 (3.00)	4.15 (2.33)	3.65 (2.36)	6.07 (3.25)	5.20 (1.74)	5.06 (1.27)		S	.30 (.21)	.38 (.72)	.34 (.37)	.42 (.71)	.43 (.39)	.77 (.45)
Dusting	B	1.83 (2.04)	3.83 (1.53)	2.00 (2.35)	4.92 (3.89)	3.80 (2.48)	2.20 (1.17)	Freeze	B	.03 (.08)	0 (0)	.03 (.08)	.10 (.22)	.03 (.08)	.03 (.08)
	S	2.05 (2.10)	2.77 (1.87)	1.08 (1.04)	5.22 (3.52)	4.05 (2.35)	2.28 (2.03)		S	3.50 (3.34)	2.98 (1.46)	2.72 (2.40)	3.52 (2.13)	1.40 (1.19)	2.21 (1.04)
Freeze/Head	B	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	Proximity	B	3.30 (2.30)	4.03 (2.06)	3.37 (2.11)	6.67 (3.76)	2.90 (2.60)	3.70 (2.99)
	S	1.94 (2.00)	1.33 (.68)	1.13 (1.11)	1.69 (1.24)	1.40 (.70)	.78 (.55)		S	5.58 (5.69)	6.30 (5.54)	5.34 (4.13)	9.04 (2.82)	7.40 (2.24)	9.28 (3.15)
Cautious Posture	B	.40 (.42)	.40 (.25)	1.03 (.99)	.63 (.97)	.97 (1.25)	1.00 (1.78)	Locomotion	B	.40 (.42)	.40 (.25)	1.03 (.99)	.63 (.97)	.97 (1.25)	1.00 (1.78)
	S	.90 (.64)	.24 (.20)	1.39 (1.56)	.20 (.20)	.89 (.62)	1.08 (1.13)		S	.90 (.64)	.24 (.20)	1.39 (1.56)	.20 (.20)	.89 (.62)	1.08 (1.13)
Locomotion	B	1.97 (1.44)	1.38 (1.66)	1.33 (.60)	1.23 (1.30)	2.40 (.91)	1.73 (.93)	Locomote/Contact	B	1.97 (1.44)	1.38 (1.66)	1.33 (.60)	1.23 (1.30)	2.40 (.91)	1.73 (.93)
	S	1.06 (.96)	1.97 (.99)	1.30 (.86)	1.76 (.61)	1.19 (.70)	1.00 (.79)		S	1.06 (.96)	1.97 (.99)	1.30 (.86)	1.76 (.61)	1.19 (.70)	1.00 (.79)
Vocalization	B	.67 (.86)	.80 (.49)	.77 (.70)	1.53 (1.27)	.23 (.19)	.70 (.41)	Gular Quiver	B	.67 (.86)	.80 (.49)	.77 (.70)	1.53 (1.27)	.23 (.19)	.70 (.41)
	S	.71 (.82)	.36 (.27)	1.72 (.92)	1.47 (.96)	.82 (.62)	1.11 (.57)		S	.71 (.82)	.36 (.27)	1.72 (.92)	1.47 (.96)	.82 (.62)	1.11 (.57)
	B	6.80 (5.57)	10.47 (.98)	10.93 (1.07)	8.10 (3.31)	7.80 (3.22)	10.37 (.98)		B	6.80 (5.57)	10.47 (.98)	10.93 (1.07)	8.10 (3.31)	7.80 (3.22)	10.37 (.98)
	S	7.13 (6.38)	9.45 (2.94)	10.06 (2.10)	3.58 (1.79)	5.78 (3.01)	7.32 (4.36)		S	7.13 (6.38)	9.45 (2.94)	10.06 (2.10)	3.58 (1.79)	5.78 (3.01)	7.32 (4.36)
	B	.40 (.38)	.60 (1.07)	.73 (1.07)	.10 (.15)	.27 (.25)	.34 (.08)		B	.40 (.38)	.60 (1.07)	.73 (1.07)	.10 (.15)	.27 (.25)	.34 (.08)
	S	.03 (.06)	.55 (.93)	.15 (.16)	.07 (.10)	.41 (.38)	.02 (.04)		S	.03 (.06)	.55 (.93)	.15 (.16)	.07 (.10)	.41 (.38)	.02 (.04)

TABLE C-2.--Analysis of Variance for Study II: Basic Analysis

Source	SS	df	MS	f	p
Preening II					
Total	42.04	59			
Between cages	29.18	29			
Signal conditions	4.34	5	.87	< 1	ns
Error (b)	24.83	24	1.03		
Within	12.86	30			
Pre-post test	.26	1	.26	< 1	ns
Signal x Test	3.80	5	.76	2.07	ns
Error (w)	8.79	24	.36		
Pecking II					
Total	328.86	59			
Between cages	245.80	29			
Signal conditions	23.07	5	4.61	< 1	ns
Error (b)	222.73	24	9.28		
Within	83.28	30			
Pre-post test	42.15	1	42.15	29.53	< .001
Signal x Test	6.86	5	1.36	< 1	ns
Error (w)	34.26	24	1.43		
Dusting II					
Total	359.23	59			
Between cages	312.53	29			
Signal conditions	90.62	5	18.12	1.96	< .20
Error (b)	221.91	24	9.24		
Within	46.69	30			
Pre-post test	.54	1	.54	< 1	ns
Signal x Test	4.90	5	.98	< 1	ns
Error (w)	41.25	24	1.72		

TABLE C-2.--Continued

Source	SS	df	MS	f	p
Freeze II					
Total	228.86	59			
Between cages	79.56	29			
Signal conditions	8.47	5	1.69	< 1	ns
Error (b)	70.69	24	2.94		
Within	149.71	30			
Pre-post tests	107.68	1	107.68	76.04	< .001
Signal x Test	8.03	5	1.61	1.13	ns
Error (w)	33.99	24	1.42		
Freeze/Head II					
Total	62.28	59			
Between cages	18.45	29			
Signal conditions	2.42	5	.48	.72	ns
Error (b)	16.03	24	.67		
Within	43.82	30			
Pre-post tests	25.15	1	25.15	37.44	< .001
Signal x Test	2.54	5	.51	.76	ns
Error (w)	16.12	24	.67		
Cautious Posture II					
Total	53.79	59			
Between cages	21.26	29			
Signal conditions	6.35	5	1.27	2.04	ns
Error (b)	14.91	24	.62		
Within	32.52	30			
Pre-post tests	.03	1	.03	.02	ns
Signal x Test	1.48	5	.29	1.53	ns
Error (w)	31.01	24	1.29		

TABLE C-2.--Continued

Source	SS	df	MS	f	p
Proximity II					
Total	856.66	59			
Between cages	522.06	29			
Signal conditions	91.56	5	18.31	1.020	ns
Error (b)	430.50	24	17.94		
Within	345.78	30			
Pre-post tests	149.84	1	149.84	21.43	< .001
Signal x Test	28.10	5	5.62	.80	ns
Error (w)	167.83	24	6.99		
Locomotion II					
Total	62.61	59			
Between cages	36.89	29			
Signal conditions	3.84	5	.77	.56	ns
Error (b)	33.05	24	1.37		
Within	25.71	30			
Pre-post tests	5.88	1	5.88	7.96	< .01
Signal x Test	2.12	5	.42	.57	ns
Error (w)	17.71	24	.74		
Locomote/Contact II					
Total	34.56	59			
Between cages	28.73	29			
Signal conditions	6.38	5	1.27	1.37	ns
Error (b)	22.35	24	.93		
Within	5.82	30			
Pre-post tests	.32	1	.32	2.11	< .10
Signal x Test	1.79	5	.36	2.33	< .10
Error (w)	3.70	24	.15		

TABLE C-2.--Continued

Source	SS	df	MS	f	p
Vocalization II					
Total	829.72	59			
Between cages	675.75	29			
Signal conditions	178.63	5	35.72	1.72	< .20
Error (b)	497.12	24	20.71		
Within	153.97	30			
Pre-post tests	51.72	1	51.72	19.17	< .001
Signal x Test	37.49	5	7.49	2.78	< .05
Error (w)	64.75	24	2.69		
Gutar quiver II					
Total	17.83	59			
Between cages	14.04	29			
Signal conditions	2.23	5	.44	< 1	ns
Error (b)	11.81	24	.49		
Within	3.79	30			
Pre-post tests	.35	1	.35	3.32	< .10
Signal x Test	.90	5	.18	1.71	< .20
Error (w)	2.54	24	.10		

APPENDIX D

DATA ANALYSIS FOR STUDY II

SIX SIGNAL CONDITIONS--HABITUATION

TABLE D-1.--Table of Means and Standard Deviations (σ) for Six Signal Conditions Over Three Stimulus Trials.
Study II--Habituation Analysis

Measure Trials	Bobwhite			Chicken			Blue Jay			Rabbit			Reverse			Food Call		
	\bar{X}	(σ)		\bar{X}	(σ)		\bar{X}	(σ)		\bar{X}	(σ)		\bar{X}	(σ)		\bar{X}	(σ)	
Pecking	1 10.60	(8.65)		9.20	(3.96)		8.40	(8.02)		11.20	(5.45)		12.20	(4.15)		9.40	(4.83)	
	2 8.40	(3.91)		10.80	(3.70)		8.00	(6.96)		12.00	(7.68)		13.00	(3.32)		13.80	(5.77)	
	3 14.80	(8.38)		11.60	(4.67)		10.00	(5.79)		14.80	(8.76)		12.20	(5.89)		11.00	(6.89)	
Dusting	1 4.40	(5.22)		5.80	(4.21)		.80	(1.30)		10.00	(6.48)		8.20	(6.76)		7.20	(7.53)	
	2 4.40	(5.97)		7.60	(5.94)		4.00	(4.30)		13.20	(9.96)		10.00	(4.95)		6.80	(8.44)	
	3 5.80	(3.90)		7.20	(5.63)		4.80	(4.87)		12.40	(8.76)		12.40	(6.31)		3.00	(4.00)	
Freeze	1 34.40	(43.49)		22.00	(28.70)		12.40	(7.83)		12.00	(6.63)		19.40	(26.73)		4.00	(1.41)	
	2 19.20	(36.83)		4.80	(3.96)		4.40	(4.28)		10.40	(7.57)		8.40	(13.24)		4.60	(7.31)	
	3 5.20	(6.60)		2.40	(1.95)		5.20	(11.63)		7.40	(4.72)		2.00	(2.55)		3.40	(4.98)	
Freeze/Head	1 22.40	(33.49)		10.00	(12.47)		7.60	(3.36)		6.80	(3.27)		6.40	(7.80)		1.60	(1.40)	
	2 13.40	(26.09)		1.40	(1.52)		2.40	(2.61)		4.60	(5.36)		2.40	(5.37)		2.00	(3.08)	
	3 2.40	(3.78)		.40	(.55)		2.80	(6.26)		3.00	(2.34)		1.20	(1.30)		1.00	(2.24)	
Proximity	1 12.00	(11.11)		12.00	(11.07)		7.80	(11.14)		19.80	(7.66)		28.40	(30.15)		20.00	(9.03)	
	2 13.00	(12.75)		11.20	(10.00)		10.80	(9.09)		22.60	(7.96)		23.80	(18.83)		25.40	(5.18)	
	3 19.60	(12.89)		18.40	(12.24)		16.60	(13.50)		22.20	(3.42)		18.20	(11.14)		23.40	(9.37)	
Cautious Posture	1 5.60	(4.98)		1.00	(2.24)		3.60	(4.33)		.20	(.45)		5.20	(5.20)		2.80	(3.83)	
	2 4.40	(3.56)		.40	(.55)		3.00	(3.32)		0	0		1.60	(3.58)		1.60	(1.95)	
	3 1.60	(2.51)		.20	(.45)		2.60	(3.58)		.20	(.45)		1.80	(1.92)		1.40	(1.95)	
Locomotion	1 2.40	(1.34)		3.80	(5.54)		3.40	(2.97)		2.40	(2.30)		3.00	(2.24)		2.00	(3.39)	
	2 5.40	(5.22)		2.60	(2.97)		2.60	(1.82)		.60	(.89)		1.80	(1.30)		1.40	(.55)	
	3 3.60	(2.30)		1.60	(1.82)		2.40	(.55)		.40	(.55)		3.20	(2.39)		2.80	(3.27)	
Vocaliza- tion	1 22.60	(36.36)		25.20	(7.39)		26.00	(9.41)		6.60	(6.65)		17.20	(12.46)		16.20	(10.76)	
	2 11.80	(15.37)		20.60	(9.02)		22.40	(5.41)		4.00	(4.00)		12.40	(11.54)		15.20	(8.26)	
	3 11.20	(15.35)		19.20	(6.09)		23.40	(15.17)		3.00	(2.00)		14.00	(8.66)		17.00	(11.36)	

TABLE D-2.--Analysis of Variance for Study II: Habituation

Source	SS	df	MS	f	p
Freezing II					
Total	28119.29	89			
Between cages	15973.29	29			
Signals	2029.55	5	405.91	< 1	ns
Error (b)	13943.73	24	580.99		
Within	12146.00	60			
Trials	2669.49	2	1334.74	8.17	< .005
Signal x Trials	1633.04	10	163.30	< 1	ns
Error (w)	7843.46	48	163.40		
Freeze/Head II					
Total	11360.10	89			
Between cages	7145.76	29			
Signals	1143.83	5	228.76	< 1	ns
Error (b)	6001.93	24	250.08		
Within	4214.33	60			
Trials	830.86	2	415.43	7.29	< .005
Signal x Trials	647.80	10	64.78	1.13	ns
Error (w)	2735.66	48	56.99		
Proximity II					
Total	14611.50	89			
Between cages	10918.26	29			
Signals	1992.80	5	398.56	1.07	ns
Error (b)	8925.44	24	371.89		
Within	3693.23	60			
Trials	144.26	2	72.13	1.23	ns
Signal x Trials	740.53	10	74.05	1.26	ns
Error (w)	2808.43	48	58.51		

TABLE D-2.--Continued

Source	SS	df	MS	f	p
Cautious Posture II					
Total	955.60	89			
Between cages	604.93	29			
Signals	164.80	5	32.96	1.79	< .20
Error (b)	440.13	24	18.34		
Within	350.66	60			
Trials	49.26	2	24.63	4.59	< .025
Signal x Trials	43.93	10	4.39	< 1	
Error (w)	257.46	48	5.36		
Dusting II					
Total	3871.95	89			
Between cages	3245.95	29			
Signals	859.02	5	171.80	1.72	< .20
Error (b)	2386.93	24	99.45		
Within	626.00	60			
Trials	42.75	2	21.38	2.29	< .20
Signal x Trials	136.98	10	13.69	1.47	< .20
Error (w)	446.26	48	9.29		
Pecking II					
Total	3129.79	89			
Between cages	1960.45	29			
Signals	150.05	5	30.01	< 1	ns
Error (b)	1810.40	24	75.43		
Within	1169.33	60			
Trials	76.42	2	38.21	1.93	< .20
Signal x Trials	142.91	10	14.29	< 1	ns
Error (w)	950.00	48	19.79		

TABLE D-2.--Continued

Source	SS	df	MS	f	p
Locomotion II					
Total	642.45	89			
Between cages	363.12	29			
Signals	58.32	5	11.66	< 1	ns
Error (b)	304.80	24	12.70		
Within	279.33	60			
Trials	4.42	2	2.21	< 1	ns
Signal x Trials	56.11	10	5.61	1.23	ns
Error (w)	218.80	48	4.56		
Vocalization II					
Total	16310.00	89			
Between cages	12190.66	29			
Signals	3440.13	65	688.02	1.88	< .20
Error (b)	8750.53	24	364.60		
Within	4119.33	60			
Trials	396.86	2	198.43	2.74	< .10
Signal x Trials	250.20	10	25.02	< 1	ns
Error (w)	3472.26	48	72.34		

APPENDIX E

DATA ANALYSIS STUDY II

SIX SIGNAL CONDITIONS: FOOD CALL VS. TRIAL 1

TABLE E-1.--Table of Means and Standard Deviations (σ) Comparing Responding During the Common Food Call Versus Responding on Trial One Over Six Signal Conditions in Study II

Measure	Bobwhite		Chicken		Blue Jay		Rabbit		Reverse		Food Call	
	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)	\bar{X}	(σ)
Pecking	FC	13.40 (8.68)	8.40 (8.50)	9.40 (7.39)	15.60 (7.79)	10.40 (4.93)	14.20 (6.72)					
	Ti	10.60 (8.65)	9.20 (3.96)	8.40 (8.02)	11.20 (5.45)	12.20 (4.15)	9.40 (4.83)					
Dusting	FC	7.00 (7.58)	6.00 (4.69)	2.20 (2.17)	11.40 (9.96)	7.40 (3.57)	5.40 (3.97)					
	Ti	4.40 (5.22)	5.80 (4.20)	.80 (1.30)	10.00 (6.48)	8.20 (6.76)	7.20 (7.53)					
Freeze	FC	18.20 (33.55)	6.40 (7.26)	5.00 (9.59)	1.80 (1.79)	4.20 (4.02)	9.00 (11.87)					
	Ti	34.40 (43.49)	22.00 (29.58)	12.40 (7.83)	12.00 (6.63)	19.40 (26.72)	4.00 (1.41)					
Freeze/Head	FC	5.60 (8.23)	3.80 (2.68)	2.60 (3.78)	.80 (.84)	2.00 (1.87)	2.40 (2.60)					
	Ti	22.40 (33.49)	10.00 (12.47)	7.60 (3.36)	6.80 (3.27)	6.40 (7.79)	1.60 (1.14)					
Proximity	FC	12.00 (11.95)	10.40 (6.30)	13.40 (11.08)	16.40 (9.89)	15.80 (10.82)	19.60 (16.05)					
	Ti	12.00 (11.11)	12.00 (11.07)	7.80 (11.14)	19.80 (7.66)	28.4 (30.15)	20.00 (9.02)					
Cautious Posture	FC	1.60 (2.30)	1.40 (.89)	3.60 (3.57)	1.60 (1.51)	2.40 (2.07)	3.60 (4.09)					
	Ti	5.60 (4.98)	1.00 (2.33)	3.60 (4.33)	.20 (.44)	5.20 (6.60)	2.80 (3.83)					
Locomotion	FC	1.40 (1.51)	2.60 (3.05)	3.80 (3.19)	3.40 (2.79)	3.60 (3.79)	2.80 (1.64)					
	Ti	2.40 (1.34)	3.80 (5.54)	3.40 (2.96)	2.40 (2.30)	3.00 (2.23)	2.00 (3.39)					
Vocalization	FC	11.60 (14.67)	20.00 (3.60)	25.80 (2.77)	18.60 (5.68)	16.00 (10.98)	19.60 (9.09)					
	Ti	22.60 (36.35)	25.20 (7.39)	26.00 (9.40)	6.60 (6.65)	17.20 (12.46)	16.20 (10.75)					

TABLE E-2.--Analysis of Variation for Study II: Food Call
versus Trial 1

Source	SS	df	MS	f	p
Pecking					
Total	2452.98	59			
Between cages	1876.98	29			
Signal condition	162.68	5	32.53	< 1	ns
Error (b)	1714.30	24	71.43		
Within	576.00	30			
Test (FC vs. T1)	43.35	1	43.35	2.35	< .20
Signal x Test	90.15	5	18.03	< 1	ns
Error (w)	442.50	24	18.43		
Dusting					
Total	2100.98	59			
Between cages	1771.48	29			
Signal condition	451.68	5	90.33	1.64	ns
Error (b)	1319.80	24	54.99		
Within	329.50	30			
Test (FC vs. T1)	3.75	1	3.75	< 1	ns
Signal x Test	40.25	5	8.05	< 1	ns
Error (w)	285.50	24	11.89		
Freezing					
Total	24926.50	59			
Between cages	19517.50	29			
Signal condition	2755.70	5	551.14	< 1	ns
Error (b)	16761.80	24	698.41		
Within	5409.00	30			
Test (FC vs. T1)	1480.16	1	1480.16	11.42	< .005
Signal x Test	819.43	5	163.88	1.26	ns
Error (w)	3109.40	24	129.56		

TABLE E-2.--Continued

Source	SS	df	MS	f	p
Freezing/Head					
Total	7748.00	59			
Between cages	4974.00	29			
Signal condition	897.00	5	179.40	< 1	ns
Error (b)	4384.93	24	182.70		
Within	2774.00	30			
Test (FC vs. T1)	589.06	1	589.06	7.99	< .01
Signal x Test	415.13	5	83.02	1.12	ns
Error (w)	1769.80	24	73.74		
Proximity					
Total	8953.93	59			
Between cages	8171.93	29			
Signal condition	1234.53	5	246.90	< 1	ns
Error (b)	6937.39	24	289.06		
Within	782.00	30			
Test (FC vs. T1)	64.06	1	64.06	5.28	< .05
Signal x Test	446.93	5	89.38	7.37	< .025
Error (w)	291.00	24	12.12		
Cautious Posture					
Total	740.18	59			
Between cages	567.68	29			
Signal condition	85.68	5	17.13	< 1	ns
Error (b)	482.00	24	20.08		
Within	172.50	30			
Test (FC vs. T1)	7.35	1	7.35	1.66	ns
Signal x Test	59.15	5	11.83	2.68	< .20
Error (w)	105.99	24	4.41		

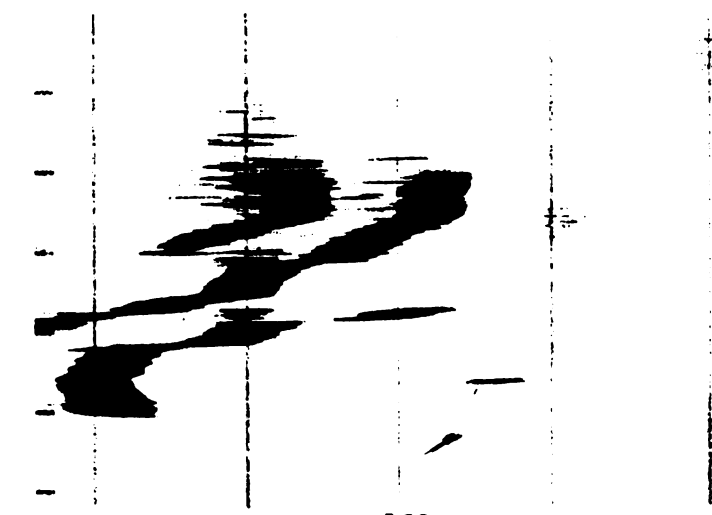
TABLE E-2.--Continued

Source	SS	df	MS	f	p
Locomotion					
Total	470.18	59			
Between cages	264.68	29			
Signal condition	19.88	5	3.97	< 1	ns
Error (b)	244.80	24	10.20		
Within	205.50	30			
Test (FC vs. T	.15	1	.15	< 1	ns
Signal	11.35	5	2.29	< 1	ns
Error (w)	193.99	24	8.08		
Vocalization					
Total	10888.18	59			
Between cages	7291.68	29			
Signal condition	1118.28	5	223.65	< 1	ns
Error (b)	6173.30	24	257.22		
Within	3596.50	30			
Test (FC vs. T	2.017	1	2.01	< 1	ns
Signal	761.08	5	152.21	1.2993	ns
Error (w)	2833.40	24	118.06		

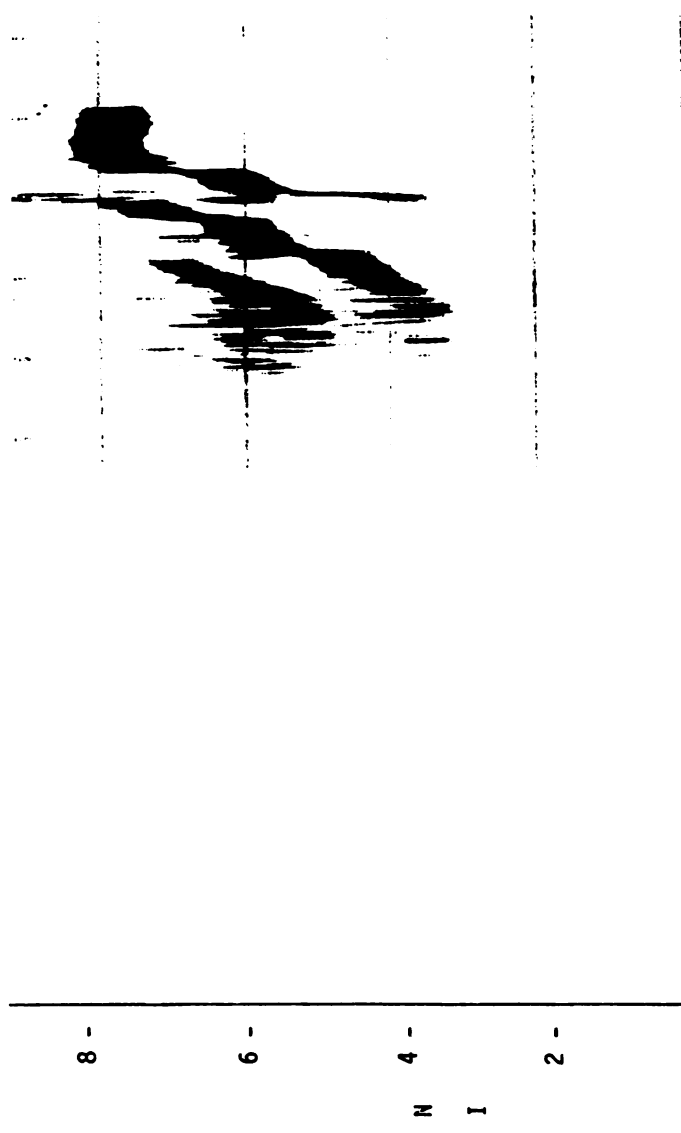
APPENDIX F

SPECTROGRAM SAMPLES OF SIGNAL STIMULI

(BROAD BAND)



Bobwhite Distress



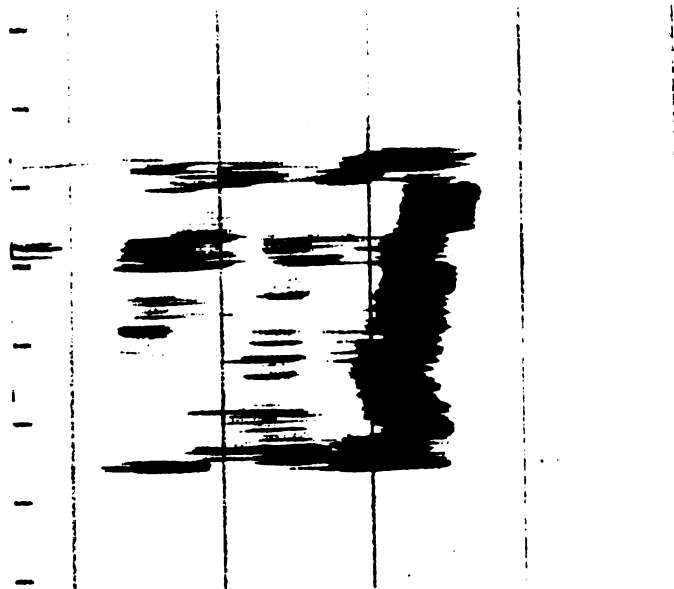
Bobwhite Reversed Distress

Milliseconds Scale

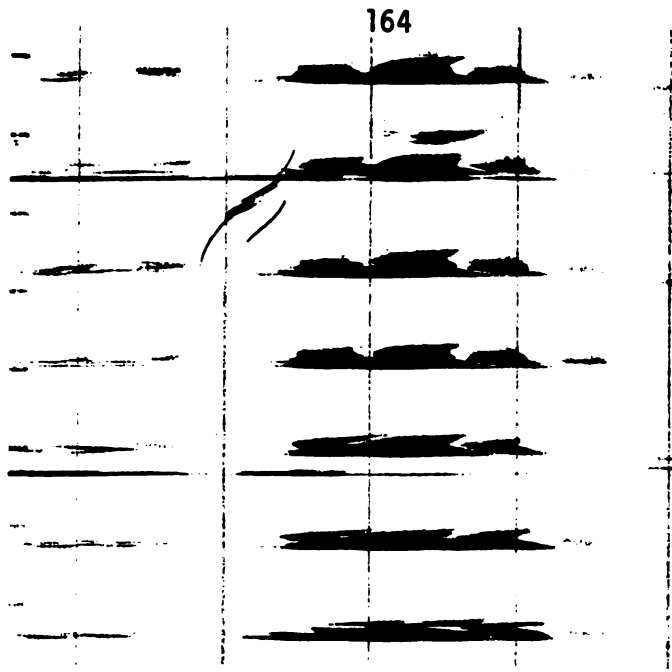
0 100 200

Time →

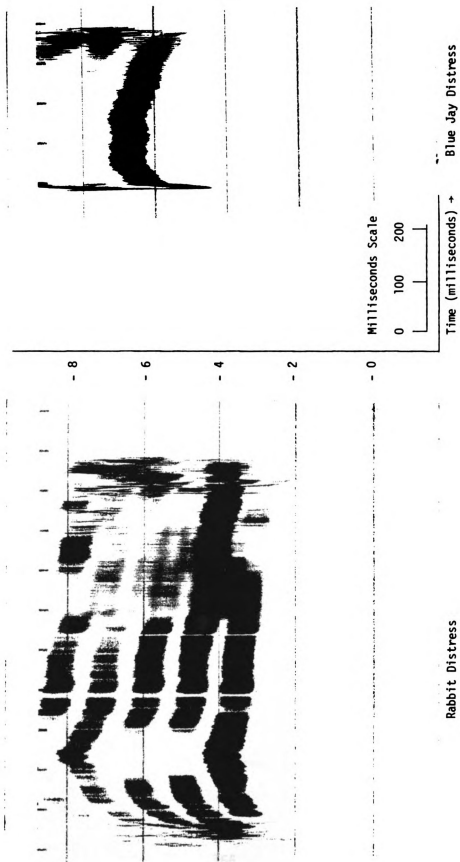
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Chicken Distress



Bobwhite Food Call



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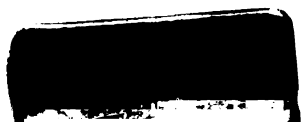
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