THE DEVELOPMENT OF FEAR DISPLAYS IN BOBWHITE QUAIL (COLINUS VIRGINIANUS)

Thesis for the Degree of M. A.

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PETER L. BORCHELT

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THESIS

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ABSTRACT

THE DEVELOPMENT OF FEAR DISPLAYS
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by

Peter L. Borchelt

The responses of animals to predators is a biologically important and behaviorally complex class of behavior. While this class of behavior has not been studied extensively in the laboratory, naturalists have long observed and described responses to predators in a wide variety of species, including birds. One conceptualization of responses to predators has been provided in the Defensive Distance model (Ratner, 1967) which states that a sequence of behaviors is emitted as a function of the distance between predator and prey. This sequence consists of freezing at long predator-prey distances, fleeing at shorter defensive distances, and fighting as the distance is reduced to zero. With prolonged predator-prey contact, the prey responds with immobility.

Data suggest that these responses function as displays which we will describe as "fear displays". Experiments and reports of observations of the development

of responses to predators (fear displays) in birds indicate the following: 1) for altricial birds (e.g., song sparrow) crouching occurs early (about 6-7 days of age) and freezing occurs about the second week as the bird develops locomotion; 2) for precocial birds (e.g., domestic chick) freezing occurs in the first few days of age (Salzen, 1962); and 3) immobility occurs in the domestic chick between 7-10 days of age (Ratner and Thompson, 1960; Salzen, 1963) at the time the bird achieves physical independence.

This information on precocial birds is from several different experiments, using a variety of strains of domesticated chickens. The present experiment was designed to trace the development of both freezing and immobility in a less domesticated precocial bird (Bobwhite quail). Four different age groups of Bobwhite quail (total N = 30) were tested for both incidence and duration of freezing and immobility. Tests were conducted in an open field apparatus. For each bird, freezing was tested first followed by the immobility test 24 hours later. Test-retest trials were conducted at additional 24 hour intervals to assess reliability. Testing ages were: Group 1, days 4-5 (retest days 6-7); Group 2, days 9-10 (11-12); Group 3, 19-20 (21-22); and Group 4, 29-30 (31-32). One-tailed Kruskal Wallis and Mann-Whitney-U tests were used.

Freezing showed a statistically significant increase

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This thesis is dedicated to my parents, to whom I owe so much.

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INTRODUCTION

Studies and observations of many species of animals have long reported responses to predators as an important class of behavior in the lives of these organisms. Aside from the morphological characteristics which have evolved to help prey elude predators (Cott, 1940), many behaviors such as freezing, fleeing, alarm calls, mobbing and other forms of attack, distraction display, and immobility have also evolved to serve this function (Denny and Ratner, 1970).

The relationship between these various responses and a predator is analyzed by Ratner (1967) in a Defensive Distance model. In general, this model describes how these responses change as the distance between the predator and the prey is reduced. At long distances, the prey freezes. At shorter distances, the prey makes escape responses, and then fights if the distance is reduced to zero. Prolonged contact (zero distance) between predator and prey results in the prey responding by immobility.

The literature that deals with immobility, variously called catelepsy, death feigning, and animal hypnosis, has been reviewed by Ratner (1967). His comparative analysis of the phenomenon concludes that: (1) the stimulus condition eliciting immobility involves restraint by some threatening or predatory stimulus condition, especially in an unfamiliar situation; (2) good preparations for the study of various aspects of immobility are identified in terms of behavior (birds), physiological processes (reptiles and rodents), and neurological processes (higher invertebrates and rodents); and (3) the response is "conceptualized as a terminal reaction in a sequence that occurs as a function of changes in the defensive distance between the threatening stimulus and the test animal" (Ratner, 1967).

A number of zoologists have discussed the adaptive significance of responses to predators. Kruuk (1964) offers an excellent description of the adaptive value of fleeing and attack as responses to different predators in the black-headed gull. He shows how attack serves to protect the brood from one type of predator and how fleeing (and "formation flight") serve to protect the adult from another.

The adaptive value of immobility was perhaps first discussed by Darwin (1900) when he called immobility "death feigning". This interpretation has often been misinterpreted by implying some need for cognition on the part of the immobile animal, but the concept of death feigning viewed as a description receives support from numerous field observations, such as those reported by Armstrong (1965), Harrison (1966), and Andrews (1956).

Harrison (1966), for example, discusses the inactivity of one bird as inhibiting attack on the part of another. Andrews (1956, p. 129) suggests that "many of the resting attitudes given during fear seem to prevent superiors from attacking . . . the birds' reduced activity seems to be of most importance in preventing attack. It no longer attracts the attention of others by moving about, and does not flee (and so give the maximal stimulus for attack) when approached." Armstrong (1965, p. 92) states that "cataleptism is dysgenic so far as the race is concerned, if associated with incubation, but has survival value for the individual in many instances when no other means of escape remains." Immobility can thus be considered as a consummatory response which serves to inhibit attack on the part of the predator.

This specific function of immobility, namely as a "last resort" response to inhibit attack, further suggests that it functions as a display or signal. Lorenz (1937) described the signaling function as a releaser and used the concept when he called an animal a "companion" when it "released" instinctive behavior in a fellow member of its species, either by bodily characteristics or by some particular behavior. Tinbergen (1939) later suggested the more general term <u>signal</u> for "releaser". Joost Ter Pelkwyk, in a letter to M. M. Nice (1943, pp. 10-11), wrote that "signals are not confined to interrelations between the individuals of one species only, but occur also between individuals of different species which influence each other in nature (predator and prey)." Many ethologists (e.g., Van Tets (1965)) use the term display to refer to behavioral signals that communicate information, that is, lead to some reliable change or lack of change in behavior in another organism.

Freezing also functions as a display, but in a different way. Here the signals take place between two or more prey animals, not between predator and prey. When one member of a group of animals freezes in response to an approaching predator, other members of the group may freeze in response to the first animal. For example, Marler (1956), in describing the behavior of the chaffinch (*Fringilla coelebs*), states that the freezing response "is also given by birds which do not perceive the initial stimulus themselves, on seeing or hearing others responding."

Most naturalistic studies of responses to predators call any or all of these responses by the general label of fear responses. Using a single concept such as fear to cover a large number of types of behaviors with a wide variety of species ranging from invertebrates to man makes experimental analysis of responses to predators difficult. However, because of the use of the term fear responses to describe observations of many species of animals responses to predators, because of the literature relating immobility and freezing to fear, and because of the previously described signal function of both immobility and freezing, the term <u>fear displays</u> might best describe these two components of responses to predators. The term fear displays is used analogously to the term courtship displays. In both cases, the behaviors involve a sequence of components which function as signals.

Many researchers investigating responses to predators have been interested in the development of these various responses. Observational studies have usually looked at the development of fear responses along with the general development of the animal studied. There are few experimental studies which have investigated the development of responses to predators, although many studies have discussed the development of fear in relation to other behaviors or processes, for instance, imprinting (Salzen, 1962; Sluckin, 1965).

This information has been largely derived from studies of birds, animals which Ratner (1967) identified as good preparations for behavioral studies of immobility. Most of this information about responses to predators in birds has come from observations of altricial birds. The slower rate of development in altricial birds is advantageous for looking at the development of behavior, but only recently (Lanyon and Lanyon, 1969) have effective methods been devised for rearing altricial birds in the laboratory. Precocial birds (especially galliformes, including turkey, chicken, and quail) are generally excellent laboratory animals, but surprisingly few studies have specifically investigated the development of their responses to predators.

In view of the above, some method is necessary to compare the development of responses to predators in altricial and precocial birds. Nice (1962) has formulated a schema for comparing the appearance of basic motor coordinations in the behavioral development of precocial, semi-precocial, and altricial birds (Table 1). She divides the development of behavior into five stages. Stage 1 (not included in Table 1) is the Post-Embryonic. This stage covers the first four days post-hatch in altricial birds and the behavioral coordinations present are limited to those concerned with nutrition. In Stages II (Preliminary) and III (Transition), locomotion and care of the plumage begin to develop. In Stage IV, the first response to predators, crouching, develops. Stage IV (Locomotory) involves the development of nest leaving, and freezing and fleeing as responses to predators. Finally, in Stage V (Socialization) flying and aggression (fighting) develop.

Table 2 shows the age at which some responses to predators develop in each of these stages for altricial birds studied by Nice (1943) and Rand (1941). The general pattern of development shows cowering or crouching in the

Table 1. Stages of appearance of basic motor coordinations in precocial, semi-precocial, and altricial birds (from Nice, 1962)

	Stage	All species	Precocials and Semi-precocials	Altricials
II	Preliminary	Yawning Preeming Standing on tarsi	Scratching head	
III	Transition	Crouching Stretching legs and wings Fanning wings Shaking self Standing on feet	Exploratory pecking	Scratching head
IV	Locomotory	Leaving nest Fleeing Picking up food Simple bathing	Play-fleeing (shorebirds, rails)	Exploratory pecking
V	Socialization	Aggression Matured bathing Flight	Play-fleeing (megapodes, ducks, White Rocks)	Play-fleeing

Table 2. Development of responses to predators in some altricial birds

	Stages			
	II (Preliminary	III (Transition)	IV (Locomotory)	V (Socialization)
Curve-billed thrasher Rand (1941)	Standing 4th day	Freezing 5-6th day Crouching 7-8th day	Escape from nest 17-18th day	Flight 25th day
Song Sparrow Nice (1943)		Cowering/crouching 6½-7 days	Leaves nest 8-11 days Flutter to escape 12-14 days	Flight 17 days Freezing 18-20 days Fighting and fear calls 19-22 days
Catbird (Nice (1943)		Cowering/crouching 6th day	Leaves nest 10-11 days Fight and fear call 13-14 days	
Redstart Nice (1943)		Cowering/crouching 9 days	Leaves nest 13-15 days Freeze 14th day	Flight 19-20 days Escape 18 days

transition stage at 5-9 days, although freezing may occur in some species. In the locomotory stage, between 8-18 days, again depending on the species, escape, fear calls, freezing, and perhaps fighting develop. By the socialization stage, between 16 and 25 days, flight has developed and fighting and fear calls become evident.

Table 3 presents the same type of analysis for precocial birds. It can be seen that Stage IV is reached in the first couple of days in domestic chickens and in 3-5 days by the oystercatcher. Responses to predators in, and prior to, this stage are crouching (with and without distress calls) and fleeing. Dewar (1920) observed that immobility in oystercatchers develops during the second week. Experiments by Ratner and Thompson (1960) and Salzen (1963) determined that the onset of immobility in domestic chickens occurred at 7-10 days. Collias (1952) states that distress calls can be heard in the newly hatched chick, and the frequency of distress calling declines with age.

Salzen (1962) discussed the development of fear in relation to imprinting. He stated that the answer to the question at what age fear develops depends on how fear is defined. If distress calls define fear, then fear is shown from hatching onwards (Collias, 1952). If flight (escape) or avoidance defines fear, then it develops sometime after the first day (Hess, 1959; Salzen, 1962).

Table 3. Development of responses to predators in some precocial birds

	Stages			
	II (Preliminary)	III (Transition)	IV (Locomotory)	V (Socialization)
Oystercatcher Dewar (1920)	Crouching (short duration)	Crouching	Crouching 3-5 days (long duration)	Immobility (inverted crouching) 7-14 days Fleeing 20-30 days Flight 5th week
Domestic Chicken Ratner & Thompson (1960) and Salzen (1963)				Immobility 7-10 days
Ratner (1965)				Aggression 10-18 days
Nice (1962)			Running 1½-2 days	Flight 10-11 days
Salzen (1962)	Passive "fear" (crouch plus distress call)- decreases with age (1-7 days) Freezing (crouch without distress call)- increases with age (1-7 days)			
Collias (1952)	Distress calls (when animal cooled)- immediately after hatching; (when isolated)- reduction in calling with age			

Continued

Table 3 continued

	Stages			
	II (Preliminary)	III (Transition)	IV (Locomotory)	V (Socialization)
Bruckner (1933)			"Fear" of loud noise less than 7 days "Fear" of rabbit in hen-brooded group - less than 7 days	"Fear" of rabbit in artificially-brooded group - 2-4 weeks

If freezing (crouch plus no distress calls) defines fear, then it occurs early and increases with age. Salzen's data (1962, p. 204, Table 3) shows that the percentage of domestic chicks freezing when placed alone in an imprinting run increases from 32 percent at 0-1 days of age to 42 percent at 3-4 days of age to 75 percent at 7 days of age. He also stated that the occurrence of fear responses in his experiments is more a function of the test situation than the age of the bird.

In general, then, the developmental sequence of responses to predators involves crouching during the first few days with immobility occurring during the stage of socialization. Salzen's (1962) study shows freezing (including crouching) to occur early and increase with age (up to the beginning of the age of socialization in domestic chickens). If the sequence of responses to predators develops in approximately the same order in altricial and precocial birds, then freezing should occur sometime between the locomotor and socialization stages in precocial birds.

An especially good preparation for studying freezing is the Bobwhite quail (Colinus virginianus). Stoddard (1931, p. 58) goes so far as to say that, while many birds and mammals freeze, "no creatures known to us have it more highly developed, or use it more effectively than do the bobwhites." Stoddard also discusses the obvious survival value of freezing for the Bobwhite in that freezing not only takes advantage of their coloration to make them blend into the slightest cover, but also that tight compression of the plumage which accompanies freezing reduces their characteristic scent.

Stoddard's (1931) observations show that Bobwhite chicks leave the nest (Stage IV) as early as 4-5 hours, but certainly within the first day. If disturbed in or around the nest, they flee for cover and give distress calls. At about two weeks of age they begin to fly (flush) when disturbed. Stokes (1967) found running to cover when the defensive distance is great and escape (flushing) when the defensive distance is much reduced as the main responses to predators in the adult Bobwhite. Responses to avian predators consisted of giving the "errk" call and freezing or crouching. Chicks (of undetermined age) respond to the "errk" call by freezing, and 1 day old chicks freeze or run to cover to a high-pitched squeek.

Unpublished experiments in our laboratory have shown that the adult Bobwhite quail responds to handling by a human predator with the immobility component of the fear display. Although no developmental studies of responses to predators have been conducted, pilot work suggests that freezing develops before immobility, and that there is a general decrease in distress calling and locomotion with age.

Statement of Problem

The developmental sequence of responses to predators in birds seems to involve crouching in the first few days, followed by freezing, and then immobility as the stage of Socialization is reached. Distress calls are given from hatching on and decrease in frequency with age. The present experiment is designed to trace the development of two components of fear display (freezing and immobility) in the Bobwhite quail. The percentage of birds showing these two responses and the duration of these responses will be determined in four different age groups. Both of these responses to predators will be tested under similar experimental conditions, and measures will be made of both locomotion and distress calls in the experimental situation.

Responses and Operational Definitions

Freezing: Some general descriptions of freezing are as follows: Armstrong (1955) describes freezing in the wren as squatting (crouching), watching, and remaining immobile. Andrew (1956, p. 126) says that while freezing "a bird is quite motionless", except for head and eye movements, and "may freeze in a normal perching attitude" or may crouch. Marler (1956) describes seven components of freezing in the chaffinch. The first four--complete immobility, horizontal body, flexed legs, and lowered head--describe crouching. Other components are sleeked feathers, concealed wing flashes, and bulging eyes (exophalmous). These descriptions of freezing were all made from observations of adult altricial birds.

Stoddard (1931, pp. 57-58) says that when adult Bobwhite quail (precocial birds) freeze, they "squat and remain absolutely motionless with tightly compressed plumage." He also mentions exophalmous as a component of freezing. A description of freezing in young precocial birds is provided by Salzen (1962) who described freezing in domestic chicks in relation to imprinting studies. He describes freezing as both the lack of locomotion (usually involving crouching) and the lack of distress calls. He differentiates freezing from "active fear" (involving jumping, walking, running, and searching) and "passive fear" which involves inactivity, but includes distress calling.

The problem of operationally defining freezing is a real one. First, most descriptions of freezing are from observations of adult birds. Secondly, in imprinting studies which observe young chicks, the type of response seen is very much a function of the test situation. The general component that runs through descriptions of adult birds is lack of locomotion. Freezing in Salzen's (1962) imprinting studies included this aspect plus the lack of distress calls. Based on the above descriptions, plus observations of Bobwhite chicks in pilot studies, an operational definition of freezing can be stated for this study. Freezing is both the lack of locomotion and the absence of distress calling. This is differentiated from locomotion with or without distress calls, and inactivity with distress calls, neither of which are considered as freezing.

Immobility: Operational definitions of immobility as used in most past studies are consistent in that the response is elicited by rapid inversion and restraint of the animal (Ratner, 1967). The usual length of restraint is 15 seconds for studies involving birds.

METHOD

Subjects

Four hundred and fifty-seven Bobwhite quail (*Colinus virginianus*) eggs from the seven year old Michigan State University Poultry Science quail colony were incubated. Of the 325 that hatched, 64 chicks were selected from the middle of the hatching distribution so that 16 *S*s were assigned to each of four groups. All *S*s in each group hatched within 2-4 hours of the other *S*s in that group. Each *S* was weighed and banded within 2 hours of hatching. A total of 34 *S*s were eliminated from the study: 10 *S*s died; 24 *S*s either could not be caught for testing, were severely pecked, or were eliminated due to procedural errors (i.e., being dropped on the floor prior to testing). Thus, the number of *S*s used in each group was: group 1, N = 8; group 2, N = 9; group 3, N = 6; group 4, N = 7.

Apparatus

Briefly, the birds were housed in cages designed so that an *S* could be removed from the cage and replaced without disturbing the other *S*s. The four cages, each 970 x 450 x 325 mm, were located in a room 4.71 x 2.82 x 2.73 m.

Each cage was constructed as follows: the floor and back was 6 mm wire and the sides and top were 10 mm thick unpainted plywood. Water was available at the rear from a 75 mm diameter metal trough. At the front were fastened five removable 150 mm square plywood food boxes with 6 mm wire floor and front. On the front of each food box was a 180 gm. paper cup for holding food (Michigan State University Quail Breeder, King Milling Company). Masonite sliding doors, each approximately 150 x 300 mm, could be slid between the cage and the food box to trap an S.

A 400 x 220 mm 2-coil electric heater was suspended at one end of each cage and provided a temperature gradient from 42-42.5°C to about 30°C. Each heater could be raised or lowered to further regulate temperature as necessary. A 450 mm long 15 watt warm white incadescent light providing continuous lighting was hung from the center of the top with a metal light shield about 30-50 mm below it. Light levels between cages were approximately equal and ranged within each cage from approximately 32 to about 430 lux.

Subjects were tested in an adjacent room 2.48 x 2.10 x 2.48 m. Tests were conducted in a 900 x 900 mm open field apparatus (OFA) with 150 mm squares marked on the floor. The floor of the OFA was 6 mm unpainted plywood and the side was a 300 mm high piece of 12 mm wire forming a circle with a diameter of 900 mm. The OFA was placed on a table 740 mm high. The light level on the floor of the

OFA was approximately 80 lux. The temperature in the testing room was 27.5°C ± .5°C.

A 150 x 300 mm piece of masonite (cover) was used to cover the open end of the food box as it was carried to and from the testing room. Data were recorded by hand on data sheets and a stopwatch was used for timing.

Procedure

The procedure for testing each S was as follows: 2-3 hours before testing, the sliding doors on the appropriate cage were lowered so that Ss could not feed. At the start of testing E opened one or two of the sliding doors and trapped one S in the food box. The food cup was removed, the food box carefully unfastened from the cage, the cover slipped behind the food box, and the food box carried approximately 3-4 m to the testing room. After closing the testing room door, E administered one of the two tests described below.

At the completion of testing, E picked up S, carefully placed S in the food box, placed the cover on the back ofthe food box, and carried the food box to the cage. The food box was replaced on the cage, the cover removed, the sliding door raised to release S, and the food box fastened with the food cup in place. This procedure was repeated until as many Ss as possible in that group had been caught and tested.

The procedure for testing freezing (Fr test) was as follows: upon entering the testing room, E positioned the food box about 10-50 mm above the center of the OFA and removed the cover so S could escape; if S did not immediately leave the food box, the food box was tilted or shaken slightly until S left (at no time was S touched). When S touched the floor of the OFA, E started counting five seconds while slowly removing the food box and placing it on a table behind E. At the end of the five second count, E started the stopwatch and recorded the time taken for S to step with both feet out of the square in which it was standing (measure of duration of freezing), and number of squares traversed and number of distress calls per minute for a minimum of five minutes. E stood about 1 m, and in full view of, the S.

The procedure for testing immobility (Im test) was as follows: upon entering the testing room, E removed the cover while reaching into the food box. The S was loosely grabbed, the food box set on a table behind E, and S positioned on its back in the middle of the OFA. The E restrained S in this position (legs free, lightly restrained) for 15 seconds and then slowly released his hands. The E counted five seconds from the release of S, then started the stopwatch and recorded duration of immobility and squares traversed and distress calls per minutes for a minimum of five minutes. E stood about 1 m from, and in full view of, the S. Duration of immobility was scored as the time from the start of the stopwatch until S righted itself. The number of squares traversed on both tests was measured by counting the number of squares entered with both feet. In the older age groups, some Ss hopped or fluttered across several squares at a time. In these cases, the number of squares between the start and end of the hop was counted. The number of distress calls on both tests was measured by counting the number of vocalizations described by Stoddard (1931) as t-s-i-e-u- calls and by Stokes (1967) as c-i-e-w calls.

The Fr test was given first to all groups followed by the Im test approximately 24 hours later. To assess reliability of results, the test sequence was repeated 24 hours later; thus, each S was tested twice on both tests. The only difference between groups was age at first test. The testing ages for each group were: Group 1, days 4 and 5 (retest days 6 and 7); Group 2, days 9 and 10 (retest 11 and 12); Group 3, days 19 and 20 (retest 21 and 22); and Group 4, days 29 and 30 (retest 31 and 32). After the last test, each S was weighed.

RESULTS

The results will be presented in three sections. The first section will present duration of response and percentages of Ss responding on each test. The second section will consider reliability of and relations between freezing and immobility. The third section will present the results of the other measures recorded. One-tailed Kruskal-Wallis and Mann Whitney U-Tests (Siegel, 1956) were used for all computations since all differences were in the expected direction.

Freezing and Immobility

Duration. The median duration in seconds of freezing and immobility on the first test for each group is shown in Figure 1. Median duration of freezing was zero at both days 4 and 9, while median duration of immobility was also zero at days 5 and 10. However, by day 19 median duration of freezing increased to four seconds and by day 29 further increased to seven seconds. Duration of immobility increased to 58 seconds by day 20 and further increased to 67 seconds by day 30.

A Kruskal-Wallis Test on duration of freezing and immobility scores in groups 2, 3, and 4 revealed overall

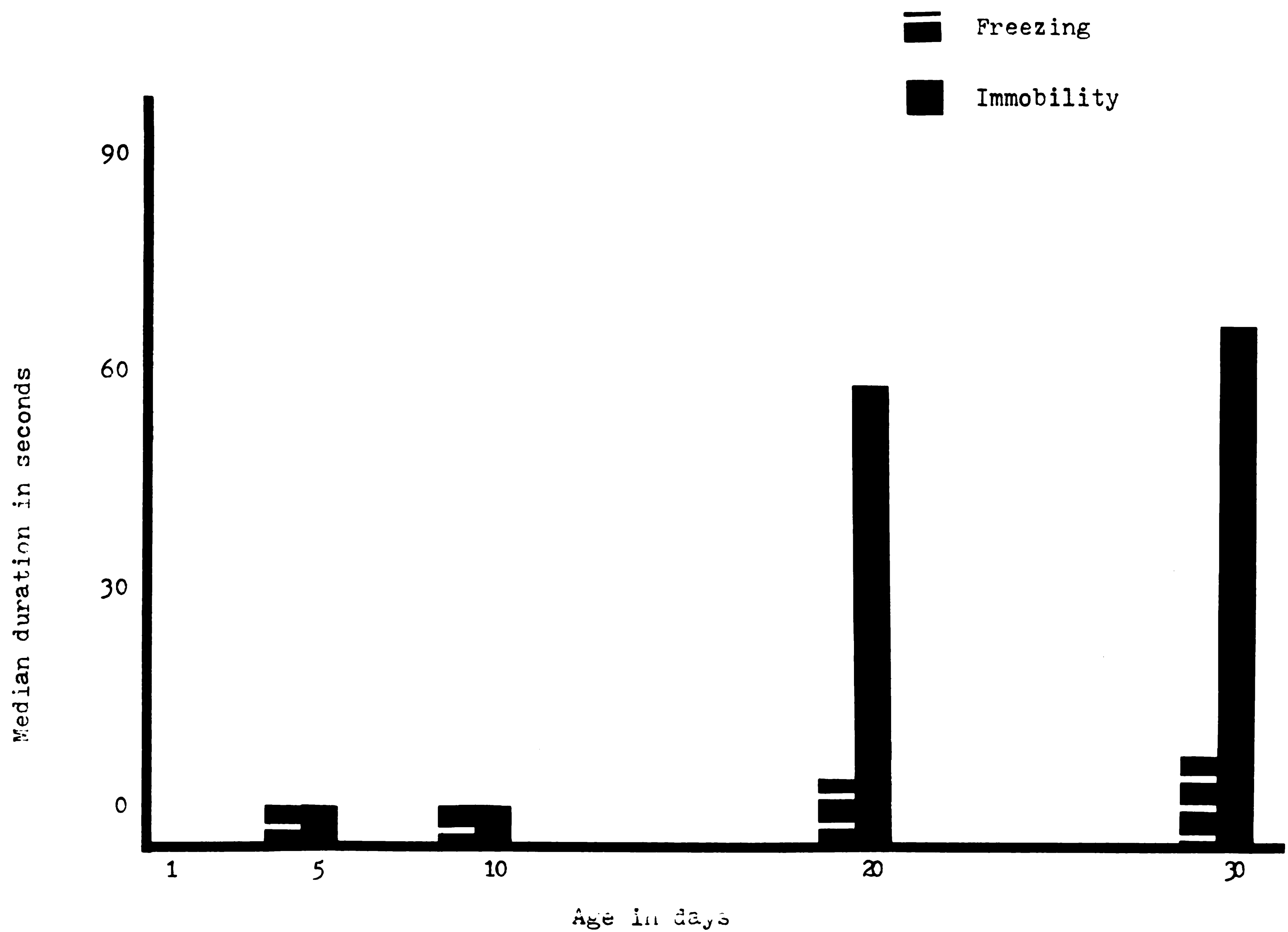

Figure 1. Median duration of freezing and immobility in each age group.

differences between age groups to be statistically significant at $p < .001$. Group 1 was excluded from the analysis because of the large number of zero scores.

Differences between individual age groups in median durations of both freezing and immobility were determined by Mann-Whitney U-Tests. A statistically significant increase in duration of freezing occurred between days 9 and 29 ($p = .05$). A statistically significant increase in duration of immobility occurred between days 10 and 20 ($p = .025$) and between days 10 and 30 ($p = .01$).

Thus, Figure 1 reveals that freezing (as indicated by group median durations in this experimental situation) began to occur somewhere between 9 and 19 days of age, but the increase did not become statistically significant until sometime between 19 and 29 days of age. Immobility, however, (as indicated by group median durations in this experimental situation) occurs reliably between 10 and 20 days of age. Both freezing and immobility continue to increase in duration at least to 30 days of age.

Percentage of Ss responding. Figure 2 shows the percentage of *S*s in each age group responding on the first Fr and Im tests. Inspection of the figure reveals a steady increase in percentages of *S*s responding from 12.5% (1/8) for both the Fr and Im tests in group 1, to 44.4% (4/9) and 22.2% (2/9) on the Fr and Im tests, respectively, in group 2, to 83.3% (5/6) on both the Fr and Im tests in

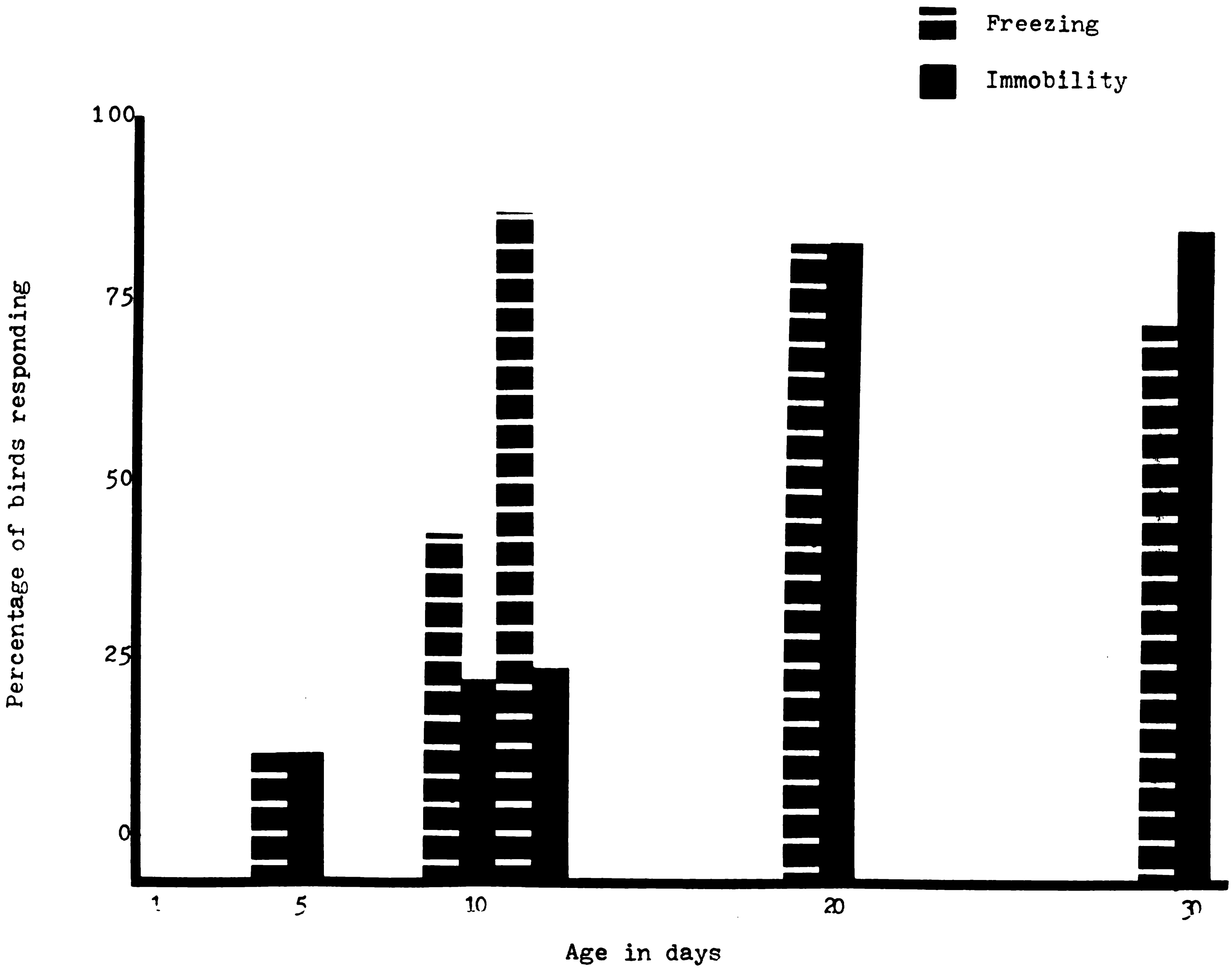

Figure 2. Percentage of birds responding in each group.

group 3. In group 4, the percentage responding on the Fr test drops slightly to 71.4% (5/7) while percentage responding on the Im test increases slightly to 85.7% (6/7).

The measure of duration of freezing and immobility gives no indication that freezing occurs before immobility, while the measure of the percentage of birds responding does. This difference in percentage of birds responding on the Fr and Im tests in group 2 was tested with the Sign Test (Siegel, 1956). A response on Fr test and no response on Im test was scored as +; no response on Fr test and response on Im test was scored as -; tied responses were eliminated. The difference was not statistically significant ($p = .25$, $N = 4$). The percentage of birds responding on the Fr and Im retests in group 2 is also shown in Figure 2. The percentage responding was 85.7% (6/7) on the Fr re-test and 28.6% (2/7) on the Im re-test. This difference was also tested with the Sign Test (longer duration on Fr than Im retest was scored as +; longer duration on Im than Fr retest was scored as -; tied responses eliminated) and was not statistically significant ($p = .109$, $N = 6$). While the Sign Tests yielded no significant differences in percentage responding on the Fr and Im test and retest in group 2, considering the low number of Ss (eliminating ties) in the analysis allows for the tentative suggestion that freezing does develop before immobility in this experimental situation.

Reliability of and relations between freezing and immobility

The rank order correlation coefficients showing reliability of freezing and immobility and the rank order correlation coefficients between freezing and immobility are presented in Table 4. Reliability of freezing and immobility durations in group 1 and reliability of immobility durations in group 2 could not be determined because of the large number of zero scores. Rank correlations between freezing and immobility in groups 1 and 2 could not be determined because of the large number of zero scores. Reliability of immobility in group 3 was not determined because all the retest scores in this group were excluded from calculations due to an apparatus failure.

The only correlation coefficient that was statistically significant for either freezing or immobility in groups 2, 3, and 4 was freezing in group 2 ($\rho = .82$, $p < .05$). The rank correlation coefficients between freezing and immobility in groups 3 and 4 were not statistically significant. Due to the number of correlation coefficients computed, the significant reliability of freezing in group 2 will not be interpreted.

Other measures recorded

Vocalizations. The median number of distress calls given in the first minute after freezing and in the first minute after immobility is shown in Figure 3 and can be

Table 4. Correlation coefficients on test-retest scores and correlations between test scores

Group	Freezing	Immobility	Freezing/Immobility
1	*	*	*
2	.82**	*	*
3	.07	***	-.78
4	-.18	-.60	-.04

* Not computed due to large number of zeroes
** $p < .05$
*** equipment failure

seen to decrease with age. A Kruskal-Wallis Test indicated the decrease on both tests to be statistically significant at $p < .001$. Mann-Whitney U-Tests between individual age groups showed a statistically significant decrease in number of vocalizations in the first minute after freezing between groups 1 and 3 ($p = .012$). The decrease in number of vocalizations between groups 1 and 4 approached significance ($p = .133$). The number of Ss in group 4 was only 3 because at this age some Ss make another response (see Escape, below).

Mann-Whitney U-Tests between age groups showed statistically significant decreases in number of vocalizations in the first minute after immobility between groups 1 and 4 ($p = .014$) and between groups 2 and 4 ($p < .01$).

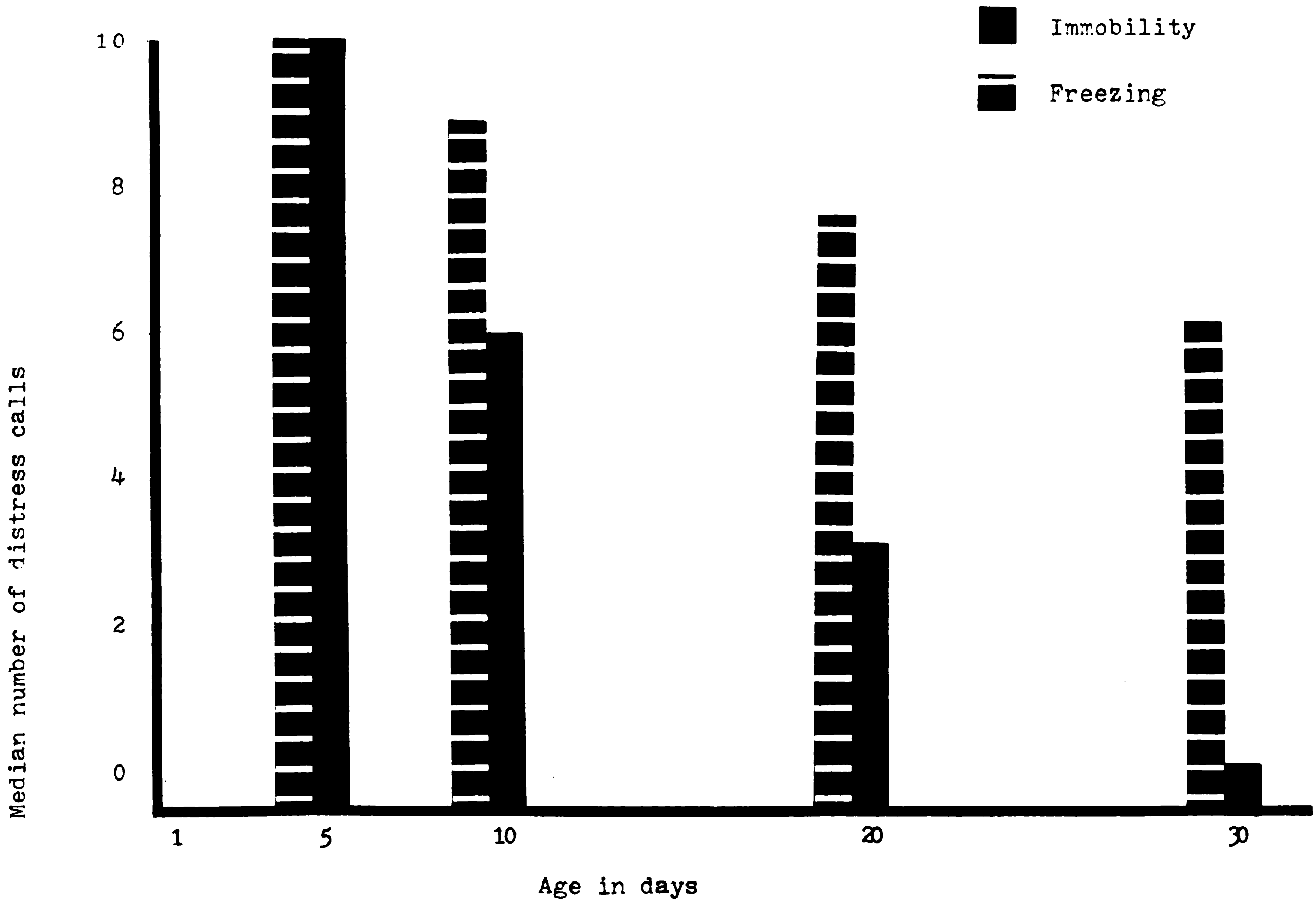

Figure 3. Median number of distress calls in each age group in the first minute after cessation of freezing and immobility.

The only within group difference between vocalizations in the first minute after freezing and immobility was in group 2 ($p = .05$) although the difference in group 4 approached significance ($p = .075$).

Figure 3 clearly shows the trend of decreasing number of vocalizations with age after freezing and immobility and also indicates that, from 10 to 30 days of age, there are fewer vocalizations after immobility than after freezing, even though the only statistically significant within group difference is in group 2.

Squares traversed. A trend similar to the reduction in vocalizations is indicated in Figure 4 which shows the median number of squares traversed in the first minute after freezing and in the first minute after immobility in all age groups. The Kruskal-Wallis Test on these data showed statistically significant overall differences at $p < .001$.

Mann-Whitney U-Tests on squares traversed in the first minute after freezing showed statistically significant decreases between groups 1 and 4 and groups 2 and 4 ($p < .001$) and between groups 3 and 4 ($p = .02$). Mann-Whitney U-Tests on squares traversed in the first minute after immobility showed no significant differences between any two individual age groups.

The differences within groups between squares traversed after freezing and squares traversed after

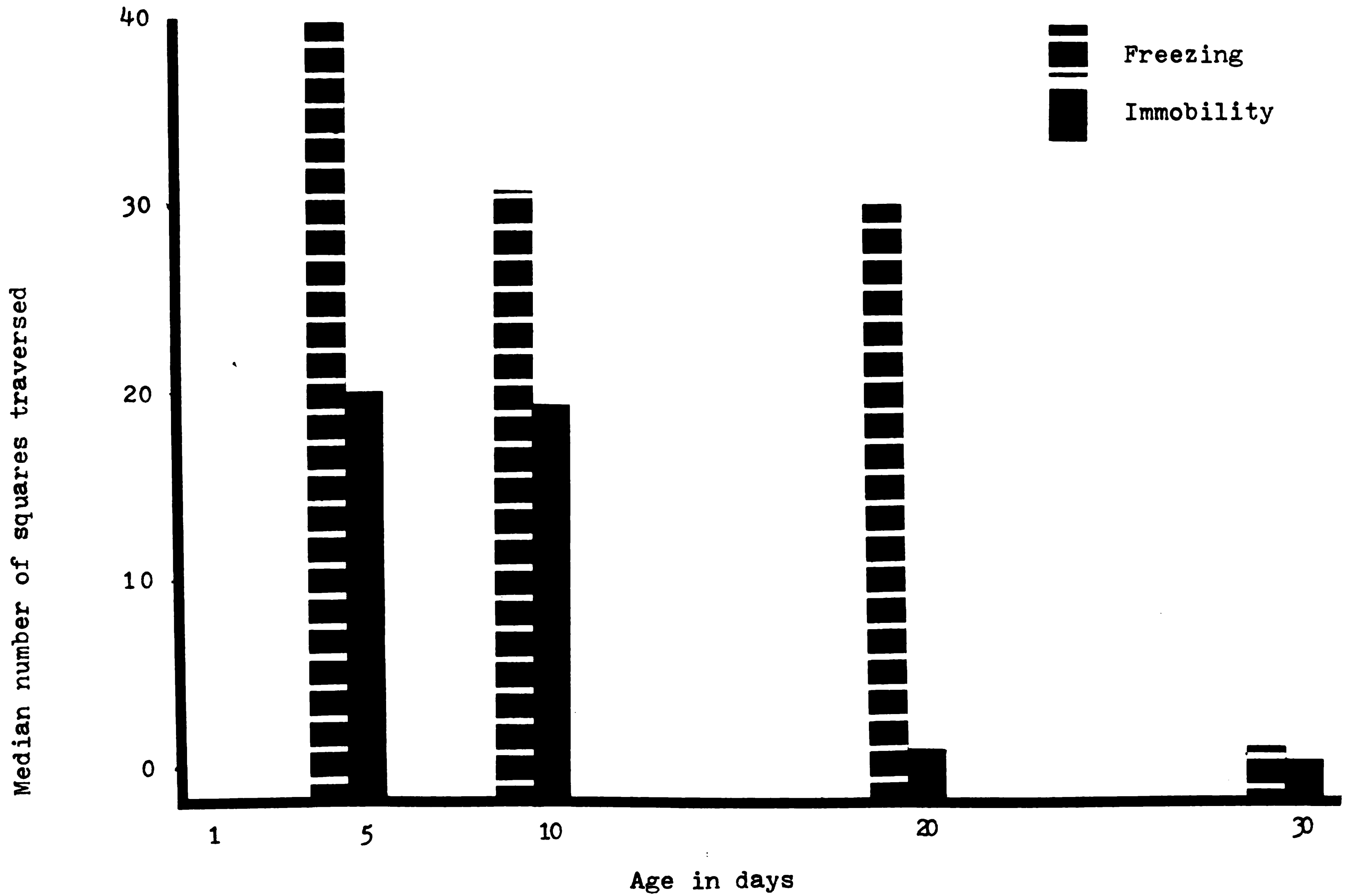

Figure 4. Median number of squares traversed in each age group in the first minute after cessation of freezing and immobility.

immobility are significant in group 1 ($p = .025$) and group 2 ($p = .05$) and approach significance in group 3 ($p = .086$). That is, Ss move more after freezing than after immobility in these groups.

Relations between vocalizations and squares traversed

Table 5 presents rank correlation coefficients computed between vocalizations and squares traversed in the first minute after both freezing and immobility for all age groups. The correlations between vocalizations and squares traversed after freezing in group 4 and after immobility in groups 3 and 4 were not determined due to a large number of zero scores. None of the coefficients were statistically significant.

Table 5. Correlation coefficients between vocalizations and squares traversed on both tests

Group	Freezing Vocalizations/ Squares traversed	Immobility Vocalizations/ Squares traversed
1	-.15	.61
2	.13	.18
3	-.25	*
4	*	*

* Not computed due to large number of zeroes.

Escapes. In groups 3 and 4, the squares traversed measure was confounded by an increase with age in the number of Ss escaping out of the OFA in the first minute after freezing and immobility. These data are shown in Figure 5 which reveals that no Ss escaped in the first minute after either freezing or immobility in groups 1 and 2. In group 3, 33.3% (2/6) escaped in the first minute after freezing while no Ss escaped in the first minute after immobility. In group 4, 57.1% (4/7) of the Ss escaped in the first minute after freezing, while only 14% (1/7) escaped in the first minute after immobility. The reliability of escapes could not be determined in groups 3 and 4 due to the small number of Ss.

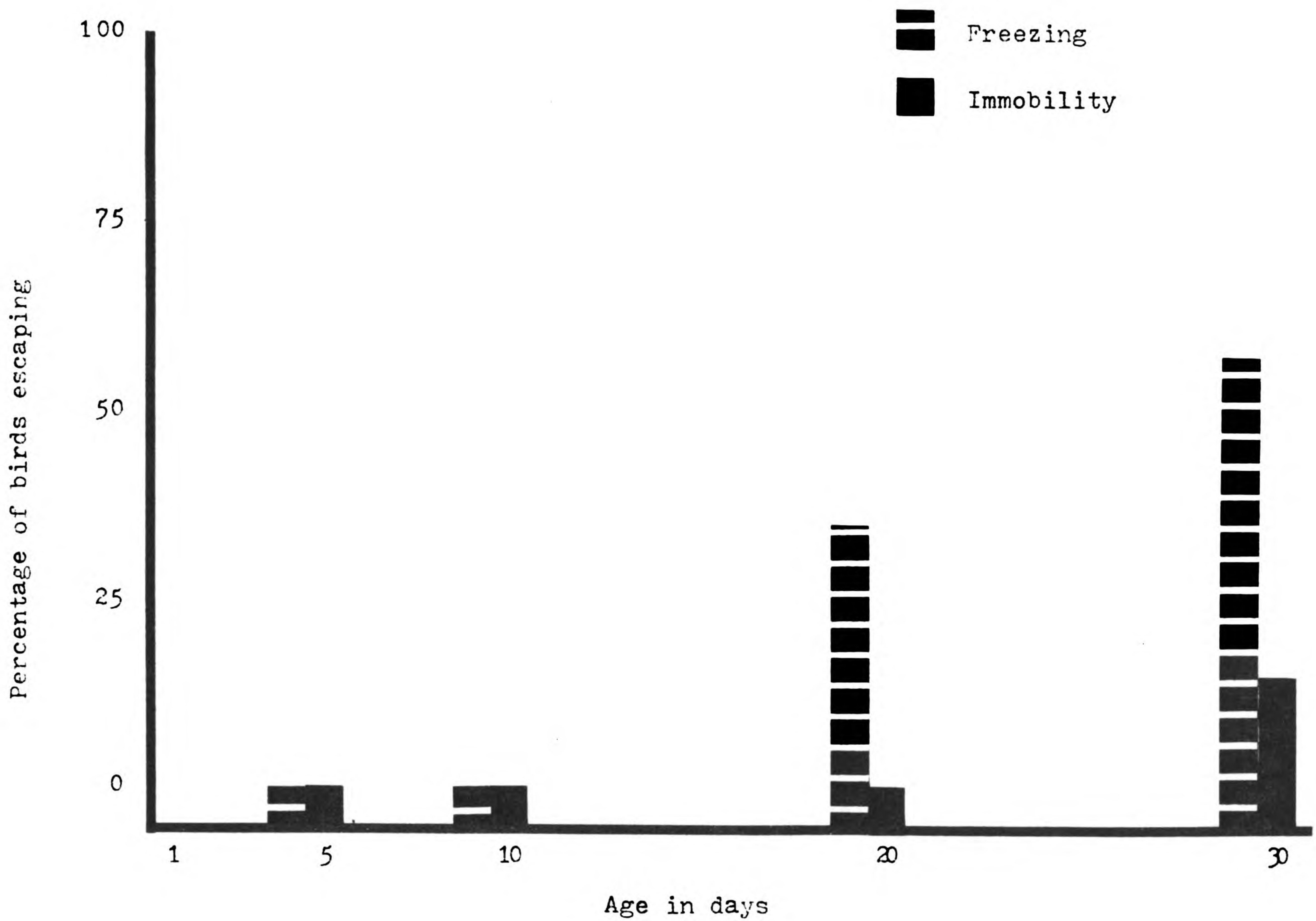

Figure 5. Percentage of birds in each age group escaping in the first minute after cessation of freezing and immobility.

DISCUSSION

The results of this experiment indicate that, for the Bobwhite quail, two components of the fear display appear at different ages. Freezing occurs between 5 and 10 days and immobility occurs between 10 and 20 days. Between 5 and 30 days there is a complex relation between components of fear display and distress calls and locomotion. Between 10 and 30 days there is an increase in escaping.

These results will be considered in terms of two general processes, namely, the developmental sequence of responses to predators in birds, and the effect of defensive distance on responses to predators.

Nice (1943, p. 53) discusses the association between the appearance of fear reactions in altricial birds and the development of physical independence. Leaving the nest first appears in the transition stage, at which time cowering or crouching occurs. There is little or no experimental research on the age at which crouching occurs in galliformes, but the response should occur during the first few days as in other precocial birds. During the locomotory stage, escape or fleeing occurs, and in this stage there is the most locomotion in the Bobwhite (Figure 4). Nice (1943) mentions freezing as also occurring in this stage. Salzen (1962) discusses freezing in relation to imprinting studies. He presented data showing the percentage of birds freezing (in an experimental situation similar to the one used in this study) to increase with age from 0-1 days to 7 days in the domestic chick; that is, the probability of freezing increases as the bird goes from the early locomotory stage to the stage of socialization. However, further research is necessary with the Bobwhite since too few birds were tested in the second age group to determine statistically whether freezing is more probable than immobility in this stage.

In the socialization stage complete physical independence is achieved. As the bird becomes independent, it regulates its body temperature and heart rate decreases to the adult level. Temperature regulation (Sturkie, 1954, p. 122) and heart rate decrease (Ringer, et al., 1957) begin to occur in the domestic chicken at approximately the same time as immobility begins to occur (Ratner and Thompson, 1960; Salzen, 1963).

The development of temperature regulation and the time course of heart rate changes have not been experimentally determined in the Bobwhite. However, Stoddard's (1931) observations concerning the age at which flight occurs (about two weeks) and the age at which the juvenile plumage starts to appear (also about two weeks) gives some indication of the development of physical independence in the Bobwhite. The results of this study indicate that the age at which the Bobwhite achieves physical independence (about two weeks) roughly corresponds to the age at which immobility occurs (between 10 and 20 days of age).

Flying as a response to predators also occurs during the socialization stage. Obviously, flying is dependent upon the development of the plumage, and thus would improve up to the time the adult plumage is attained. Attempts to fly (flutters) were seen in the present experimental situation at 9 days of age, but since escapes were only counted as flying over the 300 mm wall of the open field, it was not until 19 days of age that successful escapes were made.

Of interest is Stoddard's (1931, p. 60) observations concerning the "sitter". "Sitters" are those quail that do not flush or escape when a covery is disturbed at close range. Stoddard cites a report from a "veteran quail sportsman" suggesting that approximately 70 percent of a covey flushes, so that "sitters" comprise approximately 30 percent of a covey. Table 5 shows about 57 percent of the quail escaping at 29 days of age. The percentage of quail escaping at later ages and the reliability of the response make interesting experimental questions.

The question of the reliability of both freezing and immobility and the correlations between these responses and the other measures recorded, none of which were significant in this experiment, warrants further research. Past research with Bobwhite quail in our laboratory has shown duration of immobility to be significantly reliable, but this research has been conducted on adult birds. It is possible that duration of immobility does not become reliable until later than the ages tested in this experiment. The reliability of, and correlations between, other responses to predators in older Bobwhite quail has yet to be tested.

From the results of this study a developmental sequence of responses to predators in the Bobwhite quail can be suggested. This sequence involves crouching during the first few days followed by freezing between 5 and 10 days. Immobility and escaping (flushing) both occur between 10 and 20 days, but escaping develops more slowly than immobility. During this time there is a decrease in distress calls and a decrease in locomotion.

Collias (1952) discusses the decrease in frequency of distress calls with age in terms of their being one of a number of infantile responses which are reduced in frequency as the young bird achieves independence. However, his report of the decrease in frequency of distress calls in domestic chicks from 1 to 5 weeks of age mentions nothing about the testing conditions other than the fact that the chicks were isolated. The present study indicates that both distress calls and locomotion are affected by defensive distance. There is a general tendency towards fewer distress calls after immobility than after freezing (Figure 3) and less locomotion after immobility than after freezing (Figure 4). It is interesting to note that distress calls are not affected by the decrease in defensive distance until about 9-10 days, while locomotion is affected earlier at 4-5 days. Escapes are also affected by defensive distance since fewer escapes occur after immobility than after freezing (Figure 5).

The general effect of decreasing the defensive distance to a prolonged zero distance is a decrease in frequency of distress calls, locomotion, and escapes. The Defensive Distance model (Ratner, 1967) hypothesizes on orderly sequence of responses to predators (from freezing to immobility) as defensive distance is reduced. This sequence of responses to predators can be superimposed on a classification of behavior sequences outlined in Denny and Ratner (1970) which categorizes behavior into <u>appetitive</u> (initial and variable) components, <u>consummatory</u> (final and fixed) components, and <u>post-consummatory</u> components.

The effect of defensive distance on frequency of distress calls, locomotion, and escapes shows the differential effect of an appetitive response to predators (freezing) and a consummatory response to predators (immobility) on what might be considered in this experimental situation as post-consummatory responses (distress calls, locomotion, escapes). At least considering distress calls as post-consummatory responses is supported by Stoddard's (1931) comments that the "lost" call, which is like the "distress" call, develops with age into the "scatter" or "covey" call. The "scatter" or "covey" call functions to reunite the covey after it has been scattered by a predator. The fact that immobility reduced the frequency of these responses much more than did freezing might also verify the classification of freezing as an appetitive component and immobility as a consummatory component of responses to predators.

In summary, then, this study found a developmental sequence of responses to predators in the Bobwhite quail. Two components of the fear display occur at different ages, freezing in the locomotory stage and immobility early in the socialization stage. Escaping (flushing) occurs in the socialization stage, but develops more slowly than immobility. The developmental sequence of responses to predators in each of the stages of basic motor coordinations corresponds to that of other precocial birds. Suggestions for future research include closer determination of the age of occurrence of freezing and immobility in the Bobwhite, investigation of the effects of defensive distance on distress calls, locomotion, and escapes, investigation of the reliability of freezing and immobility at later ages, and investigation of the reliability of escaping and the overall percentage of birds escaping in a covey.

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