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SEQUENCE EFFECTS
IN THE ANTIPREDATOR BEHAVIOR
OF THE HOUSE CRICKET (ACHETA DOMESTICUS L.)

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SEQUENCE EFFECTS IN THE ANTIPREDATOR BEHAVIOR OF THE HOUSE CRICKET (ACHETA DOMESTICUS L.)

By

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ABSTRACT

SEQUENCE EFFECTS IN THE ANTIPREDATOR BEHAVIOR OF THE HOUSE CRICKET (ACHETA DOMESTICUS L.)

By

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A series of experiments was conducted on antipredator behavior in the house cricket (*Acheta domesticus* L.). First, cricket predation by rats was observed. These insects responded with autotomy (reflex separation of a metathoracic leg) or thigmotaxis, freezing, hopping, struggling, freezing after capture, and immobility. Then the eliciting stimuli for each of these behaviors were experimentally investigated. Finally, eliciting stimuli for immobility and autotomy were presented at different points in the normal sequence of behavior with the result that the eliciting stimuli were maximally effective only at their appropriate positions in the antipredator sequence. This provided evidence for a hierarchy of antipredator behavior in *A. domesticus*.

DEDICATION

This dissertation is dedicated to the memory of Dr. Stanley C. Ratner who directed this research until his death in December, 1975.

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CHAPTER I

INTRODUCTION

An expanding knowledge of the variety of behavioral strategies employed by animals in meeting the problems of survival as well as the principles by which these behaviors are organized is important to the continued development of a truly comparative psychology. Insects provide both a fascinating variety of behavior for study and many opportunities to investigate the manner in which components of behavior are assembled.

One type, or class, of behavior in which insects show this variety is antipredator behavior. For example, the aphid is usually considered to be a behaviorally uninteresting insect. Yet Dixon (1958) reported five components of antipredator behavior in response to coccinellid adults and larvae (ladybird beetles). The components were walking, dropping from the plant, kicking, dropping a leg, and "waxing." In waxing behavior, an oily liquid is secreted from the rear of the abdomen. This substance quickly solidifies to wax and if it comes into contact with the head of the predator its mouthparts are sealed in wax. This is a novel and effective defense. Dixon reported that it took the coccinellids from 42 to 94 minutes to remove the wax and free their mouthparts, thus allowing the aphids ample time to escape.

The study of behaviors like the above has delighted naturalists from many disciplines and is worthwhile as an end in itself. In addition, the presence of complex behaviors in such "simple" animals can provide us with powerful tools for the analysis of behavior. Thus the present study had two purposes. First, it explored the behaviors used by a cricket, _Acheta domesticus_, in response to a predator. Second, it investigated some relationships among these behaviors and the manner in which they are ordered.

The complex, and apparently ordered, chains of behavior in animals, especially insects, have long fascinated students of behavior. These chains have been labeled, and too often explained, by using the term instinct. J. Henri Fabre, a contemporary and correspondent of Charles Darwin, devoted his life to this study. Fabre's observations led him to believe that, once activated, an instinctive sequence of behavior must be followed to its conclusion with very little variation. An example may be found in Teale (1949):

> Because one thing has been done, a second thing must inevitably be done to complete the first or to prepare the way for its completion, and the two acts depend so closely upon each other that the performing of the first entails that

> of the second, even when, owing to casual circumstances, the second has become not only inopportune but sometimes actually opposed to the insect's interests. (p. 61)

Fabre's work is full of examples of what he called the "ignorance of instinct." This refers to situations in which normally adaptive behavior becomes grotesquely maladaptive due to the insects' inability to depart from set patterns of behavior. He described how a hunting wasp captures and feeds honey bees to its larvae. After capturing a bee, the wasp typically eats the pollen and nectar carried by the foraging bee before taking it to her larvae. If the wasp herself is captured during the consummatory stage of her feeding behavior she is unable to respond appropriately to the new situation. Again, Teale (1949) provides an example from Fabre:

> I have seen the wasp, with her prey, seized by the Mantis: the bandit was rifled by another bandit. And here is an awful detail: while the Mantis held her transfixed under the point of the double saw and was already munching her belly, the Wasp continued to lick the honey of her Bee, unable to relinquish the delicious food even amid the terrors of death. (p. 57)

Fabre chronicled inumerable examples like the above, but he did not engage in the experimental study of possible mechanisms underlying the behaviors that he observed. He assumed, on the basis of his observations, that there was an actual sequence or hierarchy involved in the behaviors that he studied. It is very easy to observe an animal performing a set of behaviors having

a common end function and conclude that an ordered sequence of behavior exists. However, even if behavior B always follows behavior A no causal relationship is necessarily implied. A third factor or a time delay function could be involved.

Recently, an increasing number of researchers have been attempting to go beyond simple description of the behavioral responses of animals to given stimuli. Descriptions of behavior are becoming more quantitative and, where apparently ordered sequences of behavior occur, transition probabilities between all behavioral components in the sequence are studied. Once a researcher has determined the components in such a sequence, questions can be asked about the manner in which the components are assembled. Baerends (1976) reviewed some of the issues involved in the study of the hierarchical and functional organization of behavior and pointed out the need for more research in this area. Sibley and McCleery (1976) carried the analysis one step farther by moving from the ordering of components in a single class of behavior such as feeding to a consideration of how two classes of behavior (in this case feeding and drinking) interact. McFarland (1974) and his associates have reported progress in the development of sophisticated techniques for the analysis of behavior based on systems analysis and decision theory. However, before these techniques can be fully utilized much basic research on behavior in a variety of species needs to be conducted in order to identify appropriate research preparations for closer analysis.

The present study represents an attempt to analyze a selected class of behavior in a single species and to obtain information about how behavior in this selected case is organized. The rationale for the present series of experiments was to identify the behaviors emitted by an animal in a given class of behavior and the proximal stimuli that are at least occasionally sufficient to elicit these behaviors. In the next stage of the study these stimuli were presented at their normal points in the apparent sequence of behavior and at earlier or later points. If these proximal stimuli always elicit responses with the same probability and topography no evidence is obtained for the existence of an order effect or a hierarchy of behavior. If, on the other hand, a stimulus is maximally effective only at its appropriate position in the sequence, evidence is privided for an organization of behavior in which previously emitted behaviors combine with incoming proximal stimuli to determine an animal's next response.

Acheta domesticus, the house or domestic cricket (formerly called Gryllus domesticus), was chosen as a general research animal after a literature review and a

series of pilot studies found that this species has a wide variety of interesting behaviors and is easy to obtain and maintain. *A. domesticus* is an Old World insect that has been introduced into the United States and Canada. An apparent sibling species, until recently thought to be a strain of *A. Domesticus*, occurs in Pakistan. However, Ghouri and McFarlane (1957) were unable to mate individuals from Pakistan with individuals of *A. domesticus* from Canada. They found no morphological differences between the two populations although the Canadian crickets were generally larger than crickets of the Pakistani strain. They did find sufficient behavioral differences between the two strains to suggest that they are reproductively isolated. Females did not respond to males from the other locality except that Canadian females "often devoured the smaller males of the Pakistani strain." Ghouri and McFarlane found that reproductive isolation in this case evidently consists in a failure of insemination but the precise mechanisms involved are unknown. Alexander (1962, 1964) has studied the behavioral isolation mechanisms in Gryllidae including *Gryllus veletis* and *G. pennsylvanicus*.

A. domesticus is commonly found in basements and refuse piles. Bate (1969a, 1969b, 1970, 1971) has studied this cricket both in the laboratory and in its natural habitat in British dumps. Bate's ecological research suggests that a laboratory environment would not be a tremendous distortion of the natural habitat of this species.

Khalifa (1949) documented the sexual behavior of the house cricket. The male produces a calling song and if a female approaches when the male has a spermatophore he changes to a mating song which, compared to the calling song, is softer but higher in frequency and is accompanied by side to side rocking movements of the body. Next the female mounts the male and/or the male pushes himself underneath the female and a spermatophore is transferred to the female. After copulation the male "watches" the female for a period that may last for over an hour.

The female oviposits in moist soil. The eggs hatch after 14 days at 30°C. and the crickets are sexually mature after 30 to 60 days. There is no care of the young behavior. The entire life cycle may be easily studied in the laboratory.

This insect is basically a scavenger and is occasionally cannibalistic. Resting, grooming, and possibly exploration occur but these behaviors have not been systematically studied.

A. domesticus was selected for research on antipredator behavior after pilot studies found that these insects respond to human predation with a defensive repertoire that includes walking, freezing, dropping appendages, hopping, struggling, and immobility.

There is little information in the literature on the defensive behavior of *A. domesticus*. Brousse-Gaury (1958) reported the occurrence of autotomy, the reflex separation of a metathoracic leg, in this insect. This report included a detailed description of the structures, muscles, and nerve impulses involved in autotomy in *A. domesticus*. The trochanter of the metathoracic leg is reduced to a thin ring that is inserted into the interior of the coxa. The trochanter-femur joint is immobile and together these two segments form a monocondyle joint with the coxa. Three muscles pass through the coxa and attach to the trochanter. Contraction of these muscles results in a rupture of the leg at the weak trochanter-femur joint. Brousse-Gaury found autotomy to be "capricious and irregular" and was unable to make any statements about possible eliciting stimuli.

CHAPTER II

EXPERIMENTS

Experiment 1:
Behaviors Elicited by Actual Predation

The purpose of this experiment was to obtain descriptive data on the topography, frequency, order, and possible function of each behavior associated with predation.

Background Observations

A series of pilot studies was conducted in order to identify a predator species for use in this experiment. A total of several hundred *A. domesticus* was exposed to predation by rats, mice, cats, ferrets, quail, a parrot, frogs, toads, snakes, and humans. The hooded rat was selected for more controlled laboratory study because rats are ecologically valid predators and these animals were the most reliable eliciters of the greatest variety of antipredator behaviors from the crickets.

Method

Subjects.--Two hundred mature *Acheta domesticus* from a larger group of crickets purchased from a commercial supplier were used in this experiment. The insects were maintained in glass terraria (25/50/30 cm. deep) containing ground corncob bedding and cardboard egg case inserts that provided shelter and resting sites. Ground chicken mash and water were always available. Adult crickets typically live for two to four weeks under these conditions. These experiments used crickets that were a few days to three weeks old. The laboratory temperature was set at 20°C. and never varied more than 4°. A 12:12 light cycle (50 lux/0 lux) was maintained. Six hooded rats were obtained from a laboratory colony at Michigan State University. The rats were housed individually in glass terraria similar to those used for crickets. The two sets of terraria were never interchanged.

Apparatus.--The apparatus for a given test consisted of a rat terrarium, a cricket terrarium, and a removable passageway that allowed a rat to climb into the cricket terrarium. This passageway was constructed of Habitrail tubing sections. When the passageway was placed between the terraria, a rat could climb a 45 cm. vertical section, cross a 45 cm. horizontal section, and descend into the cricket area through another vertical section. The crickets could not climb through the tubes.

Procedure.--A test trial consisted of a rat having access to a cricket terrarium containing 10 crickets for a period of 15 min. Four tests were conducted on each of five successive days. The following general procedure was used for each of the 20 tests.

Ten crickets (five males and five females) were haphazardly selected from the colony and placed with food, water, and fresh bedding in a terrarium and allowed to acclimate for 20 to 24 hours. Then a cricket terrarium was placed on a table next to a rat terrarium for another acclimatization period that lasted 15 min. Then the passageway was placed connecting the two terraria. The test was terminated after 15 min.

Measurement.--A tape recorder was used in an attempt to record as many observations as possible. Attention was focused on the behavior of the crickets nearest to the rat.

Results

Table 1 presents the behaviors observed in response to a rat. One hundred and five crickets were captured and 10 of these were captured twice so 115 captures were observed. Other behaviors such as stridulation, ovipositing, and grooming were common before the rat entered the cricket terrarium but all such behaviors ceased as soon as a rat entered the cricket terrarium.

Autotomy was never observed in the absence of the rat. Four individuals may have shown this response

Table 1.--Behavior Classification.

Behavior	Definition
Autotomy	Reflex separation of a metathoracic leg.
Walk	Coordinated locomotion.
Freeze	Upright posture with no movement.
Hop	A jump of more than 1 cm.
Struggle	General wiggling and pushing with legs.
Captive freeze	Cessation of movement while being held by a rat.
Immobility	Ventral side up with no movement for at least 3 sec.

but it was never possible to be absolutely sure that the rat had not torn the leg off. However, each of these cases involved a metathoracic leg and there were no signs of avulsion.

Walking was common both in the presence and absence of a rat. There were no obvious differences between walking in the presence and absence of a rat.

Freezing was also observed both before and after the arrival of a rat. There was some indication that freezing may be distinguishable from resting behavior on the basis of antennal position. Crickets freezing in response to a rat were frequently observed with their antennae in a raised position.

Hopping was observed in only one individual before the rat entered the cricket terrarium. Hopping was a very common response to the close proximity of a rat. Hopping seemed to be closely related to freezing in that most hops started from a freeze posture and after one or more hops the freeze posture was reassumed for at least a few seconds before walking occurred.

Struggling was observed in 13 of the captures and was always of short duration (one to three sec.). One of these crickets escaped after struggling but it was recaptured a few seconds later. Captive freeze, or the cessation of struggling, was observed in 12 of the above captures. Crickets remained in this posture until they were killed or released at which time they either moved away or showed immobility.

Immobility was never observed during the absence of the rat but did occur in 17 individuals. This behavior was only observed after contact with the rat. In 16 cases the cricket was captured in the rat's mouth or held down on the bedding by a paw, released ventral side up, and remained immobile. In one case an immobility response was elicited when a rat sat on a cricket. Four of the immobility reactions were terminated by the cricket righting itself and walking away. The durations of these four reactions were 13, 15, 24, and 31 sec. One immobility reaction was terminated by contact with the experimenter after 400 sec. of immobility. The rest of the immobile crickets were picked up by a rat after

4 to 266 sec. In each case struggling was resumed for a few seconds. The rat eventually ate these eleven crickets.

Table 1 lists freezing, captive freezing, and immobility as separate behaviors. Yet the classification at this point in the research was partially based on structural considerations and the concurrent behavior of a rat. For example, without recourse to physiological research there was no way to rule out the possibility of upright immobility being confused with freezing, or even resting. However, even at this point, there were some indications that the behaviors were different. No instances of freezing were observed in which a rat contacted a cricket and the cricket failed to respond, almost always with hopping. Similarly, no instances of immobility were observed in which a cricket hopped although a cricket would occasionally show some movement. A distinction was also made between captive freezing and immobility. It may be that these two behaviors are best considered as points on a continuum. Some, but not all instances of captive freezing were followed by immobility. Photographs of the behaviors described here may be found in the Summary section.

Experiment 2: Early Components of Antipredator Behavior

The results of Experiment 1 clearly identified several consummatory behaviors that are commonly emitted in response to predation. The early components of antipredator behavior remained unclear. The results of Experiment 1 were used to formulate the following hypotheses about these early responses to a predator.

1. An early component of the defensive sequence is the cessation of behavior in other classes.
2. The approach of a predator increases the frequency of freezing.
3. The approach of a predator increases the probability that a cricket will orient towards thigmotactic stimulation.

Method

Subjects.--Twenty adult *A. domesticus* (10 males and 10 females) were used in this experiment along with the female rat that was the most reliable predator in Experiment 1. The crickets were maintained as described in Experiment 1.

Apparatus.--The apparatus from Experiment 1 was used in this experiment. A cardboard screen (57/70 cm. with a 5/5 cm. hole in the center) was placed between the experimenter and the crickets in order to minimize the amount of experimenter movement visible to the cricket in the test terrarium.

Procedure.--The same procedure was used as was reported in Experiment 1 with the following exceptions. Only 1 cricket was used for each trial. On 10 tests (5 males, 5 females each) the rat could enter the cricket -errarium and on 10 tests the tube was placed in the cricket terrarium but the rat terrarium was not in the room. Running order was counterbalanced. A time sampling method was used such that behavior and location were recorded at 5 sec. intervals.

Measurement.--Cricket location was recorded in terms of position in the terrarium (wall, corner, or center) and position relative to the tube (between the tube and the wall, in the tube, on top of the tube, or next to the tube). Cricket behavior was recorded with the classification system presented in Table 1 with one addition. Thigmotaxis was scored if the cricket was in a corner, next to a wall, or behind or next to the tube.

Results.--Each experimental cricket was matched with a same sex control cricket such that the number of minutes observed (determined by how long it took for the rat to enter the cricket terrarium) was the same for each member of the pair. Thus the analysis focuses on those preconsummatory behaviors emitted before the rat actually entered the cricket terrarium. These behaviors could be in response to mechanical, visual, or chemical cues.

The time sample data were converted to percentages of the observation period (the absolute period duration differed for each pair) in order to allow the use of the Kruskal-Wallis one-way analysis of variance (Siegel, 1956) to compare the rat present condition with the control condition.

The rat entered the cricket terrarium and captured the cricket in each of the rat trials. The time for the rat to enter the cricket terrarium ranged from 1 to 5 min. with a mean of 2.18 min.

The results of this experiment did not permit the evaluation of the first hypothesis concerning the cessation of behaviors in other classes. One male cricket stridulated briefly before the rat entered the passageway in the rat condition. There were no other instances of behaviors from other classes.

The second hypothesis predicted a greater amount of freezing in the rat condition than in the control group. The crickets in the rat group responded to the distant but approaching rat by spending a mean of 76% of the time freezing as compared to a mean of 33% in the control condition. Application of the Kruskal-Wallis test found that this difference was significant at the .025 level using a one-tailed test.

The third hypothesis predicted a greater amount of thigmotaxis in the rat condition. The crickets responded to the approaching rat by spending a mean of 83% of the time in locations defined earlier as demonstrating thigmotaxis as compared with a mean of 67% in the control group. This difference was significant at the .05 level using a one-tailed test.

Discussion

This experiment does not establish the actual point at which the cricket detects the cues that signal the approach of a predator. The results do show that preconsummatory antipredator behaviors occur considerably before the predator actually reaches the immediate vicinity of the cricket. Given that this response occurs one may ask questions about the necessary stimuli for these behaviors. Experiment 3 studied freezing behavior and the roles of visual and mechanical stimuli in the elicitation of freezing.

Experiment 3:
Freezing in Response to Simulated Predation

Experiment 2 demonstrated that crickets are capable of responding to the approach of an actual predator from a distance. This experiment marks a shift from actual predation to more controlled administration of test stimuli by the experimenter. The present experiment was designed to obtain quantitative data on the topography of freezing. Some information was also obtained about the roles of visual and mechanical stimuli in the elicitation of freezing.

Method

Subjects.--Fifty crickets were haphazardly selected from a larger group in the colony terrarium. The colony was maintained as described in Experiment 1.

Apparatus.--Twenty-five clear plastic cups (5.4 cm. diameter at the base, 7.3 cm. diameter at the top, and 9.8 cm. high) were used. Each cup was used twice. A small metal weight (1.2 g.) was attached to a string and allowed to swing through an arc of 6 cm. to strike against the side of the cup to provide a reasonably constant amount of vibration.

Procedure.--One cricket was placed in each cup and all crickets were allowed to adapt for 15-45 min. The same procedure was used for all of the subjects. The experimenter approached and stopped at a distance of 2 m. from the cricket and noted the behavior of the insect and the position of its antennae. The experimenter then approached to within 10 cm. of the cup and again noted the cricket's behavior and antennal position. Then the impact stimulus as described above was administered and again the insect's behavior and antennal position were noted. If at this point the cricket was in a freezing posture, the duration of this behavior was timed with an arbitrary termination maximum set at 150 sec.

Results.--The results may be divided into two sections. First, the changes in behavior observed during approach and impact, and second, the relationship between antennal position and freezing.

Table 2 presents raw data for the frequency of three behaviors at the three data collection points that represent a gradually lessening distance between the predator (experimenter) and the cricket. Eighty-eight percent of the crickets were in a freeze posture after impact. Freeze duration ranged from one sec. to the limit of 150 sec. (n=3) with a median of seven sec.

Table 2.--Behavior at Three Data Collection Points.

Distance	Walk and Climb	Groom	Freeze
2 m.	22	6	22
10 cm.	16	6	28
Impact.	5	1	44

The cells for walking-climbing and grooming were combined and a Cochran Q test (Siegel, 1956) for k related samples was performed. There was a significant overall increase in freezing as the distance to the cricket decreased ($p < .001$). There was an increase in freezing at the 10 cm. point over the 2 m. point, but this difference was not found to be significant as a McNamar test for the significance of change (Siegel, 1956) yielded a Chi^2 value of only 3.13. The same test found a highly significant increase in freezing at impact as compared to 10 cm. ($p < .001$).

The second part of the analysis focused on the topography of freezing, especially changes in antennal position. Antennal position was recorded as horizontal, crossed, raised, or moving. The antenna were most likely to be moving if the insect was walking or climbing. The antennae were moving in 84% of active crickets, 46% of grooming crickets, and 3% of freezing crickets.

The horizontal and crossed antennal data were combined and a Cochran Q test was conducted on the data for the 22 crickets that were in a freeze posture at all three data collection points. These results show that at 2 m. 23% of these crickets had their antennae in a raised position. At the 10 cm. point, 26% had their antennae in a raised position, and after impact 59% had their antennae in the raised position. The overall change was significant at the .05 level. There were 12 crickets in which a progression was made from freeze (antennae down, crossed, or moving) to freeze with antennae in the raised position over the 2 m., 10 cm., impact observation series. In all of these cases the antennae remained raised after impact. The percentage given for those insects that raised their antennae after impact does not include seven individuals in which the antennae were already raised at the time of impact but that responded by a brief startle response (body and antennal jerk) while keeping the antennae in the raised position.

Discussion

The results of this experiment are compatible with the results of Experiment 2 in that both demonstrate that freezing is an early component of antipredator behavior. The present experiment did not find any substantial evidence for a response to an approaching potential predator over a distance. The results on the topography of freezing are interesting because they provide some basis for distinguishing between resting behavior and antipredator freezing. The position of the antennae of a resting cricket is most likely to be horizontal or moving. The antennae of a freezing cricket are most likely to be in a raised position.

It is interesting that no hopping was elicited during this experiment. This is consistent with the observations made in Experiment 1. Hopping did not occur in response to the cues associated with the approaching rat (visual and mechanical) and in fact only occurred when the rat was literally on top of and preparing to capture a cricket.

Experiment 4: Escape in Response to Simulated Predation

One of the puzzling observations made in Experiment 1 was that after the crickets moved into a corner and froze they would allow the rat to approach to within less than 1 cm. before hopping. Typically, the crickets were oriented such that they were approached from behind. It is possible that the stimulus that elicits hopping is some component (or combination of components) of the rats' breath. Pilot studies testing the response of these crickets to moving objects and the results of Experiment 3 on response to visual and mechanical stimuli, found that this stimulation may elicit freezing but does not elicit escape behavior such as hopping or running. However, breathing gently into a terrarium containing crickets always elicits a substantial amount of hopping.

It seems unlikely that a system would evolve in which air alone would elicit hopping because then any stray puff of air would elicit components of the anti-predator sequence. (But crickets in their natural habitat of basements and dumps would not be exposed to very many stray puffs of air.) It also seems unlikely that crickets would evolve a set of responses to specific predator odors. The most likley combination of stimuli that would signal the approach of most predators would be warm moist air with a high carbon dioxide content. Other insects have evolved detection systems for these substances. Gillet (1972) described such a system in the mosquito.

Testing an insect's response to carbon dioxide is complicated by the fact that this substance functions as an anesthetic at high concentrations and may have a variety of other behavioral and physiological effects. Edwards and Patton (1965) and Patton and Edwards (1968) studied what may be called the side effects of the widespread use of carbon dioxide as an anesthetic. They reported that anesthesia with carbon dioxide levels above 40% had significant effects upon general physiological variables such as growth and maturation, longevity, and heartbeat in A. domesticus.

Klopfer and Quist (1955) studied carbon dioxide avoidance in the mealworm, honeybee, and cockroach in

an air/carbon dioxide choice situation. This research represented an attempt to demonstrate avoidance at ecologically meaningful concentrations. The authors attempted to explain species differences in avoidance behavior in terms of the species' habitats. This work was greatly weakened by a total lack of carbon dioxide measurements in the habitats discussed. Klopfer and Quist did find that of the three insects studied, the cockroach was the most sensitive to carbon dioxide and reliably avoided a 10% concentration but not concentrations of 25%, 50%, or 100%. Cockroaches responded to the 10% concentration with hyperactivity. There were no instances of anesthesia below the 25% concentration level. It seems unlikely that a brief exposure to a concentration below 10% would produce anesthesia in a cricket.

A pilot study was conducted to determine the range of levels of carbon dioxide produced by potential predators. A Beckman Medical Gas Analyzer (model LB-2) was used to measure the carbon dioxide present at a point 1 cm. away from the noses of three mammalian predators--a rat, a gerbil, and a psychologist. Concentrations ranged from 1% to 4% as compared to an atmospheric baseline of .04% by volume.

Method

Subjects.--Sixty male and sixty female adult *A. domesticus* were used. Maintenance procedures were as described in Experiment 1.

Apparatus.--The air streams were obtained by valving the laboratory air supply and carbon dioxide from a tank through filters and flowmeters and combining the gases in a Y tube. The system was set up to provide air at 5 l/min., air + 4% CO_2 at 5 l/min., or nothing (tube presentation alone). A glass terrarium (25/50/30 cm. deep) was used as a test area. Teflon tubing (3 mm. inside diameter) was used to minimize extraneous chemical stimuli coming from the apparatus. Clear plastic cups were used for temporary confinement and adaptation.

Procedure.--Crickets were gently captured in test tubes and transferred to individual plastic cups. Confinement lasted for a minimum of 15 min. and a maximum of 30 min. A trial consisted of gently sliding a cricket out of its plastic cup into the test area and then presenting one of six stimulus conditions after a 1 min. adaptation period. The conditions were chosen at random and an assistant adjusted the gas apparatus and the experiment was run blind relative to the gases in the tube. Table 3 outlines the six conditions.

Table 3.--Procedure Outline for Experiment 4.

Group	Condition	Stimuli Presented
1	Control	None
2	Tube	Tube Alone
3	Air	Tube + Air Stream
4	Air + CO_2	Tube + Air + 4% CO_2
5	Freeze + Air	Vibration + Tube + Air
6	Freeze + Air + CO_2	Vibration + Tube + Air + 4% CO_2

Behavior after stimulus presentation was recorded in terms of six categories; freeze, dig, climb, walk, run, and hop. In the control condition behavior was recorded 64 sec. after release. In the rest of the conditions the tube was presented from above and its end was moved to within 1 cm. of the cricket's cerci and then withdrawn. In the freeze conditions (groups 5 and 6) vibration produced by tapping the side of the terrarium was used to elicit freezing (no body movement, antennae raised). Crickets were kept in individual cups for 24 hr. after the experiment. Data were discarded for any cricket that died during this period.

Results.--Table 4 presents the frequencies of observed behaviors and the number of surviving crickets in each of the conditions. Table 5 gives the percentage distribution of normal behavior (freeze, walk, climb, and dig), escape behavior (run and hop), and freezing considered by itself. A series of Chi^2 tests was conducted within the data in Table 4 with the significance criterion set at the .01 level.

The control data provide a baseline of normal behavior. It was not practical to distinguish between freezing as antipredator behavior and simply not moving as resting behavior. It is important to note that escape behavior (running and hopping) was totally absent from the baseline data. Presentation of the tube alone was associated with significantly more freezing than in the control group or in any other group. It seems reasonable to assume that the increase is due to an increase in antipredator freezing.

Table 4.--Escape Behavior; Raw Data.

Behavior	Control n=19	Tube n=21	Air n=21	Air + CO_2 n=20	F + Air n=14	F + Air + CO_2 n=20
Freeze	7	17	7	6	3	3
Climb	4	0	2	0	1	1
Walk	6	3	6	5	4	2
Dig	2	1	0	0	0	0
Run	0	0	2	5	3	6
Hop	0	0	4	4	3	8

All of the Air and CO_2 groups showed significantly more escape behavior than the control group. There were no significant increases in the individual CO_2 conditions compared to the corresponding Air conditions. If the two CO_2 groups are combined and compared with the combined Air groups, there was an increase in escape behavior that was significant at the .05 level. Although there was no substantial difference in amount of escape behavior between the Air and Air + CO_2 conditions, there was a significant increase in escape behavior in each of the Air and Air + CO_2 conditions compared to the presentation of the Tube alone.

Table 5.--Escape Behavior; Percentage Distributions.

Behavior	Control	Tube	Air	Air + CO_2	F + Air	F + Air + CO_2
% Normal	100	100	71	55	57	30
% Escape	0	0	29	45	43	70
% Freeze	37	81	33	30	21	15

Discussion

The results of this experiment do not support the hypothesis that carbon dioxide plays a substantial role in antipredator behavior in A. domesticus. It is interesting that the tube alone elicited freezing but the tube and any airstream elicited escape behavior. This is consistent with the results of Experiment 1 and the opinion that cerci frequently carry sensory organs sensitive to air currents. It is possible that the crickets in Experiment 1 were responding to the rat's breath.

The results of this experiment provide some information about the relationship between stimuli eliciting certain behaviors and the point in the behavioral sequence at which the stimuli are presented. However, the theory that a given eliciting stimulus will be most effective only at its appropriate point in a sequence is not supported here. Given that an air stream elicits hopping and that hopping usually follows freezing, this theory predicts an increased amount of escape behavior elicited by an air stream in the vibration-freeze groups (5 and 6) relative to the escape behavior shown in the groups that had no vibration (3 and 4). The data show a trend in the predicted direction. The vibration-freeze groups showed 70% escape behavior as compared with 45% escape behavior in the no vibration groups but this difference was not statistically significant.

Given the trends in the data, it is possible that larger sample sizes would allow finding a statistically significant response to CO_2 and some evidence for a hierarchy of behaviors. Yet it is unlikely that these effects play a major functional role in the antipredator behavior of this insect. It was for this reason that the approach used in this experiment was abandoned and the search for a more powerful preparation for the study of order effects was continued.

Experiment 5:
Struggle and Captive Freeze in Response to Simulated Predation

The purpose of this experiment was to obtain quantitative data on the behaviors of struggling and captive freeze observed in Experiment 1.

Method

Fifty crickets (25 males and 25 females) were used in this study. Each cricket was captured with forceps from the colony terrarium. Each cricket was grasped and held by one metathoracic leg in position 10 cm. above the bottom of the terrarium. The duration and topography of struggle and the duration of the captive freeze were recorded and then the cricket was released into a separate terrarium.

Results.-- Forty-one crickets responded to capture with struggle. The mean duration was 4 sec. (SD = 6 sec.). The behavior consisted of vigorous limb movements and general exploration of the forceps with the mouthparts. This behavior terminated abruptly in 39 individuals that next went into a rigid captive freeze ($\bar{x}$ = 15 sec., SD = 14 sec.). After self-termination of the captive freeze the crickets again made limb movements and explored the forceps with their mouthparts but these movements seemed distinctly less vigorous than in the initial struggling response to capture. Struggling duration ranged from 1 to 39 sec. with a median duration of 2 sec. The captive freeze duration ranged from 2 to 81 sec. with a median of 10 sec.

There were several exceptions to the usual capture-struggle-captive freeze order. Two individuals responded to capture with slow convulsive movements. Two individuals responded with a modified freeze in which the body remained still but the antennae and mouthparts moved, in one case vigorously. Eight cases of autotomy were observed, four immediately after capture, three after 2-5 sec. of struggle or jerking convulsions, and one after 1 sec. struggle followed by a 10 sec. captive freeze. All of the breaks occurred suddenly and without avulsion.

Discussion

This experiment demonstrated that the normal sequence of antipredator behavior includes a brief struggle after capture followed by a captive freeze that may or may not be similar to immobility. The results match the observations made of actual captures of crickets by the rat in Experiment 1. The occurence of autotomy in this experiment is interesting in that it demonstrates that capture is at least occasionally a stimulus that can elicit autotomy.

Experiment 6: Immobility in Response to Simulated Predation

Several cases of apparent immobility were observed in Experiment 1 and the results of this experiment suggested that chase, contact, and inversion might be involved as eliciting stimuli for this behavior. Comparative data (Ratner, 1977) suggests that capture, contact, and inversion are stimuli that commonly elicit immobility in a variety of invertebrates. The purpose of this experiment was to investigate the eliciting stimuli for, and topography of, this behavior.

Method

Subjects.--Forty *A. domesticus* were used, (20 in Treatment 1, and 20 in Treatment 2).

Apparatus.--A terrarium (50/24/30 cm. deep) filled to a depth of 2 cm. with corncob bedding was used as a test enclosure.

Procedure.--In Treatment 1, each cricket was captured, held by the metathoracic legs, and positioned ventral side up resting on the bedding at the bottom of the test enclosure. This position was maintained for 15 sec. at which time the cricket was released.

In Treatment 2, each cricket was gently removed from the colony terrarium and released into the test enclosure. Chase was simulated by flicking movements with four fingers of one hand such that intermittent contact was made with the cricket and the cricket was occasionally flipped upside down. The number of flicks required to elicit immobility, the duration of the chase, and the elapsed time until the cricket righted itself were recorded. A 3 sec. minimum duration was required for nonmovement to be scored as immobility.

Results.--Treatment 1 never elicited immobility but it did elicit struggling in 17 out of 18 crickets followed by captive freezing in 16 out of 18 crickets. The median struggle duration was 2 sec. after the cricket had been positioned on the substratum. All of the crickets immediately righted themselves upon release and walked away.

Treatment 2 elicited immobility in all of the 20 surviving crickets in this group. The mean chase time to elicit immobility was 26 sec. (SD = 15 sec.). The mean duration of immobility was 32 sec. (SD = 25 sec.). There were no significant sex differences in either chase time or in the duration of the response. The mean number of flicks per second was 1.35 (SD = .21). The range of immobility durations was 4 to 96 sec.

Discussion

The results of Treatment 1 match the results of Experiments 1 and 5 in regard to the topographies and durations of struggling and captive freeze. The failure of this procedure to elicit immobility was as clear as it was surprising as the stimuli presented are sufficient to elicit immobility in several other invertebrates.

The results of Treatment 2 clearly indicated that immobility could be reliably elicited by a combination of chase, contact, and inversion. Immobility was never elicited by chase and contact alone in this experiment.

A possible interpretation of immobility is that contact with a predator in the form of a sudden blow causes temporary injury and "stuns" the cricket. However, these insects can be dropped six feet onto a hard floor and they immediately right themselves and move away. It therefore seems unlikely that immobility is a result of a sudden blow delivered by a rat.

This experiment also demonstrated that immobility does not occur as a simple response to loss of tarsal contact with the substrate. The flicking procedure used here was an effective method to produce a loss of tarsal contact. Yet this occurred an average of 35 times before immobility occurred.

It is appropriate to add some data on the range of immobility durations from other experiments using the same procedure as outlined here. A total of several hundred immobility reactions have been elicited over a course of 3 years. The durations of immobility have ranged from the criterion of 3 sec. to 12.5 min. using this procedure. No cricket was ever encountered in which this procedure failed to elicit an immobility response. The procedure was exceptionally reliable in eliciting immobility but it was difficult to quantify and control the eliciting stimuli. Another variable that could not be controlled using this procedure was the amount that a cricket in immobility was covered with bedding. The flicking procedure resulted in varying amounts of this material being deposited on a cricket when it entered immobility. This provided a varying amount of extra and constant contact stimulation. Some evidence was obtained that the duration of immobility was positively related to the amount of bedding on top of the immobile cricket.

It seemed reasonable at this point that chase, or the opportunity to run off preconsummatory components of antipredator behavior, might be crucially important in eliciting immobility.

Experiment 7: Sequence Position as a Factor in the Effectiveness of an eliciting Stimulus

Experiment 1 demonstrated that immobility is a consummatory component of antipredator behavior in the domestic cricket. Experiment 6 found that contact and inversion will elicit immobility only if a period of chase preceded the presentation of these stimuli in which the cricket ran off the preconsummatory components of freezing, running, and hopping. However, it was necessary to design a more controlled method of presenting measurable amounts of the stimuli that elicit these preconsummatory components before experimentation could begin on their role in ordering the antipredator sequence.

Experiment 4 found that a small amount of vibration elicits freezing. Pilot studies found that larger amounts of vibration would elicit running and hopping. Pilot studies also demonstrated that immobility could be elicited by placing a cricket in a horizontal test tube and suddenly inverting the cricket by rotating the tube. A tube with a diameter of 2.5 cm. was chosen because larger tubes apparently did not provide sufficient contact and immobility was never obtained in tubes larger than 3 cm. in diameter. Immobility was easily elicited by inversion in somewhat smaller tubes but in these cases immobility frequently lasted for over 30 min. and in some cases for several hr. Such long durations were considered impractical for study.

The rationale of this experiment was to hold contact constant while presenting the eliciting stimulus for immobility (inversion) after varying amounts of vibration elicited antipredator behavior. The major hypothesis was that immobility is more likely to occur and has a longer duration if the cricket has been stressed or allowed to run off preconsummatory components of the antipredator sequence before being exposed to the eliciting stimulus for immobility. A more general statement of the same hypothesis would be that the eliciting stimulus for a given behavior is maximally effective only when presented at its appropriate point in the sequence of behavior.

Method

Subjects.--Four hundred *A*. *domesticus* adults (200 males and 200 females) were used. They were maintained under the same conditions as in Experiment 1.

Apparatus.-- Two hundred clear glass test tubes (20 cm. long and 2.5 cm. in diameter) were used. A vibrating platform driven by an electric motor with an eccentrically weighted shaft was used to elicit preconsummatory components of antipredator behavior. The platform was adjusted to swing a test tube containing a cricket through an arc of 1.5 cm. at a frequency of 7 cycles per sec.

Procedure.--Eight treatment conditions were used but they all shared the following common general procedure. Each cricket was captured in the laboratory colony by gently chasing it into a test tube. The opening of the tube was closed with a square of netting secured by a rubber band. The tube was then placed horizontally behind a screen on a table and the cricket was allowed to adapt for 1 hr. At this point a tube containing a cricket was very gently removed from the adaptation table and placed on the vibration platform that was set up behind a second screen on another table. A 1 min. adaptation period was allowed before the presentation of one of 8 treatment conditions.

Immobility was defined as remaining ventral side up with no movement for 3 sec. or more. If the first inversion failed to produce immobility the stimulus was repeated up to a total of 10 times and the number of inversions and the duration of immobility recorded. Each cricket was then placed in a separate plastic cup for 24 hr. If a cricket died during this period the data for that individual were discarded. Running order was counterbalanced by sex and by treatment and 25 males and 25 females were used in each treatment condition. Each test tube was used twice. After the first use each tube was scrubbed in tap water and stored for 10 days before being used again. Half of the subjects in each condition were run in used tubes.

Table 6 presents an outline of the treatment conditions. Treatment 1 consisted of using one hand to invert the cricket by lifting the open end of the tube through an arc of 180° above the table surface while the other end of the tube remained at a point on that surface. Treatment 2 consisted of using one hand to roll a tube through 180° across a table top in order to invert the cricket without lifting the tube from the table. Treatment 3 consisted of placing the cricket tube on the vibrating platform for 5 sec. and then inverting the tube on that platform as in Treatment 2. Treatment 4 was identical to Treatment 3 except that each cricket received 15 sec. of vibration. Treatment 5 was identical to Treatment 3 except that each cricket received 60 sec. of vibration. Treatment 6 was identical to Treatment 5 except that a probe stimulus of 2 sec. of vibration was presented to each immobile cricket after 5 sec. of immobility. Treatment 7 was a control condition. Neither vibration nor inversion were presented. Treatment 8 was a control for possible damaging effects of the vibration. In this condition each cricket received 60 sec. of vibration but no inversion.

Table 6.--Procedure Outline for Experiment 7.

Treatment	Abbreviation	Vibration	Inversion
1	F	None	Flip
2	R	None	Roll
3	5VR	5 sec.	Roll
4	15VR	15 sec.	Roll
5	60VR	60 sec.	Roll
6	60VRP2	60 sec. 2 sec. probe	Roll
7	C	None	None
8	60VC	60 sec.	None

<u>Results</u>.--A routine check for sex differences in immobility duration across all of the roll treatments found that the mean female immobility duration (105 sec.) was significantly longer than the male duration ($\overline{x}$ = 61 sec.) based on a Mann-Whitney U test ($p < .003$). This was contrary to the results of Experiment 6 and it was hypothesized that this difference was due to the larger average size of the females which would result in more contact with the test tube. An additional experiment (8) was conducted using Treatment 1 which found, as will be seen, that size accounted for the obtained differences in immobility duration. The data for males and females

in this experiment were therefore combined for purposes of further analysis.

Table 7 presents the major results of this experiment including the percentage of individuals in each treatment in which an immobility response was obtained, the mean number of inversions required to elicit immobility in these cases, and the mean log durations of obtained immobility for each condition. This table also gives the number of insects within each condition that died during the first 24 hr. following the experiment.

A test for homogeneity of variance was performed on the log duration data with the result that these data did not meet the assumptions required for the use of the analysis of variance (Winer, 1971). Therefore, nonparametric tests were used for the analysis of these results.

A Kruskal-Wallis test was performed on the log duration data and these results were significant at the .001 level. A series of Mann-Whitney U. tests found that Treatments 2, 3, and 4 all elicited significantly shorter durations than Treatment 5 ($p < .03$ in each instance). Similarly, in the % immobility obtained data, Treatments 2, 3, and 4 elicited significantly fewer immobility responses than treatment 5 ($p < .01$ in each case). Treatments 2 and 3 required significantly more inversions to obtain immobility than did Treatment 5 ($p < .02$ in both cases).

In condition 1 (Flip), only 11 immobility reactions were obtained (22%) as compared with 69% in the Roll condition. This difference was significant at the .001 level. In condition 6 in which a 2 sec. vibration probe stimulus was presented after each cricket was in immobility, only 2 out of 41 insects remained in immobility. The rest responded to the stimulus by righting themselves.

There were no significant differences in mortality across the treatment conditions even if the data were combined to compare the mortality of crickets that received vibration with the mortality of crickets that received no vibration.

Discussion

These results provide some support for the hypothesis that, in this insect and this class of behavior, there is an order effect and that previously emitted behaviors (or amount of "stress") combine with proximal stimuli to determine the next response and the topography of that response. When the condition in which 60 sec. of vibration is presented is compared with the three roll conditions with less vibration and less preconsummatory behavior, we find that less stimulation

Table 7.--Results of Experiment 7.

Treatment	Mortality	% Immobility	# Inversions $\overline{X}$	# Inversions SD	Log Duration $\overline{X}$	Log Duration SD
1 Flip	0	22	4.91	2.88	1.51	.41
2 Roll	5	69	4.16	2.62	1.47	.57
3 5VR	2	70	4.14	2.78	1.56	.55
4 15VR	2	71	3.56	2.77	1.66	.59
5 60VR	1	96	3.00	2.18	1.77	.38
6 60VRP2	4	89	3.61	2.78	----	---
7 Control	0	0	----	----	----	---
8 60V Control	0	0	----	----	----	---

(number of inversions) is required to elicit immobility. We also find that the greater amount of vibration results in increased immobility duration.

The initial analysis of the results of this experiment found a sex difference in duration. Experiment 8 investigated this finding.

Experiment 8:
Cricket Size and Immobility Duration

The purpose of this experiment was to determine if the sex difference in immobility duration found in Experiment 7 could be accounted for by the larger size of the female crickets. This larger size would result in more contact with the test tube used in inversion elicited immobility.

Method

Subjects.--Twenty male and 20 female crickets were used. The crickets were selected for size such that large males and small females were chosen.

Apparatus.--The apparatus used in Experiment 7 was used here. A pair of calipers was used to measure the crickets and a Fisher Gram-atic balance was used to weigh them.

Procedure.--The Roll procedure (Condition 2) used in Experiment 7 was duplicated here. The length and width of each subject was measured after the experiment. The subjects were kept in individual cups and allowed to die and desiccate for six months at 20°C. and a humidity of 60% before they were weighed.

Results.--The crickets were measured and the mean width and length for males was 6.4 mm. and 20.8 mm. as compared to 6.7 mm. and 19.9 mm. for females. A width X length score was calculated for each individual and a Kruskal-Wallis one-way analysis of variance was performed comparing scores of males and females. There were no significant size differences due to sex in this experiment. In the male group 18 immobility responses were obtained with a mean log duration of 1.87 sec. The female group had 16 immobility responses with a mean log duration of 1.14 sec. This difference was not significant.

Discussion

We may conclude that size can account for the sex differences in immobility duration found in the previous experiment. This is consistent with the idea that some form of contact is necessary before inversion can elicit immobility. These results are also consistent with the results of the pilot studies that were done to determine the size of the test tubes used in these experiments. Smaller diameter tubes commonly elicited durations of up to several hours making them impractical for use. Immobility was never elicited in tubes that exceeded 3 cm. in diameter, probably due to a lack of contact while the crickets were being inverted.

Experiment 9:
Autotomy

During the course of these experiments approximately 30 cases of apparent autotomy were observed. Several pilot studies were conducted under the hypothesis that there would be a positive correlation between amount of stress (vibration, etc.) and the probability of autotomy. No such relationship was observed and these experiments were uniformly uninformative. The haphazard occurrence of autotomy and its unknown position in the antipredator sequence indicated that some additional research was necessary.

Experiments 1-8 outlined a sequence of antipredator behavior and provided some support for a model of behavior based on an ordered chain of stimuli and responses. Experiment 9 was conducted to determine the probability of autotomy at each point in the known order of antipredator behavior. The basic procedure was based on the finding in Experiment 5 that sudden capture at least occasionally elicits autotomy.

Two levels of autotomy were postulated in this experiment. The first level, or actual autotomy, required that the insect drop a metathoracic leg without any mechanical stress being placed on it beyond the weight of the cricket. The second level, or potential autotomy, involved placing a mechanical stress on the metathoracic legs and required a clean separation to occur between the femur and coxa at the ring formed by the trochanter with no torn muscle tissue visible. Pilot studies indicated that the usual result of such stress was an avulsion in which the rupture occurred between the coxa and the metathorax with a substantial amount of torn muscle tissue visible and an irregular break in the sternum.

Method

Subjects.--Forty-eight male and 48 female *A. domesticus* were used in this experiment.

Apparatus.--Twenty-four plastic cups were used for individual cricket adaptation and temporary confinement. One glass terrarium (25/50/30 cm. high) with a 3 cm. deep layer of ground corncob bedding was used as a test enclosure. The gas apparatus used in Experiment 4 was also used here.

Procedure.--Table 8 outlines the procedure used. The rationale was that the probability of autotomy might vary with the position in the antipredator sequence occupied by the individual cricket. Therefore each group was taken further into the sequence than the preceding group. In Table 8, stimuli are capitalized (Capture, CO_2) and responses are in small case (freeze, immobility). For Group 1 a typical capture was accomplished by suddenly reaching into the colony terrarium and grasping a cricket by one metathoracic leg. The colony was subjected to minimal disturbance and at least five min. elapsed between capture attempts.

The same procedure (Pull) was used to test for "autotomy potential" in each group. One metathoracic leg was grasped between the thumb and forefinger of each hand with the cricket held upright with its dorsal side towards the experimenter. The legs were then pulled apart until a rupture occurred. For Group 1 this procedure was used within 4 sec. of capture.

Groups 2, 3, and 4 were tested for autotomy at successively later points in the antipredator sequence. In each group crickets were captured in the colony terrarium by gently pushing them into large test tubes. Crickets readily enter such tubes by themselves. They were then transferred to individual plastic cups for a 10 min. adaptation period. A test began when a cricket was tipped out of its cup onto the floor of the test enclosure. Chasing consisted of repeatedly touching the cricket with a finger for 10 sec. Immobility was elicited in Groups 3 and 4 by chasing the cricket with one hand and repeatedly flipping the cricket over onto its back as in Experiment 6. Twelve males and 12 females were used in each group. The groups were divided in two and an A B C D D C B A design was used to control for effects associated with running order.

Table 8.--Procedure Outline for Experiment 9.

Group	Procedure
1	Quick Capture, Pull.
2	Capture, Adaptation, Release, walk, Vibration, freeze, CO_2+Air, run or hop, Pull.
3	Capture, Adaptation, Release, walk, Vibration, freeze, CO_2+Air, run or hop, Chase, hop or run, Inversion, immobility, Pull (after 5 sec. of immobility).
4	Same as Group 3 but Pull after self termination of immobility.

<u>Results</u>.--Table 9 shows the frequency of the three types of leg separation for the four groups. Three crickets that showed autotomy in Group 1 actually escaped and had to be recaptured. The distinction between autotomy and potential autotomy may be artificial. This experiment required a leg to drop off with no mechanical stress from the experimenter to be counted

as autotomy. Several cases of potential autotomy were observed in which both legs were being held prior to "Pulling" and one leg came off without any tension being applied. There was a clear distinction between potential autotomy and avulsion and there did not seem to be varying degrees of damage caused in cases of avulsion.

Table 9.--Separation Frequency by Group and Type.

Group	Autotomy	Potential Autotomy	Avulsion
1	12	11	25
2	0	5	43
3	0	8	40
4	0	4	44

A Chi^2 test was performed after combining the cells for autotomy and potential autotomy. The results were significant at the .001 level. The overall results for potential autotomy alone were significant at the .05 level. Inspection of the data indicates that the primary effect was obtained in Group 1. It is important to note that actual autotomy never occurred after the insect began the regular sequence of antipredator behavior.

Discussion

Contrary to expectations, autotomy seems to be a very early component of antipredator behavior instead of a late component. In this experiment actual autotomy was only elicited if capture was very sudden. It also seemed that the probability of autotomy or potential autotomy was increased if the cricket was engaged in behaviors characteristic of another class such as feeding or grooming when captured. Having "run off" the first preconsummatory components of the normal sequence of antipredator behavior totally inhibited actual autotomy. Some evidence was found for a lowered probability of potential autotomy as the insect moved further into the normal antipredator sequence.

The data for actual autotomy, and to a certain extent, the data for potential autotomy, add additional support to the hypothesis that a behavioral sequence or hierarchy does exist for antipredator behavior in _A. domesticus_.

Dethier, in _To Know a Fly_ wrote:

> Although small children have taboos against stepping on ants because such actions are said to bring on rain, there has never seemed to be a taboo against pulling off the legs or wings of flies. Most children eventually outgrow this behavior. Those that do not either come to a bad end or become biologists." (p. 2)

In a certain sense, this research has discovered a third alternative outcome for such children. They can grow up to by psychologists and manipulate stimulation such that the "fly" tears its own legs off.

CHAPTER III

SUMMARY

This study set out to discover the elements of antipredator behavior found in the house cricket and to obtain some information about how these elements are ordered. The project began with basic observation of semi-natural predator-prey interactions and moved to controlled laboratory simulations to identify the stimulus-response relationships within the antipredator repertoire. Sufficient eliciting stimuli for each of these behaviors were identified.

Figure 1 outlines the sequence of antipredator behavior observed in Acheta domesticus during the course of these experiments. The gradually closing distance from the predator to the prey is a reasonable and convenient hypothetical variable around which to arrange these behaviors. If a predator is detected while still a considerable distance away, a cricket will move into a crack or similar sheltered area. If the predator continues to approach, or if detection is considerably delayed, the cricket will freeze, typically with both antennae raised. Figure 2 shows crickets in a situation similar to Experiment 1 that have moved into a corner in apparent response to cues from an approaching rat. Figure 3 shows a cricket in the typical raised antennae freeze posture. Figure 4 illustrates continued freezing in the presence of the rat. Figure 5 illustrates typical behavior a fraction of a second after that illustrated in Figure 4 in which a rat is shown beginning to open its mouth. Suddenly, hopping occurs. Figure 5 shows two crickets in mid air and one cricket already in immobility, possibly after being rolled over and stepped on by the rat. If a cricket is captured it usually struggles for a few seconds and then all movements cease. Figure 6 shows a cricket in a captive freeze or immobility being carried back through the tubing to the rat's nest and Figure 7 illustrates a typical instance of immobility.

It is interesting that during the course of some preliminary observations one rat carried 30 crickets back to her nest and piled them in a corner. Many of these were in immobility and righted themselves and moved about the rat terrarium after the rat had left. When the rat returned with another cricket all of the "escaped" crickets were recaptured (eliciting immobility) and returned to the hoard. This process was repeated four times for some individuals. This suggests that immobility may be an effective antipredator behavior.

In a natural setting the crickets could have easily escaped from a rat's nest.

The above outline covers what may be called the "normal" sequence of antipredator behavior. If, however, the predator-prey distance is effectively zero when the cricket detects the predator, an alternate sequence may occur. Figure 8 shows the results of autotomy. The metathoracic leg on the left was severed by autotomy. The leg on the right, showing a severe avulsion, illustrates what happens if a leg is removed by force after a cricket has begun its normal sequence of behavior. A cricket may return to the normal sequence after it has responded to a predator with autotomy.

An order effect or hierarchy was found to be operating in antipredator behavior in this insect. Inversion, the proximal eliciting stimulus for immobility, was found to be maximally effective only after the cricket had an opportunity to run off preconsummatory components of the sequence. Here is a situation where previous responses combine with incoming proximal stimuli to determine the next response.

An even more interesting order effect was found in the study of autotomy. Here, sudden capture, the proximal eliciting stimulus for autotomy was found to be effective only if the cricket had <u>not</u> had an opportunity to run off preconsummatory components of the "normal" sequence.

It seems that in this case, we have an example of a branching hierarchy. At the point at which the first stimuli associated with a predator are detected the cricket either begins the "normal" sequence, or, if the predator-prey distance is already 0, autotomy may be elicited. The single element autotomy sequence is apparently very unlikely to be entered once the normal sequence has begun. However, after autotomy a cricket may reenter the normal sequence.

It is unlikely that all, or even many, behavior classes are organized in this fashion. But the procedures used in this study; the combination of a real predator, laboratory simulation, and sequence analysis, offer a methodology for studying the manner in which behavior is organized.

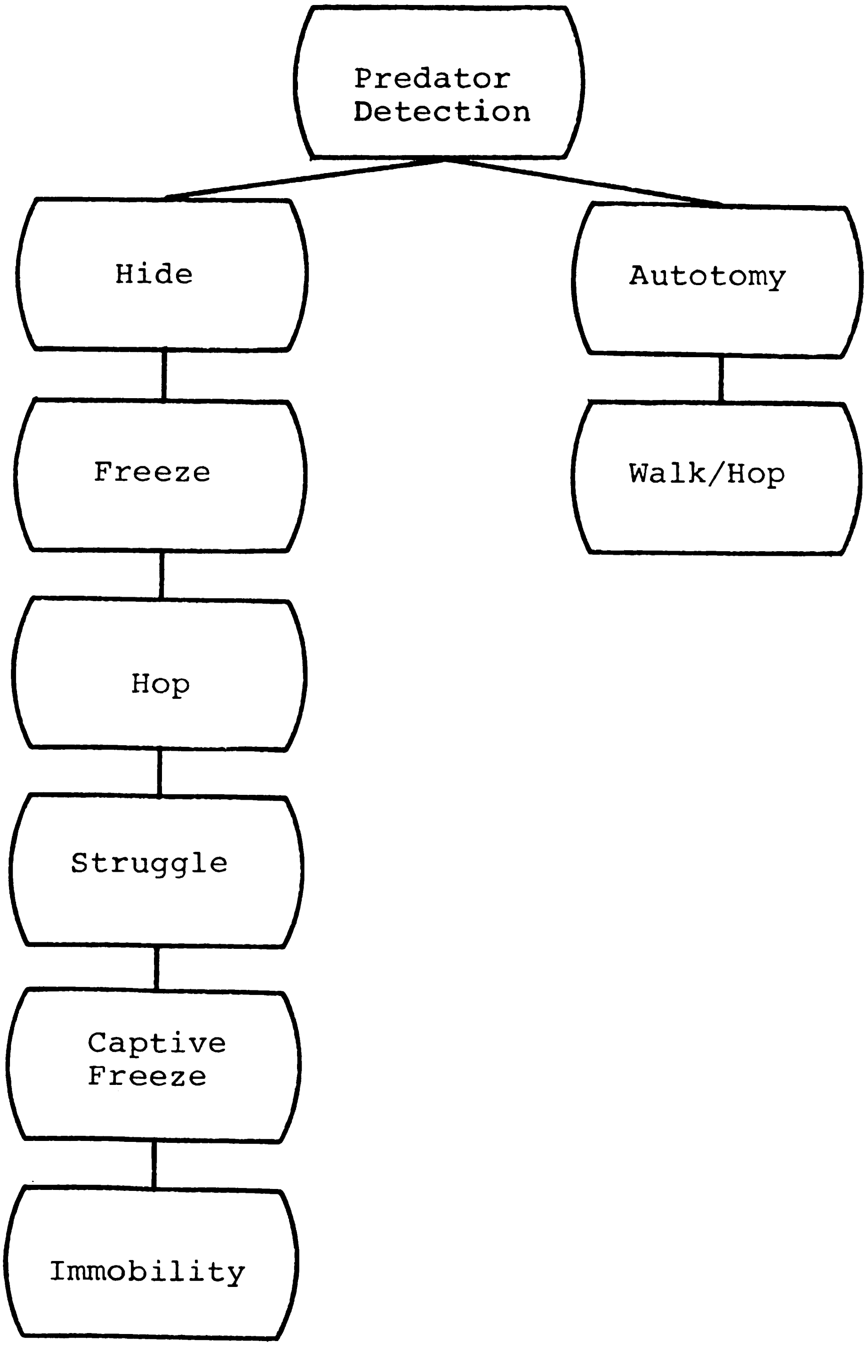

Figure 1.--Antipredator Behaviors.

Figure 2.--Thigmotaxis.

Figure 3.--Freezing.

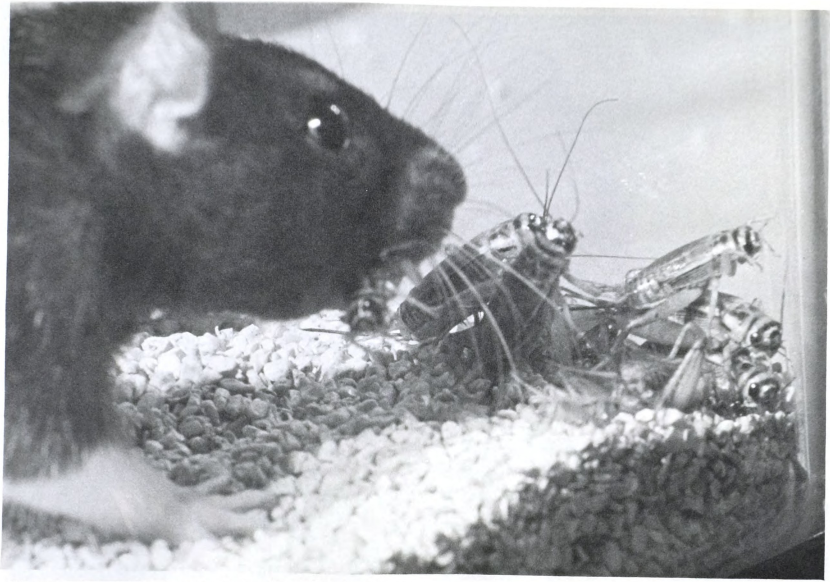

Figure 4.--Freezing in the Presence of a Rat.

Figure 5.--Escape Behavior.

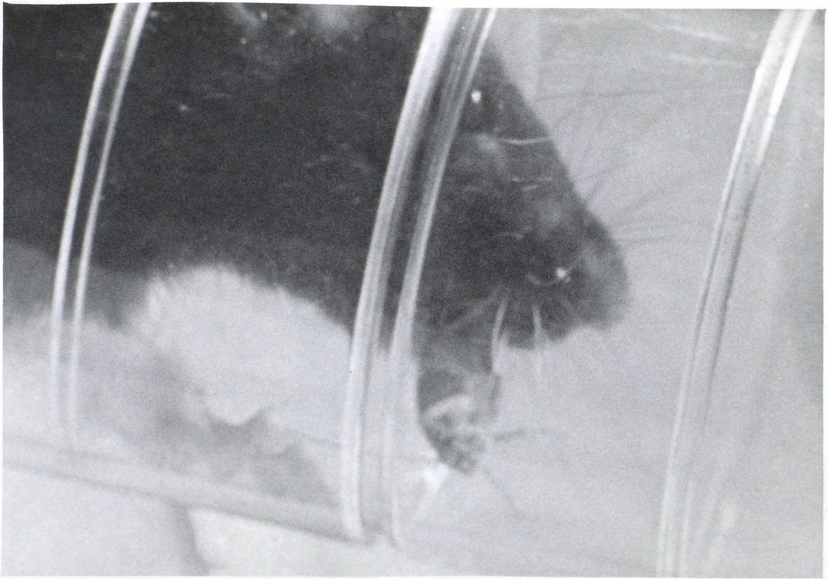

Figure 6.--Captive Freeze.

Figure 7.--Immobility.

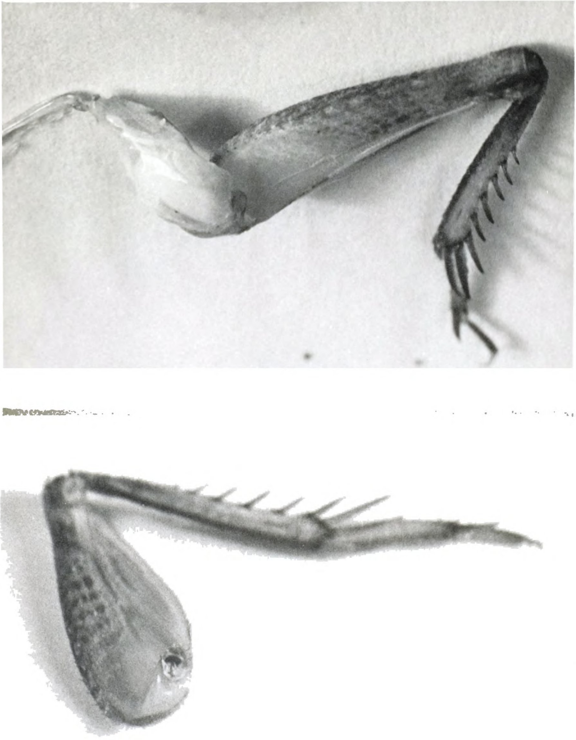

Figure 8.--Autotomy.

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