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**ON THE BEHAVIORAL RESPONSES OF FREE UINTA
GROUND SQUIRRELS TO TRAPPING**

DAVID F. BALPH

1964

ON THE BEHAVIORAL RESPONSES OF FREE UINTA GROUND
SQUIRRELS TO TRAPPING

by

David F. Balph

ACKNOWLEDGMENTS

A dissertation submitted in partial fulfillment
of the requirements for the degree

DOCTOR OF PHILOSOPHY

Wildlife Biology

Approved:

Major Professor

Head of Department

Dean of Graduate Studies

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David F. Balph

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INTRODUCTION

Biologists often trap animals to obtain information on them. If trapping is selective toward some animals, the information may be inaccurate. Most mammalogists know or suspect that their trapping techniques (reviewed by Hayne, 1949; and Stickel, 1954) contain sources of bias. Since trapping remains the only feasible way to obtain information on many animals, researchers have tried to discover sources of sampling error and refine their techniques. They have found that one major source of difficulty may lie in the behavior of animals. Individual animals seem to respond differently to trapping, both initially and through learning (Geis, 1955; Crowcroft and Jeffers, 1961; and others). However, researchers seldom observe the behavioral responses of animals to traps. They infer information from capture data. Perhaps an empirical approach would shed more light on the relationship between behavior and trapping. The present study is such an approach.

The study concerns the behavioral responses of adult Uinta ground squirrels, Citellus armatus, to trapping. I based the study on the direct observations of known individuals in a wild population. My primary objective was to learn how animals respond to a trap, to capture, and to recapture. My approach was both that of a population ecologist interested in factors affecting trapping success and that of a behaviorist interested in the effect of trapping procedures on the behavior of animals.

I conducted a broad ecological and behavioral study of the population (Balph and Stokes, 1963) before beginning the research on trap

response, which helped me select parameters and develop procedures. I also conducted a pilot study on deer mice, Peromyscus maniculatus, in the laboratory to test some procedures and the design of the trap-response investigation.

The study area was on the grounds of Utah State University, located about 10 miles northwest of Logan, Utah. I conducted most of the study on a 2-acre field, mostly open and parking lots surrounding the camp buildings. The field supported the ground squirrels with food and nesting sites and was free of other species of small mammals. It supported approximately 40 ground squirrels per acre and 100 other young mammals. Trees, brush, and grass grew in patches scattered to the west. Students used the camp from mid-June to the end of July. At other times there was only intermittent disturbance.

Ground squirrels in the study area emerge from hibernation about April 1 and emerge about the last of July.

Last spring I made the preparations for observing the response of ground squirrels to the trap. First, I marked out circular patterns on the ground to appear before the animals emerged. Each pattern consisted of two concentric circles, one 12 feet and the other 4 feet in diameter, at the center of which I would later place a trap. The patterns, hereafter called "response areas," were an aid in recording data. I located 14 test areas on the grounds. I also set traps near many of the areas. The animals had a good knowledge of the system marks before the experiments started. However, I was unable to detect any response to the marks even when the animals first encountered them.

Finally, I observed the animals nearly every day for 6 weeks following emergence in order to be able to recognize individuals before beginning the trap-response experiments. I noted differences in physical characteristics.

METHODS

The study area was on the grounds of Utah State University Forestry Camp, 20 miles northeast of Logan, Utah. I conducted most of the study on 2 acres of lawn, drives, and parking lots surrounding the camp buildings. The lawn provided the ground squirrels with food and burrow sites and me with a good view of their activity. It supported approximately 40 animals in spring and 150 after the young emerged. Trees, brush, and grass grew in areas adjacent to the lawn. Students used the camp from mid-June to the last week of July. At other times there was only intermittent disturbance from humans.

Ground squirrels in the study area emerge from hibernation about April 1 and submerge about the last of July.

Each spring I made two preparations for observing the responses of animals to the trap. First, I marked out circular patterns on the ground with gypsum before the animals emerged. Each pattern consisted of two concentric circles, one 12 feet and the other 4 feet in diameter, at the center of which I would later place a trap. The patterns, hereafter called "test areas," were an aid in recording data. I located 14 test areas on approximately 1 acre of lawn near centers of activity. The animals had 6 weeks to habituate to the gypsum marks before the experiments started. However, I was unable to detect any response to the marks even when the animals first encountered them.

Secondly, I observed the animals nearly every day for 6 weeks following emergence in order to be able to recognize individuals before beginning the trap-response experiments. I used differences in physical characteristics,

home range location, social rank, and behavioral characteristics to recognize individuals. I found that being able to capture and mark a few animals during the first days of an experiment greatly simplified the problem of recognizing all individuals.

I conducted seven experiments during May of 1960, 1961, and 1962. May was the most stable time as to movement and density and the best time to carry out the investigations. Table 1 contains a list of the experiments with the test areas, sample sizes, and times involved. The irregularities that appear in such things as the number of trials and test areas used were due to adjustments I made during the course of the study, and to difficulties associated with no control over the environment. Most of the adjustments concerned attempts to increase the number of samples. A description of each experiment follows:

1. The "standard" measured activity within the test areas without the presence or influence of a trap. The objective was to provide a standard of behavior with which I could compare behavior during later experiments. This was the only experiment in which I did not identify the individuals involved in each sample.

2. The "unbaited trap" measured the responses of animals to a functional trap which had no bait. The objectives were to see what effect the trap alone had on the behavior of animals and to probe the phenomena of capture and recapture without the influence of bait.

3. The "wired trap" measured the responses of animals to a baited trap that had the door wired open so that they could enter and leave at will. The objective was to investigate the phenomenon of repeatedly entering a trap and eating the bait without the influence of capture.

4. The "wired-trap standard" measured the activity within the test

Table 1. Experiments conducted

Experiments	Year	No. of trials	Test areas used	No. of samples
1. Standard	1962	14	14	58/22 ^a
2. Unbaited trap	1962	14	14	79/22
3. Wired trap	1960	16	4	74/10
4. Wired-trap standard	1960	16	4	55/8
5. Baited trap after prebaiting	1960	5	4	34/7
6. Baited-trap after prebaiting standard	1960	5	9	17/7
7. Baited trap	1960-61	16-18	10	187/28

^aNumber of samples/number of individuals

areas immediately after removing the wired trap. The objective was to see if animals responded to a trap location after removing the trap. My procedure was to conduct an observation period without a trap immediately after each observation period with the wired trap.

5. The "baited trap after prebaiting" measured the responses of animals to a baited and functional trap after they had been using the trap as a feeding station. The objective was to see what effect prebaiting had on the behavior of animals subsequently captured and recaptured. My procedure was to make the wired trap functional at the end of the wired-trap experiment and continue conducting trials.

6. The "baited-trap-after-prebaiting standard" measured the activity within the test areas immediately after removing the trap in the experiment with a baited trap after prebaiting. The objective and procedure were the same as those for the wired-trap standard experiment.

7. The "baited trap" measured the responses of animals to a baited and functional trap. The objective was to investigate the normal trapping situation of approaching the trap, eating the bait, being captured, and being recaptured.

Each experiment involved recording data from a group of test areas over a period of time. Each trial consisted of one 30-minute observation period on each test area used in the experiment. I conducted one trial per day on successive days on five experiments and two trials per day on two experiments. I divided the test areas to be covered each day into two groups and conducted half in the morning and half in the afternoon.

An observation period began by placing a trap in the center of a test area and ended after 30 minutes by removing the trap. I recorded data from blinds usually not more than 50 feet from a test area. I used a No. 2

National live trap (Figure 1). Rolled oats served as bait, and I did nothing to eliminate odors from the trap.

A sample began when an animal came into a test area and ended when it left or was captured. When an animal crossed the outer circle, I noted the individual, time, and began tracing its movement and recording its behavior. When the animal left the test area or was captured, I recorded the time and stopped recording data for that sample. As soon as I captured an animal, I released it, returned to the blind, and continued observations until the observation period ended. I toe-clipped and dyed a number on every animal captured for the first time. On subsequent captures I removed the animal from the trap with my hand and released it on the ground.

Three sources of information applied to each sample at the completion of an experiment. The preliminary work provided the individual's sex and home range location. The animal's performance in the sample contained its activity near the trap. Records on the animal during the experiment placed the sample in perspective by indicating the number of times the animal had previously entered test areas or had been captured.

Figure 1. No. 2 National live trap, 3 x 6 x 29 cm.

RESULTS AND DISCUSSION

In some respects this was a qualitative study—not by design, but rather by the nature of the investigation and the nature of response of animals. I had no control over the stimulus or their environment except for

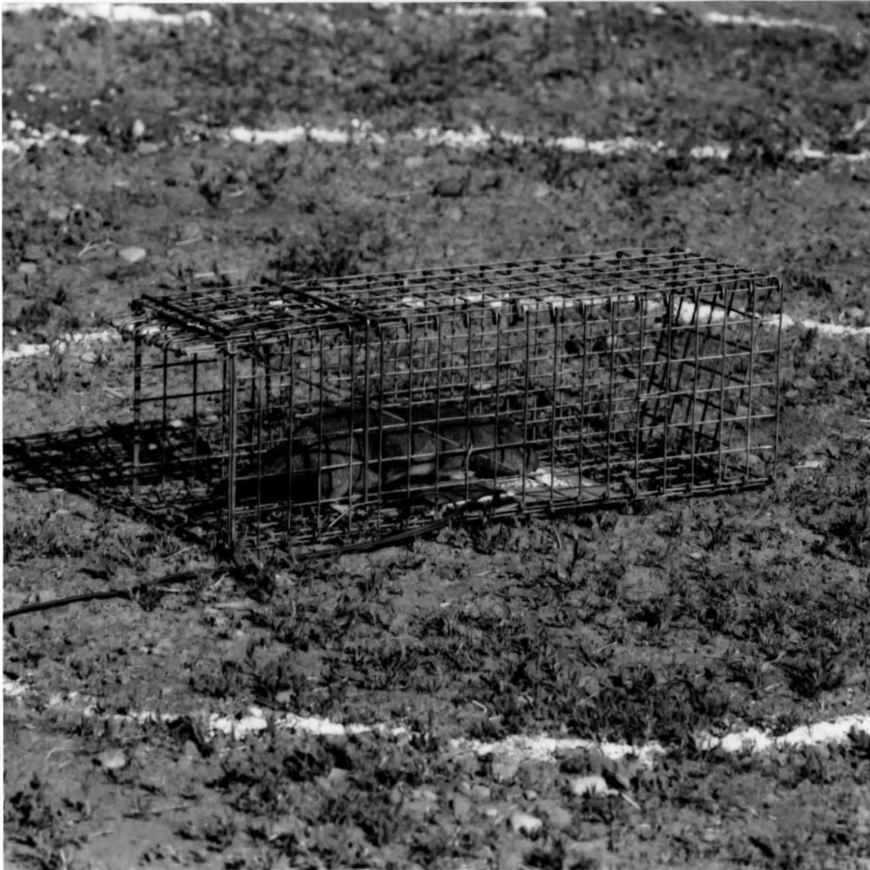


Figure 1. No. 2 National live trap, 6 x 6 x 19 inches.

by sections containing specific topics rather than by experiment. Usually more than one experiment applies to each topic. The sections are as follows: (1) activity without the influence of a trap, (2) the initial approach and capture, and (3) feeding.

RESULTS AND DISCUSSION

In some respects this was a qualitative study--not by design, but rather by the nature of the investigation and the varied response of animals. I had no control over the animals or their environment except for the trap. The type and amount of data I obtained largely have dictated the method of analysis.

I have selected those parameters that seemed most meaningful in light of the objectives. I have used data from only those animals on which I had complete trapping records during an experiment, and which had no trap experience before an experiment that might bias the results. Most data are in tables and figures, and their function is to suggest or indicate trends or the lack of them. The data appear as averages or percentages because of unequal sample sizes and differences between experiments that make their results not amenable to direct numerical comparison. The tables and figures contain the results of some statistical test done on the numerical data. Only the results appear, in keeping with the suggestion of Nelson and Hurst (1963) to present such information simply and briefly. I have discussed most large sources of variation in the text and have only indicated range in those tables and figures that contain averages.

The most succinct way to present the information on trap response is by sections containing specific topics rather than by experiment. Usually, more than one experiment applies to each topic. The sections are as follows: (1) activity without the influence of a trap, (2) the initial approach and capture, and (3) learning.

Activity Without Influence of a Trap

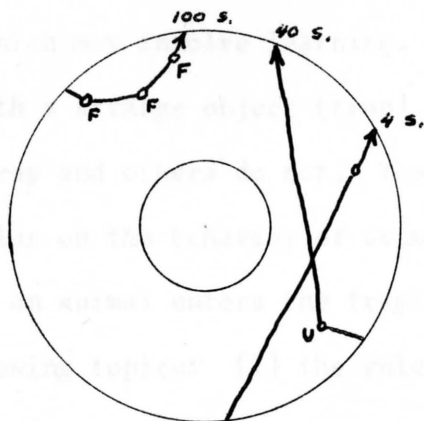
The purpose of this section is to show the movement and behavior of animals in the test areas independent of trapping procedures. To approach this objective I shall discuss and present diagrammatically some of the results of the standard experiment. Since the individuals are unknown, the results of the standard are a summation of the activity that occurred during the experiment on approximately 22 animals.

The performances of animals in the test areas fall into three categories based on movement pattern: animals entering the outer ring only (Figure 2A), animals entering the inner ring (Figure 2B), and animals passing through one or both rings but without stopping or turning (Figure 2C). The ratio of animals entering the ring only to those entering the inner ring is 5.5:1. Data which I shall present in the next section indicate that animals behave much the same in either ring when no trap is present. A computation of the expected ratio based on the assumption that movement is independent of the two rings would be complex, and unnecessary because the data form a standard and not a control.

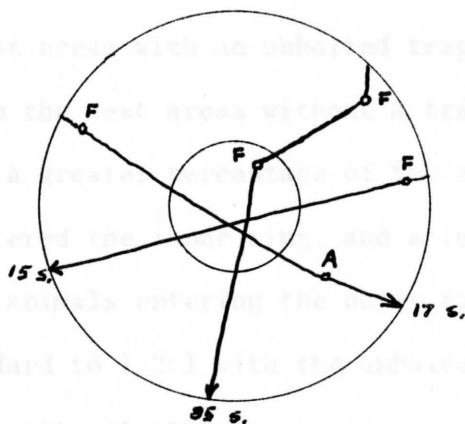
Besides movement, the activity of animals in the test areas consists of a variety of maintenance and social behavior. Animals may stop, turn (defined as a change in direction of more than 45 degrees), rest, become alert standing upright or down on all fours, attack, or escape. Figure 2 shows some of this activity, and Balph and Stokes (1963) describe it in detail.

Initial Approach and Capture

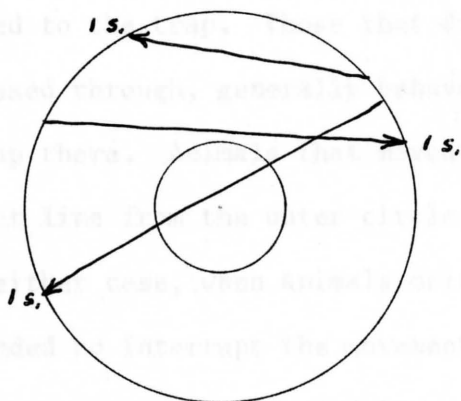
The purpose of this section is to investigate the initial responses of ground squirrels to trapping as opposed to their responses after



A. Outer ring activity only



B. Inner ring activity



C. Pass throughs

Figure 2. Diagrams of activity of animals in test areas without influence of trap. A = alert on all fours, F = feeding, S = time spent within test area in seconds, U = alert standing upright, O = stop, arrow = direction of movement.

experience with a trap which may involve learning. Setting out a trap presents animals with both a strange object (trap) and an attractor (bait). Some animals enter the trap and others do not. The questions are, what is the effect of each stimulus on the behavior of animals, and what factors determine whether or not an animal enters the trap? I shall probe these questions under the following topics: (1) the role of the trap, (2) the role of bait, and (3) the first capture.

Role of the trap

Animals in the test areas with an unbaited trap moved significantly different than those in the test areas without a trap (Table 2). With the unbaited trap present, a greater percentage of the animals that entered the outer ring also entered the inner ring, and a lesser percentage passed through. The ratio of animals entering the outer ring to inner ring changed from 5.5:1 in the standard to 1.2:1 with the unbaited trap. Hence, the unbaited trap tended to attract animals.

Animals in the outer ring behaved in one of two ways depending on whether or not they moved to the trap. Those that did not move to the trap, including those that passed through, generally behaved much the same as though there were no trap there. Animals that moved into the inner ring either did so in a direct line from the outer circle or after other activity in the outer ring. In either case, when animals oriented to and moved toward the trap they tended to interrupt the movement with a pause or two. The slight increase in occurrence of stops and turns in the outer ring with the unbaited trap compared with the standard perhaps reflected this behavior (Table 3A).

Animals in the inner ring directed nearly all of their activity toward the trap. They oriented to it, moved slowly along its edges, and often

Table 1. Occurrence of activities in (A) outer and (B) inner ring of test areas in standard, unbaited-trap, and baited-trap experiments

Table 2. Movement patterns of animals in standard, unbaited-trap, and baited-trap experiments

Movement pattern	Percent of animals entering test areas ^a		
	Standard (58/22) ^b	Unbaited trap (22/22)	Baited trap (29/29)
Entered outer ring only	84	55	38
Entered inner ring	16	45	62
Passed through	28	14	11

^aTest of independence:

Standard and unbaited trap $\chi^2 = 12.0$ ($\chi^2_{99.5} = 10.6$)

Unbaited and baited trap $\chi^2 = 1.5$

^bNumber of samples/number of individuals

Turned	.3 (0-2)	2.2 (0-5)	4.1 (0-9)
Stopped	.8 (0-2)	3.3 (0-6)	3.8 (0-7)
Fed	.7 (0-2)	.1 (0-1)	.4 (0-2)

Number of samples/number of individuals

Range in parentheses

Table 3. Occurrence of activities in (A) outer and (B) inner ring of test areas in standard, unbaited-trap, and baited-trap experiments

A. Activity in Outer Ring			
Activity	Average occurrence of activity per animal		
	Standard (58/22) ^a	Unbaited trap (22/22)	Baited trap (29/29)
Turned	.3 (0-2) ^b	.4 (0-1)	.5 (0-4)
Stopped	.9 (0-3)	1.1 (0-4)	1.3 (0-5)
Fed	.6 (0-3)	.6 (0-4)	.6 (0-5)

B. Activity in Inner Ring			
Activity	Average occurrence of activity per animal		
	Standard (9/?)	Unbaited trap (10/10)	Baited trap (19/19)
Turned	.3 (0-2)	2.2 (0-5)	4.1 (0-9)
Stopped	.8 (0-2)	3.3 (0-6)	3.9 (0-7)
Fed	.7 (0-2)	.1 (0-1)	.4 (0-2)

^aNumber of samples/number of individuals

^bRange in parentheses

stopped to probe at the wire mesh. Animals turned and stopped more but fed less than in the outer ring or either ring of the standard (Table 3). In the standard animals turned, stopped, and fed about as often in both inner and outer rings, indicating that the activity was independent of the rings. In general, animals near the trap became more active but fed less than when not near the trap.

The amount of time spent by animals in the test areas (Table 4) complements the above comparisons between the standard and unbaited-trap experiments. In the standard the largest group of animals remained in the test areas only briefly. This group contained those that passed through and others that stopped once or twice but moved on. The second largest group in the standard stayed in the test areas over 60 seconds. Feeding animals made up most of this group. With the unbaited trap the largest group of animals was in the test areas from 16-60 seconds. Most animals in this group were active about the trap. They usually left the test areas immediately after exploring the trap. The decrease from the standard in both 0-15-second and over 60-second intervals was due to fewer animals passing through and fewer feeding extensively.

The response of ground squirrels to the unbaited trap indicates that they readily approach strange objects. Ninety-one percent of those that came into test areas explored the trap at least once during the experiment. None displayed avoidance. Laboratory rats also immediately approach and explore any novelty. In contrast, wild rats, Rattus norvegicus, show strong avoidance to traps (Chitty, 1954). Chitty and Kempson (1949) give indirect evidence that voles, Microtus and Clethrionomys; shrews, Sorex; and long-tailed field mice, Apodemus, avoid traps for a day or two. Horn and Fitch (1946) state that California ground squirrels, Citellus beecheyi, are wary

of all traps. Newbecker (1958) says that Nelson antelope ground squirrels, *Citellus nelsoni*, are cautious in approaching traps but not trap-shy. Hence, Uinta ground squirrels at camp may be more prone to approach traps than other animals studied.

The environment may have contributed to the tendency of ground squirrels at camp to approach the trap. The population at camp was dense, and human habitation and the high frequency of social interaction and heterogeneity of stimuli probably created a complex environment. Standards and

Table 4. Amount of time spent by animals in test areas in standard, unbaited-trap, and baited-trap experiments

Time in seconds	Percent of animals entering test areas ^a		
	Standard (58/22) ^b	Unbaited trap (22/22)	Baited trap (29/29)
0-15	53	27	21
16-60	19	55	34
Over 60	28	18	45

^aTest of independence:

Standard and unbaited trap $\chi^2 = 3.4$ ($\chi^2_{80} = 3.2$)

Unbaited and baited trap $\chi^2 = 4.0$ ($\chi^2_{85} = 3.9$)

^bNumber of samples/number of individuals

Strange-object response is part of the larger phenomenon of exploratory behavior (reviewed by Barnett, 1958, and Barlyne, 1960). Most animals explore and reexplore their environment. The internal causes of the activity are not fully understood. Experiments on laboratory rats show that hunger, thirst, and estrous increase the activity; but some exploration is independent of immediate need or specific goal. The function of the activity lies in any benefit which animals obtain from working about while exploring and the consequent familiarity they achieve with their surroundings. An unfamiliar object in the environment releases exploration in the Uinta ground squirrels and laboratory rats, but some other animals show varying degrees of avoidance. Barnett (1963) states that wild rats are able to

of all traps. Hawbecker (1958) says that Nelson antelope ground squirrels, Citellus nelsoni, are cautious in approaching traps but not trap-shy. Hence, Uinta ground squirrels at camp may be more prone to approach traps than other animals studied.

The environment may have contributed to the tendency of ground squirrels at camp to approach the trap. The population at camp was dense, and human habitation exposed animals to many novel stimuli. Both the high frequency of social interaction and heterogeneity of stimuli probably created a complex environment. Zimbardo and Montgomery (1957) found that laboratory rats raised in a complex environment explored more than those raised in a simple environment. Montgomery (1955), Hebb (1946), and others found that exploratory behavior had an element of fear in it, but repeated exposure to strange objects reduced the fear. If the same learning occurs in Uinta ground squirrels, the animals at camp would be more prone to approach traps than those in a sparse and undisturbed population. Qualitative observations on such a population 1 mile from camp tend to support this hypothesis.

Strange-object response is part of the larger phenomenon of exploratory behavior (reviewed by Barnett, 1958, and Berlyne, 1960). Most animals explore and reexplore their environment. The internal causes of the activity are not fully understood. Experiments on laboratory rats show that hunger, thirst, and estrous increase the activity; but some exploration is independent of immediate need or specific goal. The function of the activity lies in any benefit which animals obtain from moving about while exploring and the consequent familiarity they achieve with their surroundings. An unfamiliar object in the environment releases exploration in the Uinta ground squirrels and laboratory rats, but some other animals show varying degrees of avoidance. Barnett (1963) states that wild rats are able to

make the most of the environment with a balance between exploring, which provides information on the area's resources, and avoiding unfamiliar objects, which may be sources of danger. He suggests that the strong avoidance which rats display is a product of selection caused by methods used in controlling them.

Role of the bait

Trappers usually bait traps to lure animals. However, rolled oats is not the natural food of ground squirrels, and the trap itself acts as a lure. What then is the role of bait in an animal's first encounter with a trap? To probe this question I shall consider some of the results of the unbaited and baited-trap experiments.

More animals that entered the outer ring also entered the inner ring and less passed through with a baited trap than with an unbaited trap (Table 2). The ratio of outer to inner-ring activity changed from 1.2:1 with the unbaited trap to 0.6:1 with the baited trap. Therefore, bait seemed to add to the trap's attraction. However, the chi square value and the change in ratio was not as great as between the standard and unbaited-trap experiments. The trap appeared to be more important than the bait in drawing animals into the inner ring.

I am not sure how bait accomplishes the added attraction. Perhaps animals recognize the bait as food from a distance and come to the trap to feed. But bait also increases the trap's visual and olfactory clues. Perhaps increasing the complexity of the stimulus merely increases the exploratory tendency (tendency as defined by Hinde, 1955-56, as the probability of the activity occurring) as it does in laboratory rats (Montgomery, 1951). Other studies indicate that herbivores tend to come upon bait by chance rather than the bait actually drawing them (Rowley, 1960). Bait

may act as a greater lure for animals that normally seek food by olfaction.

With a baited trap animals in the outer ring behaved much the same as they did with the unbaited trap. The added attraction of the bait probably was responsible for the slight increase in turns and stops (Table 3A).

Animals were more active in the inner ring with a baited trap than with an unbaited trap. They turned, stopped, and fed more times (Table 3B). Most of the turns and stops resulted from animals moving about the trap. A clue to the cause of increased feeding activity appears later in a comparison of the results of the standard and the wired-trap experiments. Apparently, animals that want to eat bait and are unable to do so, here because they can not move directly to the bait, redirect their feeding activity to grass.

Animals moved about the unbaited trap in a rather uniform way. Most oriented first to the side of the trap and then moved along its edge toward the rear of the trap. Presumably, the movement toward the rear was due to more visual clues there. They usually turned the rear of the trap and moved up the other side, probing occasionally as they went. The number of probes at the trap front, rear, and sides was about equal considering the relative area (Table 5). Animals seldom reversed their direction of movement at the side of the trap.

Animals moved about the baited trap more actively. They probed, turned trap corners, and reversed direction at the side of the trap more times than with an unbaited trap (Table 5). However, the greatest increase was in probes at the rear, reversals of direction at the side, and trap corners turned at the rear. Hence, animals were most active at the rear of the trap where the bait was located.

The baited trap may both increase and decrease the probability of an animal's capture. The bait tends to attract more animals, increase their

Table 5. Occurrence of activities at the trap in unbaited and baited-trap experiments

Activities	Average occurrence of activity per animal	
	Unbaited trap (10/10) ^a	Baited trap (19/19)
Probed at trap front	.3 (0-1) ^b	.5 (0-1)
Probed at trap rear	.3 (0-1)	.7 (0-2)
Probed at trap side	1.5 (0-3)	2.0 (0-3)
Turned corners at trap front	.3 (0-1)	.4 (0-1)
Turned corners at trap rear	.6 (0-2)	1.6 (0-7)
Reversed direction at trap side	.1 (0-1)	.3 (0-3)

^aNumber of samples/number of individuals

^bRange in parentheses

activity at the trap, and hold them in the test areas longer (Table 4). The bait also tends to hold animals at the rear of the trap and away from the entrance. The two effects cancel each other, and the probability of capture for those animals entering the inner ring with the trap for the first time is approximately the same for both an unbaited and baited trap (30 and 32 percent, respectively). Obviously, a better trap for ground squirrels would be one which they could enter from any direction. Such a trap would close by dropping over the animals. The trap would then take advantage of even a slight tendency to explore and would not present the problem of "finding" the entrance.

First capture

Biologists know they seldom if ever trap all the animals in an area. Some animals enter traps and some do not. Here, my objective is to determine what activity leads to an animal's first capture and what activity does not. To approach the objective I shall compare the performances near a baited trap of animals that enter the trap with those that do not. Neither group has been captured before, but both groups include animals that have approached a trap before.

Animals coming into the inner ring usually oriented to the side of the trap. Even animals that approached the ends of the trap generally swung to one side or the other and stopped first at the trap side. The initial orientation to the trap did not seem to be an important factor in the probability of capture (Table 6).

Animals that were captured probed at the front, side, and turned the front corners of the trap more times than did animals that were not captured (Table 7). In contrast, animals that were not captured probed at the rear, reversed directions at the side, and turned the rear corners

Table 6. First orientation to baited trap of animals captured and not captured

First orientation	Percent of animals entering inner ring ^a	
	Captured (18/18) ^b	Not captured (23/12)
Front of trap	6	9
Rear of trap	11	13
Side of trap	83	69
No orientation to trap	0	9

^aTest of independence: $\chi^2 = 2.0$

^bNumber of samples/number of individuals

Table 7. Occurrence of activities at edge of baited trap of animals captured and not captured

Activity	Average occurrence of activity per animal	
	Captured (18/18) ^a	Not captured (23/12)
Probed at trap front	1.0 (1)	.3 (0-1)
Probed at trap rear	.4 (0-1)	.7 (0-2)
Probed at trap side	1.8 (0-3)	1.2 (0-5)
Turned corners at trap front	.9 (0-1)	.3 (0-2)
Turned corners at trap rear	1.2 (0-3)	1.5 (0-7)
Reversed direction at trap side	.1 (0-1)	.3 (0-3)

^aNumber of samples/number of individuals

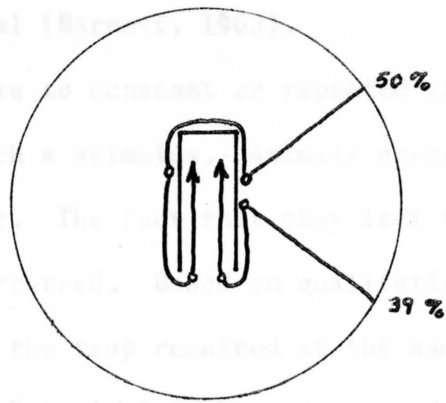
^bRange in parentheses

of the trap more times than did animals that were captured. This further suggests that bait decreases the probability of capture by keeping animals at the rear of the trap.

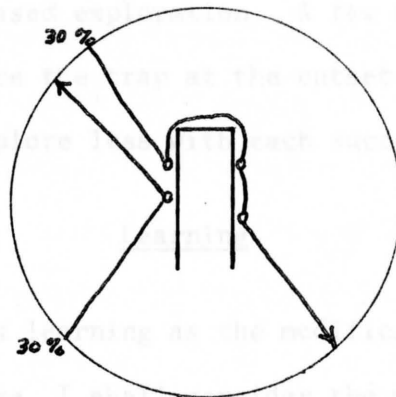
Animals that were captured generally moved about the outside of the trap steadily in one direction and stayed close to its edge. Fifty percent moved down one side of the trap, around the rear, and up the other side to the entrance (Figure 3A). Thirty-nine percent moved from the rear or side of the trap up the side to the entrance (Figure 3B). Animals that were captured seemed to be intent on exploring the trap and came upon the entrance by chance and entered.

Animals that were not captured showed more variable activity. Thirty percent of them moved down one side of the trap, around the rear to the other side, but then left the test area (Figure 3B). Thirty percent either did not stop at the trap or moved along the trap edge briefly and left the area (Figure 3B). Seventeen percent moved from one side of the trap to the other repeatedly by way of the rear of the trap (Figure 3C).

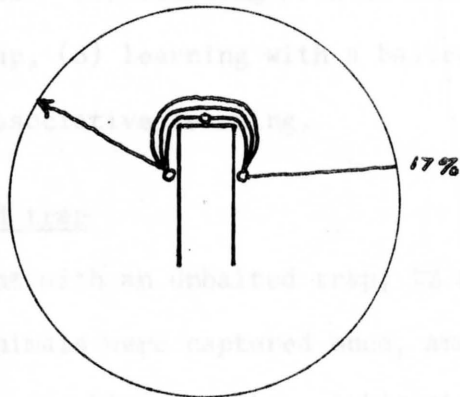
The apparent reasons why each of the above groups was not captured were chance, little tendency to explore the trap, and great interest in the bait, respectively. Chance was involved with those animals that were active about the trap but failed to come upon the entrance before they moved away. Some animals showed lack of interest in the trap even on first encountering it. Animals that had high interest in the bait displayed detour behavior by becoming fixed to the rear of the trap. The classic detour problem is that of a barrier (trap) between the animal and the goal (bait). To solve the problem the animal must first move away from the goal and go around the barrier. An animal that cannot solve the problem moves back and forth along the barrier opposite the goal. Animals below primates seldom solve a detour



A. Captured



B. Not captured



C. Not captured

Figure 3. Generalized movement patterns of animals in inner circle with baited trap resulting in (A) capture and (B and C) noncapture. Percentage refers to number of animals either captured or not captured displaying specific movement pattern.

problem on the first trial (Barnett, 1963).

Animals may habituate to constant or repeated exposure to stimuli. The trap seemed to act as such a stimulus. Animals encountering a trap first explored it and then left. The fact that they left the trap indicates that short-term habituation occurred. Based on qualitative observations it appeared that the longer the trap remained at the same location, the fewer the exploratory visits. But placing the trap at a different location or removing the trap for a few hours or days and then replacing it at the same location again released exploration. A few animals--those that had little tendency to explore the trap at the outset--showed long-term habituation. They seemed to explore less with each successive exposure to the trap.

Learning

Scott (1958) defines learning as the modification of behavior through previous experience. Here, I shall consider the modification of behavior that occurred in ground squirrels after various experiences with a trap under the following topics: (1) learning with an unbaited trap, (2) learning with a wired trap, (3) learning with a baited trap, (4) the effect of prebaiting, and (5) associative learning.

Learning with an unbaited trap

During the experiment with an unbaited trap, 22 animals entered test areas 79 times. Eight animals were captured once, and one of these was taken twice. The animals caught were taken within the first 6 out of 14 trials. Therefore, they had ample opportunity to enter the test areas again before the experiment ended. After first capture, two of the eight animals never returned. The other six returned to the test areas 17 times.

A comparison of the behavior of animals before and after their initial capture should be a measure of learning resulting from capture. After capture animals entered the inner ring and were caught less frequently than before capture (Table 8). After capture they were less active in the inner ring, especially at the edge of the trap in activity such as probing (Table 9), and spent less time in the test areas (Table 10). Therefore, capture in an unbaited trap decreased the tendency of animals to approach and be active near the trap.

Animals that encountered the trap after capture did one of two things: avoided the trap immediately or first approached it and then avoided. Those that immediately avoided usually came upon the trap while engaged in other activities. They detoured around it, often avoiding the test area entirely. Typically, those that approached and then avoided first moved hesitantly toward the trap. Before reaching it they turned and fled. Only twice did animals move to the trap edge. One animal was recaptured, but this was at a test area different from that of original capture. The recapture involved a problem in associative learning that I shall discuss later. After second capture the animal avoided the trap.

Capture involved confinement, handling, and toe-clipping for the animals. While confined and handled, they frequently defecated and squealed. Uinta ground squirrels often squeal when bitten or closely pursued by a conspecific or predator (Balph, 1964). They also show indications of physiological stress in confinement (Noble, 1961). Golley (1961) states that adrenal weights of cotton rats, Sigmodon, increase when subjected to trapping. Researchers sometimes use the frequency of defecation in laboratory rats as a measure of fear (Bindra, 1953). These facts indicate that capture was probably an "unpleasant" experience for the ground squirrels. They

Table 8. Movement patterns of animals before and after capture in unbaited trap

Movement pattern	Percent of animals entering test areas ^a	
	Before capture (17/8) ^b	After capture (17/6)
Entered outer ring only	29	59
Entered inner ring	71	41
Passed through	6	6
Resulted in capture	41	6

^aTest of independence: $\chi^2 = 5.8$ ($\chi^2_{.85} = 5.4$)

^bNumber of samples/number of individuals

Table 9. Occurrence of activities in inner ring of test areas before and after capture in unbaited trap

Activity	Average occurrence of activity per animal	
	Before capture (12/8) ^a	After capture (7/6)
Turned	2.4 (0-7) ^b	1.3 (0-4)
Stopped	4.4 (0-9)	2.0 (0-5)
Probed	2.7 (0-6)	.3 (0-1)
Trap corners turned	1.4 (0-5)	.0 (0)

^aNumber of samples/number of individuals

^bRange in parentheses

Table 10. Amount of time spent in test areas by animals before and after capture in unbaited trap

Time in seconds	Percent of animals entering test areas ^a	
	Before capture (17/8) ^b	After capture (17/6)
0-15	18	59
16-60	47	24
Over 60	35	17

^aTest of independence: $\chi^2 = 6.1$ ($\chi^2_{.95} = 6.0$)

^bNumber of samples/number of individuals

associated punishment with the trap and learned to avoid it.

Animals avoided at varying distances from the trap. Some never entered test areas again, and others moved to the trap edge before fleeing. Campbell and Kraeling (1953) state that in laboratory rats the strength of avoidance is proportional to the strength of punishment. Brown (1948) states that strength of avoidance is also inversely proportional to the distance from the punishing object. Therefore, the variation in avoidance response of the squirrels likely reflected the amount of effect the punishing experience had on each individual.

Learning with a wired trap

The objective is to see how eating bait in a nonfunctional trap affects subsequent responses of animals to the trap. During the experiment with a wired trap, 10 animals entered test areas 74 times. Six animals entered the trap and ate bait. They all returned to the trap and ate bait again from 1-13 times.

Changes in movement patterns of the six ground squirrels before and after eating bait were not significant (Table 11). However, many more performances ended in eating bait after they had eaten bait once. But the amount of activity and the time they took changed considerably. The more times animals entered the trap and ate bait, the more directly they went to the bait. They turned, stopped, probed, and turned trap corners less on each successive trap entry (Figure 4). The only major exception was that on the second entry animals probed more than on the first (Figure 4C). The increase was due to some animals having a strong tendency to reach the bait without having learned yet how to enter the trap directly. Animals also took less time to reach the bait on each successive trap entry (Table 12).

The above changes in behavior and time reflect both a shift in tendency

Table 11. Movement patterns of animals in the test areas before and after eating bait in wired trap

Movement pattern	Percent of animals entering test areas ^a	
	Before eating bait (15/6) ^b	After eating bait (46/6)
Entered outer ring only	7	9
Entered inner ring	93	91
Passed through	0	9
Resulted in eating bait	40	74

^aTest of independence: $\chi^2 = 2.5$

^bNumber of samples/number of individuals

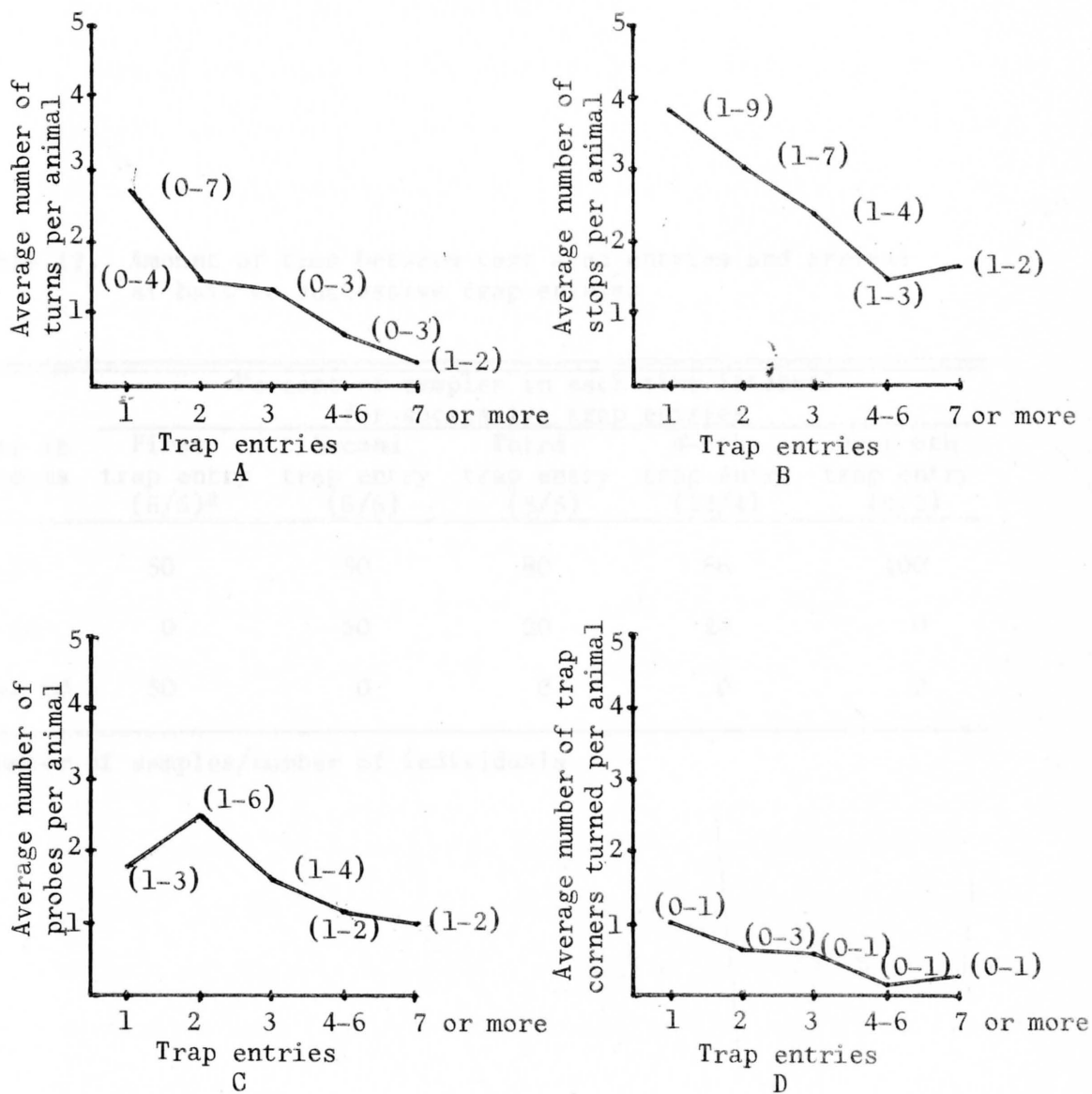


Figure 4. Occurrence of activities in inner ring of test areas on successive entries into wired trap.

and a reinforcement of the shift. Before eating bait most animals tended to explore the edges of the trap. After eating bait they directed their activity toward reaching the bait. Animals moved steadily up the sides of the trap to the entrance and showed no difficulty in solving the detour problem. None of the animals spent over 10 seconds in reaching the bait. They spent less time in appetitive behavior on each successive trap entry. These results agree with the results of experiments on reinforcement in

Table 12. Amount of time between test area entries and arrival at bait on successive trap entries

Time in seconds	Percent of samples in each time interval for successive trap entries				
	First trap entry (6/6) ^a	Second trap entry (6/6)	Third trap entry (5/5)	4-6th trap entry (12/4)	Over 6th trap entry (9/2)
0-15	50	50	80	86	100
16-60	0	50	20	14	0
Over 60	50	0	0	0	0

^aNumber of samples/number of individuals

Further evidence of the relative value of bait as a reward came from observations of captive ground squirrels which I fed grass and oatmeal. All the animals ate grass readily, but some ate more oatmeal than others. Two of 31 captive animals did not eat oatmeal, either as food in the pen or as bait in the trap.

Based on the above evidence and on observing ground squirrels visit bait in traps many times, I think that the desirability of the bait varies from unobtainable for some to highly desirable for others. I think that the level of desirability of the bait for an animal is a major factor in the number of times it will register a wired trap.

and a reinforcement of the shift. Before eating bait most animals tended to explore the edges of the trap. After eating bait they directed their activity toward reaching the bait. Animals moved steadily up the sides of the trap to the entrance and showed no difficulty in solving the detour problem. None of the animals spent over 60 seconds in reaching the bait. They spent less time in appetitive behavior on each successive trap entry. These results agree with the results of experiments on reinforcement in laboratory rats (reviewed by Spence, 1956). The more rats are reinforced, the quicker is their response to the reinforcing stimulus. For ground squirrels, eating bait acts as a rewarding stimulus. There is a linear relationship between eating the bait and returning to the trap (Figure 5). Eating the bait reinforces entering the trap again for bait.

The number of times animals returned to the trap and ate bait varied. Three animals ate bait on the first trial. Each of their home ranges contained at least two test areas. They returned to eat the bait 1, 5, and 13 times respectively. This indicates that the attractiveness of the bait varied for each individual.

Further evidence of the relative value of bait as a reward came from observations of captive ground squirrels which I fed grass and oatmeal. All the animals ate grass readily, but some ate more oatmeal than others. Four of 31 captive animals did not eat oatmeal, either as food in the pen or as bait in the trap.

Based on the above evidence and on observing ground squirrels eat bait in traps many times, I think that the desirability of the bait varies from undesirable for some to highly desirable for others. I think that the level of desirability of the bait for an animal is a major factor in the number of times it will reenter a wired trap.

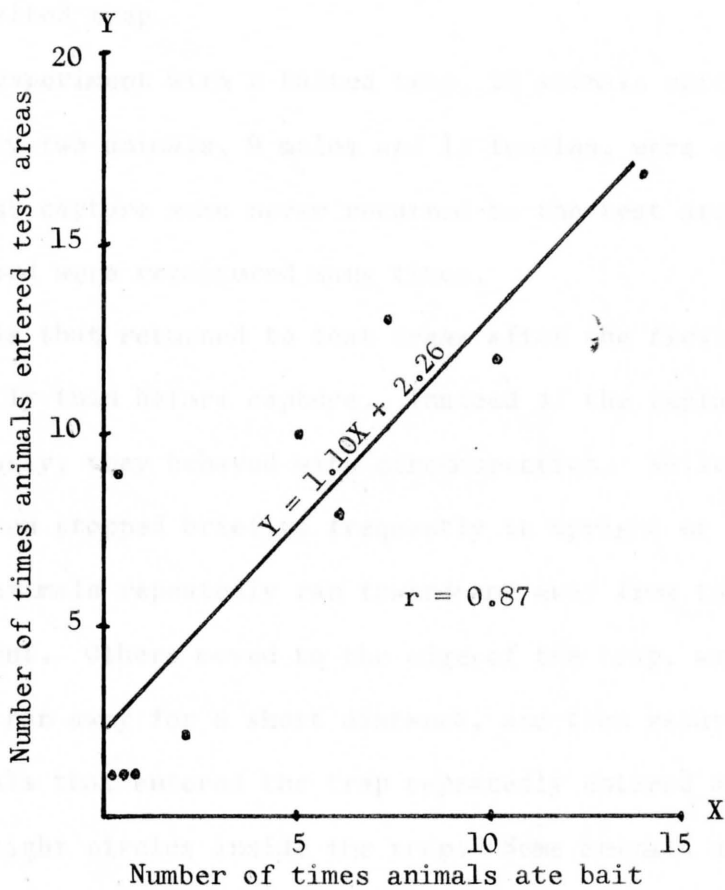


Figure 5. Comparison between number of times animals ate bait in wired trap and number of times they returned to test areas.

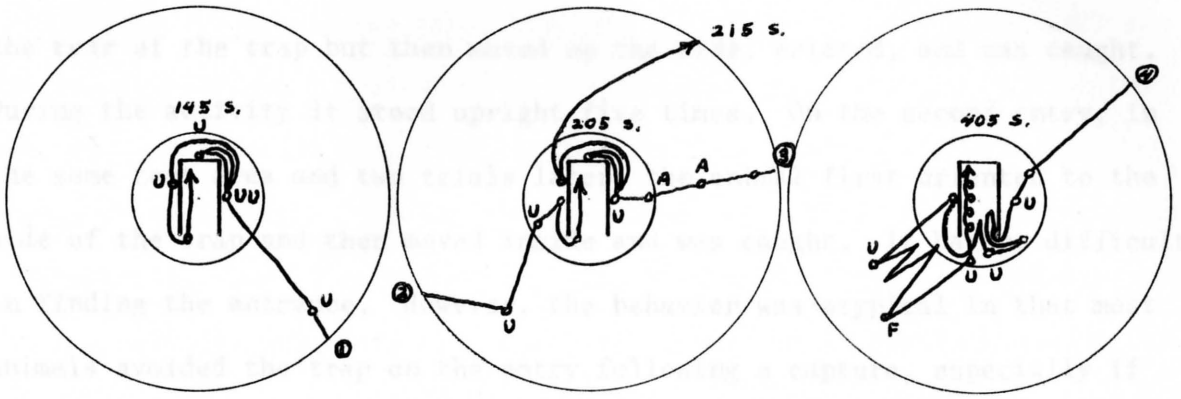
Learning with a baited trap

In the previous two topics I have dealt with the separate effects of bait and capture on the responses of ground squirrels to the trap. In this topic I shall consider the combined effects of bait and capture on their responses to a baited trap.

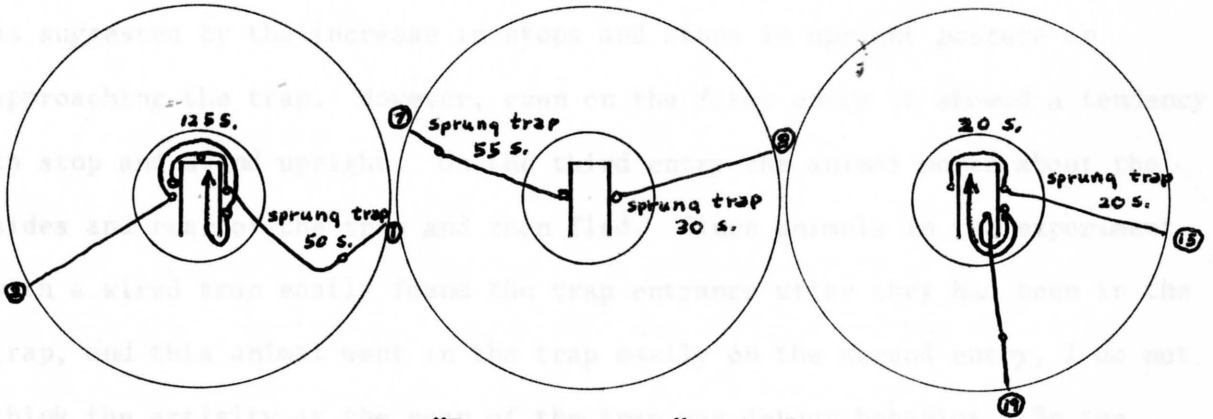
During the experiment with a baited trap, 28 animals entered test areas 187 times. Twenty-two animals, 9 males and 13 females, were caught at least once. After first capture some never returned to the test areas, while others returned and were recaptured many times.

Those animals that returned to test areas after the first capture behaved differently than before capture. Instead of the exploratory activity described previously, they behaved with circumspection. While moving toward the trap they often stopped briefly, frequently in upright or down-alert postures. Some animals repeatedly ran toward and away from the trap in ambivalent movement. Others moved to the edge of the trap, walked or ran along its edges, ran away for a short distance, and then returned to the trap. Some animals that entered the trap repeatedly entered and withdrew or turned about in tight circles inside the trap. Some animals displayed an elongated posture in the trap while moving toward the bait. They stretched their bodies full length and slowly and hesitantly moved forward. When reaching the bait they usually began eating immediately and were recaptured. At any point in the approach to the trap or bait an animal may have turned and left the area. To illustrate the activity more fully and also show its diversity, the following are trap-response histories of three animals:

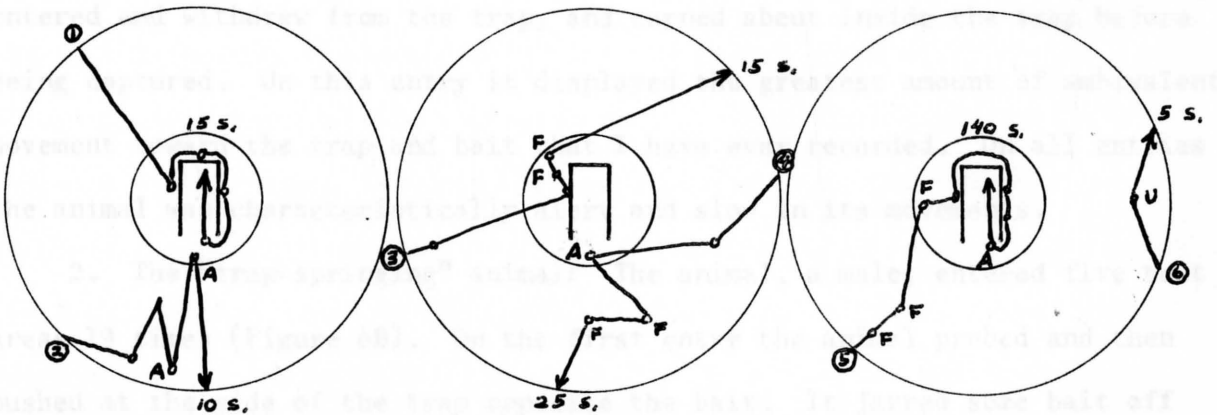
1. The "alert" animal: the animal, a male, entered two test areas four times (Figure 6A). On the first entry the animal approached the trap directly and oriented to the side. It showed some tendency to remain at



A. "Alert" animal



B. "Trap-springing" animal



C. "Typical" animal

Figure 6. Diagrams of activity of the (A) "Alert," (B) "Trap-springing," and (C) "Typical" animals on some successive entries into test areas with a baited trap. Symbols are as in Figure 3.

the rear of the trap but then moved up the side, entered, and was caught. During the activity it stood upright five times. On the second entry, in the same test area and two trials later, the animal first oriented to the side of the trap and then moved inside and was caught. It had no difficulty in finding the entrance. However, the behavior was atypical in that most animals avoided the trap on the entry following a capture, especially if the test area was the same and time between entries was short. Perhaps it was somewhat more hesitant in approaching the trap after the first capture as suggested by the increase in stops and stops in upright posture in approaching the trap. However, even on the first entry it showed a tendency to stop and stand upright. On the third entry the animal moved about the sides and rear of the trap and then fled. Since animals in the experiment with a wired trap easily found the trap entrance after they had been in the trap, and this animal went in the trap easily on the second entry, I do not think the activity at the rear of the trap was detour behavior. On the fourth entry the animal repeatedly moved toward and away from the trap, entered and withdrew from the trap, and turned about inside the trap before being captured. On this entry it displayed the greatest amount of ambivalent movement toward the trap and bait that I have ever recorded. On all entries the animal was characteristically alert and slow in its movements.

2. The "trap-springing" animal: The animal, a male, entered five test areas 19 times (Figure 6B). On the first entry the animal probed and then pushed at the side of the trap opposite the bait. It jarred some bait off the treadle, ate it, and finally sprung the trap. On the second entry it repeated the activity except that the trap remained set. Finally, it moved up the side, entered, and was caught. On the third entry, a different test area, the animal moved directly into the trap and was captured. On the

fourth entry it sprung the trap. On the fifth through nineteenth entries the animal continued the pattern of either jarring the trap and eating the bait or moving inside and being captured. Occasionally it approached and then avoided the trap. During the experiment the animal pushed the trap on 12 entries, sprung it on 9 entries, was captured on 5 entries, and approached and then avoided on 4 entries. Since the animal often obtained bait without being caught, I have excluded it from further consideration. During the experiments 5 of 60 animals sprung traps at least once. Many animals pushed at the sides of the trap or tried to dig under it with varying degrees of intensity.

3. The "typical" animal: The animal, a female, entered two test areas six times (Figure 6C). On the first entry the animal moved about the trap steadily, reached the entrance, entered, and was captured. On the second entry, a different test area, it approached and then avoided the trap twice. On the third entry the animal moved to the side of the trap, probed once, but then moved away and twice fed briefly before leaving the area. The feeding activity may have been redirected, displacement, or normal. The fourth entry was a continuation of the third in that the animal moved off the test area, stopped, and moved onto the test area again. This time it did not move to the edge of the trap but stopped in alert posture near the entrance and fed. On the fifth entry the animal approached the trap while feeding, moved about the trap, entered, and was captured. On the sixth entry the animal stopped once in upright posture and then moved on. It may or may not have been responding to the trap. The pattern that this animal displayed--capture followed by several entries in which it was not captured and showed conflict and then recapture--was the most common pattern among animals captured more than once in a baited trap.

Due to the variety of responses, an overall analysis of the data would have little meaning. Therefore, I shall present and discuss the results of the experiment with respect to individuals and groups of individuals based on the number of times they were captured and other factors that set them apart.

Nine animals, two males and seven females, were caught only once. The trial in which capture occurred varied from the first to the sixteenth with the average being the eighth (Table 13A). After capture they returned to the test areas 0-13 times with the average being 4 times (Table 13B). After capture three animals never returned to the test areas. Two had little opportunity to do so since only one trial remained in the experiment. The other animal was captured on its fifth entry into the test areas with seven trials remaining in the experiment. This animal did not eat bait. It was captured while exploring the inside of the trap and showed no interest in the bait. Other animals also may not have eaten the bait on the first capture. I could not always determine if an animal took bait before depressing the treadle. Closure of the trap door usually startled animals, and they stopped responding to the bait.

The remaining six animals captured only once returned to the test areas. On some entries they avoided the trap; on others they moved to the trap and probed its edges. One animal moved a few inches inside the trap before escaping. However, the result was always the same--at some point before reaching the bait they turned and fled. Except for one animal none moved repeatedly toward and away from the trap in ambivalence or entered the trap.

The activity of animals captured only once in a baited trap was similar to that of animals captured in an unbaited trap in that both groups showed strong avoidance. In both groups a few animals never returned to the test

Table 13. Average number of (A) trials and (B) entries into test areas before first capture and between successive captures

	Average number			
	Animals captured only 1 time (9) ^a	Animals captured only 2 times (6)	Animals captured only 3 times (3)	Animals captured 4 or more times (3)
A. Trials				
Before first capture	8.1 (0-16) ^b	2.8 (0-6)	3.0 (0-6)	3.0 (1-5)
Between cap. 1 and 2	8.0 ^c (1-15)	7.3 (2-12)	2.3 (0-6)	.3 (0-1)
Between cap. 2 and 3		5.5 ^c (0-10)	3.7 (3-4)	1.3 (0-4)
Between cap. 3 and 4			5.3 ^c (4-8)	.3 (0-1)
Between cap. 4 and 5				1.3 (0-3)
Between cap. 5 and 6				2.0 ^c (0-3)
B. Entries				
Before first capture	2.2 (1-4)	.2 (0-1)	.0 (0)	2.3 (1-5)
Between cap. 1 and 2	3.2 ^c (0-13)	1.3 (0-4)	.3 (0-1)	.3 (0-1)
Between cap. 2 and 3		.3 ^c (0-1)	1.3 (0-3)	1.0 (0-3)
Between cap. 3 and 4			.7 ^c (0-1)	1.0 (0-2)
Between cap. 4 and 5				2.0 (0-4)
Between cap. 5 and 6				.7 ^c (0-1)

^aNumber of individuals

^bRange in parentheses

^cValue before experiment ended

areas. Of those returning after capture, 44 percent entered the inner ring with the baited trap, and 41 percent entered the inner ring with the unbaited trap. However, 33 percent moved to the baited trap, and only 12 percent moved to the unbaited trap. This suggests that those captured only once in a baited trap subsequently had a greater tendency to approach closer to the trap before avoiding than did animals captured in an unbaited trap.

During the experiment 12 animals were captured more than once. Each was first captured within the first six trials. The number of times animals were captured more than once seemed to be independent of the trials remaining in the experiment at the time of first capture (Table 13A).

Six animals, three males and three females, were caught only twice. Before first capture they responded quickly to the trap and were captured either on the first or second test-area entry (Table 13A and B). An average of 7.3 trials went by before they were captured again. During this interval between captures they entered test areas 0-4 times. On these entries they displayed the full gamut of activity described previously. After the second capture an average of 5.5 trials remained in the experiment. However, only two animals returned, and they escaped before entering the inner ring.

Three animals, two males and one female, were captured only three times. Their response was similar to those captured twice. The number of trials between captures increased with each capture. Calhoun (1962) also noted this in wild rats. The number of entries between captures also increased until the third capture. After the third capture an average of 5.3 trials remained in the experiment. Two animals returned, but both avoided before entering the inner ring.

Of three animals captured 4 or more times, one male was captured 5 times, one male 7 times, and one female 12 times. The number of trials

between captures tended to increase with the number of captures. The animals of this group entered test areas more times before first capture than the two previous groups (Table 13B). The reason for this was that they tended to remain near the end of the trap and display detour behavior.

Those captured four or more times responded more like animals rewarded in a wired trap than any other group. They continued to return to the trap and be caught. They entered the inner ring, moved to the trap, and were captured more often per entry into the test areas than any other group (Figure 7A, B, and C). However, those captured four or more times also typified the circumspect behavior. They moved ambivalently, entered and withdrew from the trap, and displayed elongated posture more often per entry than any other group (Figure 7C, D, and E).

The major factor contributing to the behavior of ground squirrels after capture in a baited trap lay in the experience that the trap afforded. The unbaited trap offered punishment to animals. After capture they avoided the trap. The strength of avoidance tendency varied for individuals, but it was generally high enough to prevent recaptures (Figure 8A). The wired trap offered reward to animals. After eating bait they approached the trap. The strength of approach tendency also varied for these individuals, but it caused a majority to return repeatedly to the trap and eat bait (Figure 8B). The baited trap offered both punishment and reward to animals. The tendency of those that received both was to approach and avoid at the same time. The conflicting tendencies produced by the baited trap resulted in a capture distribution intermediate between that produced by the unbaited and wired trap (Figure 8C). The conflict also produced the circumspect behavior described previously--behavior typical of animals with opposing tendencies (Miller, 1937; Bastock et al., 1953). Masserman (1946) produced "experimental

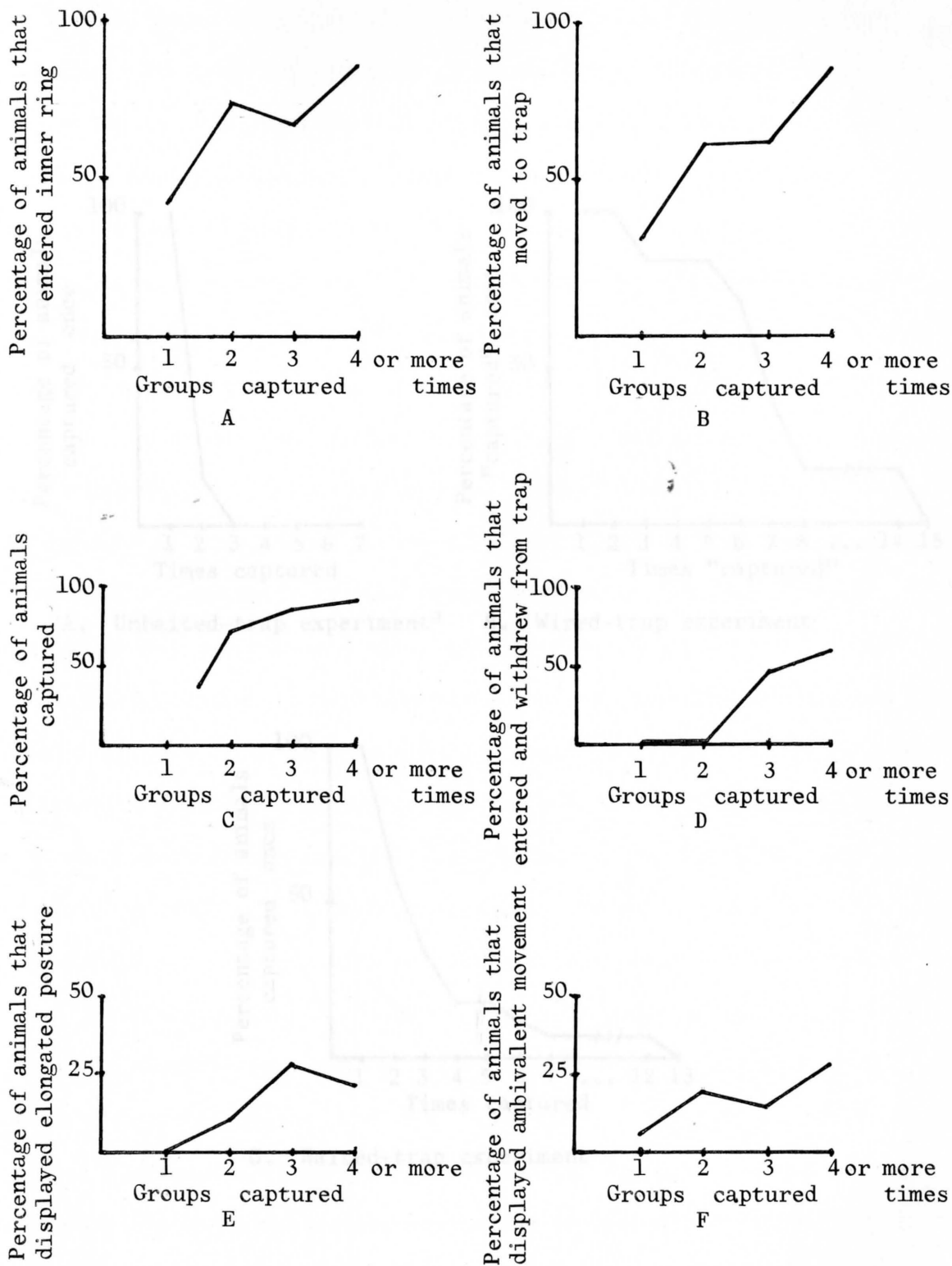
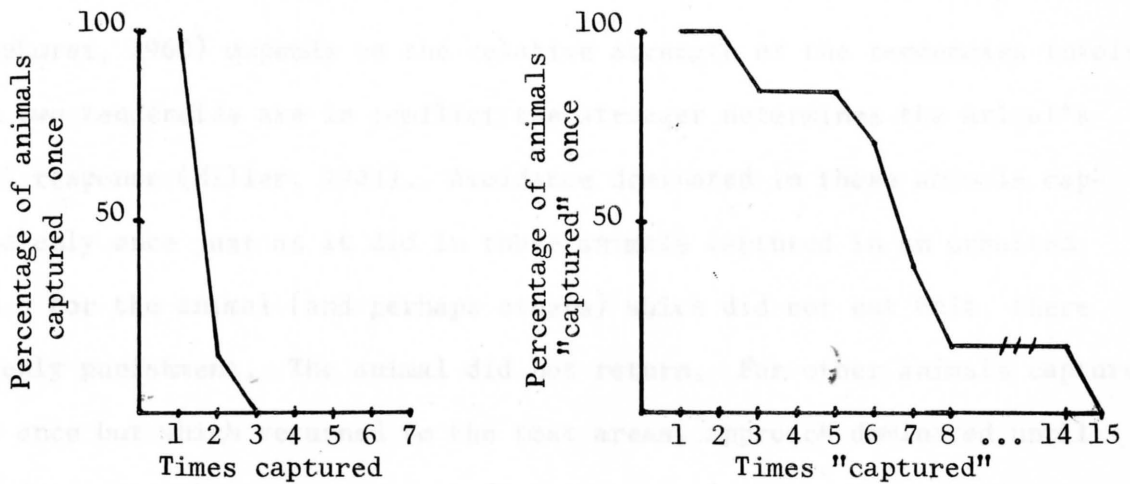
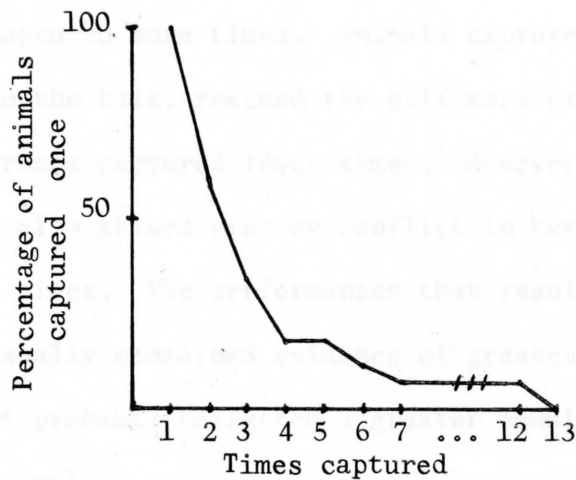


Figure 7. Activities in test areas of groups of animals captured only 1, 2, 3, and 4 or more times during the baited-trap experiment.



A. Unbaited-trap experiment^a B. Wired-trap experiment



C. Baited-trap experiment

Figure 8. Distribution of number of times animals were captured in three experiments.

^aNumber of individuals

neurosis" in domestic cats by simultaneously offering them reward and punishment. The cats responded to the stimuli with overt indication of conflict and certain physiological changes associated with stress.

The behavioral result of a conflict in tendencies (reviewed by Broadhurst, 1960) depends on the relative strength of the tendencies involved. When two tendencies are in conflict the stronger determines the animal's final response (Miller, 1944). Avoidance dominated in those animals captured only once just as it did in those animals captured in an unbaited trap. For the animal (and perhaps others) which did not eat bait, there was only punishment. The animal did not return. For other animals captured only once but which returned to the test areas, approach dominated until they drew near the trap. At some distance short of the trap or bait, avoidance became dominant and they left the test areas.

Approach relative to avoidance tendency was generally stronger in those groups of animals captured more times. Animals captured four or more times approached closer to the bait, reached the bait more often, and were recaptured sooner than groups captured fewer times. However, groups of animals captured more times also showed greater conflict in tendency than did groups caught fewer times. The performances that resulted in recapture or near recapture usually contained evidence of greatest conflict. The increase in conflict probably reflected a greater equality between the tendencies near the goal.

The performances of ground squirrels after capture in a baited trap were consistent with the results of studies on approach-avoidance gradients in laboratory rats (reviewed by Miller, 1959). As rats move closer to the goal, both the tendency to approach and avoid become stronger. However, the strength of avoidance increases more rapidly than the tendency to

approach (Brown, 1948). Animals with a weaker approach than avoidance tendency may readily approach the goal if it is at some distance. However, the animal will turn and flee short of the goal. Animals with a higher tendency to approach than avoid may move to the goal, but at the goal they are apt to be under the most conflict.

In ground squirrels recapture probably reinforced both approach and avoidance. The fact that the number of trials between successive captures tended to increase indicated that the strength of reinforcement for each tendency was not equal. Avoiding became stronger relative to approaching.

Based upon the performances of individuals in the unbaited, wired, and baited-trap experiments, I think the relative difference in level between the tendencies to approach for reward and to avoid the punishment determines whether or not an animal is recaptured. The desirability of the bait and the undesirability of capture determines the level of the two tendencies for each animal. Further, the relative difference in level between these conflicting tendencies after first capture and the differences in strength of reinforcement for each tendency on each successive capture determines the number of times an animal is recaptured within a specific period.

The results of the above three experiments shed some light on factors influencing recapture distributions. Biologists have tested the hypothesis that trapping captures animals at random by testing the fitness of capture distributions with the expected distribution. The expected distribution under the assumption of random capture is that of the Poisson or binomial type. Some researchers find that their capture data fit the expected distribution (Tanaka, 1956), while others find that they do not (Huber, 1962). Data that do not fit usually indicate a large group of animals are not caught or are caught only once, and that a few animals are caught many

more times than expected. Biologists interpret these results in several ways. Andrzejewski and Wierzbowski (1960) and others deal with the large group captured once as migrant animals. Many researchers have surmised that some animals must be characteristically trap-prone or trap-shy (Young et al., 1952; King, 1955; and others), or that learning somehow affects the recapture data (Thompson, 1953; Sealander et al., 1958; Calhoun, 1962; and others).

Uinta ground squirrels did learn from experience with a trap. If they did not, recapture distributions for the three experiments (Figure 8) would be the same. The distribution of animals captured in a baited trap did not fit the expected distribution under the assumption of random capture ($\chi^2 =$ over 100). However, the question of whether or not the distribution fits the expected is immaterial with respect to the question of whether or not trapping selects animals at random. The behavioral responses of ground squirrels to trapping violates the definition of randomness: that each animal in the population has an equal and independent chance of being captured and recaptured. The recapture distribution obtained by trapping is really the product of variation among individuals in their responses to the trapping experience.

Effect of prebaiting

The objective of this topic is to investigate the effect of prebaiting on the responses of animals to a baited and functional trap. In this topic I shall consider the performances of two groups of animals: one group subjected to prebaiting procedures represented by the 10 animals that entered test areas during 16 trials with a wired trap, and the other not subjected to prebaiting represented by the 28 animals that entered the test areas during 16 trials with a baited and functional trap. I shall compare

the performances of animals in the first 5 and first 16 trials of the baited-trap experiment with those in the 5 trials of the experiment with a baited trap after prebaiting. The latter experiment was a continuation of the one with a wired trap in that I made the trap functional after 16 trials and continued the experiment for 5 more trials.

On five trials a greater percentage of animals subjected to prebaiting subsequently moved into the test areas and were caught than the animals not subjected to prebaiting (Table 14). However, on 16 trials all animals not subjected to prebaiting entered the test areas (by definition), and the percentage captured exceeded the percentage captured on 5 trials in the prebaited group (Table 14). These data indicate that animals subjected to prebaiting are captured more quickly than those not subjected to prebaiting. Capture data on voles suggest much the same thing (Chitty and Kempson, 1949).

On the 10 animals that had experienced prebaiting procedures, 5 showed no response to the trap, and 5 were captured 13 times. Of those that showed no response, two entered test areas, and three did not. However, those that did not respond did approach the trap during the prebaiting procedure. But after exploring the trap a few times they displayed little further interest in it. Their lack of interest continued after I made the trap functional.

In contrast to the prebaited group, the animals that were not prebaited did not show the bifurcation of response into capture or no apparent response. Some animals repeatedly approached the trap but were never captured. Others were captured on the first approach and never returned. Still others were captured repeatedly.

The difference in response between the two groups indicates that prebaiting reduces the variability of response to trapping. It does this

Table 14. Percentage of animals in prebaited and nonprebaited groups that entered test areas and were captured

Results	Percent of animals entering test areas		
	Animals subjected to prebaiting	Animals not subjected to prebaiting	
	(10) ^a 5 trials	(28) ^a 5 trials	(28) ^a 16 trials
Entered test areas	70	22	100
Captured	50	7	71

^aNumber of individuals

by decreasing the number of animals responding to the trap to a core of individuals that readily enter the trap. Prebaiting tends to eliminate from around the trap those animals that have little interest in the bait but yet may be captured while investigating the trap. In this way prebaiting may reduce the total number captured in an area over the long term. The reduction may not apply to other species that use olfaction to find food and/or avoid strange objects.

Prebaited animals responded rather uniformly to the trap. During prebaiting five animals began using the trap as a feeding station. After I made the trap functional, all were caught on their first entry into the test areas. In each case they entered the trap directly. On the second entry into the test areas all approached, three avoided, and two were recaptured. On the third entry all approached and then avoided. After five trials all five animals were recaptured at least once. In contrast, animals not subjected to prebaiting seldom entered the trap directly, none were recaptured within five trials, and a large percentage were not recaptured in 16 trials (Table 15).

The factors that contributed to the more uniform response of prebaited animals than animals not prebaited were associated with the learning that occurred during prebaiting. During prebaiting animals became oriented to the bait as a goal and learned how to enter the trap directly. Eating the bait repeatedly without capture reinforced approach to the trap. After capture the tendency to approach remained strong, at least over five trials, as evidenced by the strong tendency to return to the trap and eat the bait again. Laboratory rats show the same tendency of moving to the goal despite punishment, if previously they are repeatedly rewarded for approaching the goal (Kaufman and Miller, 1949).

Table 15. Percentage of prebaited and nonprebaited animals entering test areas that were recaptured

Recaptured	Percent of animals captured once		
	Prebaited animals 5 trials (5) ^a	Nonprebaited animals 5 trials (2) ^a	16 trials (20) ^a
One or more times	100	0	60
Two or more times	40	0	35
Three or more times	20	0	20

^aNumber of individuals

Associative learning

My first objective in this topic is to see if ground squirrels associate trap experience with trap location without the presence of the trap. To approach this objective I shall compare the results of three experiments: the standard (activity without the influence of trapping), wired-trap standard (activity during the 30-minute period following removal of the wired trap which offered reward), and baited-trap-after-prebaiting standard (activity during the 30-minute period following removal of the baited trap after prebaiting which offered reward and punishment.

A comparison between the performances of animals in the standard and wired-trap standard shows that trap experience significantly modifies the subsequent behavior of animals at the location (Table 16). A larger percentage of the animals that entered test areas also entered the inner ring in the wired-trap standard than in the standard. They also turned, stopped, and fed more than in the standard (Table 17). Animals entered test areas at a rate of 1.7 per observation hour in the wired trap standard and 1.1 in the standard. Hence, animals tend to return to a trapping location where they have received reward, at least during the 30-minute period after removing the trap.

The tendency to explore and feed may have contributed to the return of animals to the rewarding location. In the test areas animals often moved directly to the spot where the trap had been stopped, sniffed at the ground, and appeared to explore the area. Removal of the trap constituted a change in the environment. Barnett (1963) states that a change in the environment often releases exploratory behavior in animals. Most ground squirrels fed when they came into the test areas after removal of the trap. Since the animals had been using the trap as a feeding station, they may have approached

Table 16. Movement patterns of animals in test areas in standard, wired-trap standard, and baited-trap-after-prebaiting standard experiments

Movement pattern	Percent of animals entering test areas ^a		
	Standard (58/22) ^b	Wired-trap standard (55/8)	Prebaited standard (17/7)
Entered outer ring only	85	49	76
Entered inner ring	16	51	24
Passed through	28	31	18

^aTest of independence: standard and wired-trap standard,
 $\chi^2 = 16.5$ ($\chi^2_{.99} = 9.2$)

wired-trap standard and prebaited standard,
 $\chi^2 = 4.8$ ($\chi^2_{.90} = 4.6$)

^bNumber of samples/number of individuals

Table 17. Activities of animals in inner ring of test area in standard and wired-trap standard experiments

Activity	Average occurrence of activity per animal	
	Standard (9/?) ^b	Prebaited standard (28/7)
Turned	.3 (0-2) ^a	.6 (0-3)
Stopped	.8 (0-2)	1.2 (0-4)
Fed	.7 (0-2)	1.0 (0-3)

^aRange in parentheses

^bNumber of samples/number of individuals

the area to feed on bait. Finding the trap absent they perhaps redirected feeding from bait to grass.

A comparison between the performances of animals in the wired-trap standard and baited-trap standard should show if the type of trap experience affects subsequent responses to the trap locations. A lesser percentage of the animals that entered the test areas also enter the inner ring in the prebaited standard than in the wired-trap standard (Table 16). The percentage becomes even less when considering only the activity of animals at the location after they have been captured. After capture only one animal returned to the inner ring after removal of the trap. It displayed ambivalent movement and alert behavior but also fed. Others approached the area where the trap had been but turned off before reaching the inner ring. They still tended to stop and feed in the outer ring. These facts suggest that animals are more hesitant about approaching locations where they have received both reward and punishment than where they have received only reward. Hence, capture likely added avoidance to the exploratory and feeding tendencies discussed previously.

I think that in general ground squirrels respond to the trapping location the same as they would if the trap were still present except at a lower intensity. They associate trap experience with trap location. Laboratory rats also display a location response--the response being consistent with the type of experience they have received at the location (Mowrer, 1960). However, the above discussion regarding ground squirrels only concerns the 30-minute period following removal of the trap. I have no information on habituation to the trap location.

My second objective in this topic is to see if ground squirrels captured once display the same response on the next approach to the trap at the same

location as they do to the trap at a different location. To approach the objective I shall consider those animals that were captured once in a baited trap and that subsequently returned either to a trap at the same or different location.

Before capture and on the second entry into a test area, 60 percent of the animals entered the same test area they did on the first entry. After first entry the average number of entries into different test areas before they returned to the initial test area was .8. In contrast, after first capture 47 percent of the animals entered the same test area in which they were captured. The average number of entries into different test areas before they returned to the test area of capture was 1.9. These data suggest that before capture animals tend to return to the same test areas, but after capture they tend to go to a test area other than the one in which they were first captured.

On the first entry into a test area after first capture, 9 animals entered the same and 10 animals entered a different test area. A lesser percentage of the animals that entered the same test area also entered the inner ring and were captured than those that entered a different test area (Table 18). Only animals entering the same test area displayed the elongated posture of conflict while in the trap (Table 18). Animals entering a different test area were more active in the inner ring than those entering the same test area. They turned, stopped, probed, and turned trap corners more (Table 19). These data suggest that animals show more hesitancy in approaching the trap and bait in the test area of first capture than they do in a different test area.

Since ground squirrels respond to both trap and trap location, moving the trap to a new location modifies the stimulus causing the approach and

Table 18. Movement patterns in test areas of animals on first test-area entry after first capture at same and different location

Movement pattern	Percent of animals entering test areas ^a	
	Same area (NS9) ^b	Different area (NS10)
Entered inner ring	77	90
Captured	33	50
Elongated posture	22	0

^aTest of independence: $\chi^2 = 5.3$ ($\chi^2_{.90} = 4.6$)

^bNumber of individuals

Table 19. Activities of animals in inner ring of test areas on first test-area entry after capture at same and different location

Activity	Average occurrence of activity per animal	
	Same area (7) ^b	Different area (9)
Turned	2.3 (1-4) ^a	3.7 (1-7)
Stopped	2.4 (1-4)	3.0 (1-6)
Probed	2.0 (0-4)	2.3 (0-4)
Turned trap corner	.9 (0-2)	2.6 (0-5)

^aRange in parentheses

^bNumber of individuals

avoidance tendencies. Modification of the stimulus caused by moving the trap apparently decreases the avoidance tendency relative to the approach tendency, thus allowing the animals to more readily approach the trap in a new location. Stimulus generalization for laboratory rats also weakens the tendency to avoid more than to approach (Murray and Miller, 1952; Miller and Kraeling, 1952).

The behavior of animals, for example, of usually attracts the animals, a trapper should do everything possible to take them away from the trap. If a flag attached to the trap accomplishes this without causing avoidance, then he should use flags. If the capture experience causes strong avoidance to the trap, he should do everything possible to increase the reward aspect and decrease the punishment aspect of the capture experience. If a trapper is concerned with capturing as many different ground squirrels as possible, he should not prowl. The point is that with a knowledge of how animals respond to trapping, one can design procedures that will take advantage of their behavior in obtaining the type of information desired.

I think the study also illustrates the need for a closer relationship between both biologists and psychologists interested in the behavior of animals. Experimental psychologists have studied learning for years using the laboratory rat as the experimental animal. However, they have not actively bred the rat for laboratory use and have conducted most experiments in the sterile environment of the Skinner box or maze. Many biologists and psychologists have ventured how much of the information gained on laboratory rats can be applied to wild species in their natural environments. The fact that many of the responses of ground squirrels to the trap could have been predicted on the basis of what is known about learning in laboratory rats makes obvious the value of the research done by psychologists for field biologists interested in animal behavior.

GENERAL CONCLUSIONS

Behavior is an important consideration in trapping animals. For efficient trapping, the procedures should be built around a knowledge of the behavior of animals. For example, if novelty attracts the animals, a trapper should do everything possible to make them aware of the trap. If a flag attached to the trap accomplishes this without causing avoidance, then he should use flags. If the capture experience causes strong avoidance to the trap, he should do everything possible to increase the reward aspect and decrease the punishment aspect of the capture experience. If a trapper is concerned with capturing as many different ground squirrels as possible, he should not prebait. The point is that with a knowledge of how animals respond to trapping, one can design procedures that will take advantage of their behavior in obtaining the type of information desired.

I think ^{Little} the study also illustrates the need for a closer relationship between both biologists and psychologists interested in the behavior of animals. Experimental psychologists have studied learning for years using the laboratory rat as the experimental animal. However, they have selectively bred the rat for laboratory use, and have conducted most experiments in the sterile environment of the Skinner box or maze. Many biologists and psychologists have wondered how much of the information gained on laboratory rats can be applied to wild species in their natural environments. The fact that many of the responses of ground squirrels to the trap could have been predicted on the basis of what is known about learning in laboratory rats makes obvious the value of the research done by psychologists for field biologists interested in animal behavior.

SUMMARY

This study concerned the behavioral responses of adult Uinta ground squirrels, Citellus armatus, to trapping. The objective was to learn how animals responded to a trap, to capture, and to recapture. I based the study on the direct observation of the performances of known individuals in seven experiments conducted on a wild population.

The following is an outline of the sections and topics contained in the report and the major points brought out in each:

I. Activity without the influence of a trap. The purpose of this section was to show the movement and behavior of animals in the test areas independent of trapping procedures.

II. The initial approach and capture. The purpose of this section was to investigate the initial responses of ground squirrels to trapping as opposed to their responses after trap experience which may have involved learning.

1. Role of the trap: The objective was to see how animals responded to an unbaited trap when first encountering it.

a. The unbaited trap tended to attract animals.

b. Environmental factors may have contributed to the strong tendency of animals to approach and explore the trap.

2. Role of bait: The objective was to see what role the bait played in an animal's first encounter with a trap.

a. Bait added to the trap's attraction, but the trap seemed to be the primary attractor.

b. Animals were more active and stayed longer around a baited trap than an unbaited trap. However, bait tended to hold animals at the rear of the trap and away from the entrance. The two effects cancelled one another, and the probability of capture on the first encounter was the same in both baited and unbaited traps.

c. A better trap for the ground squirrel would be one in which they could enter from any direction. Such a trap would then take advantage of even a slight tendency to explore, and would not present the problem of "finding" the entrance.

3. The first capture: The objective was to determine what activity led to an animal's first capture and what activity did not.

a. Animals that were captured generally moved about the trap in one direction and stayed close to its edge.

b. Animals that were not captured either did not chance upon the trap entrance, showed little interest in the trap, or showed strong interest in the bait and became fixed to the rear of the trap.

III. Learning. The purpose of this section was to investigate the responses of animals to various experiences with a trap.

1. Learning with an unbaited trap: The objective was to see how capture in an unbaited trap affected subsequent responses of animals to the trap.

a. Capture punished animals, and they learned to avoid the trap.

b. The strength of avoidance caused by capture experience varied among individuals.

2. Learning with a wired trap: The objective was to see how eating

bait in a nonfunctional trap affected subsequent responses of animals to the trap.

a. Eating bait rewarded animals, and they learned to enter the trap to get bait.

b. The more times animals ate bait, the more directly they went to the bait.

c. The amount of attraction bait had varied for each individual, and was probably a major factor in the number of times they returned to the trap to get bait.

3. Learning with a baited trap: The objective was to see how both bait and capture combined affected the responses of animals to the trap.

a. The baited trap produced conflict between the tendencies to approach and to avoid.

b. The relative difference in strength between the tendencies to approach for reward and to avoid the punishment probably determined whether or not an animal was recaptured.

c. The relative difference in strength between the conflicting tendencies after first capture and the difference in strength of reinforcement for each tendency on each successive capture determined the number of times animals were recaptured during the experiment.

4. The effect of prebaiting: The objective was to see how prebaiting affected the responses of animals to a baited and functional trap.

a. Animals subjected to prebaiting were captured more quickly than those not subjected to prebaiting.

b. Prebaiting decreased the number of animals responding to

the trap to a core of individuals that readily entered the trap.

c. Prebaiting functioned to reinforce entering the trap for bait. After capture the tendency to enter the trap remained strong.

5. Associative learning: The first objective was to see if animals associated trap experience with trap location.

a. Animals tended to return to a trapping location where they had received reward.

b. Animals tended to avoid a trapping location where they had received both reward and punishment.

The second objective was to see if animals captured once responded the same on the next approach to the trap at the same location as they did to the trap at a different location.

a. Animals showed more hesitancy in approaching the trap and bait in the test area of first capture than they did in a different test area.

b. The trap at a new location apparently decreased the avoidance tendency relative to the approach tendency, thus allowing the animals to more readily approach the trap at a new location.

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