OLFACTION AS A POSSIBLE MECHANISM FOR PREY SELECTION IN THE LEAST WEASEL, MUSTELA NIVALIS

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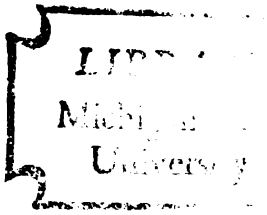

ABSTRACT

OLFACTION AS A POSSIBLE MECHANISM FOR PREY SELECTION IN THE LEAST WEASEL, MUSTELA NIVALIS

By Danny G. Herman

Three least weasels were tested in a plexiglass y-maze to determine the extent to which this species could effectively use olfaction in prey detection. Prior to testing individual animals it was necessary to verify the non-selective nature of the maze (Test I). The results showed no indication that the arm of the maze chosen by test animals was accomplished by anything but random choice.

Three separate tests were performed on the test animals. The first two of these tests consisted of running a potential prey animal through the maze (one arm only) then allowing the weasel to run the maze. Test II (2) was conducted in daylight while Test III(3) was conducted in the dark. The fourth (4) test was carried out by running one prey animal through the maze and placing another prey animal in the opposite arm of the maze and allowing the weasel to then run the maze.

Results were analyzed using the Chi-square analysis for goodness of fit. It was concluded that the least weasel can use olfactory cues alone to detect and find potential prey. The results also suggest that under the conditions of these tests, the weasel detected the prey animals by substrate borne rather than air borne olfactory cues.

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by

Danny G. Herman

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The least weasel (Mustela nivalis Linnaeus) smallest of all known carnivors, is holarctic in distribution (Ellerman and Morrison-Scott, 1966; Hall and Kelson, 1959; Hall, 1951) and inhabits primarily ecotonal or transitional areas between woodlands, bogs and grasslands (Beer, 1949 and 1950; Soper, 1946) throughout all of Michigan (Allen, 1940; Hatt, 1940; Dearborn, 1932). It appears to prey exclusively on rodents occuring in the same type of habitat, such as Reithrodontomys sp. (Polderboer, 1942) Peromyscus maniculatus (Polderboer, 1942; Seton, 1929) Clethrionomys gapperi and Microtus pennsylvanicus (Criddle, 1947). Although there have been occasions where it was believed that M. nivalis was consuming insects and other invertebrates (Abbott, 1884; Seton, 1929) there is no critical evidence to indicate that this is indeed true. This lack of evidence does not preclude the possibility that at some times the least weasel may feed on invertebrates or other small vertebrates (i.e. birds, reptiles, amphibians, etc.).

The least weasel being relatively small, 40-50 grams (Burt, 1967) must spend a sizable amount of energy in capturing prey (Short, 1961). Although the weasel restricts himself to the la. size prey class (Rosenzweig, 1966) which consists of animals from zero to 50 grams, it is very likely that it would at times be required to attempt to kill an animal of equal or greater body weight than his own. This little carnivor has, however, a prey handling mechanism, killing by bitting through the base of the skull, (Heidt, 1970; Moore, 1945; Glover, 1943; Llewellyn, 1942; Allen, 1938; Hamilton, 1933; Seton, 1929)

which greatly reduces prey handling time and thus may decrease the energy required to successfully acquire food.

Another source of energy loss in the prey seeking activities of not only the least weasel but of all non-sessile food gathers, is the energy expenditure required to move the food seeking animal from one energy source to the next. Whether this avenue of energy loss occurs to any large extent in the least weasel is irrelevant; the reduction of this energy loss no matter how small could be of great advantage to the individual (Emlen, 1966). Therefore, any additional mechanisms, behavioral and/or physiological, which accomplish this reduction would also be advantageous to the animal possessing them.

It is the feeling of this investigator that the ability to detect potential prey at a distance, using whatever environmental sampling or sensing devices available to the animal, would greatly increase its energy gathering ability over that of a strictly random, chance encounter, foraging strategy and in so doing also increase its potential for survival. Taking into consideration the type of environment that the least weasel inhabits (i.e. thick brushy areas of low visability) and the type of sensing devices available to it, it appears to this investigator that the sense which would be most likely employed to best advantage for remote prey detection is olfaction. It will, therefore, be the intent of this research to attempt to discover whether or not the capability for using this scent detecting device exists. If the capability exists then the ability of the weasel to use it to detect prey will be investigated.

METHODS AND MATERIALS

Experimental Animals and Maintenance

All weasels used in this study were wild caught using either Sherman live traps or the modified starling trap as shown in Figure 1. The latter was constructed of .635 cm hardware cloth and contained three inverted cones which projected through the end walls and one side of the trap. The trap measured 45.74 cm x 45.74 cm x 91.44 cm. Each of the cones was 22.86 cm long with a 15.24 cm exterior opening and a 2.54 cm interior opening.

Prior to placement into the colony individuals were weighed, had their sex determined, and assigned a sequence identification number. This information pertinent to either the animal's identification or natural history was recorded. One copy was attached to the animal's cage and the other was maintained in a file. Due to reports by other investigators concerning unexplainable deaths of least weasels in captivity (Heidt, 1970; Short, 1961; Phillips, 1949) it was decided that toe clipping for identification purposes would not be employed. This investigator felt that this practice would introduce a needless possible source of infection which would greatly overshadow any advantage it might have in keeping animals separated. It was also felt that it might lead to a reduction in killing effectiveness as a result of the reduction of digits. During the course of this study, elimination of toe clipping did not prove to be an identification problem principally because of the low numbers of individuals maintained at any one time and also the practice of housing animals separately. However, if large numbers of animals are to be kept and dormatory housing is to be

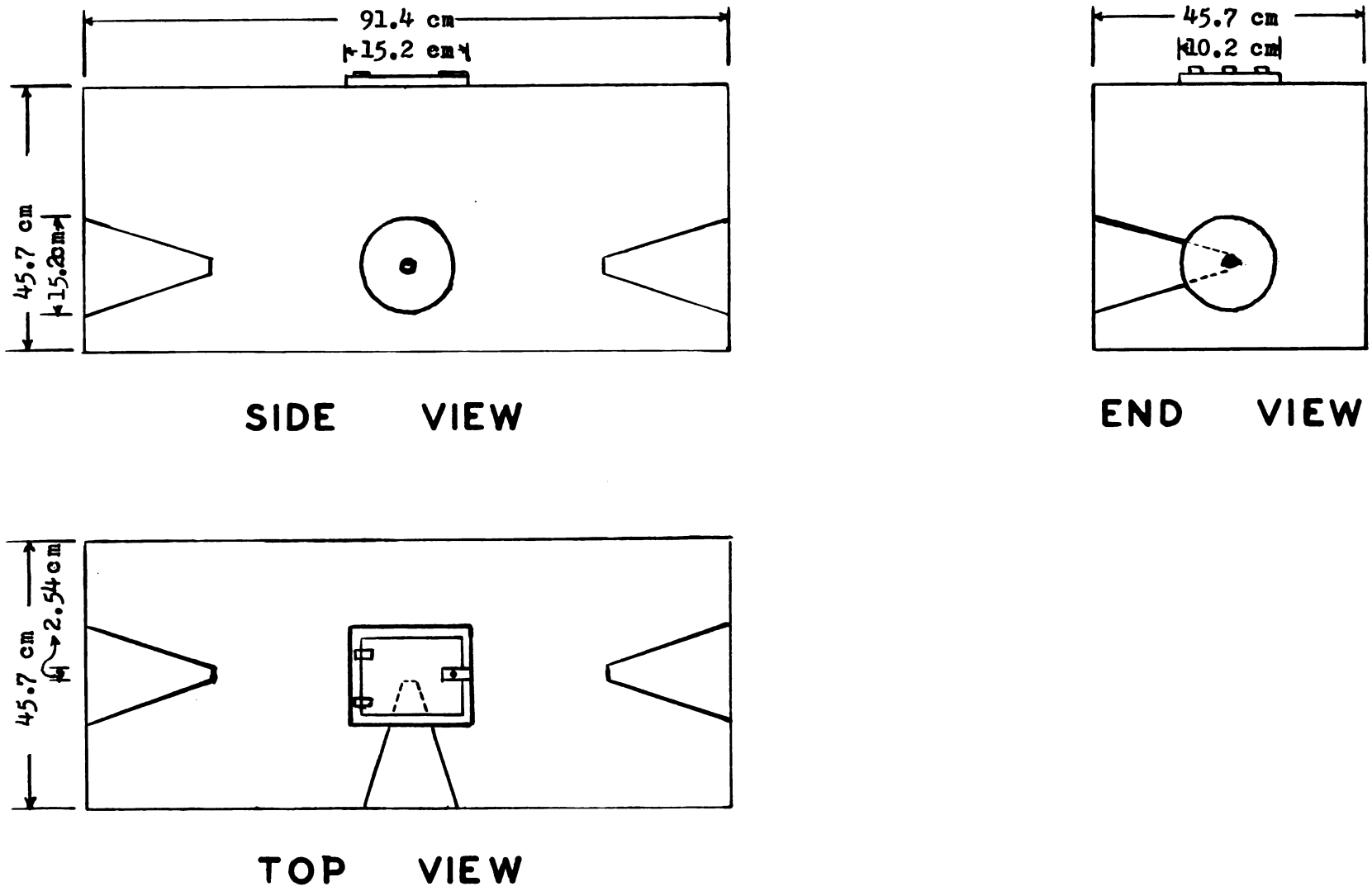

Figure 1: Modified starling trap used to capture Mustela nivalis. Basic design taken from Marsh and Clark (1968)

employed, toe clipping would be strongly advised.

Any animals that died during the study were added to the MSU Museum collection, all pertinent information being recorded in the Museum catalogue at the time the study skins were prepared. Animals remaining alive at the end of the study were given to the Museum for further study.

Housing and Nutrition

All weasels were initially placed in duel-compartment standard cages (Heidt, 1970) which measured 86.3 x 30.5 x 38.00 cm. The cages were basically of wood construction, the entrance to which was gained through twin wooden framed .635 cm hardware cloth tops. For ease of viewing animals the cage fronts were made of plate glass. The ends of the cages had 15 x 18 cm ventilation ports cut into them which were also covered with .635 cm hardware cloth. Each cage was divided into two compartments of equal size, and were separated by a sliding partition of either plywood or .635 cm hardware cloth. This screen could be removed at any time by lifting it through a slot cut in the top of the cage provided expressly for this purpose. Wood shavings were chosen as bedding material due to their absorbancy, deoderizing effect, relative low cost, and availability. For sanitation purposes all bedding was changed weekly although it did not appear to be necessary to change the bedding that frequently.

Wooden nest boxes 15 x 10 x 10 cm were placed in each compartment containing an animal. A 2.54 cm hole was placed in one end of the nest box to act as an entry way. The tops of the boxes were hinged to facilitate occasional observation and cleaning.

Toward the end of this study all animals were transferred to standard metal lab cages (30.48 x 34.56 x 52.07 cm) with hinged screen tops. This was done to meet federal standards as prescribed by Parts 1, 2, 3 of Subchapter A, Chapter I, Title 9, Code of Federal Regulations which set the guidelines for housing and maintenance of captive experimental animals. Bedding, nest boxes, and cage care were the same as used in the wooden cages.

Weasels were fed live rodents every 24 hours either in their cage or in the test apparatus. Mus musculus was the most frequently used food source although Peromyscus, Microtus, Sigmodon, and Zapus were used on occasion. In addition to live mice each weasel was provided with lab chow, which appeared to receive very little attention. Mink food consisting of whole ground fish and chicken was given when possible, but if this was not available a commercially prepared dog or cat food was substituted. Mixed foods and lab chow were placed in glass finger bowls to prevent fouling of the bedding and contamination of the food. These were cleaned and refilled daily. Water bottles were placed in each compartment to provide a constant supply of water.

Animals used as prey species in this study consisted of Mus musculus taken from a laboratory colony maintained by the Psychology Department of Michigan State University, Peromyscus sp. provided by the Behavioral Research Laboratory of the Zoology Department of Michigan State University, and Microtus pennsylvanicus which were captured in Sherman live traps on the Michigan State University campus or supplied by Dr. F. Elliott of the Department of Crop and Soil Science, Michigan State University.

Prey animals were maintained in 20.32 x 20.32 x 40.64 cm plastic cages with perforated stainless steel tops. Wood shavings were also used as bedding in these cages. Mice were fed Purina lab chow placed in 5.08 x 10.16 x 15.24 cm metal food hoppers hung from the inside of the cage wall. Water was continuously supplied from water bottles, the nozzles of which were projected through the top of the cage. The cages containing these animals were maintained separately from the weasels and were kept on cage racks in the Michigan State University Museum Small Animal Colony.

Test Apparatus

Directional responses to olfactory stimulants were tested using a y-maze constructed of acrylic plate. The y-maze constructed (see Figure 2) consisted of four distinct interlocking components: A-one combination trap and holding compartment, B-one holding compartment and maze entrance, C-two maze arms and D-two pivot door box traps attached to the end of each maze arm. Except for the entrance way of compartment A, which was constructed of 2.54 cm pine board, the entire maze was made of .317 cm acrylic plate all immovable components of which were bonded together with an acrylic solvent, methylene chloride. Compartment A, 11.43 x 11.43 x 20.32 cm with a guillotine type door at each end was used to trap the weasel and remove him from his cage and transport him to the study area. This eliminated the necessity for direct handling of the weasel or a transfer operation from a non-integral trap to the test apparatus. A 2.54 cm diameter hole was bored in the front, wooden partition through which the weasel entered the trap compartment,

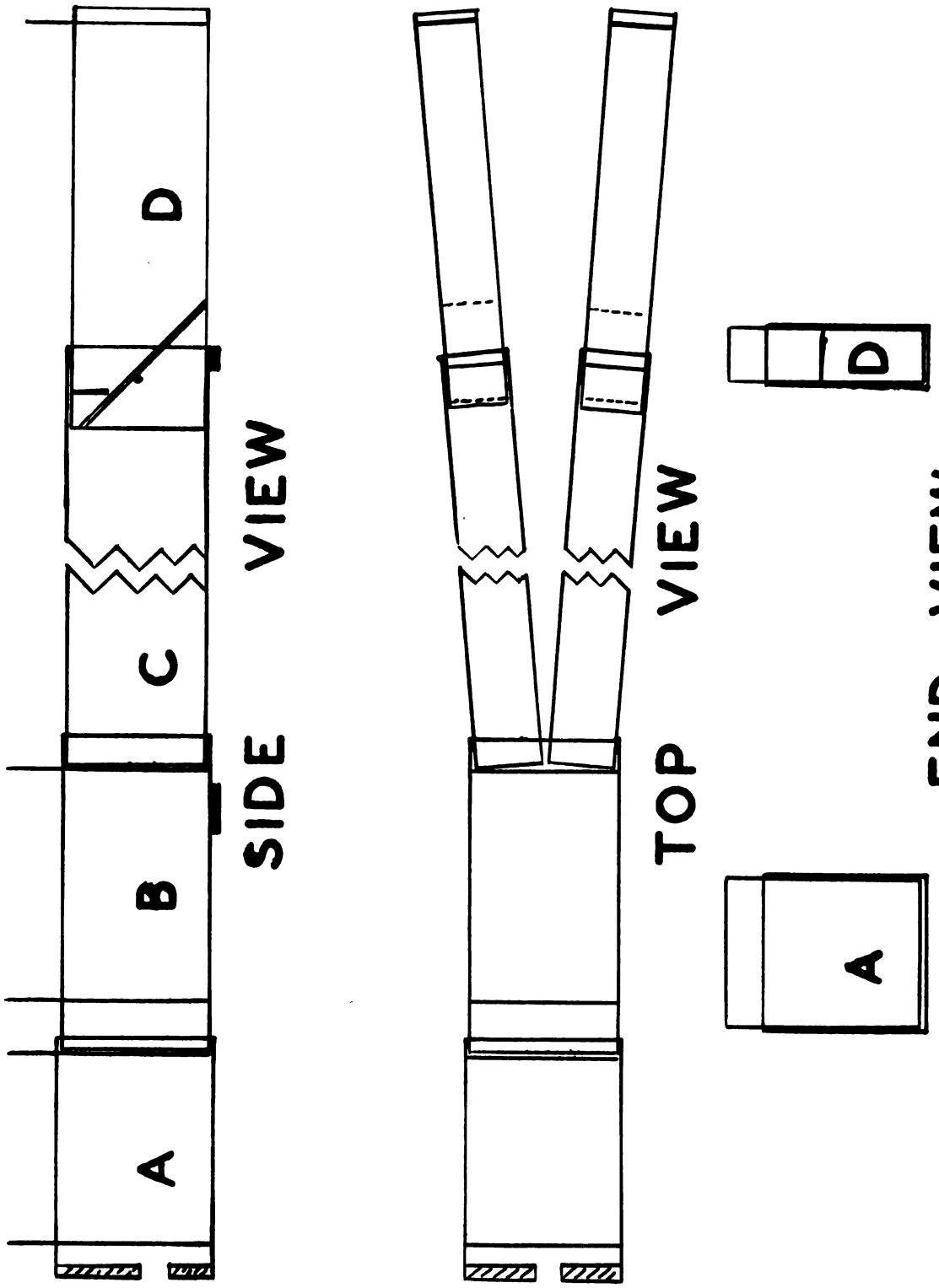

Figure 2: Y-maze used to test the directional response of weasels

the guillotine door being lowered behind him. In this way the weasel could be handled and transported with only limited disturbance to the subject and very little chance of escape.

The second compartment in the series measured 10.8 x 10.8 x 25.4 cm with quillotine doors at each end and was used as an acclimation chamber in the first test and as a prey holding and maze entrance in the remaining three tests. This is referred to as compartment B in Figure 2.

Each of the maze arms, component C, measured 5.08 x 10.16 x 152.5 cm and was provided with a removable top to facilitate cleaning and maintenance. In order to insure as little scent transfer and holdover as possible from trial to trial, the arms of the maze were lined with saran-wrap which was removed and replaced after each trial.

Granulated clay of the type used for cat litter, was employed as the maze arm substrate upon which both the prey species and the intended predator were required to run. This substance was chosen because of uniformity of particle size, moisture content, cleanliness and its unscented characteristics. The clay was placed on both arms of the maze, to a depth of approximately .635 cm and smoothed out with a piece of acrylic plate cut for this purpose.

The last section of the maze consisted of two pivot door traps, 4.45 x 9.52 x 22.86 cm which when in use were inserted about 1.27 cm into the terminal end of the maze arm. The weasel, in order to enter the trap was required to lift the base of the pivot door, which was taped over to prevent the weasel from seeing the prey or visa versa, and crawl under it. The door was

supplied with top and bottom guard plates so that once inside the weasel could no longer operate the door. The rear of the trap was closed off by a final guillotine type door used to either replace the animal in the first compartment of the maze or return the animal to its cage.

After each trial run the clay was removed and the entire maze washed out with tap water and allowed to air dry.

Test I

The first series of tests required no prey species in the maze. It was designed to test for the possibility of unique characteristics inherent in the maze or setting of the test area that would cause a directional response in the weasel, independent of that due to a prey species being present. The weasel, randomly chosen as to order, was placed in chamber A, and allowed to acclimitize for a period of 10 minutes. After this period of time all quillotine doors leading to the maze arms were removed and the weasel allowed to run the maze.

A total of three weasels were used to conduct this test and each completed the test on thirty (30) different occasions. In all cases the weasel upon entering the maze remained in that arm until it entered the terminal pivot trap at the end of that arm. At no time was there an occurence of backtracking and either re-entering the same arm or the opposite arm. Therefore, each run was considered completed when the weasel entered the trap.

Test II

This test was conducted using one prey animal, either Microtus pennsylvanicus, Peromyscus sp., or Mus musculus, all species which might be expected to be encountered in the field by a weasel. Both the prey species and the weasel chosen to run the maze were taken from a predetermined listing. This "Master List" assigned a particular weasel by number, to a particular prey species/maze arm combination. The order of such pairings was arrived at by drawing entries from a table of random numbers and was completed for the entire test before any test was conducted. An alternative method could have been used here, that is, just allowing the mice to randomly run the maze before releasing the weasel, instead of determining, randomly, which arm the mouse was to run. This, however, would have required a second set of tests identical to Test I only in this case allowing the mice to run the maze for position effect.

In each case a prey animal was first placed into compartment B. The two maze arms with their pivot traps in place, as previously described, were then placed in position in the end of compartment "B". The mouse was, after a five minute acclimation period, allowed to run the arm of the maze as determined by the master list, being then detained in the pivot trap until the weasel was allowed to make the run. The weasel, also taken according to the master list was then caught in compartment A which was then locked into position with compartment B. After 10 minutes the doors of both compartments A and B were raised allowing the weasel entrance to the maze.

It should be noted here that the prey animals were left alive in the trap portion of the maze throughout the entire test. Leaving the prey in the trap was for the purpose of acting as a reward, in hopes that the weasel would by the presence of food be prompted to continue responding to the olfactory stimulants provided. The animals were left alive to reduce or prevent the possibility of the animal, in the act of dying, releasing new or larger amounts of scents or olfactory stimulants thus deviating from that which would be expected to be emitted or left behind by a normal non-stressed animal.

Test III

This test was conducted in exactly the same manner as Test II, except for the fact that it was conducted in the dark (in this case darkness was provided by the natural subdued lighting of night, therefore some incident light may have existed). It was recognized that it might be possible for the weasel to be receiving some visual cues while in the arm of the maze, left behind by the prey animal that could not be detected by the experimenter. Although the clay substrate was in part chosen for its relative coarseness, in order to preclude the possibility of blatant tracks being left by the prey, there was no way to completely guarantee that this would not occur. Nor did it alleviate the possible deposition of hair, dander or traces of moisture which might be detected and followed by the weasel. Removing light may effectively remove all of these factors as uncontrollable variables. Three animals and 30 trials each were used to complete this test.

Test IV

Due to the afore mentioned fact that the prey animals were all left alive in the trap portion of the maze until dispatched by the weasel it seemed plausible that the weasel might be receiving auditory stimulation and was using that to key in on the position of the prey. During the whole of the testing period in all tests involving a prey animal, all prey animals were observed to sit almost completely motionless in the trap until the weasel entered the trap himself, at that time activity markedly increased on the part of both animals until the mouse was dead. It was, therefore, felt improbable that the prey animals were making sufficient noise to attract the weasel. However, not being certin of the actual auditory acuity of the least weasel and not wanting to kill the prey animal for the reasons already set down, it seemed reasonable to conduct a test to attempt to rule out sound reception as a source of error.

The method finally decided upon was to run a prey animal as in the two previous tests but in this case, before releasing the weasel into the maze, a second prey animal of the same species was placed in the remaining trap. This was not done in the normal manner, that is, by not providing entry through the pivot door from the maze arm side but rather through the guillotine door on the opposite end of the trap. If the weasel were keying on sound, he should then respond to either arm with equal probability.

Unlike the other tests only two weasels were available. Each weasel, as in the other tests was run through 30 trials.

Diseases

All weasels maintained for the purposes of this study died either during or shortly after the conclusion of the study. On three different occasions animals were sent to the pathology lab of the Michigan State University Veterinary Clinic but only in one case were any diagnostic findings made. Two juvenile, female least weasels, captured by hand 29 October 1971, were brought into the Museum colony and maintained in individual cages in a room separate from the rest of the colony. Using a weight/age chart (Heidt, 1970) it was estimated that the animals were approximately 4 weeks of age and most likely unweaned. After the first day in captivity they began feeding on freshly killed and eviserated rodents. Both gained weight steadily until the 5th or 6th day when their weight stabilized. By the end of the 8th day they were beginning to loose weight. It was at this time that what appeared to be small nematode worms were noted in the feces of both animals. On the 9th day both weasels were found dead. They were immediately sent to the pathology lab for autopsy which showed, Nematodiasis, focal interstitial pneumonitis, and acute focal encephalitis. The report also stated that "It is possible that the lesions in the lung and brain may be related to parasite migration". It was felt that the damage to tissue was of recent origin and it is not known whether the animals came into the colony with the infestation or were possibly inoculated through the rodents given as food.

All other reports came back with cause of death undetermined.

Killing Behaviour

Although killing behavior in the least weasel and other North American mustelids has been well documented and described by several investigators (Allen, 1938; Hamilton, 1933; Polderboer et al. 1941; Glover, 1943; Moore, 1945; Llewellyn, 1942; and Heidt, 1970) this investigator feels that the following observation is worthy of mention. Two female least weasels, the same two as described in the disease section of this writing, were observed very closely in reference to their killing and feeding behavior. It is believed that these animals had not been weaned although they may have been presented with and consumed meat prior to receiving it from me. After the initial prepared meal consisting of a freshly killed meadow vole with entrails exposed, young live Microtus pennsylvanicus were placed in the containers with the weasels. As soon as a vole was placed in the cage, the weasel immediately and with no hesitation attacked the vole. Upon seizing the prey each weasel emitted a series of rather sharp chirps accompanied by the characteristic release of musk. At this juncture all similarities to Llewellyn's or anyone elses, description of weasel killing behavior ceased. The young weasels grabbed not the characteristic nape of the neck but any appendage or anatomical feature which presented itself, in one case this was a hind leg in another the tail and in still another a patch of skin over the flank of the mouse. Both predator and prey then rolled violently around the cage, the weasel apparently attempting to secure a firmer hold and the mouse attempting to escape.

The first time this occured the two were allowed to be thus engaged for a

period of 15 minutes. At that time no further progress appeared to be being made by either party so the vole was removed, killed, and returned to the cage, at which time the weasel approached cautiously and then began licking the junction of the neck and head. The base of the brain case was then opened and its contents consumed before directions were reversed and the remaining posterior portions of the body eaten. These inept attempts at securing prey continued through the fourth day for the large female and the fifth day for the smaller female at which time both apparently caught on and were able to complete the kill unaided. From that point until their death weasels continued capturing prey in the typical weasel manner by inflicting mortal wounds to the base of the prey's skull. This observation may suggest that although weasels are born with the innate ability to kill in this manner, in order to successfully use it they must either learn the behaviour (Heidt, 1966) from a parent animal or stumble on to the correct and most efficient method through trial and error, as was apparently the case in these instances.

RESULTS

The Chi-square values and levels of significance for all four tests are summarized in Table I.

In each test a single choice was required of each weasel being tested, i.e., to enter either the left or right arm of the maze and continue down that arm. Then, through the expenditure of energy, it was necessary for the weasel to open the pivot door of the trap and enter that trap. Any time that the weasel entered the trap containing a mouse in either Test II or III, it was recorded as a correct response. In Test IV a correct response consisted of the weasel entering the trap that contained the mouse that had himself run the maze. Each trial was recorded as either correct or incorrect as determined by the above criteria.

Test I

A Chi-square test for goodness of fit was used to determine, in the first test, whether or not there existed any maze characteristic which might lead to a position effect. The test statistic is: $X^2 = \frac{(O-E)^2}{E}$. Results from each animal were totaled and compared with an expected value of $E(x) = 15$, as should be generated by a random two alternative, single choice decision making process (see Table II).

The value for Chi-square computed from the data was extremely low $X^2 = .80$, as compared with the tabular X^2 value of .386, with an alpha greater than

Table I: Results of Chi-square analysis

Test Number	Weasel Number	Correct Response Number of	Incorrect Response Number of	X^2	signif-icant level
I	1	16	14	.8	N.S.
	2	17	13		
	3	14	16		
II	1	2	28	64.8	>.005
	2	1	29		
	3	4	26		
III	1	3	27	45.33	>.005
	2	1	29		
IV	1	0	30	56.13	>.005
	2	1	29		

.5 and 2 degrees of freedom. This suggests strongly that there is no reason to believe that the results noted are anything but random. It then follows that there is no reason to believe that any position effect exists, therefore, the responses made in future tests can be assumed to vary only as a result of the experimental manipulation and not cue to characteristics of the maze itself.

Test II

The results of the second test which was conducted using 3 weasels, 30 trials per weasel and 1 prey species (in the presence of light) were subjected to a Chi-square test. An expected value of E(x) = 15 was assumed for this, and the remainder of the tests. Substituting the experimental results into the expression outlined in Test I results, a computed value of X^2 =64.8 was derived. This value was determined to be significant above the .005 level. The actual tabular value for X^2, .005, v=2, =10.597. This is so much higher than expected that it very strongly suggests that the weasel was not relying on chance alone to find prey, but was in some way able to correctly detect and pursue the prey species in the maze (see Table III).

Test III

In the third test only two animals were run in a sequence of 30 trials each. Their correct responses totaled and substituted into the Chi-squared formula and compared to an expected value of 15. The corrected Chi-square value obtained was X^2 = 45.33 which is very highly significant, X^2, .005, v=1, =7.879. These results indicate that in the absence of normal visual cues the least weasel is still able to effectively detect and locate prey (see Table IV).

Test IV

Test number four revealed some interesting results. As in the previous two tests the X^2 value was very high $X^2 = 56.13$ above the .005 level. This suggests that the weasels were either not responding to sounds produced by the mice or the mice were not making sounds at levels that the weasel could detect. A second, incidental result was obtained while running this test. Mice were present in both traps of the maze and the pivot doors were not sufficiently air tight to prevent the passage of air from a trap into the maze arm. If air were diffusing into the maze it should carry the odor of the mouse along with it. This leads to several possible conclusions, for example: (1) The weasel is not able to detect air borne olfactory stimulants; (2) the scents that the weasel is following and recognizes or detects are only those laid down by feet of rodents which may adhere strongly to the substrate and are not readily vaporized, therefore, not readily diffused; or (3) that a weasel cannot follow a scent gradient in the air (see Table V).

Time Analysis

During the course of these tests the time required for each weasel to run the maze on a particular trial, i.e., first, second, third, etc. was recorded along with the results of that trial. The individual times that each of the three weasels in the second test and the two weasels in the third and fourth tests, spent in the maze were averaged according to trial number and plotted as seen in Figure 3. Also plotted in Figure 3, as a separate line, are the averages for each trial of the times of the three weasels ran in Test I. This is meant to be

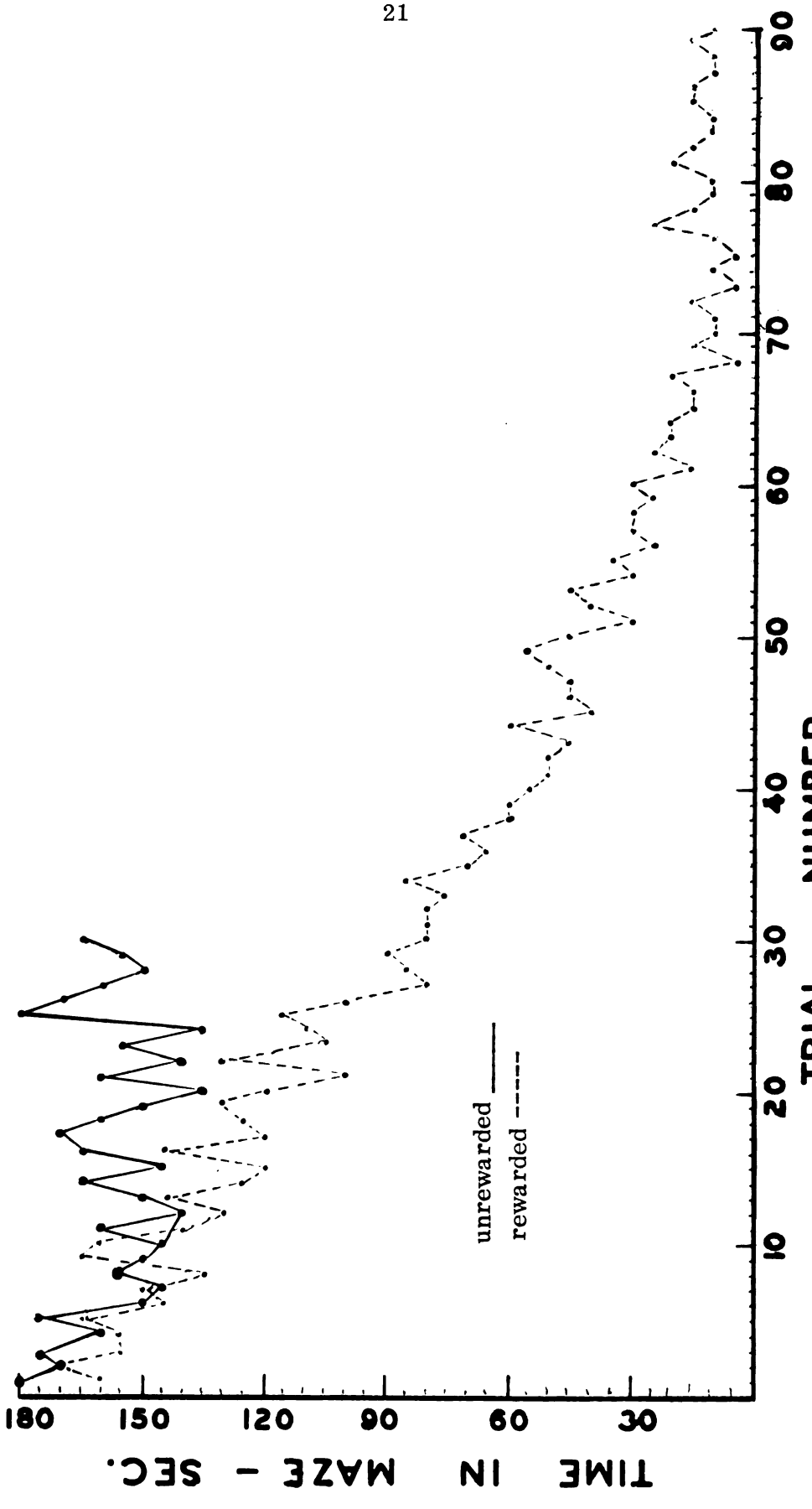

Figure 3: Reduction in maze running time as a result of a food reward.

used as a point of comparison between a rewarded and a non-rewarded weasel.

The lapsed times were taken with the sweep second hand of a Bulova wrist watch and, therefore, are only approximate.

Table II: Results of choices made by weasel with no prey in the maze

Weasel	I		II		III	
Trial No.	W-N	W-D	W-N	W-D	W-N	W-D
1	1	R	3	R	2	R
2	1	L	3	L	2	L
3	3	L	1	L	2	L
4	2	L	1	L	3	R
5	1	R	3	L	2	L
6	2	L	3	L	1	R
7	3	L	2	R	1	L
8	1	R	2	R	3	R
9	3	R	1	L	2	L
10	3	R	2	R	1	L
11	3	R	1	L	2	L
12	2	R	3	L	1	R
13	1	L	3	R	2	R
14	3	R	1	L	2	L
15	2	L	3	L	1	L
16	1	R	2	R	3	L
17	3	R	1	R	2	L
18	1	R	2	R	3	L
19	2	R	3	L	1	L
20	1	L	2	R	3	L
21	2	R	3	R	1	R
22	2	L	3	L	1	L
23	2	R	1	R	3	L
24	1	R	3	R	2	L
25	1	R	2	R	3	R
26	2	L	1	L	3	R
27	2	L	3	R	1	R
28	3	R	1	L	2	L
29	1	L	2	L	3	R
30	1	R	2	L	3	L

W-N = Weasel order number (i.e. 1st, 2nd, 3rd)
W-D = Direction weasel took in maze (i.e. right R, or left L)

Table III: Results of choices made by weasel with one prey species run in the light.

Weasel No.	I				II				III			
Trial No.	W-N	P-A	D	W-D	W-N	P-A	D	W-D	W-N	P-A	D	W-D
1	3	P	L	L	1	Mic	L	L	2	P	R	R
2	3	Mus	R	R	1	Mus	L	L	2	Mic	L	R
3	1	P	L	L	3	Mus	R	R	2	Mic	L	L
4	1	P	L	L	3	Mic	R	R	2	Mus	R	R
5	2	P	R	R	1	P	R	R	3	Mic	L	L
6	3	P	L	L	1	P	L	L	2	P	L	L
7	1	Mic	L	L	2	P	L	L	3	P	L	L
8	3	Mic	L	R	2	Mus	R	R	1	Mus	L	L
9	2	Mic	R	R	1	Mic	L	L	3	P	R	R
10	2	P	R	R	1	Mus	L	L	3	Mus	L	R
11	2	P	R	R	3	Mus	L	R	1	P	R	R
12	3	P	R	R	2	Mus	R	R	1	P	L	L
13	1	Mic	R	R	3	P	L	L	2	P	L	L
14	2	Mus	R	R	3	Mus	R	R	1	P	R	L
15	3	Mus	R	L	2	Mic	L	L	1	P	L	L
16	3	Mic	R	R	1	Mus	L	L	2	P	R	R
17	3	Mic	R	R	1	Mic	R	R	2	Mic	L	L
18	1	Mic	L	L	3	P	R	R	2	Mus	L	L
19	3	P	R	R	2	Mic	L	L	1	Mic	L	L
20	2	Mic	L	L	1	Mus	R	R	3	Mic	R	R
21	1	P	R	R	2	P	L	L	3	Mus	R	R
22	1	P	L	L	3	P	L	L	2	Mic	R	R
23	1	Mus	R	R	2	P	L	L	3	Mus	R	R
24	1	Mus	R	R	2	Mus	R	R	3	Mic	L	L
25	3	P	L	L	2	Mic	R	R	1	Mus	R	L
26	2	Mus	R	R	3	P	L	L	1	Mic	R	R
27	1	Mus	R	R	3	P	R	R	2	P	L	L
28	1	Mic	L	L	3	Mus	R	R	2	Mic	L	L
29	3	P	L	L	1	Mic	L	L	2	Mus	R	R
30	3	Mic	L	L	2	Mus	R	R	1	Mus	L	L

W-N= The weasel order number (i.e. 1st, 2nd, 3rd)
P-A= Prey animal (P=Peromyscus, Mic=Microtus, Mus=Mus musculus).
D= The direction the prey species was assigned (i.e. right=R, left-L).
W-D= The direction chosen by the weasel

Table IV: Results of choices made by weasel with one prey species run in the dark.

Weasel No.	I				II			
Trial No.	W-N	P-A	D	W-D	W-N	P-A	D	W-D
1	2	Mus	R	R	1	Mic	L	L
2	1	Mic	R	R	2	Mus	L	L
3	2	P	L	L	1	P	L	L
4	1	Mus	R	R	2	Mic	R	R
5	2	Mus	R	R	1	P	L	L
6	1	P	L	L	2	Mic	R	R
7	1	Mus	R	L	2	P	L	L
8	1	Mus	R	R	2	Mic	R	R
9	2	Mus	L	L	1	Mic	L	L
10	1	P	R	R	2	Mus	R	R
11	1	P	L	L	2	Mus	L	L
12	1	Mus	L	L	2	P	R	R
13	1	Mus	R	R	2	Mic	L	L
14	2	Mus	R	R	1	Mic	L	L
15	2	Mus	L	L	1	Mic	L	L
16	2	Mus	R	L	1	P	R	R
17	1	P	L	R	2	P	L	L
18	1	Mic	R	R	2	Mic	R	R
19	1	Mus	R	R	2	Mus	L	L
20	2	Mus	R	R	1	Mic	R	R
21	2	Mic	L	L	1	Mus	R	R
22	1	Mus	L	L	2	P	R	R
23	1	P	R	R	2	Mus	R	R
24	1	Mus	R	R	2	Mus	R	R
25	2	Mic	R	R	1	Mic	R	R
26	2	Mic	L	L	1	P	R	R
27	2	Mic	L	L	1	Mic	L	L
28	2	P	L	L	1	Mic	L	L
29	2	Mic	L	L	1	Mus	R	R
30	1	Mic	R	R	2	Mus	R	L

W-N= The weasel order number (i.e. 1st or 2nd)
P-A= Prey animal (P=Peromyscus, Mic=Microtus, Mus=Mus musculus).
D= The direction the prey species was assigned (i.e. right=R, left=L).
W-D= The direction chosen by the weasel.

Table V: Results of choices made by weasel with one prey species run through the maze and one placed in the opposite trap.

Weasel No.	I				II			
Trial No.	W-N	P-A	D	W-D	W-N	P-A	D	W-D
1	1	P	L	L	2	Mic	L	L
2	2	Mus	L	L	1	Mus	R	R
3	2	P	L	L	1	Mic	L	L
4	2	P	L	L	1	P	L	L
5	2	Mic	L	L	1	P	L	L
6	2	Mus	R	R	1	P	L	L
7	2	Mus	R	R	1	P	R	R
8	2	Mic	L	L	1	Mic	R	R
9	2	Mus	L	L	1	P	R	R
10	2	Mus	L	L	1	Mus	R	R
11	1	Mic	R	R	2	P	R	R
12	1	Mus	L	L	2	Mus	R	R
13	1	Mic	L	L	2	P	L	L
14	1	P	L	L	2	Mic	R	R
15	1	Mic	R	R	2	Mic	L	L
16	2	Mic	R	R	1	Mic	L	L
17	2	Mus	R	R	1	P	R	R
18	2	Mus	R	R	1	Mic	L	L
19	2	Mic	L	L	1	P	L	L
20	2	P	L	L	1	P	L	L
21	2	P	R	R	1	Mus	L	L
22	2	Mic	L	L	1	Mic	L	L
23	1	P	L	L	2	Mic	L	L
24	1	Mic	L	L	2	P	L	L
25	1	Mus	R	R	2	P	R	R
26	2	P	R	R	1	Mus	R	R
27	2	Mus	R	R	1	P	R	L
28	2	Mic	L	L	1	Mic	R	R
29	2	Mus	R	R	1	Mus	L	L
30	2	Mic	R	R	1	P	R	R

W-N= The weasel order number (i.e. 1st or 2nd).
P-A= Prey animal (P=Peromyscus, Mic=Microtus, Mus=Mus musculus).
D= the direction the prey species was assigned (i.e. right=R, left=L).
W-D= the direction chosen by the weasel.

DISCUSSION

Rosenzweig (1966), while looking at the community structure in some sympatric carnivora, noted that the least weasel preyed exclusively within what he termed the la size class. This class ranges from 0 - 50 grams and includes most invertebrates and many of the smaller rodents, birds, etc. Evidence of larger vertebrates has never been discovered in either scats or gut contents of the least weasel. This does not, however, preclude the possibility that the least weasel can and may actually prey upon larger animals under certain circumstances.

Prey specificity appears to be a rather wide spread characteristic of both invertebrate (Menge, 1972) and vertebrate (MacLulich, 1937) predators. It has been hypothesized that the rational behind food specificity is that for each predator there exists a particular size range of prey species within which it is most economical to function (Hall et al., 1970; Dodson, 1970; Schoener, 1969; Brooks, 1968; Galbraith, 1967). That is, the energy required for location, pursuit, capture, dispatch and consumption of prey within this range will be off-set or compensated for by the net energy gain available to the predator upon assimilation of the prey.

Within Rosenzweig's (la) prey class there is a multitude of animals which occur sympatrically with the least weasel. These animals range from fossorial to arboreal species and possess very different life styles and escape mechanisms. Relative abundance, speed, evasive ability, and differential escape patterns

of the prey species would affect their desirability (Christian, 1973), as possible prey for the weasel. For instance, a small meadow vole (Microtus) and a jumping mouse (Zapus) may have approximately the same nutrient and caloric value. However, the saltatorial behavior of the latter which may increase its evasive ability thus increasing the energy cost of capture, may make it less desirable than the relatively slow moving, runway inhabiting Microtus. Whether or not the weasel can distinguish, by olfaction or any other means, between these potential prey species is a testable question which lies beyond the scope of this study.

Just as grass eating rodents are possibly able to reduce risk (i.e. exposure to predators, etc.) in their food gathering (Baker, 1971) by feeding under concealment of their runway systems so may the least weasel lessen the same type of risk (Craighead, 1956; Handley, 1949; Latham, 1952) by being able to reduce the actual time required to seek and capture prey. It has already been noted that the weasel has been able to kill prey animals very rapidly (see references in introduction). It, therefore, remains only to reduce the time required to locate that prey.

It would be of great advantage to a predator to be able to detect prey animals prior to actually confronting and attempting to take the prey. If this were possible, it would reduce energy loss and exposure to disadvantageous situations by eliminating excessive time spent in random, chance encounter, search patterns which may or may not end in the successful acquisition of energy.

In a tidal aquatic environment one would expect that at least in some predators olfactory detection at a distance would probably be of little value. Menge (1972) looking at this problem in Leptasterias, an intertidal predatory starfish, found this to be true and attributed it to the fact that considerable mixing of water occurs in this region, therefore, making any traceable scent gradient non-existent. For the same reason one would expect the same type of scent usage to be lacking or reduced in animals of aerial life style (i.e. birds, bats, etc.). Terrestrial animals, mammals in particular, have been noticed apparently sampling, olfactorally, air and ground, although I know of no instance where terrestrial mammals obtain olfactory cues for food or prey detection from bodies of water. This may exist, however, in Cetaceans, pinnipeds, and other aquatic and marine mammals. The ability to detect the presence of chemical stimulants by olfactory means appears to be both an important and widespread implementation among mammals. For instance, scent marking to lay out territories, to establish dominance hierarchies, or to express intolerance for the presence of others is among mammals very common (Ralls, 1971). Just as common is the ability of other mammals, conspecifics or not, to detect these markings and possibly respond in some manner.

Olfaction plays an integral role in initiating reproductive activity in a number of mammals (Doty, 1970) and in some invertebrates (Karlson and Butemandt, 1959). Congregations of male dogs that appear suddenly when a female dog enters estrous have been shown to have been attracted as a result of an olfactory stimulant present in the urine of such females (Beach and Gilmore, 1949).

The importance of olfaction in the mating behaviors of a number of rodent species is well documented (Beach, 1942; Heimer and Larson, 1967) as is the effects of bulbectomys, which effectively eliminate the ability of an animal to detect any olfactory stimulus (Carter, Doty, & Clemens, 1970; Murphy & Schneider, 1970) and the general preference by male mice for estrous over diestrous females (Carr & Caul, 1962; Carr & Pender, 1958; Carr, Solberg & Pfaffman, 1962; Le Magnen, 1952). Aggressive behavior, which may in many cases be related to reproductive behavior, has been demonstrated to be correlated to odors of conspecifics in some mice (Mackintosh & Grant, 1966; Ropartz, 1968; Archer, 1968; Archer, 1969). This type of olfactory social stimuli may have physiological effects such as weight change of the adrenal cortex which may cause changes in adrenocortical responses (Archer, 1968; Christian, 1955; Louch & Higginbothan, 1967). Changes of this sort may drastically alter what are usually considered to be normal behavior patterns.

Rodents feeding on conifer seeds in reforestation areas generated interest in mechanisms for food detection by these animals (Smith and Aldous, 1947; Spencer, 1954; Tevis, 1956; Dick et al., 1958; Hooven, 1958; Abbott, 1961). In a series of experiments it was determined that deer mice, Peromyscus maniculatus, could detect the presence and location of seeds buried under the soil using olfactory rather than visual cues (Howard et al., 1968).

Even taking into consideration the extremely small sample size that was used to generate the data collected in this study it appears that the least weasel, as with the animals previously mentioned, uses olfaction to effectively sample

its immediate environment. Specifically M. nivalis, can by scent detection alone, successfully secure food. The sensitivity of this animal's ability to respond to olfactory stimulants has not been quantified. Care was taken to reproduce as closely as possible a scent residue similar to that which a weasel might encounter in his environment.

At least in one case it has been suggested that weasels are capable of controlling rodent populations (Matler, 1967). It has also been suggested that weasels are able, by some mechanism, to key in on large or increasing local populations of rodents and reduce them to low level before moving on to another localized population (Cooper, 1972). The mechanism, as determined by this study, could be olfaction, and for the relative large distances existing between localized populations, is probably the only plausible one. If a weasel were using olfactory cues to detect and locate prey animals and would only continually hunt in a given area when the number stimulations resulting from prey scent encounter occur with a certain threshold frequency it would follow that he would continue searching until that minimum stimulation requirement was met. If this minimum threshold were not very large, in other words the weasel was very sensitive to population densities, then the possibility of missing a fairly sizable aggregation of potential prey would be relatively low. For instance, if a weasel were foraging and received a stimulus revealing the presence of a prey animal the weasel would track, capture and consume that prey animal. Sometime after completing the feeding activity the weasel would again start foraging, but receiving no immediate stimulus would continue searching non-directionally

which might take him completely out of the area. If on the other hand the weasel were to receive a second stimulus after a short period of time, the weasel by responding to that stimulus would be kept in the area. If the population were large the weasel would be detained by its repeated responses to the prey stimuli in its immmediate environment until such time as he had reduced that population to a level from which it would be just as likely to encounter a new stimulus by moving out of the area as by staying in that area. If the weasel were able to learn, as is suggested by the marked reduction in time required for the animal to run the maze as this study progressed, that given areas give high stimulation rates, it might be possible for the weasel to establish "prey routes", moving continuously from areas of low stimulation frequency to areas of high stimulation frequency thus generating a population cycle. If this were all true it would certainly lend credence to the statements by Matler and Cooper.

There is room for further research in applying olfaction and other environment sampling devices to autecology, particularily in the area of predation. Along with being able to detect potential prey at a distance it would be advantageous for a predator such as the least weasel to be able to determine optimal prey animals prior to actual confrontation. An animal able to use olfaction in this manner would reduce the number of attempts to capture prey either too small or evasive to give adequate returns or so large that injury or even death of the predator might result. By accomplishing the above task the animal would further increase its survival potential by economizing its energy expenditure, energy intake ratio.

Summary

Three least weasels, Mustela nivalis, were tested for their ability to use olfaction in prey detection. Tests were conducted by allowing small rodents to leave scent trails on an earth like substrate in a y-maze. The weasels tested were found to be able to detect the presence of prey provided and to locate prey in the maze by olfactory means alone.

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