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# Utilization of Heat Sensitivity in Crotalidae

James Cordrey Miller

*Eastern Illinois University*

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UTILIZATION OF HEAT SENSITIVITY IN CROTALIDAE

(TITLE)

BY

JAMES CORDREY MILLER

B.S., Eastern Illinois University, 1973

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS  
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Master of Science

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY  
CHARLESTON, ILLINOIS

1978

YEAR

I HEREBY RECOMMEND THIS THESIS BE ACCEPTED AS FULFILLING  
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DEPARTMENT HEAD

UTILIZATION OF HEAT SENSITIVITY IN CROTALIDAE

BY

JAMES CORDREY MILLER

B.S., Eastern Illinois University, 1973

ABSTRACT OF A THESIS

Submitted in partial fulfillment of the requirements  
for the degree of Master of Science in Zoology at the Graduate  
School of Eastern Illinois University

CHARLESTON, ILLINOIS

1978

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Specimens of five genera of snakes (Crotalus, Agkistrodon, Bitis, Epicrates, and Elaphe) were tested for use of thermal cues in food selection. Results indicate that pit vipers (Crotalus and Agkistrodon) and boas (Epicrates) utilize thermal radiation in selection of food. It was also indicated that Crotalus (rattlesnakes) do not invariably show a reflexive strike before food is investigated or ingested.

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## INTRODUCTION

The pit organs of the snakes in the family Crotalidae have long been used as a major descriptive character to distinguish the pit vipers from the Old World Vipers or Viperidae. The earliest settlers of North America noticed the rattle of the Crotalus and Sistrurus and learned to avoid the pit viper's bite. Nevertheless, it was not until 1937 that the function of the facial pits as radiant energy receptors was hinted at by Noble and Schmidt.

The first recorded dissection of the facial pits was by Tyson in 1683 (Klauber, 1972). Tyson thought that the pits could be ears, but could find no support for his idea in the anatomy of the structures. In 1804, Home, after an anatomical examination of the facial pits, decided they could not be ears, but he could not reach a conclusion as to what function they might perform (Klauber, 1972). He suggested a possible analogy of the pits to the tear sacs of certain ruminants. Later Desmoulins, in 1824, wrote of the rich innervation of the pits and proposed a possible olfactory function for the facial pits (Barrett, 1970). West, in 1900, was the first author to write a comprehensive anatomical account of the facial pits. He proposed that the pits were similar in function to the lateral line sense organs in fishes (Klauber, 1972).

Lynn (1931) reviewed earlier studies and summarized seven earlier theories of the function of the pit organs

and added an eighth of his own. Through his anatomical studies of the facial pits Lynn could find no connections with other sense organs of the head and concluded that because of its structure the pit should respond to tactile stimuli from air vibrations.

The idea that the facial pits would respond to air vibrations was also suggested by Noble (1934). The author stated that turbulence in the air caused by passing prey or enemies enabled the snake to become aroused and strike with accuracy. In 1935, Ros showed that the labial pits of a python might be sensitive to radiant energy (Barrett, 1970). Subsequently, Noble and Schmidt (1937) reported new experiments which showed the facial pits as primarily temperature-differential receptors. The sensing of air vibrations by the facial pits was considered a secondary function.

Noble and Schmidt (1937) used both boids and pit vipers as subjects in their experiment. Their experiments used light bulbs or dead rats as stimuli for the snakes. The light bulbs were turned on to simulate warm targets and were presented to the snakes either mounted on a fly wheel or waved by hand in front of the snake. In certain sessions the light bulbs were presented along with freshly killed rats. The snakes were tested in various stages of mutilation from all organs of the head functioning properly to every organ but facial pits, blocked or destroyed. It was

discovered that the snakes could accurately strike at warm targets even though all the sensory organs except facial pits were covered or destroyed. When the pit was filled with collodion a strike was no longer elicited by warm targets. The authors also found that pit vipers will strike at cold targets if warm ones are not available, when all sense organs but facial pits are blocked. These results led Noble and Schmidt to conclude that the facial pits of pit vipers and labial pits of certain boids function as temperature-differential receptors. With this ability the snakes could determine the location of prey which have a higher body temperature than the environment, a tremendous help in locating homeothermic prey. However, Noble and Schmidt thought the facial pits detected air temperatures in the general area of the snakes head, instead of radiant energy from the body of the prey as is now believed.

Bullock and Cowles (1952) and later Bullock and Diecke (1956) showed with electrophysiological data that the facial pits were receptors for infrared radiation. Using drugged rattlesnakes, the authors cut one of the nerves ramifying into the pit membrane. Then using various stimuli they recorded the responses to those stimuli. There were no responses from the pit organ to sound, odor, vibration of substratum, or to heat filtered light of "moderate" intensity. However, deformation of the pit membrane by touching or a puff of air did produce some response. The membrane showed

a high degree of sensitivity to radiant heat falling on it. Bullock and Cowles found that the membrane of the facial pit has a continuous rate of nerve discharge which is not dependent upon the snake's body temperature. This level of nerve discharge is somehow dependent on the average radiation of objects in the facial pits sensory field. The rate of response went up whenever an object warmer than the background temperature entered the receptor field and the rate decreased when a cooler object entered the receptor field. These data indicate that pit vipers can potentially detect either warm or cool objects in front of them. The field of response of the facial pits is cone-shaped from each pit, horizontally extending from a right angle to the snakes head to approximately  $10^{\circ}$  across the midline, and vertically from  $45^{\circ}$  above to  $35^{\circ}$  below the horizontal line. These fields of reception overlap in the middle and therefore give the pit vipers a stereoscopic "view" of objects in front of them. This ability would potentially be of great value in targeting prey or in defense.

More recent experimenters have expanded on Bullock and Cowles' work. Bullock and Barrett (1968), using similar techniques, showed that the labial pits of pythons and boas are electrophysiologically similar to the facial pits of pit vipers. However, the labial pits of Boidae are "about four times less sensitive" than the facial pits of Crotalidae and they respond to stimuli which are warmer than the

general environmental temperature. The authors discovered that certain boas which do not have visible labial pits are still sensitive to radiant heat.

In 1973, Gamow and Harris experimented with boids to determine whether the labial pits were photochemical, frequency detectors or were energy detectors. In a photochemical frequency detector, entering infrared radiation would trigger the release of energy already stored in the nerve as in the eye. The energy detector would absorb the incoming radiation directly. The authors tested the snakes with microwave radiation and a CO<sub>2</sub> laser. They concluded that the pits are energy detectors because of the clear responses obtained from both infrared and microwave radiation.

The most recent experiments with pit vipers have been by Chiszar and Radcliffe, (1976b), and Chiszar et al (1976a,c). The experiments compared rattlesnakes with garter snakes or other Colubridae and dealt with food seeking behavior in both groups. The authors formed the hypothesis that rattlesnakes rely primarily on visual and/or thermal cues to orient on prey and strike, and subsequently stimuli from the strike activates tongue-flicking, enabling the snake to detect olfactory stimuli from the prey. This idea is similar to the proposals of Bullock and Barrett (1968) which stated that the strike reflex is triggered by firing of the heat receptors and then another system of sensory stimuli determine following behaviors.

The structural make up of the facial pits has been thoroughly studied (see Barrett, 1970 for a review). Basically they are pits located on either side of a pit viper's head between the eye and nostril. The pit occupies a depression in the maxillary bone and is divided by a membrane into two chambers. The two chambers are connected by a small pore in the membrane located under the bottom edge of the lower preocular scale.

The membrane which divides the two chambers is approximately  $10\mu$  thick and is richly supplied with nerves from the ophthalmic and supramaxillary branches of the fifth cranial nerve (Barrett, 1970). The receptors in the membrane are almost entirely heat receptors which are inhibited by cold. The responses to heat stimuli by the receptors is mainly phasic; the rate of response returns to a normal level very quickly in spite of continuous stimuli.

Because the facial pits of the Crotalidae and the labial pits of Boidae are radiant heat receptors they could be used to detect prey, homeothermic enemies, or to scan the environment for suitable terrain. The heat sensing ability enables the pit vipers to use thermal cues to acquire prey. Since pit vipers often release their prey after envenomation, allowing the prey to crawl away before dying, thermal cues from the still warm body along with olfactory cues would enable the snake to find the dead prey. Its potential use as an aid to finding dead prey is the basis for this study.

The following experiments were designed to determine if pit vipers or other snakes would preferentially select as food "warm" mice over "cool" mice using thermal cues.



## Materials and Methods

## Subjects:

Six adult pit vipers (two Crotalus atrox, two Agkistrodon contortrix, and two A. piscivorus); two adult old world vipers (Bitis arietans); two adult rainbow boas (Epicrates cenchria); and two fox snakes (Elaphe vulpina) were used in the experiment. All animals had been maintained in captivity at least two years and were regularly feeding on mice. The eight vipers were housed individually in wooden cages (approximately 40x25x28 cm) with sliding glass front, containing water and a paper floor covering. The boas and fox snakes were housed individually in wooden cages (50x30x28 cm) with sliding glass front, containing water and a paper floor covering. Room temperature was kept at 75-80° F. throughout the experimental period, except for the next to last day of testing at which time the temperature had dropped to 68° F.

For two months prior to the beginning of experimentation each snake was fed one dead mouse per week in its home cage. The mouse was left in the cage for at least three hours and then removed if not eaten. Food was only offered once a week and no attempt was made to force feed subjects which refused mice. During the testing period water was changed twice a week, once at least 48 hours before a testing session, and once while the subject was in the test box. The home cage was cleaned while the subject was in the test

box, as necessary.

#### Apparatus:

An open box constructed of finished  $\frac{1}{4}$  inch plywood with 1 x 2 inch posts in the corners for support was used in the experiment. The floor was 60 cm wide and 121 cm in length with the walls 91 cm high (Fig. 1). Target positions A and B were located approximately two inches from either wall in their respective corners. Point C was half way between the right and left corners at the opposite end, and X was the position from which observations during the experiment were made.

#### Procedure:

The twelve snakes were divided into two groups for convenience of testing, with group A including all the pit vipers, and group B including the puff adders, rainbow boas, and fox snakes. Each group was tested once a week with group A being tested on Thursdays and group B on Fridays. The order of testing within each group was always kept the same; group A: Agkistrodon contortrix first, A. piscivorus second, then Crotalus atrox; group B: Bitis arietans first, Epicrates cenchria second, and Elaphe vulpina last.

A trial was started after a "warm" mouse was placed in its scheduled position, A or B, and a "cool" mouse had been placed in the remaining position (Fig. 1). The "warm" targets were mice which were killed within five minutes of the beginning of the trial. The "cool" targets were mice

which had been killed earlier and placed in a refrigerator until their body temperature was approximately 5° F. ( 1 ) below room temperature. These mice were then returned to the testing room and allowed to warm to room temperature (approximately 10-15 minutes). The positioning of the "warm" and "cool" mice were reversed after each trial. The presentations were such that the positions of the targets for one week were reversed for the next week so that each snake would be presented with the "warm" mouse in A position for one half of the trials and in B position the other half.

After the mice were in proper position the subject was placed in the experimental box at position C (Fig. 1). A stop watch was started as the subjects were released at point C. Observations of the subject's movements during the trial were recorded on paper. The trial was completed as soon as the subject either gripped a mouse with its mouth or fifteen minutes passed without seizure of either target. If a subject gripped one of the mice it was allowed to totally consume the mouse before it was returned to its home cage. The subjects which did not accept a mouse during a trial were returned to their home cages and a freshly killed mouse was left in the cage for at least three hours. If the mouse was then not accepted it was removed from the home cage, acceptance or refusal being recorded at this time.

In all phases of the experiment the vipers were handled to and from their cages with a snake hook and the

boas and fox snakes by hand.

Standard data recorded for each trial were subject, time, date, latency to first contact, latency to consumption, position of "warm" and "cool" mice, acceptance or non-acceptance of mouse, position of selected mouse, and occurrence or absence of a strike. Latency to first contact was recorded for both positions, and was recorded as the time from release of the snake in the box to first contact with either mouse. This time was recorded for both positions if both were touched. The latency to consumption was the time from beginning of a trial to the time the subject first gripped with its mouth either mouse. The position of the "warm" and "cool" mice was either A or B (see Fig. 1). Acceptance of a mouse was recorded if either mouse was accepted. If one of the mice was eaten, the position of the selected mouse (A or B), and its nature ("warm" or "cool"), was recorded. Occurrence of a strike was recorded if a strike occurred.

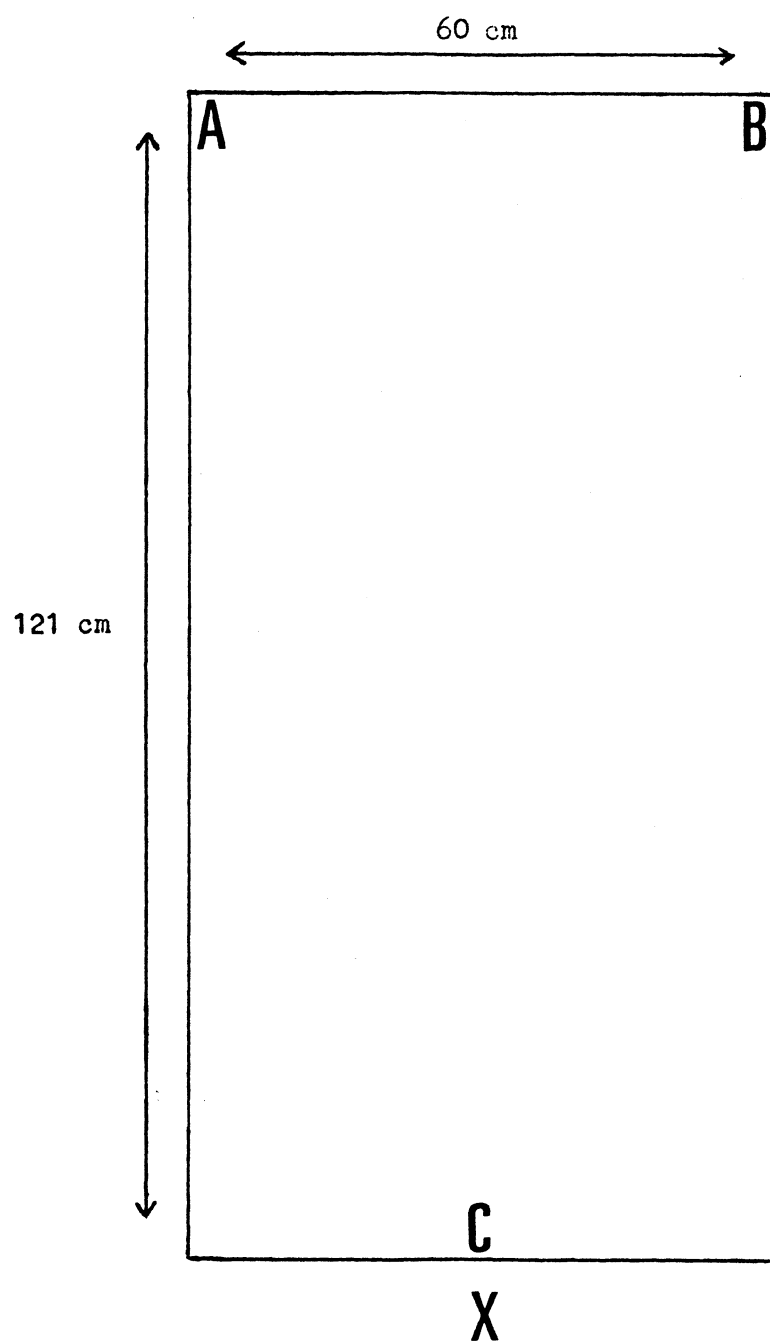


Figure 1. Floor dimensions in cm of experimental box and positions used in experimentation.

## Results

Each of the twelve snakes were run in 16 trials. In all 192 trials were run; in 95 of those trials a mouse was accepted and consumed; 97 trials resulted in no acceptance. In 73 of the 95 trials in which a mouse was taken only one mouse was contacted before acceptance. Both mice were contacted in the other 22 trials before one was accepted. In all of the trials in which both mice were contacted the "warm" mouse was accepted.

For the purpose of identification during the experiment each snake was given a two letter and one number code. The two letter code was made from the first letter of the snake's generic and species name e.g. Crotalus atrox -- CA. The number used in the code was either one or two.

Of the twelve snakes used as subjects four failed to respond positively in any trial. Those subjects include both Agkistrodon contortrix (AC-1 and AC-2), one Epicrates cenchria (EC-2), and one Bitis areitans (BA-1). None of these four snakes accepted a mouse during testing. BA-1 accepted all the mice offered to it in its home cage after testing. The other three snakes (AC-1, AC-2, and EC-2) accepted the mice in their home cages less than half the time they were offered.

Table 1 shows the number of mice accepted by each of the eight reacting snakes over 16 trials. It also includes a breakdown of how many of those mice accepted

were "warm" or "cool" and what position they were in when selected, A or B. It can be seen that both pit vipers and boas selected "warm" targets significantly more often than "cool" targets while no temperature preferences were observed in the non-heat sensitive species.<sup>1</sup>

Figures 2-5 present data on each snake from the first trial to the sixteenth. The data includes trial number, acceptance of a mouse (yes or no), position of accepted mouse (A or B), strike occurrence (yes or no), and type of mouse selected (warm or cool).

All subjects consistently approached mice along a wall of the experimental box except one Bitis arietans (BA-1). In the 14 trials in which BA-2 accepted a mouse it approached the mouse along the wall in eight trials and it approached and contacted the mouse from the middle of the box in six trials.

1. Non-heat sensitive as used here refers to species with no known specialized heat receptor organ.

Table 1. Target Selection data for individual subjects through 16 trials

	Pit Vipers					Boa	Non-Heat Sensitive				
	AP-1	AP-2	CA-1	CA-2	$\Sigma X$	EC-1	BA-2	EV-1	EV-2	$\Sigma X$	
Number Accepted	4	2	14	13	33	16	14	16	16	46	
Number "Warm" Selected	3	2	13	8	26**	12*	4	11	7	22	15
Number "Cool" Selected	1	0	1	5	7**	4*	10	5	9	24	
Number Position A Selected	2	1	7	6	16	4*	10	9	11	30*	
Number Position B Selected	2	1	7	7	17	12*	4	7	5	16*	

\*\* Difference significant at the .01 level

\* Difference significant at the .05 level



CA-1

	Y	N	A	B	Y	N	W	C
Trial 1	/			/	/		/	
2		/		/		/		/
3	/			/	/		/	
4	/		/		/		/	
5	/		/		/		/	
6	/			/	/		/	
7	/		/		/		/	
8	/			/	/		/	
9	/		/		/		/	
10	/			/	/		/	
11	/		/		/		/	
12	/			/	/		/	
13	/		/		/		/	
14		/				/		
15		/				/		
16	/		/		/		/	

CA-2

	Y	N	A	B	Y	N	W	C
Trial 1	/			/	/		/	
2	/		/		/		/	
3	/			/	/		/	
4	/		/		/		/	
5	/		/		/		/	
6		/				/		
7	/		/		/		/	
8		/				/		
9		/				/		
10	/		/		/		/	
11	/		/		/		/	
12	/		/		/		/	
13	/		/		/		/	
14	/		/		/		/	
15	/		/		/		/	
16	/		/		/		/	

Figure 2. Data for Crotalus atrox subjects (CA-1, CA-2) for 16 trials in chronological order.

Key: Col. 1. Acceptance of mice (Y = yes, N = no)  
 Col. 2. Position selected (A, B)  
 Col. 3. Occurrence of strike (Y = yes, N = no)  
 Col. 4. Temperature of mouse selected (W = "warm", C = "cool")

AP-1

	Y	N	A	B	Y	N	W	C
Trial 1								
2								
3								
4								
5								
6								
7								
8								
9								
10								
11								
12								
13								
14								
15								
16								

AP-2

	Y	N	A	B	Y	N	W	C
Trial 1								
2								
3								
4								
5								
6								
7								
8								
9								
10								
11								
12								
13								
14								
15								
16								

Figure 3. Data for Agkistrodon piscivorus subjects (AP-1, AP-2) for 16 trials in chronological order.

Key: Col. 1. Acceptance of mice (Y = yes, N = no)  
 Col. 2. Position selected (A, B)  
 Col. 3. Occurrence of strike (Y = yes, N = no)  
 Col. 4. Temperature of mouse selected (W = "warm", C = "cool")

**EV-1**

	Y	N	A	B	Y	N	W	C
Trial1	/	/	/	/	/	/	/	/
2	/	/	/	/	/	/	/	/
3	/	/	/	/	/	/	/	/
4	/	/	/	/	/	/	/	/
5	/	/	/	/	/	/	/	/
6	/	/	/	/	/	/	/	/
7	/	/	/	/	/	/	/	/
8	/	/	/	/	/	/	/	/
9	/	/	/	/	/	/	/	/
10	/	/	/	/	/	/	/	/
11	/	/	/	/	/	/	/	/
12	/	/	/	/	/	/	/	/
13	/	/	/	/	/	/	/	/
14	/	/	/	/	/	/	/	/
15	/	/	/	/	/	/	/	/
16	/	/	/	/	/	/	/	/

**EV-2**

	Y	N	A	B	Y	N	W	C
Trial1	/	/	/	/	/	/	/	/
2	/	/	/	/	/	/	/	/
3	/	/	/	/	/	/	/	/
4	/	/	/	/	/	/	/	/
5	/	/	/	/	/	/	/	/
6	/	/	/	/	/	/	/	/
7	/	/	/	/	/	/	/	/
8	/	/	/	/	/	/	/	/
9	/	/	/	/	/	/	/	/
10	/	/	/	/	/	/	/	/
11	/	/	/	/	/	/	/	/
12	/	/	/	/	/	/	/	/
13	/	/	/	/	/	/	/	/
14	/	/	/	/	/	/	/	/
15	/	/	/	/	/	/	/	/
16	/	/	/	/	/	/	/	/

Figure 4. Data for Elaphe vulpina subjects (EV-1, EV-2) for 16 trials in chronological order.

Key: Col. 1. Acceptance of mice (Y = yes, N = no)  
 Col. 2. Position selected (A, B)  
 Col. 3. Occurrence of strike (Y = yes, N = no)  
 Col. 4. Temperature of mouse selected (W = "warm", C = "cool")

EC-1

	Y	N	A	B	Y	N	W	C
Trial 1	/			/	/		/	
2	/		/		/		/	
3	/			/	/		/	
4	/			/	/		/	
5	/			/	/		/	
6	/			/	/		/	
7	/			/	/		/	
8	/			/	/		/	
9	/		/		/		/	
10	/			/	/		/	
11	/		/		/		/	
12	/			/	/		/	
13	/			/	/		/	
14	/			/	/		/	
15	/			/	/		/	
16	/		/		/		/	

BA-2

	Y	N	A	B	Y	N	W	C
Trial 1	/			/	/		/	
2	/			/	/		/	
3	/			/	/		/	
4	/			/	/		/	
5	/			/	/		/	
6	/		/		/		/	
7	/		/		/		/	
8	/		/		/		/	
9	/		/		/		/	
10	/		/		/		/	
11	/		/		/		/	
12	/		/		/		/	
13	/			/	/		/	
14	/			/	/		/	
15	/		/		/		/	
16	/		/		/		/	

Figure 5. Data for Epicrates cenchria and Bitis areitans subjects (EC-1, BA-2) for 16 trials in chronological order.

Key: Col. 1. Acceptance of mice (Y = yes, N = no)  
 Col. 2. Position selected (A, B)  
 Col. 3. Occurrence of strike (Y = yes, N = no)  
 Col. 4. Temperature of mouse selected (W = "warm", C = "cool")

## DISCUSSION

The results presented in Table 1 indicate that both captive pit vipers and boas significantly select "warm" over "cool" targets, although the targets differed only in temperature. The snakes had no olfactory trails to follow, and all other known stimulus factors were controlled, except body temperature of the target mice and mouse size. Since all mice used were adults, the size factor was considered negligible. It is known that pit vipers will behaviorally respond to thermal stimuli as far away as 35 cm (Noble and Schmidt, 1937) and it is believed that pit vipers can recognize a warm object at a greater distance (Klauber, 1972). This ability to thermally recognize the "warm" target at distances greater than 35 cm explains the higher number of "warm" mice selected. The extreme limits of thermal detecting ability in pit vipers and boas are not known. However, it is possible that the pit vipers and boas detected the "warm" mice from as far away as 121 cm (Fig. 1). The snakes may identify the "warm" mouse at a greater distance than it can identify either target through other sensory modalities. This capacity would be valuable under the natural conditions in which a rattlesnake or boa captures prey. In the normal pattern of feeding behavior rattlesnakes typically envenomate their prey and then release it. The prey may move some distance away from the snake before it dies. It seems probable that pit vipers use thermal cues from the still warm body to find the prey, in addition to

olfactory cues used by snakes in general. With boas the normal feeding pattern is grasping prey and coiling around it to strangle it. The prey is never released. However, the boas are mostly nocturnal feeders and therefore the ability to locate warm prey in the dark would be a great advantage. The non-heat sensitive group (fox snakes and puff adder) did not show any significant choice of either "warm" or "cool" targets.

Table 1 shows significant positional preferences in two groups (boa and non-heat sensitive). The boa showed a significant preference for position B and the "non-heat sensitive" showed a significant preference for position A. The positional preference could be explained by operant conditioning with the mouse as a food reinforcer. All the subjects except one (BA-2) had a distinct wall-seeking behavior. This wall-seeking would have led the subjects directly to one of the mice. The mouse would reinforce the behavior chain of the snake and therefore increase the likelihood that the snake will take the same wall on the next trial. This whole sequence would result in a positional preference for either A or B developing. That a snake can acquire a positional preference in a relative few trials has been shown in previous experiments with snakes. (Schmitz and Goodrich, 1977).

The data gathered in this experiment on striking behavior do not support the idea that the heat receptors are the

primary receptors that trigger a strike reflex in pit vipers as suggested by Bullock and Barrett (1972). Of the 33 trials in which a pit viper accepted a mouse, in only 11 cases did a snake strike at one of the target mice (Figs. 2 and 3). It is almost certainly the visual stimulus of the moving prey in conjunction with thermal stimuli which normally elicits a strike. The normal sequence of acquiring prey is: sighting; striking; following dying prey, or location of dead prey; followed by investigation and ingestion of prey. However, with this experimental procedure, there was no visual stimulus of moving prey and the normal sequence was sighting or other detection of non-moving prey and subsequent investigation and ingestion.

Of the 95 trials in which a mouse was accepted, in 73 of them only one mouse was contacted and it was then eaten. In the 22 trials in which both mice were contacted before either was accepted, the "warm" mouse was always accepted. Notably, 15 of these 22 "double contacts" were trials involving pit vipers. It can be assumed that the temperature of the "warm" mouse more closely approximated that of the snake's normal prey.

During the two months before experimentation began all subjects regularly accepted dead mice in their home cages. However, during testing, four of the subjects (AC-1, AC-2, BA-1, and ED-2) did not accept a mouse under experimental

consitions. Three of those snakes (AC-1, AC-2, and EC-2) accepted mice offered them in their home cages after experimental sessions in relatively few cases: AC-1 accepted seven times: AC-2 accepted four times; and EC-2 accepted four times. The fourth subject (BA-1) accepted a mouse offered in the home cage after failure to respond in the experimental situation in all sixteen trials. Two other subjects (AP-1 and AP-2) also showed very low response rates during experimental sessions (Fig. 3). Their subsequent acceptance rates in the home cages were also low; AP-1 accepted one time and AP-2 accepted four times. These low acceptance rates both under experimental conditions and in home cages are believed to be due to stress as a result of handling the subjects in transporting them between the home cage and the experimental box, despite all efforts to keep this stress to a minimum. It had been hoped that the length of time the subjects were in captivity involving weekly handling associated with cage cleaning activities would have habituated them to the handling required in the present study.



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