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THE PREDATORY BEHAVIOR OF THE NORTHERN PACIFIC RATTLESNAKE (*CROTALUS VIRIDIS OREGANUS*): LABORATORY VERSUS WILD MICE AS PREY

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ABSTRACT: Predatory behavior of rattlesnakes is dependent upon or modified by particular routes of sensory input. Experimental studies examining the effects of sensory input commonly use laboratory strains of mice, but this raises the question of how faithfully such mice present a prey stimulus equivalent to that of natural, wild rodents. To examine these effects, I studied the comparative predatory behavior of rattlesnakes using laboratory mice and wild mice under various schedules of sensory deprivation: blindfolded and covering of infrared facial pit. Of 56 scored predatory variables, in only three did rattlesnakes show significant differences in their predatory behavior between laboratory and wild mice. Most such differences were likely related to the more cautious behavior of wild mice. Our conclusions agree with others, namely that with only a few exceptions, laboratory mice elicit predatory behaviors of rattlesnakes equivalent to those of natural rodent prey.

Key Words: *Crotalus; Peromyscus;* Rattlesnake behavior; Predation; Sensory deprivation; Trailing; Chemoreception; Photoreception

THE predatory behavior of rattlesnakes has received considerable attention leading to characterization of the pre-strike, strike, and post-strike hunting repertoire. Largely, this has been possible because of the development of laboratory techniques that help quantify the components of behavior (e.g., Burghardt, 1970, 1980) and documentation of stereotypic aspects [e.g., strike induced chemosensory searching (SICS); Chiszar et al., 1977, 1980, 1981*a*] For the most part, previous studies used laboratory mice, *Mus musculus*, as prey. Reasonably, use of laboratory mice takes advantage of their convenience (easily raised in animal facilities), genetic consistency (standardizing of various strains), and repeatability (laboratories can test results obtained elsewhere). However, use of laboratory mice does raise the question of how faithfully they present the rattlesnake with a prey stimulus equivalent to its natural prey and to which its behavioral repertoire is presumably most keenly adapted. Laboratory and wild mice present different visual stimuli (white versus dark) and odors

(strong versus weak; Dice 1957); although not quantified, personal observation and incidental comments in the literature (e.g., Hayes and Galusha, 1984) suggest that wild mice placed before rattlesnakes under laboratory conditions offer a much more cautious, quick reacting prey than laboratory mice. The several studies comparing laboratory versus wild mice found few differences in responses of rattlesnakes to both types of prey, and envenomation effectiveness (time to death) was essentially equivalent (Furry et al., 1991), whereas others did find selective differences in death rates of prey, but not in distance run post-strike (Kuhn et al., 1991). As a companion study to a series of sensory deprivation experiments of rattlesnakes (Kardong, 1992), I compared the stimulus equivalence of laboratory mice to wild mice under similar deprivation treatments. This comparison revealed differences and similarities to previous literature reports (e.g., Chiszar et al., 1981*b*; Dullemeijer, 1961; Naulleau, 1965). The purpose of this paper is to report these findings and to use this as the occasion to discuss the larger issue of the use of laboratory mice in feeding studies in rattlesnakes.

Materials and Methods

All rattlesnakes were *Crotalus viridis oreganus*, part of a permanent long-term colony (over 4 yr), originally captured in Whitman County, Washington. Rattlesnakes in this region feed, as adults, almost exclusively on rodents (Fitch, 1949; Kardong, 1974). While in captivity, all snakes used in this study were similarly fed dead mice (frozen). All used in this study were defined as large (Kardong, 1986*a*), >70 cm snout–vent length, males and females. Previous studies (Kardong, 1986*a*) found no significant differences in predatory behavior between the sexes of rattlesnakes. The same individual snakes were used across the two experiments.

Two sets of experiments were undertaken. In the first set of experiments, predatory variables for the rattlesnakes were scored for snakes striking laboratory compared to wild mice. The two specific species of mice used were white laboratory mice (Swiss Webster), *Mus musculus*, and wild deer mice, *Peromyscus maniculatus*. Laboratory mice ranged in size from 19.2–27.6 g, of mixed sex, raised under controlled laboratory conditions. The wild mice ranged in size from 15.9–24.8 g, of mixed sex, and were live trapped in Latah County, Idaho 1–4 wk prior to use in experiments. During this time, wild mice, like laboratory mice, were fed commercial mouse chow (Purina®) and were kept on a bedding of wood shavings. No near-term, pregnant females were used; previous studies (Kardong, 1986*a*) found no significant differences between male and female (non-pregnant) mice within the scored variables of these experiments.

Comparisons of laboratory and wild mice were made under three treatments of rattlesnakes: normal, eyes covered, and facial pit covered. Specific techniques are defined elsewhere (Kardong, 1992), but generally both eyes were covered with diamond shaped patches of black electrical tape; both facial pits were first filled with a small ball of Styrofoam then covered with a rectangular piece of black electrical tape. Snakes were physically restrained and were grasped behind the head during application of the sensory covers. The procedure took no more than 5 min, after which each snake was returned to its home cage and allowed to acclimate for at least 1 h before feeding trials were begun. Sham treatments included placing donut-shaped pieces of electrical tape around the eyes or facial pits but with a hole in the middle so that the sensory organ was exposed. Such sham treatments produced no statistically significant effects (Kardong, 1992). Therefore, in normal snakes, sensory organs were not covered nor were they encircled with pieces of electrical tape. Safety considerations (e.g., Gans and Taub, 1964) precluded actual pinning and grasping normal snakes, but otherwise they were treated similarly to experimental animals; namely, prior to experimental trials, normal snakes were removed by hook for at least 5 min, returned to the cage, and also allowed to acclimate for at least 1 h.

The second experiment compared predatory behavior of rattlesnakes between

normal Swiss Webster laboratory mice (white) and color dyed Swiss Webster laboratory mice (black/brown). The hair of Swiss Webster mice, normally white in appearance, was hand spread with liquid hair dye (Clairol®, 20-Dark Rich Brown, hypoallergenic) making sure to work the dye over the face and entire body producing a light black/brown color to the mouse hair. This produces laboratory mice closer in color to the usually gray buff of natural prey, *Peromyscus maniculatus*. As soon as the dye dried (about 10 min), these laboratory mice were used in feeding trials.

In both experiments, the feeding trials followed the same protocol (see Kardong, 1992, for details). Generally, rattlesnakes were maintained in individual cages (50 × 50 × 90 cm) with a clear plastic top. Three sides were covered with thick newspaper to block any view of persons in the room; an incandescent light was shown through the fourth side that otherwise faced a blank wall. At opposite ends of the cage, two circular, opaque plastic chutes (8 cm diameter) were suspended through two tight fitting holes in the clear lid to within 6 cm of the floor of the cage. Additional blinds blocked any view of the experimentor. Mice were presented by lowering them down the chute furthermost from where the snake had taken up residence within the cage. After the strike, mice were retrieved immediately by a monofilament line tied earlier to their tails; a dead mouse of the same species and approximate size was immediately reintroduced to replace the struck mouse. An overhead video camera connected to recording and monitoring equipment in an adjacent room permitted continuous viewing of ensuing events. Scoring of predatory variables was done later by playback of the videotape.

Details of variables can be found elsewhere (Kardong, 1992), but generally include 14 dependent variables: tongue flicks per minute taken in the 1 min before the strike (INTROTFR); time (s) from introduction of mouse to initiation of the strike (TIMESTR); time (seconds) for prey to die after being struck (TIME-TO-DEATH); shortest distance from snake-to-mouse immediately before the strike (RANGE); sequential location on the mouse where fangs entered, from head/shoulders (1), midbody (2), to rump (3) (SITE); whether mouse was released (0) or held (1) following the strike (HOLD/RELEASE); number of times the snake struck at the prey (STRIKES); time (s) from reintroduction of the dead mouse to when the snake discovered the mouse (SEARCH); tongue-flick rate, tongue flicks taken during the minute immediately before swallowing began (INVESTTFR); time (s) from discovery of dead mouse to when first swallowing tries began (INVESTIM); whether the mouse was (1) or was not (0) swallowed (SWALLOW2); number of attempts to swallow prey (TRIES); whether swallowing began at the head or anus end of the mouse (HDANUS); time to swallow the dead mouse (DEGLUTIT).

As the number of independent contrasts are scored in an experiment, each at α level of significance, the probability of making a Type I error increases, namely the probability of obtaining spuriously significant results increases (Kirk, 1982). Because the design in this study included experiment-wise comparisons, a Bonferroni t procedure was used to control the experiment-wise Type I error (Milliken and Johnson, 1984). Taken together in the two experiments, there were totally 56 comparisons (14 variables, four treatments). At a comparisonwise error rate of $\alpha = 0.05$, the experiment-wise error rate $\alpha^* = 0.05/56 = 0.00089$. This experiment-wise α^* was used to establish the level of significance in each of the four treatments respectively: $F_{1,\ 25,\ 0.00089} = 14.21$; $F_{1,\ 19,\ 0.00089} = 15.47$; $F_{1,\ 17,\ 0.0089} = 16.14$; $F_{1,\ 9,\ 0.0089} = 23.64$.

Results

Experiment 1: Laboratory versus Wild Mice, Sensory Deprivation

Across the three sensory deprivation treatments, none of the 14 variables were significantly different between laboratory and wild mice (Table 1). However, several variables scored for laboratory and wild mice were significantly different within one of the three treatments. Laboratory

TABLE 1.—Laboratory versus wild mice. Comparison of dependent variables of rattlesnakes normal (control), blindfolded (eyes covered), or facial pits covered presented laboratory versus wild mice. Respectively, 26, 20, and 18 snakes were used in each treatment. Means of scored variables are given, and below each in brackets is 1 SD.

	Treatments								
	Control			Eyes covered			Facial pits covered		
	Lab	Wild		Lab	Wild		Lab	Wild	
Dependent variables	$\bar{x}$ (26)	$\bar{x}$ (26)	F	$\bar{x}$ (20)	$\bar{x}$ (20)	F	$\bar{x}$ (18)	$\bar{x}$ (18)	F
INTROTFR	17.7	11.7	1.02	23.7	30.3	1.26	15.6	5.4	1.01
	[12.2]	[12.3]		[16.1]	[14.4]		[9.5]	[9.4]	
TIMESTR (s)	24.6	34.4	4.63	24.4	168.3	140.08*	19.9	25.0	3.62
	[37.9]	[81.7]		[13.1]	[154.6]		[20.9]	[39.9]	
TIME-TO-DEATH	663.5	152.1	43.60*	176.8	124.0	1.81	415.0	250.6	2.40
	[1494.9]	[226.5]		[167.9]	[226.2]		[493.1]	[317.9]	
RANGE	8.3	8.8	1.04	3.8	2.7	4.12	7.5	9.0	1.55
	[3.7]	[3.6]		[3.3]	[1.6]		[3.2]	[4.0]	
SITE	1.4	1.9	6.05	1.9	1.8	1.18	1.4	1.8	2.02
	[0.6]	[1.4]		[1.1]	[1.2]		[0.8]	[1.2]	
HOLD/RELEASE	0.0	0.0	0.00	0.0	0.0	0.00	0.0	0.0	0.00
	[0.1]	[0.0]		[0.0]	[0.0]		[0.0]	[0.0]	
STRIKES	1.3	1.8	4.12	1.2	1.5	17.05*	1.4	1.7	3.74
	[0.5]	[1.0]		[0.3]	[1.2]		[0.7]	[1.3]	
SEARCH (s)	168.2	178.0	1.39	102.0	91.7	1.11	126.8	103.5	2.56
	[230.2]	[271.7]		[62.5]	[59.4]		[83.7]	[52.3]	
INVESTTFR	66.8	75.0	1.49	69.5	70.8	1.54	70.7	67.5	1.00
	[12.7]	[15.5]		[13.5]	[10.9]		[15.3]	[15.2]	
INVESTIM (s)	93.5	120.2	6.72	82.9	223.0	12.21	80.0	190.1	13.71
	[113.0]	[293.1]		[76.1]	[265.7]		[86.5]	[320.4]	
SWALLOW2	0.97	0.96	3.84	0.98	0.98	1.78	0.94	1.0	1.00
	[0.1]	[0.2]		[0.1]	[0.1]		[0.2]	[0.0]	
TRIES	1.5	1.2	1.44	1.8	1.5	1.72	1.4	1.5	2.61
	[0.7]	[0.6]		[1.0]	[0.0]		[0.6]	[0.9]	
HDANUS	0.98	0.96	9.00	1.0	1.0	1.00	1.0	1.0	1.00
	[0.07]	[0.20]		[0.0]	[0.0]		[0.0]	[0.0]	
DEGLUTIT (s)	469.2	454.8	2.03	424.5	393.2	1.10	444.9	376.8	1.45
	[140.6]	[98.8]		[107.6]	[102.7]		[102.0]	[84.8]	

* $P < 0.05$ adjusted for experimentwise comparison giving a significance level of $F = 14.21$ (control), $F = 15.47$ (eyes covered), $F = 16.14$ (facial pits covered).

(s) indicates scored in seconds; INTROTFR, tongue-flick rate before strike; TIMESTR, time from prey introduction to strike; TIME-TO-DEATH, time for struck prey to die; RANGE, snake to prey strike distance; SITE, location of fang penetration on prey; HOLD/RELEASE, mouse held or released after strike; STRIKES, number of times snake struck prey; SEARCH, poststrike time to discover dead mouse; INVESTTFR, tongue-flick rate immediately before swallowing; INVESTIM, time discovery of mouse to beginning of swallowing; SWALLOW2, whether or not recovered mouse was swallowed; TRIES, number of swallowing attempts; HDANUS, whether prey was swallowed head- or anus-first; DEGLUTIT, swallowing time.

mice struck by normal rattlesnakes (no sensory organs covered) took significantly longer to die (TIME-TO-DEATH) than wild mice (663.5 versus 152.1 s)

Blindfolded rattlesnakes launched a successful strike (TIMESTR) sooner when laboratory mice were presented than when wild mice were presented (24.4 versus 168.3 s). Blindfolded rattlesnakes also struck fewer times at laboratory mice before landing a successful strike (STRIKES) than when presented with wild mice (1.2 versus 1.5 times).

When facial pits were covered, rattlesnakes exhibited no selective difference in the 14 variables.

Experiment 2: Laboratory (White) versus Laboratory (Dyed Black/brown) Mice

Rattlesnakes showed no statistical differences in predatory behavior whether white-fur or dyed black/brown-fur laboratory mice were presented (Table 2).

DISCUSSION AND CONCLUSIONS

Differences in time-to-death of the two mice species emerged only where snakes were normal (no sensory deprivation). Why

similar statistical differences did not emerge when eyes or facial pits were covered is not known. Perhaps when sensory input is reduced, venom delivery may be altered to increase certainty of results. These experiments did not address this issue. However, the fact that differences in mouse death rate struck by normal rattlesnakes did emerge is in contrast to some reports of rattlesnake performance (Furry et al., 1991), but in keeping with other reports (Kuhn et al., 1991). Perhaps these differences in results reflect the fact that different subspecies of rattlesnakes were used in the studies and/or that slightly different methods of mouse presentation were employed. However, I would like to stress, as done by others (Kuhn et al., 1991), the great variation in death rate; most mice die quickly in under 60 s, but a few survive much longer. The reasons for such variation in death rate may relate to disruption of the strike (Kardong, 1986*b*) and/or to the site on the mouse where venom is injected (Hayes, 1991; Kardong, 1986*a*). Although the mean death rates (laboratory to wild) were significantly different, both showed considerable variation in the present study (23–7200 s versus 15–767 s, respectively, laboratory versus wild mice). The important biological point to emphasize is that the post-strike repertoire of rattlesnakes must be sufficient to recover struck and released mice that on occasion may scamper significant distances before becoming immobile.

The selective differences in variables between the three treatments may also be related to the differences in elusive behavior of the two species of mice. As noted earlier, wild mice offer a more alert, wary, and elusive target than laboratory mice. Such especially cautious behavior of wild mice likely accounts for the longer time that blindfolded rattlesnakes take in finally launching a successful strike and in the larger number of missed strikes before then.

Previous work documents a decrease in striking range if rattlesnakes are blindfolded (Kardong, 1992), and that is reflected in the present study between laboratory mice (8.3 to 3.8 cm control to blindfolded). This decrease in range has been hypothesized to result from the different capabilities of the sensory system of the rattlesnake (Kardong, 1992). Blindfolding the snakes leaves them the infrared sensitive pits as the primary source of sensory input guiding the strike, but apparently the snake's ability to form a differentiated infrared image of the prey is less than the eyes, so the snakes must approach closer to the prey before launching a strike (Benson and Hartline, 1988; Kardong, 1992). Thus, both characteristics of the sensory systems (visual versus infrared) and the prey (evasiveness) help explain modifications of predatory behavior of the rattlesnakes.

Black/brown laboratory mice elicited predatory behavior statistically equivalent

TABLE 2.—Responses of rattlesnakes (n = 10) to white fur versus dyed black/brown fur laboratory mice. Means of scored variables are given and below each in brackets is 1 SD.

Dependent variables	Laboratory mice: White $\bar{x}$ (10)	Laboratory mice: Brown $\bar{x}$ (10)	F
INTROTFR	13.9 [12.5]	2.2 [6.2]	3.95
TIMESTR (s)	7.2 [4.9]	7.4 [9.9]	4.19
TIME-TO-DEATH	547.3 [786.7]	584.6 [518.0]	2.31
RANGE	8.2 [4.5]	8.8 [4.0]	1.23
SITE	1.2 [0.4]	1.5 [1.1]	8.14
HOLD/RELEASE	0.0 [0.0]	0.0 [0.0]	0.0
STRIKES	1.5 [0.6]	1.4 [0.7]	1.5
SEARCH (s)	109.5 [63.2]	104.5 [64.1]	1.03
INVESTTFR	71.1 [10.1]	60.5 [12.8]	1.59
INVESTIM (s)	96.4 [110.1]	177.9 [320.1]	8.45
SWALLOW2	1.0 [0.0]	0.9 [0.3]	1.00
TRIES	1.5 [0.9]	1.4 [0.9]	1.89
HDANUS	1.0 [0.0]	1.0 [0.0]	1.00
DEGLUTIT (s)	506.3 [125.4]	488.8 [230.1]	3.37

* $F < 0.05$; adjusted for experimentwise comparison giving a significance level of $F = 23.64$.

(s) indicates scored in seconds. For description of variables, see legend for Table 1.

to white laboratory mice. This suggests that the difference in pelage color of laboratory to wild mice (white to black/brown) is a relatively unimportant difference between the two as a predatory stimulus.

Although implicit within the discussion of statistical analysis, it bears emphasis to state that the general absence of significant difference between pairwise comparisons does not constitute proof on behalf of the null hypothesis. And, as with all laboratory studies, one must keep in mind the possibility of introducing artifacts compared to natural predatory conditions. Further, other experimental conditions are imaginable and reasonable (Furry et al. 1991; Gillingham and Clark, 1981; Graves and Duvall, 1985; Halpern, 1987; Hayes and Duvall, 1991; Kuhn et al., 1991; Proske, 1969) in which to compare behavioral responses to laboratory and wild mice. However, the experimental conditions of the present study seem to simulate reasonably natural hunting approaches of rattlesnakes (Duvall et al., 1985, 1990). Thus, this study is in agreement with others (e.g., Furry et al., 1991), namely that with few exceptions, laboratory mice elicit predatory behaviors of rattlesnakes equivalent to their predatory responses to natural rodent prey.

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CUES INVOLVED IN RELOCATION OF STRUCK PREY BY RATTLESNAKES, *CROTALUS VIRIDIS OREGANUS*

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ABSTRACT: Following release of an envenomated mouse, a rattlesnake begins a post-strike trailing behavior that allows it to track chemically and to recover the dispatched prey. The rattlesnake can discriminate the trail of the mouse that it struck from trails of other unstruck mice, suggesting that the struck mouse produces a chemically unique odor trail. The purpose of this study was to determine generally what those chemical cues might be and what emphasis the rattlesnake might give to each during post-strike trailing. Taking advantage of venomoid (venomless) rattlesnakes, four experiments were performed in which we examined the ability of rattlesnakes to discriminate trails of mice receiving fang punctures (but no venom), mice artificially struck by hand (no venom), different individual mouse scents, and the effects of venom on post-strike trailing ability. We found that fang puncture alone was sufficient to produce a distinctive odor trail, but that this was subordinate to the distinctiveness of individual mice odors; envenomated mice produced the most distinctive trail. Our results indicate that alone the mechanical effects of fang penetration of the integument produce a chemical uniqueness in the mouse, but that can be overridden by mouse odor and venom effects. Thus, rattlesnakes biting mice have available ranked odors unique to the struck mouse: venom > mouse odor > fang puncture.

Key words: Rattlesnakes; Predation; Post-strike trailing; Chemosensory cues; Envenomation

RODENT prey, released immediately by a rattlesnake after an envenomating strike, dash a varying distance before dying (Hayes and Galusha, 1984; Kuhn et al., 1991). Shortly thereafter, the rattlesnake begins a pattern of post-strike behavior that includes elevated levels of tongue-flicking (Chiszar et al., 1983) and use of chemical information associated with the prey (Melcer and Chiszar, 1989*a*,*b*) that facilitates discrimination of the victim's scent trail from that deposited by unstruck rodents (Furry et al., 1991). The rate of post-strike tongue-flicking depends at least upon as-