

Department of Zoology, Washington State University, Pullman, WA, U.S.A.

Proximate Factors Affecting Guidance of the Rattlesnake Strike

KENNETH V. KARDONG

With 2 Tables

Abstract

Rattlesnakes, *Crotalus viridis oreganus*, were deprived of the 3 primary sensory organs – eyes, facial pits, vomeronasal organ – either individually or together (eyes plus facial pits), and the effects on 14 dependent variables of predatory behavior quantified. Of these 3 sensory organs, the eyes and facial pits were confirmed to be the most important during the strike behavior. Further, each alone was able to compensate equivalently for the absence of the other and maintain a high level of predatory performance. The only exception was that strikes dependent upon facial pits (eyes covered) were initiated when much closer to the prey. The vomeronasal organ was important during prestrike and poststrike behavior but its absence had no statistical affect upon the strike itself.

1. Introduction

For the rattlesnake, successful predatory behavior often comes down to a rapid strike during which a single pulse of venom is delivered. Following the strike, the rodent prey is usually released. Thereafter the rattlesnake follows the scent trail left by the envenomated rodent to recover and swallow the dispatched quarry. Since killing of prey is largely the result of chemical envenomation, the delivery of venom during the strike is critical to subsequent successful discovery and swallowing of the prey. Yet, delivery of venom occurs in a very brief period, usually less than 0.5 sec, during which the prey may take evasive action and the snake adjust for any initial errors in placement of its fangs. Guidance of the cranio-cervical system of rattlesnakes brings the venom apparatus quickly into the vicinity of the prey and delivers the pulse of venom. During this rapid strike, as well as during prestrike preparation and poststrike recovery of prey, a multisensory system monitors a variety of proximate factors critical to the overall hunting success of the rattlesnake.

Among the various sensory receptors, the vomeronasal organ (*VNO*), eyes, and facial pits all likely contribute to the sensory configuration of the prey during predation. The vomeronasal organ is certainly important after the strike when the snake searches to recover the dispatched victim (COWLES and PHELAN 1958; DULLEMEIJER 1961; DUVALL et al. 1980; CHISZAR et al. 1980, 1983; GILLINGHAM and BAKER 1981; O'CONNELL et al. 1981). There is even some evidence (GRAVES and DUVALL 1985; GILLINGHAM and CLARK 1981) that it plays a role in prestrike behavior, although its specific role remains uncertain (cf. CHISZAR et al. 1977).

Chemical cues may play a more general role in confirming identity of prey (GRAVES and DUVAL 1985). In natricine snakes chemical cues are used to identify, track, and strike prey (BURGHARDT 1970, 1980; CHISZAR et al. 1981a, b). In a series of extensive studies with garter snakes, the VNO has been implicated in trailing as well as the actual attacks upon prey (HALPERN 1983; HALPERN and FRUMIN 1979; HALPERN and KUBIE 1983, 1984; KUBIE and HALPERN 1979; HELLER and HALPERN 1982). It has also been implicated in social behavior (HELLER and HALPERN 1982), but in a complicated way (HELLER and HALPERN 1982; KUBIE et al. 1978). However, in crotaline snakes, vision and thermoreception are apparently the most important senses immediately affecting orientation to the prey and during the strike itself (SCUDDER 1982; DE COCK BUNING 1983a).

The exact roles played by the eyes and the facial pits in directing the strike are not known. Although sometimes awkward, blindfolded crotaline snakes will still strike at live mice (DE COCK BUNING et al. 1981). If the facial pit is plugged, some crotalines will (DE COCK BUNING et al. 1981) and others will not (DULLEMEIJER 1961) strike at mice. Their roles are complicated, perhaps interrelated, but the eyes and the facial pits seem to be important factors in the strike. They are thus likely the sense organs most important in gathering information about the prey that is translated into what has been termed a differentiated image within the central nervous system that can be used to discriminate prey form (KARDONG 1986a; BERSON and HARTLINE 1988; KARDONG and MACKESSY 1991).

The purpose of this study is twofold. First, it tests for the separate roles of these 3 primary sensory receptors—eyes, facial pits, vomeronasal organ—in the predatory behavior of the rattlesnake. Thus, second, this study compares the effects of multiple deprivation of eyes and facial pits together upon the hunting behavior of rattlesnakes.

2. Materials and Methods

2.1. General Procedures

All snakes used were northern Pacific rattlesnakes, *Crotalus viridis oreganus*, collected from eastern counties (GRANT and WHITMAN) of the state of Washington (USA), constituting a common laboratory colony kept in an isolated reptile room and where experimental trials were also conducted. This reptile room was kept warm year around (27 to 32 C) and maintained on a 12:12 h = light/dark cycle. Each snake was housed individually in a glass terrarium approximately 50 × 50 × 90 cm the floor of which was covered by newspaper. A newly caught snake was considered acclimated when it began striking and swallowing live mice presented. Access to the room was limited to authorized personnel (3 persons) familiar with the experiments and safety procedures (GANS and TAUB 1964). All snakes used in the study measured over 70 cm SVL and had been in captivity at least 6 months when feeding trials began.

2.2. Feeding Trials

The predatory behavior was divided into 3 phases—prestrike, rapid strike, and poststrike. During each of these 3 phases, 15 variables (see below) were scored, some immediately, most later by playback of a videotape recording of the entire feeding trial.

Videotape recording: 2 Panasonic video cameras were used. One camera, held above the cage on a tripod, obtained an image of the entire area of the cage floor; the other camera, outside the reptile room, was focused upon specific feeding trial data (snake identification, real time, date, comments). Through an intervening video mixer, both images were brought to simultaneous viewing on split screen and recorded on a VHS video recorder with pause and video field-by-field advance. This video system was not high-speed so images of the strike were blurred. Nevertheless, these images were sufficient to confirm scoring of strike variables, and certainly the slower prestrike and poststrike behaviors could be accurately scored later (1 to 7 d) during playback of the video. This later scoring was done by the same individual throughout the entire study who quantified the particular variables directly from the screen (tongue flicks, range, etc).

Presentation of the Mouse: 3 to 24 h before a feeding trial, the snake in its own cage was placed upon a counter top within the reptile room. The screen cage top was replaced with a clear plastic lid with 2 holes (6 cm dia) at opposite ends. Visually opaque tight-fitting tubes of PVC plastic were suspended through these holes to a level about 7 cm above the cage floor. These tubes were the chutes down which mice were introduced during the feeding trial. The back of the cage faced a blank wall. Directed in this side of the cage was an incandescent light that both served as the sole illumination of the cage and could be adjusted to keep the temperature in the cage between 30 to 32 °C during feeding trials. The 3 other sides of the cage, that gave the snake a view of the room, were covered with thick sheets of newspaper and tagboard. Further blinds were placed strategically around the cage and entrance to the chutes so that the snake could not see the experimenter at anytime during presentation of the mouse. The overhead lights in the room were turned off to further reduce possible distractions. Finally, a video camera was positioned over the cage.

During a feeding trial, a live, preweighed mouse was gently lowered, by a long monofilament line tied to its tail, down the chute furthest from where the snake had taken up residence within the cage. Immediately (<5 s) following the strike, the mouse was retrieved, via the line tied to its tail, and the ensuing death rate scored. Immediate retrieval of the struck mouse was necessary so that any reflex actions of the mouse (KARDONG 1986a) did not stimulate a 2nd or 3rd snake strike. Further, the mouse spasms did not always occur and thus would have confounded the poststrike stimuli from trial-to-trial. However, the retrieved mouse was replaced with a dead mouse of approximately equal weight introduced back down the chute thus presenting the snake with actual, but non-moving, poststrike prey. If no strike was initiated within 15 min the trial was ended. At least 2 weeks separated feeding trials.

2.3. Treatments

In separate feeding trials, each snake was entered in control treatments and in up to 3 different experimental treatments that selectively deprived it of one of its primary routes of sensory input – eyes, facial pit, vomeronasal organ.

Control: Control treatments were of normal snakes with no sensory organ covered.

Eyes: To eliminate visual input, both eyes were covered with black plastic, electrical tape. Snakes were lifted from their cages by a long hook, placed on a flat counter top, and pinned behind the head with a long bar. The snake was then grasped by hand immediately behind the head taking care that at no time during the procedure did the snake prematurely release venom. A small dab of petroleum jelly was touched to each eye to make later removal of tape easier. A precut piece of this opaque tape (approx. 6 × 6 mm) was placed over each eye and pressed around its edges to affix it in place. Care was taken not to cover adjacent sensory organs or leave gaps in this tape blindfold. The snake was returned to its cage within 2 min overall, allowed to acclimate for at least 1 h, and then a feeding trial was begun. Immediately after the feeding trial, the snake was similarly pinned, the plastic blindfold of each side inspected to be sure it still completely covered the eye, and then it was removed.

Facial pit: To eliminate infrared input via the facial pits, both pits were covered. Once pinned, as described above, a small ball of styrofoam was inserted into each pit; then a narrow piece of black plastic, electrical tape (approx. 3 × 6 mm) was affixed across the pit further covering it and holding the styrofoam in place. The snake was returned to its cage within about 4 min overall, allowed to acclimate for at least 1 h, then a feeding trial was begun. Immediately after the feeding trial, the snake was pinned, the covers over its facial pits inspected, and then the covers were removed.

Vomer onasal Organ: To eliminate chemosensory input via the vomeronasal organ, the 2 ducts leading from the mouth to this organ were covered. In the past, 2 methods of externally blocking these ducts have been used in reptiles. One involves suturing loose folds of oral epithelium across the duct openings (KUBIE and HALPERN 1979); the other involves the use of a drop of tissue glue to temporarily block these openings. In a pilot study, we tried both techniques, and decided on the use of glue. We preferred glue because, after some practice, we felt it presented less of a mechanical obstruction to tongue protrusion compared to suture thread. Further, we found we could apply the glue without anesthetization of the snake. This removed any doubt about whether the snake might carry into a feeding trial any lingering effects of the anesthetic and allowed us to begin feeding trials soon (within 1 h) thus leaving the glue in place for only a short time.

The snake, pinned and grasped as above, was held beneath a low magnification dissecting microscope. Its mouth was gently opened, the ducts in the roof of the mouth identified, and a small drop of cyanoacrylate glue (Superglue®) touched to the area of these openings. The snake was held, with mouth open, until the glue hardened. As with other treatments, if venom premeautrally spilled from one or both fangs during the procedure, then that snake was not entered in a feeding trial that day. Otherwise, the snake was returned to its cage withing about 15 min overall, allowed to acclimate for at least 1 h, then a feeding trial was begun. Immediately after the feeding trial, the snake was pinned, the drop of glue inspected to be sure it was still in place, then the glue was removed gently with forceps.

2.4. Variables

Certainly many factors could contribute to successful predatory behavior. However, in this study 16 were followed during each feeding trial. These represent factors that seemed might be important from our work (KARDONG 1986a; KARDONG and MACKESSY 1991; ROBINSON and KARDONG 1991) and that of others (NAULLEAU 1965; CHISZAR et al. 1977, 1981 a, b; HAYES 1991). For example, tongue flicks have been counted during various snake activities and their variation and frequency used to help interpret behaviors (O'CONNELL et al. 1981). Tongue protrusion/retraction cycles were counted from videos and expressed in tongue flicks/min. If counts were scored for less than 1 min, then the score was extrapolated to a min^{-1} basis.

2.5. Prestrike

Prior: Tongue flicks taken in the 1 min before the introduction of a mouse.

Introduction: Tongue flicks during the minute before the strike.

Timestrike: The time [sec] elapsing from the introduction of a mouse at the bottom of chute to the point at which the snake launches its strike.

2.6. Strike

Detailed descriptions and rationale of strike variables are given elsewhere (Kardong 1986a). Generally, the following were scored during the strike or were a consequence of the strike.

The prey used were of Swiss-Webster "white" laboratory mice, *Mus musculus*. 2 weight classes of laboratory mice were used, small (8.0 to 11.0 g) and large (20.0 to 28.7 g). The time to nearest second for prey to die (last muscular twitch) following the strike was the death rate. The hold/release behavior refers to whether the snake continued to hold

(score = 1) a struck mouse or immediately (1 to 2 s) released (score = 0) the mouse. The site struck scores the location on the body of the mouse where the fangs made contact — site 1 (head/shoulders), site 2 (mid body), site 3 (rump). Only 1 size class of snake was used, large snakes, 70 to 85 cm, SVL; only 1 mouse was presented during a feeding trial.

Range: The distance at strike between the tip of the snake's snout to the closest part of the mouse constituted the strike range. The video tape was paused just before the rapid strike was launched and the distance measured on the video monitor (later calibrated and expressed in actual cm).

2.7. Poststrike

Search: The time interval [sec] from when the replacement mouse was introduced until investigation movements of the snake brought the tip of the snake's snout to within 1 cm of the mouse was the search time.

Swallow: Dependent variable that scores whether snake eventually did (1) or did not (0) swallow the presented mouse within 3 h of experimental trial.

Investon: Tongue flicks taken in the minute immediately before swallowing begins.

Investim: Time from when investigation of the mouse first begins (snout within 1 cm) to when first swallowing try begins (jaws open, first reciprocating motions of the jaws).

Deglutit: Time from start of swallowing (first reciprocating movements of jaws) to end of swallowing (point at which last part of the prey, not including the tail, could no longer be seen in overhead view). If the snake stopped swallowing, regurgitated the mouse, but later began again, the deglutition time was for the final, successful swallowing attempt.

Tries: Often after several seconds of swallowing, the snake might stop, reverse swallowing, and eject the mouse from its mouth. One such behavior constituted one swallowing try. The number of such tries was scored.

Hdanus: The site (head/shoulders = 1, midbody = 2, rump = 3) on the prey were swallowing began was also scored. Usually this was the head, but on several occasions the snake began at another part of the body. If several swallowing attempts were made, then this score was for the last successful swallowing.

2.8. Experimental Design/Statistical Tests

Most dependent variables met assumptions of parametric tests and therefore 2 tests for statistical significance were used, analysis of variance (ANOVA) and Z-tests. A repeated measures design was used in which each individual snake was run as a control and in an experimental treatment (paired, random order). In a sense, each snake was its own control (WIENER 1971). Results from all snakes so tested were pooled and a Z-test run on performance of control vs experimental treatment for each variable. A further analysis of variance was used, in particular the general least squares package, Statistical Analysis Systems (SAS, PROC GLM). The effects of each variable were statistically eliminated in a stepwise fashion. Thus, each variable under each treatment was separately isolated and tested for its single effects on snake predatory behavior. Where distributed scores of dependent variables were skewed, data were rank-transformed prior to Z-test or t-test (CONOVER 1980).

During pretesting, sham operations were performed. For eyes and facial pits, this consisted of patches of black electrical tape as in the experimental protocol, except a hole was cut in the middle so that the eye or facial pit itself remained exposed but the patch was otherwise positioned as in experimental procedures. For the vomeronasal organ, sham operation consisted of sutures sewn or glue applied to the oral epithelium adjacent to the ducts but not occluding them. Sham operations produced no statistical effects. Further, all snakes were tested in feeding trials before and again after the experimental trials, about 18 months. This confirmed that no statistical change occurred in predatory behavior during the course of the experimental treatments.

2.9. Experiments

Study 1: The individual roles of the 3 sensory receptors were examined by comparison of controls (normal) to experimental treatments (deprivation of sensory input) in 3 experiments – Experiment 1 (eyes), Experiment 2 (facial pit), Experiment 3 (vomeronasal organ). From the captive colony of rattlesnakes, 24 individuals were used in experiment 1, 37 in experiment 2, and 19 in experiment 3.

Study 2: The possible role of the VNO alone was examined by an experiment in which eyes and facial pit were covered simultaneously. The same snakes were presented, in separate feeding trials, with laboratory mice.

3. Results

3.1. Study 1

Snakes were presented with all 3 experimental treatments (covered eyes, facial pit, VNO) and the effects on variables compared to the control treatment.

3.1.1. Site, Hold/Release, Death rate, Tries

Snakes in all treatments struck site 1 (head/shoulders) more frequently (about 70% of the time) than any other location on the prey. This tendency to strike site 1 was statistically equivalent in all 3 experimental treatments compared to control treatments. Snakes were also statistically equivalent in their tendency to release prey following the strike (80% of the time), although like controls, under all 3 experimental treatments the tendency to release mice declined (75%) if small mice were presented. None of the treatments produced a statistically significant change in death-rate; mice struck by snakes with eyes, or facial pit, or VNO covered died as quickly as mice struck during control trials. There were no “dry bites“. Death rates varied, but all struck mice died; 50% of all struck mice were dead in less than 60 s. In all control trials (100%), snakes presented with prey struck the prey; when eyes or facial pits were covered, this percent fell only slightly to 99% (97/98) and 93.7% (104/111), respectively. However, when the VNO was covered, strike attempts fell significantly ($Z^2 = 19.29$, $P > 0.001$) so that only 79.7% (55/69) of the snakes struck at mice presented. Most effects of experimental treatments upon predatory behavior arose during prestrike and in poststrike phases.

3.1.2. Range, Timestrike, Intro, Search, Investon, Investim

The RANGE and TIMESTRIKE were affected when eyes of the snake were covered, but not during any other treatments. Blindfolded snakes did not launch a strike until much closer to the prey, almost twice as close, than controls (Tables 1, 2). In blindfolded snakes, the time to initiate a strike following introduction of prey significantly increased. None of the other dependent variables scored showed any change from normal (control) predatory behavior when snakes were blindfolded.

Table 1. Small mice (≤ 11 g) as prey. Descriptive statistics are shown for dependent variables during prestrike, strike, and poststrike predatory behavior of the rattlesnake, *Crotalus viridis oreganus*.

Dependent variable	Treatment					
	Control		Covered Eyes		Control	
	Control	Covered Eyes	Control	Covered Facial Pit	Control	Covered VNO
	$n = 32$	$n = 32$	$n = 36$	$n = 36$	$n = 22$	$n = 22$
	\bar{X}	\bar{X}	\bar{X}	\bar{X}	\bar{X}	\bar{X}
INTRO	13.1	19.9	14.0	13.9	12.9	.02***
TIMESTRIKE	44.9	92.8	53.2	45.7	40.9	64.3
DEATH RATE	214.6	242.5	196.0	268.2	176.6	114.7
RANGE	5.5	2.2***	6.7	5.6	5.8	4.8
SITE	1.6	1.9	1.7	1.6	1.6	1.5
HOLD/RELEASE	0.28	0.31	0.20	0.29	0.26	0.23
STRIKES	1.2	1.1	1.1	1.2	1.1	1.3
SEARCH	182.8	95.5	131.1	210.1	124.6	239.1*
INVESTON	55.9	63.9	58.7	67.5	57.1	6.2***
INVESTIM	104.8	137.2	121.9	85.0	106.7	276.5
SWALLOW	1.0	1.0	1.0	1.0	1.0	0.9
TRIES	1.8	1.4	1.8	1.6	1.7	1.5
HDANUS	1.2	1.0	1.2	1.1	1.2	1.2
DEGLUTIT	280.9	250.1	310.9	233.5	284.3	240.0

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Snakes with ducts to VNO covered, however, showed significant changes in 1 prestrike and 4 poststrike dependent variables (Table 1, 2). If the VNO was covered, the number of tongue flicks prior to the strike (INTRO) significantly declined. Of poststrike variables, snakes with covered VNO took longer to rediscover prey (SEARCH), exhibited reduced tongue flick rate before beginning swallowing (INVESTON), and investigated the prey longer before beginning swallowing (INVESTIM). Further, if large mice were presented, snakes with VNO covered exhibited reduced tendency to swallow (SWALLOW) dispatched prey (for presented small mice, this statistical difference did not emerge).

3.2. Study 2

When both eyes and facial pits were covered simultaneously, the number of strikes fell precipitously to 57.1% (8/14). The snakes did not strike randomly and succeeded only 8 times. This decline from 100% (control) was a consequence of the failure of the snakes to initiate any strike at all. In those 8 strikes, the site at which the snake struck was less often placed in the anterior of the mouse, and the range significantly declined, 7.7 cm to 3.6 cm. But, in all other dependent variables there was no significant difference from control trials.

Normal (control) predatory behavior, as characterized by these 14 dependent variables, did not change within an individual snake during the course of the

Table 2. Large mice (>20 g) as prey. Descriptive statistics are shown for dependent variables during prestrike, strike, and poststrike predatory behavior of the rattlesnake, *Crotalus viridis oreganus*.

Dependent variable	Treatment					
	Control		Covered Eyes		Control	
	Control	Covered Eyes	Control	Covered Facial Pit	Control	Covered VNO
	$n = 24$	$n = 24$	$n = 35$	$n = 35$	$n = 27$	$n = 27$
	\bar{X}	\bar{X}	\bar{X}	\bar{X}	\bar{X}	\bar{X}
INTRO	15.7	22.5	16.9	15.8	15.6	.4***
TIMESTRIKE	28.7	46.1*	32.7	22.4	14.5	11.6
DEATH RATE	323.6	229.6	350.9	389.1	665.6	657.5
RANGE	8.1	4.9*	9.0	7.3	9.2	7.9
SITE	1.5	1.8	1.6	1.3	1.6	1.3
HOLD/RELEASE	0.01	0.00	0.01	0.00	0.01	0.03
STRIKES	1.5	1.2*	1.4	1.3	1.5	1.4
SEARCH	117.1	99.9	160.2	158.8	107.5	237.0**
INVESTON	68.2	67.5	64.9	66.2	67.9	10.2***
INVESTIM	109.1	100.7	92.4	86.3	94.6	312.4
SWALLOW	1.0	1.0	1.0	0.9	1.0	0.8
TRIES	1.4	1.9	1.4	1.4	1.4	1.9
HDANUS	1.1	1.0	1.1	1.0	1.0	1.1
DEGLUTIT	461.4	476.1	481.8	478.1	457.8	508.1

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

approximately 18 months of the feeding trials ($p < 0.87$, $n = 36$). However, between snakes, there were a few that were significantly and consistently different than all others taken together in the death rate their strikes produced.

4. Discussion

The tendency for rattlesnakes to deliver strikes preferentially to the anterior region of the prey was not affected by any of the treatments in which deprivation was of single sensory organs. This suggests that when deprived of one of the 3 primary sensory organs, the remaining sensory organs can compensate to maintain strike accuracy. When both eyes and facial pits were covered, this accuracy declined suggesting that formation of a differentiated image of the prey resides primarily within both organs. Covering the eyes produced changes in the range at which the strike was initiated, namely closer to the prey. This suggests that the facial pit is more distance limited than the eyes. Conversely, absence of any statistical change in predatory behavior when the facial pit was covered suggests that comparatively, the eyes offer a slightly more complete compensation for facial pit deprivations, than the other way around.

Deprivation of the VNO reduced the number of strikes, but produced no significant alteration of the strike performance itself (c. f. GRAVES and DUVAL

1985). Rather, 1 prestrike (reduced INTRO) and 4 poststrike (SEARCH, INVESTON, INVESTIM, SWALLOW) variables were affected. This is consistent with the view (DE COCK BUNING 1983a) that the role of the VNO in hunting behavior centers upon chemoreception of pertinent odors.

Whether the VNO can (with chemosensory stimuli) produce a differentiated image of the prey equivalent to eyes and to facial pits is a difficult issue to interpret. In many vertebrates, the vomeronasal organ plays a surprising role in behavior. It is hypothesized to mediate the unconditioned reinforcing properties of naturally occurring prey odors; visual, tactile, and olfactory cues become paired with VNO stimulation (HALPERN 1987). Vomeronasal removal or lesions may lead to gradual extinction of responses paired with VNO stimuli in, for example, guinea pigs (BEAUCHAMP et al. 1982, 1985) and garter snakes (KUBIE and HALPERN 1979). In this current study, the reported drop in rattlesnake strike responses following VNO deprivation to 79.7% would be consistent with the view that in rattlesnakes the VNO also mediates unconditioned reinforcement of paired stimuli. Whether rattlesnake strikes would have continued to decline with continued VNO deprivation was not addressed in my study.

On the other hand, a patent VNO but without visual and infrared input (eyes and facial pits closed) was nevertheless also accompanied by precipitous decline in strikes (to 57.1%). Even snakes that do not strike exhibit predatory interest in the prey (they do not rattle their tails defensively, but show head turning and some approach to temporarily stationary prey). Absence of a strike does not seem to be a consequence of absence of interest. Thus, aside from the possible role the VNO of rattlesnakes may necessarily play in conditioning, the VNO input of experienced rattlesnakes does not produce a strike releasing pattern within the nervous system that is equivalent to that of eyes or facial pits alone. I hypothesize that the reason for this absence of a sufficient releasing pattern is that the VNO and areas of the brain to which it projects do not form a sufficiently differentiated image of the prey. This would also account for the finding that field tested rattlesnakes strike at prey models despite the absence of chemosensory stimuli (HAYES and DUVAL 1991), and that rattlesnakes with nostrils closed and tongue tips amputated (thus presumably no VNO input) show normal strike behavior (DULLEMEIJER 1961).

In crotaline snakes, an attempt has been made to characterize the relative importance of various sensory inputs during phases of hunting behavior and to recognize chemically oriented and vision/heat oriented species (DE COCK BUNING 1983a, b). In *Agkistrodon blomhoffii* (chemically oriented), visual deprivation resulted in hunting mistakes in the final adjustments before the strike; heat deprivation (pits covered) was even more disruptive resulting in near extinction of normal hunting behavior (DE COCK BUNING et al. 1981). In *Crotalus ruber*, with pits plugged, strike behavior (but not swallowing) was largely eliminated (DULLEMEIJER 1961).

A somewhat different picture emerges in the present study. In *Crotalus viridis oreganus*, visual and thermal inputs are predominant in all phases of hunting behavior compared to other sensory inputs. When deprived of facial pits, eyes

compensate completely; when eyes were covered, facial pits compensated completely (except strikes were initiated closer to the prey). This coincides with the natural behavior of the rattlesnake in which foraging occurs both in the presence of visual information (diurnal) and in the absence of visual information [(nocturnal, down burrows); FITCH (1949), DUVALL et al. (1985, 1990)]. Thus this species of rattlesnake is able to switch from visually to thermally based hunting and maintain a high level of predatory performance.

The dramatic drop in initiation of strikes, following simultaneous deprivation of eyes and facial pits, implies that eyes and facial pits, as other have argued (e.g. DE COCK BUNING 1983a, b; KARDONG and MACKESSY 1991), are the primary sensory systems relied upon during the rattlesnake strike. Certainly snakes possess other possible sensory systems including the nasal passage (KUBIE and HALPERN 1979), mechanoreceptors in the skin (PROSKE 1969), and possibly accessory thermal organs (HENSEL 1973; CHISZAR et al. 1986). However, this inability or disinclination to strike with eyes and facial pits covered implies that remaining sensory organs (vomeronasal plus these others) are collectively insufficient to compensate equally for the absence of visual and thermal information. Conversely this implies that rattlesnakes can use either the eyes or the facial pits to produce a visual or thermal image of the prey that is sufficient to elicit the strike and differentiated enough to permit discrimination of form (e.g. BENSON and HARTLINE 1988) so that strikes can be accurately targeted.

Acknowledgements

Special thanks go to K. KREBS for help analyzing the video data and to M. BELNAP, S. GULLORY, and M. KINDELSPIRE for further data analysis and to D. CHISZAR for comments on the manuscript. Assistance with the running of feeding trials is gratefully acknowledged to J. HERMAN, B. KUHN, M. ROCHELLE, and P. SMITH; statistical consultation with D. RATKOWSKY and M. EVANS, Program in Statistics at Washington State University, and with W. K. HAYES is very much appreciated. Supported in part by NSF grant (BNS 8820091).

References

- BEAUCHAMP, G. K., I. G. MARTIN, C. J. WYSOCKI, and J. L. WELLINGTON: Chemoinvestigatory and sexual behavior of male guinea pigs following vomeronasal organ removal. *Physiol. Behav.* **29** (1982) 329–336.
- C. J. WYSOCKI, and J. L. WELLINGTON: Extinction of response to urine odor as a consequence of vomeronasal organ removal in male guinea pigs. **99** (1985) 950–955.
- BERSON, D. M., and P. H. HARTLINE: A tecto-rotundo-telencephalic pathway in the rattlesnake: Evidence for a forebrain representation of the infrared sense. *J. Neurosci.* **8** (1988) 1074–1088.
- BURGHARDT, G. M.: Chemical perception in reptiles. In: J. W. JOHNSTON Jr., D. G. MOULTON and A. TURK (eds.), Vol. 1. *Communication by Chemical Signals: Advances in Chemoreception*. Appleton-Century-Crofts, New York 1970, 241–308.
- Behavioral and stimulus correlates of vomeronasal functioning in reptiles: Feeding, grouping, sex, and tongue use. In: D. MÜLLER-SCHWARZE and R. M. SILVERSTEIN (eds.), *Chemical Signals: Vertebrates and Aquatic Invertebrates*. Plenum Press, New York 1980, 275–301.

- CHISZAR, D., C. W. RADCLIFFE, and K. M. SCUDDER: Analysis of behavioral sequence emitted by rattlesnakes during feeding episodes. I. Striking and chemosensory searching. *Behav. Biol.* **21** (1977) 418–425.
- D. DICKMAN, and J. COLTON: Sensitivity to thermal stimulation in prairie rattlesnakes (*Crotalus viridis*) after bilateral anesthetization of facial pits. *Behav. Neural Biol.* **45** (1986) 143–149.
- D. DUVALL, K. SCUDDER, and C. W. RADCLIFFE: Simultaneous and successive discrimination between envenomated and non-envenomated mice by rattlesnakes (*Crotalus durissus* and *C. viridis*). *Behav. Neural Biol.* **29** (1980) 518–521.
- C. W. RADCLIFFE, F. FEILER, B. O'CONNELL, and H. M. SMITH: Predatory behavior in a congenitally alingual Russell's viper (*Vipera russelli*) 2. Trail-following behavior. *Bull. Maryland Herpetol. Soc.* **19** (1983) 15–23.
- – B. O'CONNELL, and H. M. SMITH: Strike-induced chemosensory searching in rattlesnakes (*Crotalus viridis*) as a function of disturbance prior to presentation of rodent prey. *Psychol. Rec.* **31** (1981 a) 57–62.
- C. W. TAYLOR, C. W. RADCLIFFE, H. M. SMITH, and O'CONNELL: Effects of chemical and visual stimuli upon chemosensory searching by garter snakes and rattlesnakes. *J. Herpetol.* **15** (1981 b) 415–425.
- CONOVER, W. J.: *Practical Nonparametric Statistics*. 2nd ed. New York: Wiley & Sons. 1980.
- COWLES, R. B., and R. L. PHELAN: Olfaction in rattlesnakes. *Copeia* **1958** (1958) 77–83.
- DE COCK BUNING, T.: Thermal sensitivity as a specialization for prey capture and feeding in snakes. *Amer. Zool.* **23** (1983a) 363–375.
- Thresholds of infrared sensitive tectal neurons in *Python reticulatus*, *Boa constrictor*, and *Agkistrodon rhodostoma*. *J. Comp. Physiol.* **151** (1983b) 461–467.
- R. C. GORIS, and S. TERASHIMA: The role of the thermosensitivity in the feeding behavior of the pit viper *Agkistrodon blomhoffi brevicaudus*. *Japanese J. Herp.* **9** (1981) 7–27.
- DULLEMEIJER, P.: Some remarks on the feeding behavior of rattlesnakes. *Proc. Kon. Nederl. Akad.* **64** (1961) 383–396.
- DUVALL, D., M. J. GOODE, W. K. HAYES, J. K. LEONHARDT, and D. G. BROWN: Prairie rattlesnake vernal migration: Field experimental analysis and survival value. *Nat. Geograph. Res.* **6** (1990) 457–469.
- M. B. KING, and K. J. GUTZWILLER: Behavioral ecology and ethology of the prairie rattlesnake. *Nat. Geograph. Res.* **1** (1985) 80–111.
- K. M. SCUDDER, and D. CHISZAR: Rattlesnake predatory behavior: Mediation of prey discrimination and release of swallowing by cues arising from envenomated mice. *Anim. Behav.* **28** (1980) 674–683.
- FITCH, H. S.: Study of snake populations in central California. *Amer. Midl. Nat.* **41** (1949) 513–579.
- GANS, C., and A. TAUB: Precautions for keeping poisonous snakes in captivity. *Curator* **7** (1964) 196–205.
- GILLINGHAM, C., and R. E. BAKER: Evidence for scavenging behavior in the western diamondback rattlesnake (*Crotalus atrox*). *Z. Tierpsychol.* **55** (1981) 217–227.
- and D. L. CLARK: An analysis of prey searching behavior in the western diamondback rattlesnake, *Crotalus atrox*. *Behav. Neural Biol.* **32** (1981) 235–240.
- GRAVES, B. M., and D. DUVALL: Avomic prairie rattlesnakes (*Crotalus viridis*) fail to attack rodent prey. *Z. Tierpsychol.* **67** (1985) 161–166.
- HALPERN, M.: Nasal chemical senses in snakes. *Adv. Vertebr. Neuroethol.* **56** (1983) 141–176.
- HALPERN, M.: Vomeronasal system functions: Role in mediating the reinforcing properties of chemical stimuli. In: SCHWERTFEGER and SMEETS (eds.), *The Forebrain of Reptiles*. Basel: Karger 1987 pp. 142–150.
- and N. FRUMIN: Roles of the vomeronasal and olfactory system in prey attack and feeding in adult garter snakes. *Physiol. & Behavior* **22** (1979) 1183–1189.

- and J. L. KUBIE: Snake tongue flicking behavior: Glues to vomeronasal system functions. In: *Chemical Signals in Vertebrates. III.* New York: Plenum (1983) 45–72.
- – The role of the ophidian vomeronasal system in species-typical behavior. *Trends Neuro-Scil.* 7/12 (1984) 472–477.
- HAYES, W. K.: Envenomation strategies of prairie rattlesnakes. Ph. D. Thesis, Univ. Wyoming 1991, pp. 156.
- and D. DUVALL: A field study of prairie rattlesnake predatory strikes. *Herpetologica* 49 (1991) 78–81.
- HELLER, S. B., and M. HALPERN: Laboratory observations of aggregative behavior of garter snakes, *Thamnophis sirtalis*. *J. Comp. Physiol., Physiol., Psychol.* 96; (1982) 967–983.
- – Laboratory observations of aggregative behavior of garter snakes, *Thamnophis sirtalis*: roles of the visual, olfactory, and vomeronasal senses. *J. Comp. Physiol. Psychol.* 96; (1982) 984–999.
- HENSEL, H.: Cutaneous thermoreceptors. In: A. IGGO (ed.), *Handbook of Sensory Physiology* 2 Springer New York 1973, pp. 79–110.
- KARDONG, K. V.: The strike behavior of the rattlesnake, *Crotalus viridis oreganus*. *J. Comp. Psychol.* 3 (1986a) 314–324.
- The predatory strike of the rattlesnake: When things go amiss. *Copeia* 1986 (1986b) 816–820.
- and S. P. MACKESSY: The strike behavior of a congenitally blind rattlesnake. *J. Herpetol.* 25 (1991) 208–211.
- KUBIE, J. L., M. HALPERN, and A. VAGVOLGYI: Roles of the vomeronasal and olfactory systems in courtship behavior of male garter snakes. *J. Comp. Physiol. Psychol.* 92; (1978) 627–641.
- – Chemical senses involved in garter snake prey trailing. *J. Comp. Physiol. Psychol.* 93 (1979) 648–667.
- NAULLEAU, G.: La biologie et le comportement prédateur de *Vipera aspis* au laboratoire et dans la nature. *Bull. Biol. France Belg.* 99 (1965) 295–524.
- O'CONNELL, B., D. CHISZAR, and H. M. SMITH: Effect of poststrike disturbance on strike-induced chemosensory searching in the prairie rattlesnake (*Crotalus v. viridis*). *Behav. Neural Biol.* 32 (1981) 343–349.
- PROSKE, U.: Vibration-sensitive mechanoreceptors in snake skin. *Exp. Neurol.* 23 (1969) 187–194.
- ROBINSON, B. G., and K. V. KARDONG: Relocation of struck prey by venomoid (venom-less) rattlesnakes, *Crotalus viridis oreganus*. *Bull. Maryland Herp. Soc.* 27 (1991) 23–30.
- SCUDDER, K. M.: Mechanisms mediating the sequential aspects of rattlesnake predatory behavior. Ph. D. Dissertation, Univ. Colorado. 1982.
- WIENER, B. J.: *Statistical Principles in Experimental Design.* McGraw-Hill, New York 1971.

Received August 31, 1991

Accepted May 15, 1992

Author's address: Dr. K. V. KARDONG Department of Zoology Washington State University Pullman, WA 99164-4236, USA