Proximate Factors Affecting the Predatory Behavior of the Red Spitting Cobra, *Naja mossambica pallida*

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ABSTRACT.—Cobras lack infrared facial pits, are largely diurnal hunters, and exhibit active hunting behavior, suggesting that proximate visual stimuli may be of primary importance in guiding or releasing predatory behaviors. Further, predatory behavior in some snakes involves a hierarchical evaluation of multiple sensory stimuli by the central nervous system assigning some stimuli primary roles and others subordinate roles in eliciting specific foraging behaviors. To test these possibilities in cobras, mice were presented to five red spitting cobras with and without their eyes covered, and 13 dependent predatory variables scored in each treatment. We found that cobras with the use of their eyes struck prey sooner, and from greater range, than when they were blindfolded, results consistent with the view that red spitting cobras are primarily visual predators. Blindfolded cobras exhibited elevated rates of tongue flicking prior to striking but they took longer to locate prey, changed locomotor behavior (increased movement, sweeping motions of head), and usually struck only after making actual tactile contact with the prey. In the absence of visual stimuli, red spitting cobras increase their reliance on chemical cues, but this did not allow them to maintain a level of predatory performance equivalent to that seen in the control condition. We conclude that switching within the central nervous system between sensory modalities is fundamentally different in cobras than in pit vipers.

Elements of the predatory behavior of snakes are released by proximate stimuli mediated by eyes, facial pits, vomeronasal organ, sensory olfactory epithelium (Chiszar and Radcliffe, 1977; Chiszar and Scudder, 1980; Chiszar et al., 1977, 1981a,b, 1991, 1990; Halpern and Frumin, 1979; de Cock Buning, 1983a; Halpern and Kubie, 1983; Kardong and Mackessy, 1991; Furry et al., 1991; Kardong, 1992; Alving and Kardong, 1996) and perhaps by other sensory systems as well (Proske, 1969; Hartline, 1971; Robinson and Kardong, 1991; Haverly and Kardong, 1996). However, these sensory stimuli are evaluated in a hierarchical order by the nervous system giving some a primary and others a subordinate role in eliciting specific foraging behaviors (Kardong, 1992; Lavin-Murcio et al., 1993; Lavin-Murcio and Kardong, 1995). Switching between proximate stimuli may represent adjustments of foraging behavior to availability or absence of information under changing environmental conditions, such as diurnal/nocturnal availability of visible light, or when hunting in burrows or when direct line of vision to prey is obstructed (Gillingham and Clark, 1981). A close examination of such a sensory hierarchy within selected members of various snake families has been the basis for developing hypotheses about the evolution of foraging and sensory systems (de Cock Buning, 1983a).

Elapids have received much less attention than colubrids or viperids. Generally, elapids are recognized as active foragers (Mushinsky, 1987). Less typical ambush hunting among elapids apparently represents a condition convergent with Viperidae (Shine, 1980). Laboratory studies seem to confirm that cobra hunting behaviors include some features distinct from viperids (Kardong, 1982), but the dependence on various sensory modalities is not well delineated. The purpose of this study was to provide an initial evaluation of the sensory hierarchy important in cobra predatory behavior.

MATERIALS AND METHODS

Five red spitting cobras were used. The taxonomy is presently under review (e.g., Wüster and Thrope, 1992) and until settled we retain their former scientific name, *Naja mossambica pallida*. They were born in captivity and used in earlier experiments as described elsewhere (Radcliffe et. al., 1983, 1984; Rasmussen et al., 1995). These animals were donated to us as adults (128.1–134.0 cm, snout-vent length) for these experiments. They were housed in an isolated reptile room, at 27–32° C and with a photophase from 0900–2100 h. Each snake was kept in a home cage, a glass terrarium (50 × 27 × 30 cm) the floor of which was covered with newspaper. They had been in captivity since their birth, and had been in our colony for a minimum of two months, during which time they were fed live and dead mice on an irregular schedule. During feeding trials, laboratory reared mice of

mean mass 23.6g (19.0–27.9) were used as prey. At least 1 wk separated feeding trials. Safety precautions followed Gans and Taub (1964).

Treatments.—Control and sensory-deprived treatments were used in this experiment, generally following procedures described elsewhere for rattlesnakes (Kardong, 1992). In the sensory-deprived treatment, each snake was gently lifted on a hook from the feeding arena, pinned across its neck with a long bar, and grasped by hand behind the head. The eyes were covered with small diamond shaped (10 × 10 mm) pieces of electrical tape. The snakes were then returned to the feeding trial arena and left undisturbed for at least one hour. In the control treatment, no sensory organs were covered. However, as above, each snake was lifted by hook from the test arena, pinned, and grasped by hand for two minutes. Then the snake was returned to the test arena and left undisturbed for at least one hour. At no time during these procedures did snakes release venom.

Feeding Trials.—During a feeding trial, an individual snake was placed into a large wooden arena (120 × 55 × 50 cm) lined on all interior sides with white butcher paper and covered with a plexiglas top with two holes (7 cm dia.) cut at opposite ends. Black plastic tubes (PVC) were inserted through these holes and suspended from the plexiglas about 10 cm from the bottom of the arena. Two Panasonic video cameras, held with tripods above and at opposite ends of the arena permitted video recording of behavioral events. Following a period of acclimation (> 1 h), the video system was turned on for one minute. A preweighed, live mouse was lowered down the tube furthermost from the head of the snake and left with the snake after the strike. After introduction of the mouse, the investigator left the room and monitored events via the continuing videotaping of subsequent behavior. Behaviors occurring during the feeding trials were recorded on a VHS video recorder (Panasonic, AG 1230, Super 4 heads) and viewed simultaneously on split screen.

Variables.—Predatory behavior was divided into three phases: prestrike, strike, and poststrike, and the following variables occurring during each were observed during normal speed playback and by pause, frame-by-frame analysis of the recorded trials (Kardong, 1986, 1992; Hayes, 1991): RTF—Before Strike, the tongue flick rate during the minute before the strike; TIMESTRIKE, the time (secs) from introduction of the prey to initiation of the strike; RANGE, the distance from the mouse to the snake immediately before it struck; TIME-TO-DEATH, the time (secs) for the prey to die; SITE, locations on the body of the prey where the fangs entered, coded as head/shoulders (1),

midbody (2), hindquarters (3); STRIKES, the number of times the snake struck at the mouse; Hold or Release, whether the snake held the mouse (> 2s), or released it (< 2s); RTF—After Strike, the tongue flick rate during the minute immediately after the strike; SEARCH, the time from when the mouse was released until body/head movement brought the tip of the snake's snout within 1 cm of the prey; ENDRTF, tongue flick rate in the minute immediately before the snake relocated the prey (snakes snout within 1 cm of the prey); INVESTRTF, the tongue flick rate in the minute before swallowing of the prey began; INVESTIM, the time from the first relocation of the prey until the first swallowing attempt; DEGLUTIT, the time to swallow the dead mouse (when the last part of the prey, the hindquarters, was no longer visible from an overhead view); TRIES, the number of swallowing attempts. These variables were scored by the same two people throughout all experiments. One snake (blindfolded, large mouse) failed to strike successfully within the 15 min allotted following mouse introduction and these scores were not included in analyses. Each of the five cobras was tested twice in both control and sensory-deprived treatments administered in random order. For each snake, we averaged control scores and scores for the sensory-deprived treatment. Thus, these statistical means constitute observations from a randomized complete block design (Zar, 1974). They were analyzed using Wilcoxon signed-rank statistic (StatMost, DataMost, Corp.) and are presented in Table 1 (α = 0.05).

Sham Treatments.—Separate from the experimental treatments described above, the five cobras were tested for possible effects of the tape blindfolds on behavior. A hole (6 mm dia) was punched in the center of each tape diamond so that when applied, the hole left the eye uncovered, but surrounded it with tape in a position otherwise the same as in the blindfolded experimental condition. Control treatment was the same; the sham treatment involved pinning the snake and applying the hole-punched tape around each eye. Each snake was run once in each treatment, control and sham-taped, in random order. After handling, each snake was placed in the test arena and left undisturbed for at least one hour, before two minutes of behavior were recorded.

RESULTS

Qualitative.—In the hour or more before introduction of prey, cobras in the control treatment usually settled into an activity pattern characterized by long (more than 180 sec) periods of movement about the arena accompanied by tongue flicking interrupted by brief (30–180 sec)

TABLE 1. Means, standard deviations [in brackets], and z-scores from Wilcoxon signed-rank test of variables. *Significant at $P < 0.05$.

	Dependent variable	Control $\bar{x}$	Sensory-deprived $\bar{x}$	z-score
Scene	Phase			
PRESTRIKE				
	RTF—Before Strike	37.4	79.6	2.701*
		[25.4]	[15.7]	
	TIMESTRIKE	21.6	219.2	2.369*
		[9.57]	[223.9]	
STRIKE				
	RANGE	4.9	0.3	2.666*
		[0.12]	[0.06]	
	TIME-TO-DEATH	41.7	155.7	1.24
		[43.5]	[319.3]	
	SITE	2.8	2.7	0.2096
		[0.8]	[1.1]	
	STRIKES	1.8	2.1	0.56
		[1.1]	[1.0]	
	Hold or Release	0.6	0.6	0.00
		[0.52]	[0.52]	
POSTSTRIKE				
	RTF—After Strike	0.1	7.1	1.34
		[0.32]	[18.8]	
	SEARCH	146.0	257.2	0.3654
		[112.7]	[386.5]	
	ENDRTF	45.9	29.3	0.734
		[41.4]	[13.9]	
	INVESTIM	53.6	19.6	1.540
		[65.99]	[39.4]	
	DEGLUTIT	164.9	146.6	0.888
		[95.69]	[45.2]	
	TRIES	1.1	1.4	1.095
		[0.32]	[0.73]	

pauses in which no movement or tongue flicks occurred. It was unusual to find active cobras pushing their heads into corners or trying to escape, but often the activity seemed to be exploratory, involving movement about the full range of the arena. Upon introduction of the mouse, a moving cobra in the control treatment stopped, oriented its head toward the mouse, and then moved very quickly toward the prey, exhibiting tongue flicks as it approached. A cobra stationary at the time of introduction of the mouse similarly oriented its head toward the mouse, and, exhibiting tongue flicks, moved quickly toward the prey.

In the sensory-deprived treatment, blindfolded cobras exhibited similar activity patterns before introduction of the mouse, except their intervals of no movement seemed longer. When the prey was introduced, cobras momentarily ceased movement in the direction of prior travel, then usually started moving very actively about the cage. Cobras motionless at the time of prey introduction, similarly became suddenly animated, moving actively about the cage. In blindfolded cobras, this movement did not always carry them in the direction of the prey. Such movement often brought them into contact with the sides of the cage or bumped them into contact with their own bodies, which was sometimes followed by a light biting of cage wall or even of their own body. On several occasions this movement was accompanied by head sweeping motions with the jaws slightly parted. The head was moved from side to side held about 2 to 5 cm above the floor. When sweeps of the head brought the open jaws into apparent random contact with the mouse, the cobra quickly struck.

Quantitative.—In the minute prior to introduction of the mouse, the RTF was statistically equivalent between the two treatments (z-score = 0.6166, $P = 0.54$). Compared to the RTF before mouse introduction, the RTF after introduction of the mouse remained statistically the same in the control treatment (45.6 to 37.4, z-score = 0.8401, $P < 0.4$), but increased signifi-

cantly (52.6 to 79.6, z-score = 2.0732, P < 0.04) in the sensory-deprived treatment. As shown in Table 1, this postintroduction RTF in the sensory-deprived snakes was also significantly above control treatments (37.4 versus 79.6 RTF, z-score = 2.071, P = 0.007).

As further summarized in Table 1, cobras in the control treatment on average struck the introduced mouse sooner (21.6 sec versus 219.2 sec) and from a greater range (4.9 cm versus 0.3 cm) than when blindfolded. However, in all other scored predatory variables, there were no significant differences between control and sensory-deprived treatments. For example, the time mice took to die was statistically equivalent (TIME-TO-DEATH: 41.7 sec versus 155.7 sec) as was the number of times the snakes struck the presented prey (STRIKES: 1.8 versus 2.1) and the tendency to hold struck mice (HLDREL: 0.6 versus 0.6).

Often, struck prey were held until dead, then the cobra began swallowing from where its jaws already held the prey. If they released the prey, then a search followed the strike to recover the dead prey. This occurred on 4 and 5 trials (control, sensory-deprived respectively), but showed no significant difference in recovery time (SEARCH: 146.0 versus 257.2 sec). As the number of retaliatory bites by mice increased, the number of strikes by snakes increased (z-score = 3.7235, P < 0.0002).

Sham Treatment.—After handling, snakes often moved about the cage, occasionally exhibiting probing or head-rubbing against the cage. However, by the end of one undisturbed hour, attempts ceased to rub hole-punched tape from the head. There was no significant difference in RTF between control and sham-taped snakes (z-score = 0.4045, P = 0.69).

DISCUSSION

Results of these experiments are consistent with the view the red spitting cobra is primarily a visual predator. Cobras with use of their eyes struck prey sooner, and from greater distances, than when they were deprived of vision. Certainly there is some evidence that these cobras compensate for the absence of visual information. When blindfolded, cobras exhibited an elevated RTF when prey were introduced suggesting some switching to a chemosensory modality to adjust for lost visual input.

Both control and blindfolded cobras completed their search for envenomated prey in equivalent times, suggesting that poststrike relocation of prey is mediated primarily through chemosensory cues. If visual input were primary during poststrike searching, then we would expect a significant change in this phase of behavior when cobras were blindfolded.

However, even though some compensation in predatory behavior occurs when visual information is denied, during prestrike and strike phases of prey capture, cobras did not switch to alternative sensory modalities sufficient to maintain an equivalent level of predatory performance. A comparison to rattlesnake predatory behavior is useful as a contrast to another chemical-based (venom) predatory system.

In rattlesnakes, most strikes are delivered predominantly to the head and shoulder region of the prey (Kardong, 1986), even if eyes or facial pits are separately covered (Kardong, 1992). In red spitting cobras, strikes are delivered anywhere on the prey, without one region receiving most strikes.

In rattlesnakes, the distinct facial pits offer, in addition to the eyes, a route of photosensory input (infrared). With the eyes covered, rattlesnakes continue a high level of predatory performance by switching to infrared information gathered via these facial pits (Kardong, 1992). In rattlesnakes, as in cobras, covering the eyes results in a decrease in range to prey before the strike. However in rattlesnakes, this decrease in range is not so close as to bring the snake into actual contact with the prey before the strike. The strike is stimulated by infrared stimuli, but from a closer position, perhaps because of the more limited ability of infrared cues to produce stimuli equivalent to visual cues (de Cock Buning, et al. 1981; de Cock Buning, 1983b). In blindfolded cobras, head sweeping and increased random movement usually bring the head into actual contact with the prey before striking. What appears to occur in blindfolded cobras is that they increase locomotor activity, often accompanied by sweeping or swinging of their heads until making contact with the prey. Upon contact, the cobra initiates its strike in the direction of physical contact. If this interpretation is correct, it suggests that switching within the central nervous systems between prey cues is fundamentally different in rattlesnakes and cobras.

As reviewed by Mushinsky (1987), water snakes may strike below the surface as fish pass within range, although these strikes may miss (Cope, 1869). Such a foraging behavior was termed "fishing" (Evans, 1942) and may include side-to-side sweeping motions of the head until making contact with prey (Mushinsky and Hebrard, 1977). In moving water (Gillingham and Rush, 1974) or turbid water, visual information may be unavailable leading to these fishing behaviors by terrestrial snakes. Our results with cobras suggest that in the absence of visual information, a similar head sweeping and random movement behavior emerges during the prestrike phase.

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Breeding Migration of *Ambystoma cingulatum* in Florida

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ABSTRACT.—The movement of *Ambystoma cingulatum* was monitored at a 0.8 ha breeding site in Oka-loosa County, Florida with a drift fence and funnel traps for two consecutive breeding seasons (1993–1995). In 1993–1994, 198 salamanders were captured, 76% in the months of October and November; yearlings com-prised 66% of the catch. A total of 59 salamanders was captured in 1994–1995, only 10% of which were year-lings. Differences in number of yearlings captured between years may be the result of annual variation in either the amount and distribution of rainfall or recruitment of juveniles in previous years. Salamander movement was positively correlated with precipitation and minimum air temperature. The sex ratio was female-biased in 1993–1994, but no different than parity in 1994–1995. In 1993–1994, salamanders that en-tered and exited the breeding site only once remained in the basin for an average of 38 days, and exited within an average of 44 m from the point of entry. More salamanders immigrated from mesic longleaf/slash pine flatwoods than from xeric longleaf/sand pine flatwoods.

Reported declines of reptile and amphibian populations have increased in recent years (Petranka et al., 1993; Blaustein and Wake, 1995). In the Coastal Plain of the southeastern United States, declines of herpetofaunal populations have been attributed to the drastic reduction and fragmentation of the longleaf pine ecosys-tem (Auffenberg and Franz, 1982; Moler, 1992; Dodd and LaClaire, 1995). The flatwoods salamander (*Ambystoma cingulatum*), which is restricted to the southeastern Coastal Plain (Co-nant and Collins, 1991), is believed to have un-dergone a rangewide population decline as a re-sult of habitat conversion (Bury et al., 1980; Means, 1986; Means et al., 1996). It is considered rare in Georgia (L. LaClaire, pers. comm.), Florida (Ashton, 1992), and Alabama (Means, 1986); endangered in South Carolina (S. Bennett, pers. comm.); and is a candidate for federal list-ing (U. S. Fish and Wildlife Service, 1994).

Anderson and Williamson (1976) noted that

less is known of the life history of the flatwoods salamander than any other species of *Ambys-toma.* Little new information regarding the natu-ral history of this secretive species has surfaced in recent years. Most recent literature regarding *A. cingulatum* has addressed its endangerment status while summarizing what is already known of its biology (Bury et al., 1980; Means, 1986; Ashton, 1992; Palis, 1996). Palis (1995) de-scribed larval growth, development and meta-morphosis for two Florida populations. Means et al. (1996) reported the decline of a population during a 22 yr period apparently as a result of habitat alteration associated with plantation for-estry.

Recent surveys in Alabama (J. Godwin, pers. comm.), Florida (Palis, unpubl. data), Georgia (L. LaClaire, pers. comm.) and South Carolina (S. Bennett, pers. comm.) have failed to detect *A. cingulatum* at many historic locations. Infor-mation regarding the timing of reproduction, environmental factors influencing migration, and size and structure of breeding populations is necessary to make management and conser-vation decisions. To this end, I studied a popu-

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