PROXIMATE FACTORS INVOLVED IN RATTLESNAKE PREDATORY BEHAVIOR: A REVIEW

KENNETH V. KARDONG AND TAMARA L. SMITH

ABSTRACT: Prey capture in rattlesnakes is built around chemichal means of predation (venom), replacing mechanical means (constriction, overpower). This provides a safer way to dispatch prey without the risks of injury from retaliation. Such a predatory strategy is based on an accurate strike, release of prey, and a precise subsequent relocation of struck prey. Radiation receptors (eyes, facial pits) represent input routes to guide the critical strike. Chemosensory inputs (olfactory, vomeronasal) guide the post-strike relocation of envenomated prey. As might occur in nature, rattlesnakes switch almost equivalently between eyes and facial pits in aiming and launching a predatory strike. During post-strike, however, they do not switch between olfactory and vomeronasal inputs to track the envenomated rodent. These limits are reflected in the organization of the central nervous system, where radiation receptors merge in common areas of the optic tectum but chemosensory receptors do not merge extensively. Further, the absence of compensation in this multi-modal system is correlated with an absence of convergence of radiation and chemical information. Consequently, in rattlesnakes there is a correlation between predatory strategy and organization of the central nervous system. In rattlesnakes, chemical predation also includes release of prey followed by precise post-strike recovery. Post-strike recovery is selective, discriminating the struck mouse trail from others, and the strike itself may be necessary to release selective trailing behavior. The strike permits gathering of unique prey odors during contact, but the altered prey odor, produced by fang penetration and venom injection, occurs after release. A rattlesnake's chemosensory image of the envenomated prey may thus be composed of chemical cues gathered directly upon contact with the prey and/or of induced chemical cues produced following envenomation. The result is to produce a distinctive chemosensory profile of the prey, retained for an extended period and used for selective post-strike trailing.

INTRODUCTION

The predatory behavior of rattlesnakes (genera *Crotalus* and *Sistrurus*) usually includes an envenomating strike that immobilizes and kills the selected prey (Klauber, 1956; Kardong, 1986a). Depending upon research context, as few as three phases (e.g., Chiszar et al., 1977) or as many as nine (e.g., de Cock Buning, 1983) have been recognized to describe this behavior. Additionally, this predatory behavior is preceded by efforts of the rattlesnake to locate itself near likely concentrations of prey (Duvall et al., 1985; Duvall et al., 1990). However, these recognized components of overall predatory behavior are often released within specific contexts (Gove and Burghardt, 1983; Chiszar et al., 1992), and often include accompanying stereotypic motor patterns (e.g., strike-induced chemosensory searching, SICS; Chiszar et al., 1977; see Stiles et al., this volume) that exhibit some modifications (Chiszar et al., 1979; Gillingham and Clark, 1981). Several of these motor patterns may represent modal action patterns (Barlow, 1977). These behavioral components may be released by seasonality (Duvall et al, 1990), by a key event such as the strike (Chiszar et al., 1992), or by other environmental cues (Chiszar et al., 1977; Gillingham and Clark, 1981; Holtzman, 1998). Therefore, they can be conceptualized not just as conveniences but also as modular units, which are distinct activity elements with some neurological and behavioral independence (see Bolker, 1999; Gilbert et al., 1999). We propose to view predatory behavior as composed of modular units, including nine phases, in turn, composed of distinct stages (Fig. 1). These should be treated as working hypotheses, to be tested by subsequent behavioral and neurological experiments. This conceptualization offers a way of thinking about homologous units of predatory behavior of squamates (e.g., Chiszar et al., 1982; Cooper, 1990), similar to studies of anatomical structures. The presence of similar patterns and levels of rates of tongue-flicking (RTF) in various basal squamate groups (Cooper and Alberts, 1991; Cooper, 1992a, b; Cooper, 1994) suggests that the evolution of many predatory motor patterns evolved prior to appearance of vipers (Chiszar et al., 1992). Consequently, these modular units of predatory behavior may eventually be treated as character states, applicable to phylogenetic analyses (see Martins et al., this volume).

Predatory behavior requires doing many things well, but often this comes down to a rapid strike, during which venom is injected and the envenomated prey is quickly released, thereby reducing the risk of injury to the snake from retaliation by the prey. Therefore, this review begins with an examination of the rattlesnake strike, followed by an examination of the various sensory modalities important in targeting of the strike and sensory inputs important during subsequent relocation of the released, envenomated prey.

School of Biological Sciences, Washington State University, Pullman, Washington 99164-4236, USA
E-mail (KVK): kkardong@wsu.edu

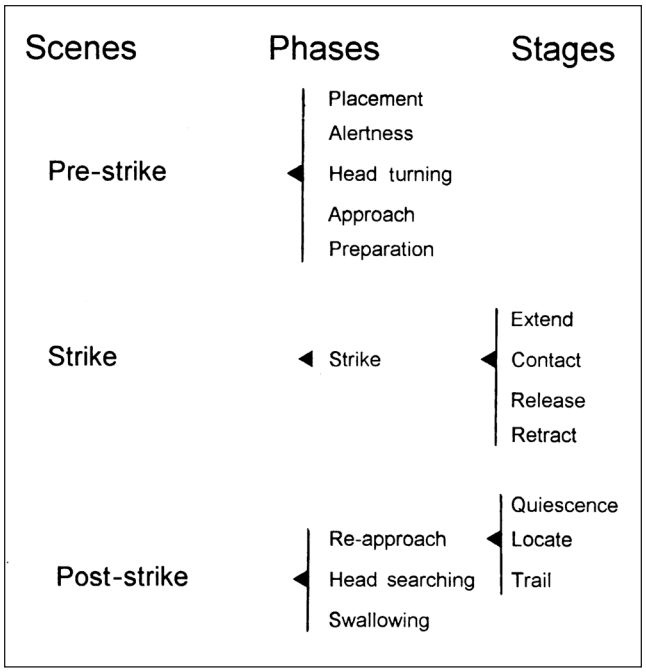

Fig. 1. Predatory behavior. Pre-strike, strike, and post-strike are composed of distinctive phases, in turn of specific stages. After de Cock Buning (1983).

RATTLESNAKE PREDATORY STRIKE

The predatory strike of rattlesnakes is usually completed in less than 0.5 sec, placing a premium on an accurate strike that produces no significant errors in fang placement, penetration, and venom injection. Such errors could result in poor envenomation, where released prey might escape beyond a recovery range. As discussed below, poor envenomation might produce a weak scent trail of the struck mouse, making relocation less likely. High-speed cinematography permits slow-motion viewing of the rapid rattlesnake strike. Beginning with the onset of the typical strike (Fig. 2), the mouth opens and the fangs are rotated forward during the extend stage until the snake makes contact with the prey. The jaws close driving the fangs into the prey and the jaws subsequently open rapidly disengaging from the prey and breaking contact, resulting in release of the prey and withdrawal of the head from the vicinity of the prey (Kardong and Bels, 1998).

Occasionally, complex modifications of the basic pattern occur. For example, in Figure 3, the snake makes its first strike but misses (time = 0 to 0.08 sec); then strikes again and misses again (time = 0.12 to 0.16 sec); finally it turns, approaching the mouse, to implant its fangs (time = 0.34 sec), then retracts (Fig. 3). Other high speed sequences (not shown) reveal strikes wide of the prey, missing it entirely, and strikes in which only one fang initially penetrates. Usually where the initial strike is poorly delivered, the snake rotates its head around, re-erects the fang failing to penetrate, and embeds it into the prey.

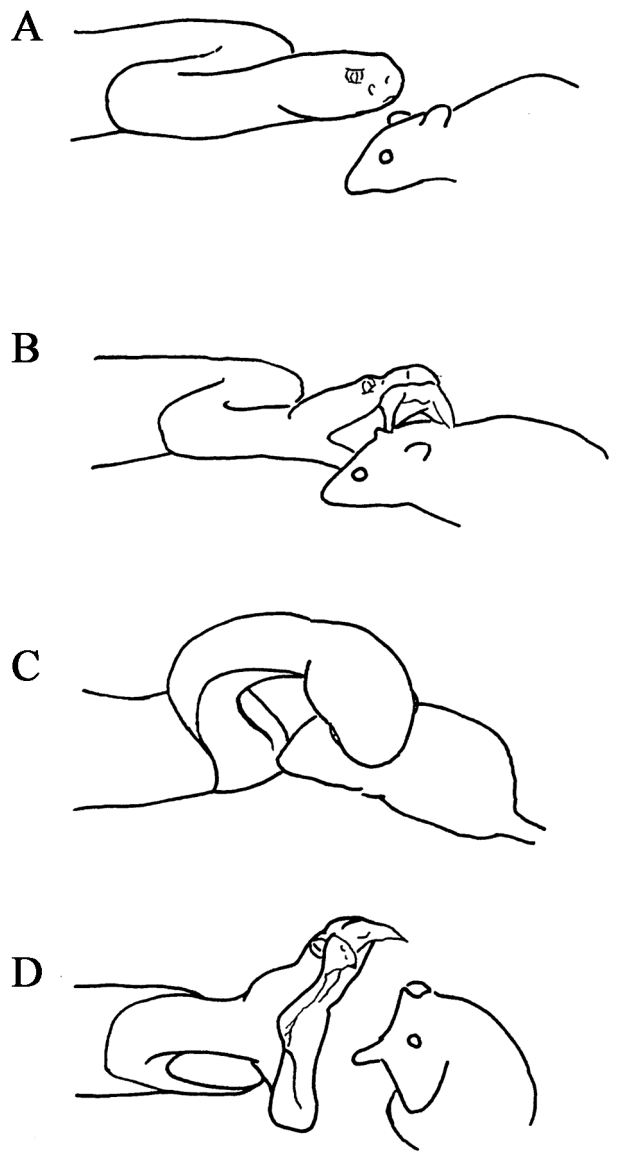

Fig. 2. Typical rattlesnake strike. The preparation phase (A) ends pre-strike. As the strike begins, the body extends and fangs rotate forward (B), contact is made as venom is injected (C), and the jaws release and are thrown clear of the prey as the head retracts (D).

All strikes are very rapid. Even in a strike (Fig. 3) where misses initially occur, the entire sequence is completed in < 1.0 sec. During this time the head moves quickly to the prey, fangs are erected and penetrate the prey, venom is injected, and the head of the snake is withdrawn. Missed fang placement, inaccurate targeting of the prey, and/or an insufficient pulse of venom may cause released prey to escape beyond recovery range, resulting in an unsuccessful predatory episode for the snake. However, the rat-

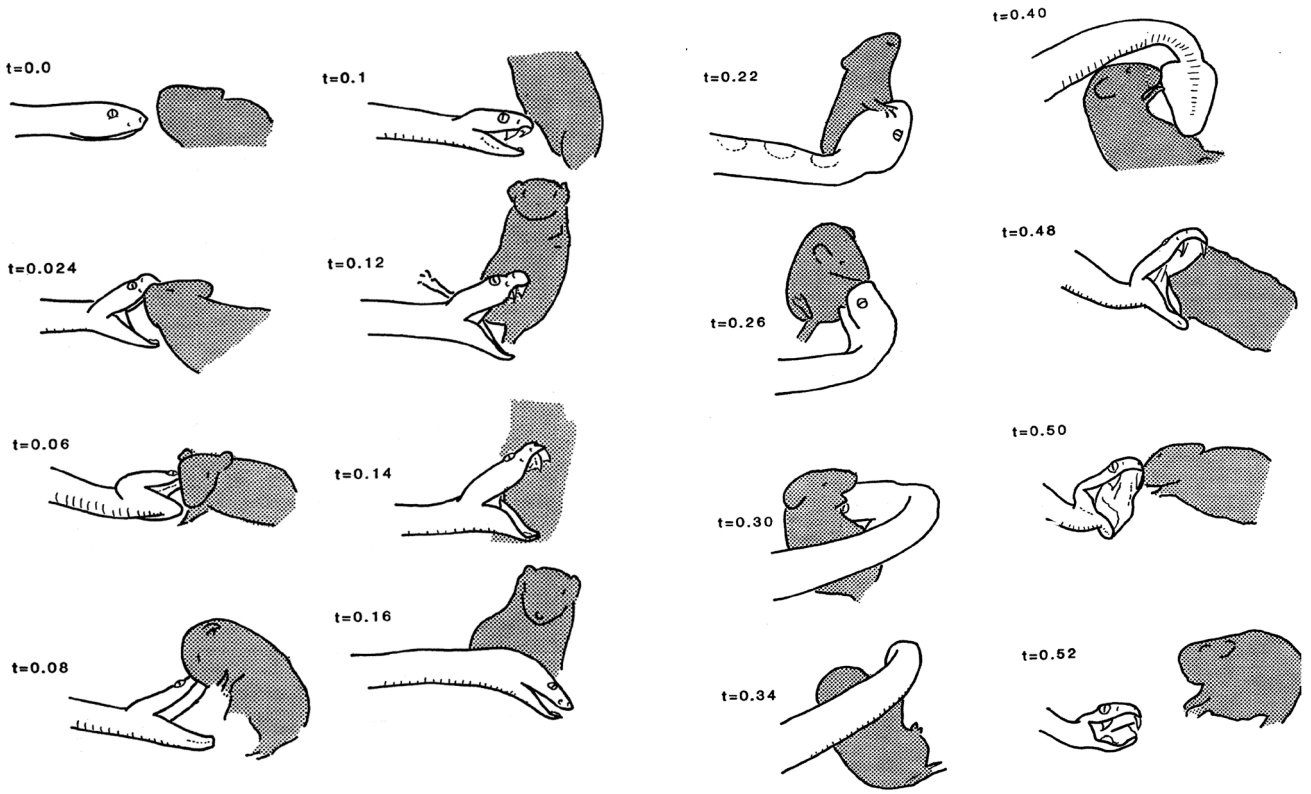

Fig. 3. Complex rattlesnake strike. After initiation of the strike (time = 0 to 0.024 sec), the snake failed to implant its fangs (time = 0.06 to 0.08 sec) and became separated from the mouse (time = 0.1 sec), which leaped upwards. The snake opened (time = 0.12 sec) then closed (time = 0.16 sec) its jaws, missing the mouse again. It then turned (time = 0.22 sec), opened its jaws, and now for a third time approached the mouse (time = 0.34 sec) to implant its fangs successfully. As the retract stage began (time = 0.40 sec), the mouse bit the upper lip of the snake (time = 0.50 sec), until the snake moved away from the envenomated mouse (time = 0.52 sec).

tlesnake strike is usually targeted precisely (Kardong, 1986a), the quantity of venom is metered to prey size (Hayes et al., 1995; this volume), and the prey is released, with death ensuing quickly (Kardong, 1986a). To accomplish this high level of predatory performance, proximate sensory input must be precisely integrated with motor outputs during the strike. In the following section we discuss what these sensory inputs might be, when they are important during various predatory phases, and the relative importance of various modalities.

PRE-STRIKE TO STRIKE: SENSORY COMPONENTS

The rattlesnake strike is not based equally on all available sensory stimuli. Visual and infrared receptions are more important than chemical cues in eliciting alertness and tongue-flick behaviors (Scudder, 1982; de Cock Buning, 1983; Chiszar et al., 1981). Further, in the absence of the strike, rattlesnakes do not respond to prey odors with an increase in rate of tongue-flicking (RTF) unless they are hungry and/or are exposed to prolonged rodent odor (Cowles and Phelan, 1958; Chiszar et al., 1977; Gillingham and Clark, 1981). Chemical and somatosensory cues may also affect behavior (Proske, 1969; Chiszar et al., 1980), although in a subordinate role to visual and infrared stimuli (Kardong, 1986b; Haverly and Kardong, 1996).

The success of the rattlesnake strike may depend upon adjustments within the central nervous system to different available stimuli. Sensory systems assimilate a variety of environmental cues (Cowles and Phelan, 1958; Dullemeijer, 1961; Proske, 1969). Each sensory component (or organ) responds to particular proximate stimuli (Hartline, 1971; Gillingham and Baker, 1981; Dickman et al., 1987). Since predatory conditions may change (e.g., diurnal/nocturnal, prey species, evasive prey behavior), availability of sensory cues may change as well (e.g. Duvall et al., 1985). Consequently, the success of the strike depends on how the nervous system adjusts to the availability of these sensory cues. The predatory behavior of rattlesnakes involves the integration of

sensory information primarily from the eyes, facial pits, sensory nasal epithelium (olfactory), and vomeronasal organs (vomerolfaction), all of which monitor a variety of proximate factors directly affecting the pre-strike, strike, and post-strike motor patterns (de Cock Buning, 1983; Graves, 1985; Chiszar et al., 1986). Deprivation of sensory cues, as might occur at night or in a burrow, may alter the sequence or the degree to which other senses are utilized (Chiszar et al., 1981; Kardong, 1992).

Predatory behavioral patterns and the ability to adjust to available sensory cues from the prey probably depend on the underlying neurological organization of the central nervous system, and projections within and to the motor areas. We recognize two classes of primary proximate stimuli: radiation and chemosensory.

Radiation receptors.—The two primary radiation receptors in rattlesnakes are the eyes and facial pits. When deprived of input from one of these radiation receptors, rattlesnakes maintain a high level of pre-strike and strike performance (Kardong, 1992). The anatomical convergence of visual (eyes) and infrared (facial pits) information in the optic tectum is correlated with this ability to compensate behaviorally during the predatory strike (Hartline et al., 1978; Kass et al., 1978; Gruberg et al., 1979; Kishida et al., 1980; Newman et al., 1980; Stanford and Hartline, 1980; Newman and Hartline, 1981; Schroeder, 1981, 1985).

Chemosensory receptors.—The two primary chemosensory receptors in rattlesnakes are the sensory olfactory epithelium and the vomeronasal organ. When deprived of vomeronasal input, strikes decline by about one-half, and post-strike trailing is extinguished (Kardong, 1992; Alving and Kardong, 1996). This suggests that, compared to vomeronasal input, olfactory input is not equivalent and does not permit recovery of these behaviors. The processing of chemosensory information or differences in the chemical cues themselves may account for the absence of effective behavioral switching based on chemical input (Halpern, 1976, 1992; Lohman and Smeets, 1993; Lanuza and Halpern, 1998).

Multisensory modalities.—When deprived of both radiation receptors (eyes and facial pits), rattlesnakes do not switch to chemosensory modalities to maintain a high level of predatory performance when aiming and launching a strike (Haverly and Kardong, 1996). This lack of adjustment correlates with the absence of significant convergence in the central nervous system between pathways of radiation and chemosensory inputs (Kardong and Berkhoudt, 1999).

POST-STRIKE: SENSORY COMPONENTS

Details of the strike and its complexity are essential to explain behavioral events that ensue. Not only does the rapid strike introduce immobilizing toxins, but it also releases the next phase of predatory behavior, the selective post-strike recovery of the envenomated prey. Further, the strike presents a brief moment of contact when the rattlesnake can gather unique prey odors, contributing to the chemosensory image used to track the envenomated and released prey.

Examination of post-strike behavior, and of some of the associated stereotypic motor patterns such as strike-induced chemosensory searching (SICS) (Chiszar et al., 1977, 1982; Stiles et al., this volume), have come primarily from viperid snakes (Naulleau, 1965; 1967), rattlesnakes in particular (Chiszar et al., 1982, 1983, 1990, 1991, 1992; Robinson and Kardong, 1991; Lavín-Murcio et al., 1993; Boyer et al., 1995; Lavín-Murcio and Kardong, 1995; Busch et al., 1996). However, species of colubrid snakes and lizards also show evidence of SICS (Cooper 1989, Cooper et al., 1989; Burghardt and Chimura, 1993), although these species do not typically adopt a strike-release-trail behavior. Thus, rattlesnake predatory behavior, pre-strike and post-strike have become both highly specialized and stereotyped.

Chemosensory Stimuli and Predatory Plasticity

Release of the envenomated prey reduces exposure of the snake to retaliation from a severe bite, but released prey may scamper beyond the immediate vicinity of the snake and must be relocated. Relocation presents another set of problems to the snake. Envenomated fishes or frogs in a current of water might be carried away, or birds on land might fly beyond a recovery range, and these prey are sometimes held by the snake (Hayes and Duvall, 1991). Some arboreal vipers commonly hold struck prey (K. Kardong, unpublished), which would otherwise be lost to the forest floor. Even released prey (e.g., rodents) may travel some distance and disappear from visual or thermal view, leaving only a chemical trail of cues to follow. Further, these scent trails of the envenomated prey cross the scent trails of other rodents within the local colony potentially compromising the ability of the snake to track the envenomated prey. However, rattlesnakes can distinguish the scent of an envenomated mouse from that of a littermate (Chiszar et al., 1983; Furry et al., 1991), and even from a mouse's own pre-strike scent (Chiszar et al., 1982; Robinson and Kardong, 1991). This ability to discrim-

inate the envenomated trail is retained for an extended period of time (Smith et al., 2000). Therefore, the chemosensory ability of rattlesnakes is very acute, discriminating between subtle differences in rodent scent.

Examining Post-strike Trailing: Methods

Snakes.—Our studies of post-strike trailing have been performed with Northern Pacific Rattlesnakes, *Crotalus viridis oreganus* (= *C. oreganus*; see Douglas et al., this volume). All individuals are members of a long-term laboratory colony, originally collected in Whitman County, Washington. Snakes are maintained individually in glass terraria and offered white laboratory mice (Balb/c or Swiss Webster) twice a month, and provided with water ad libitum. Safety procedures for handling snakes follow those of Gans and Taub (1964).

Post-strike trials.—All trailing experiments were conducted in a square-test arena (1.25 m side x 0.5 m high) described elsewhere in detail (Robinson and Kardong, 1991; Lavín-Murcio and Kardong, 1993; Alving and Kardong, 1996). A Y-shaped outline made of black tape was placed on the floor of the arena, and covered with a new piece of white butcher paper before each trial. The Y- outline, a 50 cm base and 50 cm each arm, could be seen through the white paper and was used to guide the placement of the scent trails. Each trial began by placing one snake in a holding box located at the base of the Y-outline for an acclimation period of not less than 6 h. After a period of acclimation, a removable chute, used to introduce prey, was placed in a slot in front of the holding box. A pre-weighed mouse was introduced, down the chute to the rattlesnake in the box, struck by the snake, and then retrieved via fishing line tied to the base of the rodent's tail. The door to the holding box was replaced, and the chute was removed. Pairs of non-overlapping scent trails were made for each trial, placed from the holding box out the base of the Y then out one arm. Depending on protocol, the control trail was either distilled water (DW) or a non-struck mouse (NS); the experimental trail was the struck mouse (S). The water trail was made with a cotton-tipped applicator. A mouse trail, NS or S, was made by holding the mouse by the nape of the neck with long forceps, and in one, continuous, slow motion, slid belly-side down, along the base of the trail and out one arm, completing the laying of the scent trail within 14 sec ± 2 sec. After the trail was laid the mouse was removed from the test arena. The door to the wooden holding box was opened and subsequent trailing behavior recorded via a VHS video camera. Playback of the video permitted scoring of trailing variables. We considered a snake to be following a trail if its head stayed within the 10 cm guidelines placed on either side of the black-tape Y-shaped trail. When the snake went outside these guidelines for over 30 sec, or when it ceased to leave the holding box within the trial period of 20 min, the snake was scored as not trailing.

Selective Post-strike vs General Chemosensory Searching

The rattlesnake strike is an important releaser of selective post-strike trailing. Unlike pre-strike behavior, wherein rattlesnakes settle into ambush positions (Duvall and Chiszar, 1985; Duvall et al., 1990), post-strike behavior is characterized by a selective trailing behavior, wherein the scent trail of the particular envenomated rodent is followed (e.g. Robinson and Kardong, 1991; Lavín-Murcio and Kardong, 1995). In the absence of a strike, rattlesnakes do not trail (Smith et al., 2000), although snakes presented with NS mice exhibited some behaviors indicative of a general hunting strategy (elevated RTF and limited scent investigation at the base of the trail), these were not equivalent to post-strike behaviors. Prey odor alone (but no strike) did not release selective trailing. Although slightly elevated, RTF was significantly below that exhibited following an envenomating strike (Smith et al., 2000). Certainly, rattlesnakes in nature use general chemosensory information to locate habitats occupied by rodents and wait in ambush (e.g., Duvall et al., 1985); however, the use of a distinctive chemosensory odor associated with a particular rodent is preceded by an envenomating strike.

In post-strike trailing, some snakes maintain the selective trailing behavior for up to 24 h post-strike, although the frequency declines over time (Smith et al., 2000). Snakes that trailed stayed close to the scent trail. If putrefaction enhanced perceptibility, then trailing success should increase with time. This, however, does not happen. At 24 h, the trailing success continues to decline. This suggests that the trailing snakes maintain the memory of chemical cues collected during the strike for a considerable amount of time. Consequently, relocation of prey is not simply a matter of chance encounter with dead prey, the result of general searching, or hunting behavior. Instead, selective trailing behavior, released by the strike, is maintained at a significant level for an extended period of time. It also suggests that the snake retains the unique suite of chemosensory cues

used to discriminate the prey trail for an extended period of time at post-strike. Further, the particular features of the scent trail were maintained as well (Smith et al., 2000). For example, once trailing behavior was initiated, RTF reached a high level characteristic of SICS and remained at a high level for all time periods, although slightly declining in longer delays. There was no evidence that delay in trailing led to adjustments in chemosensory searching by changes in RTF. In other words, lingual sampling rates stayed constant, even as delay times increased (Smith et al., 2000).

Exactly how long rattlesnakes in nature might be able to trail cannot be answered with laboratory experiments. Wild mice, compared to laboratory mice, in some respects react differently to envenomation (Kuhn et al., 1991). Wild mice, for example, may produce a more perceptible, longer lasting post-strike scent trail. The above experiments demonstrate, nonetheless, that rattlesnakes retain a memory of chemical cues of the mouse they struck for extended periods post-strike.

It is not known what environmental cues or internal mechanisms might prompt a snake to trail or not to trail. Field observations of rattlesnakes swallowing putrefying prey have been interpreted as evidence for scavenging (Klauber, 1956; Gillingham and Baker, 1981), and this may be so. Other field observations suggest, however, that rattlesnakes may continue to try and relocate prey they envenomated up to several days post-strike (Diller, 1990).

This selective post-strike trailing is distinct from the more general pre-strike hunting behaviors seen in the rattlesnake and in other species. The pre-strike behaviors (NS) appeared to be analogous to ambush behavior in Nature, wherein the snake initially locates an area with high prey density and then sets up in ambush (Duvall et al. 1985, 1990). During pre-strike, there is little advantage for a snake to indiscriminately follow odor trails of non-envenomated mice. After envenomation, the rattlesnake has invested energy (e.g., movement, venom) and subjugated a prey (dead) likely to be recovered. Locating this particular prey now becomes advantageous. Consequently, post-strike trailing, released by the strike, is selective with the rattlesnake restricting its searching efforts to the particular mouse it struck.

Formation of Post-strike Search Image

The chemosensory cues that characterize the post-strike trail of the prey are gathered during the strike upon contact with the prey, but also arise from envenomation immediately after release of the prey.

Prey odors.—A rattlesnake in ambush conceivably gathers chemosensory cues about the various rodents in its vicinity. But for selective trailing to occur, the acquisition of the unique suite of scents arising from one particular prey must occur during the rapid strike when the rattlesnake is briefly in contact with the prey. Artificial scents (Melcer and Chiszar, 1989a, b) or diets/bedding (Melcer et al., 1990) add unique chemosensory cues to prey that rattlesnakes appear to learn during the process of envenomation. In fact, the chemical cues can be picked up by the fangs alone. Rattlesnakes were induced to strike latex condoms, packed either with mouse homogenate or with water soaked cotton (Chiszar et al., 1991a). Only a strike to the mouse packed condom produced characteristic post-strike SICS. Presumably the fangs penetrated the wall of the condom, and carried away mouse (and latex) scent sufficient to elicit SICS.

Envenomation induced odors.—In addition to diet and environmental scents giving prey individualized odors, genetic differences of mice could be involved as well (Chiszar et al., 1992). But the process of envenomation itself increases the perceptibility of the post-strike rodent trail (Chiszar et al., 1981; Robinson and Kardong, 1991; Lavín-Murcio et al., 1993). Because the strike is so rapid and time of contact so brief (Kardong and Bels, 1998), whatever envenomation does to enhance prey perceptibility must occur after release of the prey. The post-strike rattlesnake tracks prey trails using a scent image composed of chemosensory cues collected from the prey during the strike and chemosensory cues arising after the strike. Because the envenomated mouse dashes off after the strike, these induced post-strike chemosensory cues could not be learned at the time of contact. Instead, this induced component of the scent image must be innately recognized by the post-strike trailing chemosensory system.

Ordered Priority

Not all prey scents are equal. Selective trailing of the prey scent image occurs post-strike. Rattlesnakes, however, seem to prefer some chemical components of this chemosensory image over others.

Envenomation > mouse odor.—In trailing experiments (Robinson and Kardong, 1991; Lavín-Murcio et al., 1993), when mouse odor is controlled, rattlesnakes prefer the scent trail of the envenomated mouse over all other natural scents. This was shown

Table 1. Rattlesnakes exhibit a scent priority, preferring first scent trails produced during envenomation, then differences in prey odor, and last, chemical cues from mechanical fang puncture. Mouse treatment: non-struck (NS), snake-struck (SS), hand-struck (HS). * = preferred choice in paired post-strike trials.

Scent priority	Control	Experimental
Envenomation > mouse odor		
a) Different mice envenomation (E)	NS	SS*
b) Same mouse envenomation (E)	NS	SS*
Mouse odor > fang puncture		
a) Different mice venectomized	NS	SS*
b) Same mouse venectomized	HS	SS
c) Different mice venectomized	HS	SS*

by using the same mouse to lay the NS and S trails. A live mouse held by the nape of the neck with long forceps is slid along one side of a Y-maze, and then presented to and struck by an acclimated rattlesnake in a hold box at the beginning of the maze. As soon as the envenomated mouse is dead or immobilized (knockdown), it is slid similarly along the other side of the Y-maze. Rattlesnakes preferred the trail of the envenomated mouse (Table 1). If different mice were used in producing the paired trails, thereby adding distinctive individual prey odors to paired scent trails, the rattlesnakes nevertheless still preferred the envenomated mouse trail (Table 1). Therefore, even when distinctive mouse odors are available, scents that rattlesnakes prefer are related to envenomation and not individual mouse odor.

Mouse odor > fang puncture.—When the effects of venom are removed, rattlesnakes can use alternative odors. This was shown by surgically tying off the main venom ducts of rattlesnakes, thereby eliminating venom chemicals from delivery to the mouse during the predatory strike. In all other respects, the predatory strike was normal. In the absence of venom-induced chemosensory cues, rattlesnakes nevertheless preferentially trailed the mouse they struck (but no venom) (Robinson and Kardong, 1991). This suggests that, in the absence of venom effects, individual prey odor is sufficient to permit rattlesnakes to carry away from the strike distinct prey odor cues used to subsequently trail the struck mouse.

Finally, we note that fang penetration of the skin might itself add to subsequent trail perceptibility. To test this, we used the same venectomized snakes (Lavín-Murcio et al., 1993). To simulate fang puncture, we used two fangs, about normal distance apart affixed to a small board as artificial fangs. With these artificial fangs, we "hand struck" (HS) a mouse and used this mouse to lay the first trail. This same mouse was presented next to the rattlesnake and struck (but no venom), and used to make the second trail. Rattlesnakes did not trail preferentially, but essentially selected each trail equally. However, when different mice were used (e.g., hand-struck vs snake-struck), rattlesnakes preferred the trail of the mouse they struck. This reveals two features of the predatory strike. First, fang puncture had an effect on perceptibility of the post-strike mouse trail, but second, if individual mouse odor was available, this was used over fang puncture effects to trail struck mice.

Taken together, we note an ordered priority of available post-strike scent cues. Effects of normal envenomation override effects of individual mouse odor. Individual mouse odor overrides effects of fang penetrations. Overall rattlesnakes exhibit preference for ranked odors unique to the struck mouse: envenomation > mouse odor > fang puncture.

Chemical Cues Used for Discrimination

Venom.—Envenomation is the most important factor contributing to the chemosensory prey image post-strike. But venom, per se, is not the proximate chemical cue in the post-strike trail. Following an envenomating bite, small quantities of venom remain on the surface of the prey (Hayes et al., 1992; Hayes et al., 1995). In theory, this could add chemical cues to the environmental trail of the struck mouse. However, this is not the case. Cotton balls, either soaked with reconstituted lyophilized venom or with water (control), were presented in pairs to snakes that had just struck a mouse to elicit normal post-strike behavior. These snakes showed no preference for either. The same negative results occurred if mice carcasses were soaked directly with venom or with water, and similarly presented to a post-strike rattlesnake (Chiszar et al., 1992). On the other hand, if venom ducts are tied off, thereby preventing venom delivery during the

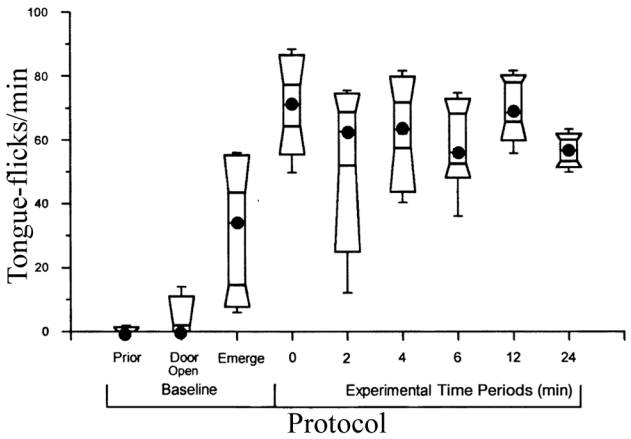

Fig. 4. Rates of tongue-flicking (RTF), baseline (pre-strike) and delayed trailing (post-strike, but held in holding box for six time intervals). RTF expressed in tongue-flicks per minute (TF/min) for each experiment collected at two minutes Prior to trial onset, Door Open, 1 minute after emergence (Emerge) from the holding box, and all experimental time periods (0, 2, 4, 6, 12, 24 min). Box-and-whisker plots show distribution of data. Horizontal lines denote the minimum and maximum, and the 10th, 25th, 50th, 75th, and 90th percentile points. From Smith et al. (2000).

strike, snakes still selectively trailed, preferring the trail of the mouse they struck (Robinson and Kardong, 1991).

Individual mouse odor.—The individual rodent carries unique cues, apart from envenomation induced cues, that allow the rattlesnake to distinguish one mouse from another (Furry et al., 1991). These may be integumentary materials, perhaps arising from dander, sebaceous glands, Harderian glands, and/or from glands located on various other body parts (Chiszar et al., 1992). These cues are apparently learned at contact during the strike, but they seem secondary or enhanced by the process of envenomation itself.

Envenomation.—Envenomated mice are preferred over non-envenomated mice during post-strike behavior. It has been suggested that venom includes a special chemical principal, not necessarily with lethality or toxicity, but with the function of enhancing the salience of envenomated prey and their post-strike trails (Chiszar et al., 1999). But if venom per se does not enhance post-strike perception of prey, then envenomation (strike, fang penetration, venom injection, release) must indirectly lead to enhancement of scents following envenomation. Nearly all experimental work on rattlesnake post-strike behavior has been performed with rodents. Field reports indicate, however, that rattlesnakes also successfully follow the post-strike trail of lizards (Chiszar et al., 1993b). Therefore, whatever indirect effects envenomation has on prey, it is not restricted to mammalian (e.g., rodent) physiology.

We suggest that one consequence of envenomation is elevated trauma upon the cellular physiology of the prey. Such trauma can have a cascading effect on the cellular and tissue physiology of the prey, leading to enhanced chemosensory cues. Evidence for this comes from experimental work (Chiszar et al., 1999). Rodents were injected with graded doses of reconstituted lyophilized venom, and the ability of rattlesnakes to discriminate "envenomated" (E) from "non-envenomated" (NE) rodents was tested. Using RTF as an indication of rattlesnake response, RTF increased with increasing venom dose. Because the rodents, E and NE, were euthanized immediately before injection of venom, alarm pheromones should be equal and therefore not produce differential cues between the two treatments. Effects of graded venom doses upon post-strike trailing success were not measured, only RTF. This complicates the interpretation of scent enhancement via envenomation, as we will see next.

Source of post-strike scent cues.—The chemosensory cues produced or enhanced by envenomation must arise quickly following the strike. Toxic components of the venom kill prey, but before death venom also disrupts the locomotor system of the rodent, reducing the distance it travels following the strike (Kardong, 1986a). This time to motor disruption has been termed the "Knockdown Time" (Minton, 1969), distinguished from time-to-death (see Kardong, 1986a), which lasts slightly longer. The two are related, but knockdown time, although more subjective to score, is perhaps the more biologically important consequence of envenomation because it is a measure of the time the prey can distance itself from the snake. Or put a different way, knockdown time is indicative of the trailing task facing the snake during post-strike. Knockdown time can be only a few seconds (Fig. 5), wherein the rodent scrambles and hops away from the snake and becomes immobile. During these few seconds, the distinctive post-strike odor must be produced and released to the environment, thereby leaving the distinctive odor trail. The route to the environment and the medium in which envenomation scents are carried have been investigated.

Urine droplets released by the struck rodent might produce an odor trail, but urine does not seem to carry the distinctive scent. Presented with urine droplets, integumentary materials, or water, Prairie Rattlesnakes (*Crotalus viridis*) did not follow urine or water cues,

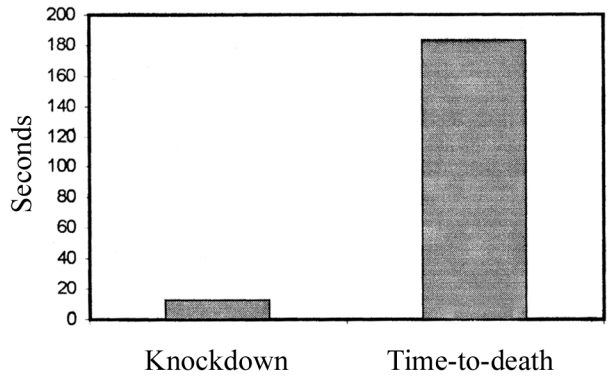

Fig. 5. Knockdown vs time-to-death. Knockdown denotes the time from the rattlesnake strike to when the locomotor system of the prey is immobilized, preventing any further increase in recovery distance (N = 30).

but did follow integumentary cues (Chiszar et al., 1990; Duvall and Chiszar, 1990b) at about the same efficiency as with ordinary rodent trails (Golan et al., 1982; Chiszar et al., 1983, 1986).

Blood presented on cotton or euthanized rodent carcasses has been shown to elicit, in post-strike rattlesnakes, increased RTF directed at the blood carrying objects compared to controls (Chiszar et al., 1993a). To determine whether blood from envenomated rodents carried scents sufficient to guide post-strike trailing, we (K. Kardong and T. Smith, unpublished) presented rattlesnakes with paired choices, water versus blood. This was done following similar procedures as described above. A mouse was presented to an acclimated rattlesnake in the holding box, struck, then removed. Upon death produced by the envenomation, the thoracic cavity was opened and blood gathered directly on a cotton swab or with a syringe needle to the heart, then transferred to a cotton swab. As we harvested blood, care was taken not to include integumentary cues. This collected blood was immediately spread along one side of the Y-maze with the cotton swab. The door to the hold box was then opened and the snake allowed access to the paired trails (water vs blood). All snakes (N = 16) exited the hold box, and exhibited elevated RTF, but none followed the blood trail to its end. This suggests to us that whatever the effects of envenomation might be, they are not carried in the blood at perceptible levels. This is consistent with the view that envenomation effects do not require systemic integrity of the intact circulatory system (Chiszar et al., 1992, 1999). It does, however, raise this question: why is blood of interest in one context (Chiszar et al., 1993a) but not during trailing?

Acquiring the trail.—Re-approach (Fig. 1) during post-strike trailing may involve several sets of stimuli and require distinctive behavioral units. This is suggested by the distinctive RTF post-strike (Fig. 6). Immediately after the strike, rattlesnakes exhibit a short stillness with only slightly elevated RTF. This is usually brief and often ends with a yawn, leading to a substantially elevated RTF when the snake emerges from the holding box. Following this, RTF drops slightly when the snake is on the scent trail.

Not surprisingly, RTF is low at pre-strike (Fig. 6). Note that once the rattlesnake emerges from the holding box, the RTF rate rises significantly and is at the highest rate during the post-strike episode. As it emerges, it sweeps its anterior body left and right, usually "anchoring" its posterior body in a fixed position (see Chiszar et al., 1992). During successful trailing, this phase gives way to active trailing, wherein the sweeping head swings are less extensive and become more localized to either side of the scent trail. As RTF declines slightly, the snake slowly courses along the scent trail to its end. The different RTF, accompanied by different behaviors, suggest that re-approach includes three distinctive stages: (1) quiescence, (2) locate, and (3) trail.

The quiescence stage occurs immediately after the strike, is brief, and includes slightly elevated RTF, compared to pre-strike. It often ends with yawning or mouth gaping. Locate stage includes a very elevated RTF, is accompanied by wide sweeping of the anterior body, and is concentrated around the beginning of the rodent scent trail. Trail stage is characterized by lower, but still high RTF, more precise localization to the scent trail, and faster progress along the trail.

We hypothesize that each of these stages of re-approach addresses different behavioral functions. The quiescent stage is short and refractory after the strike. The envenomation-enhanced prey scent trail may require several seconds to reach perceptibile levels. Also, it may occur when the central nervous system "builds" a chemosensory image of the envenomated mouse. The locate stage represents the stage during which the snake acquires the beginning of the rodent trail, but also examines the spatial relationship of this trail to the immediate environment. The departing mouse may provide visual cues to the snake (Lee et al., 1988). But when a rodent is struck, it bounds off in an erratic manner, often ending out-of-view with no further visual or thermal cues to reveal its location. The sweeping motions of the snake, therefore, may help to confirm the direction of the rodent. By inves-

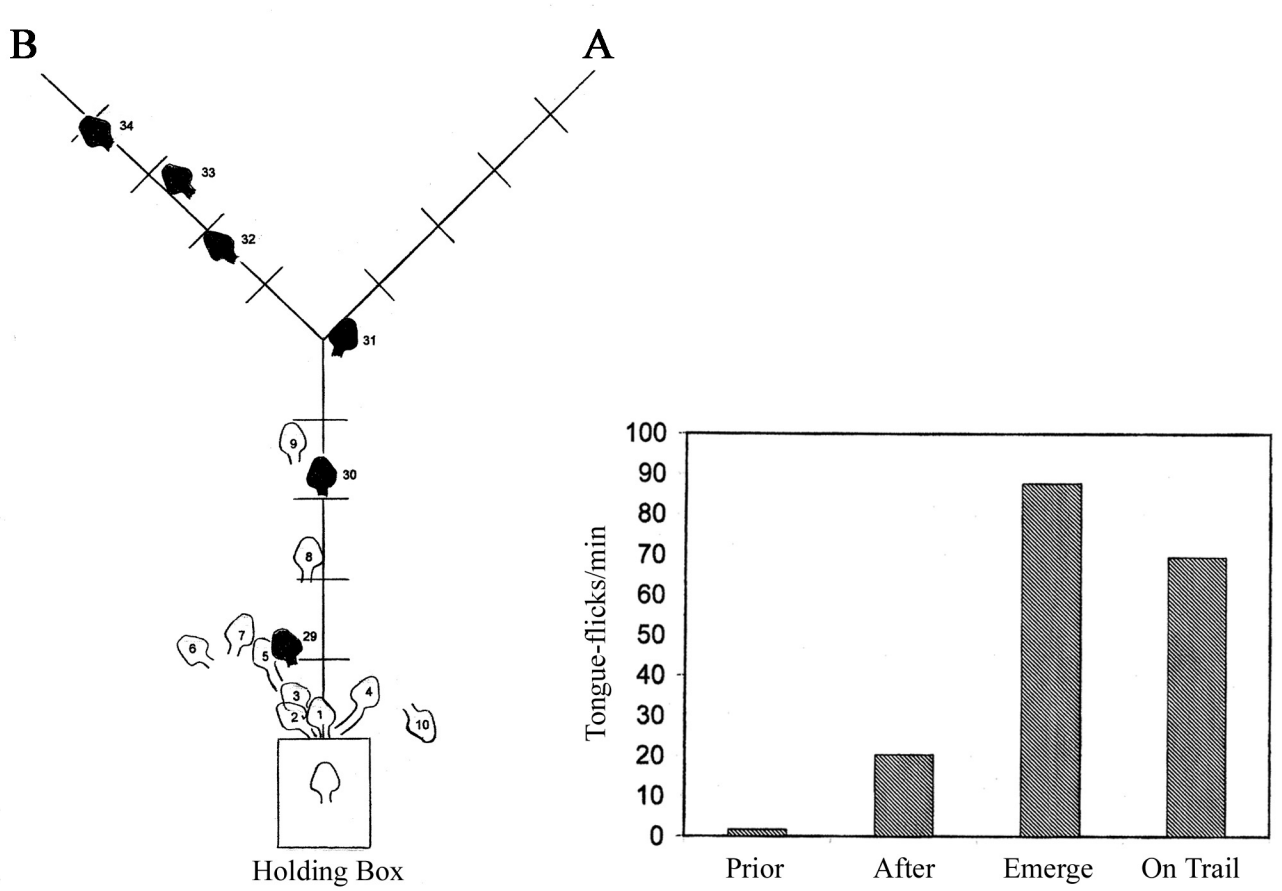

Fig. 6. Post-strike trailing. Left: During a trailing sequence, the head of the rattlesnake is traced in position at 30 sec intervals and numbered in sequence. Note that most of the sweeping Emerge positions (open silhouettes) are concentrated along the base of the trail. The On trail sequences (solid silhouettes) are along the trail close to the scent. Unstruck odor trail A; struck mouse odor trail B. Right: RTF at various points during trailing: immediately pre- and post-strike, when the snake first emerges (Emerge) from the holding box, and finally when on the scent trail (On trail) (N = 16).

tigating its immediate surroundings upon emergence, the rattlesnake can confirm the relationship of rodent scent trail to environmental orientation. This locate stage, with elevated RTF and sweeping motions, may also represent a behavioral response to match the chemosensory image with the unique chemical characteristics of the envenomated mouse trail. Apparently, once this is determined, the rattlesnake enters the trail stage, wherein it more precisely follows the now well-differentiated scent of the envenomated rodent.

Post-strike Conclusions

The collective work on rattlesnake predatory behavior we reviewed clarifies the behavioral components important in post-strike. The rapid strike itself, wherein contact with the prey is made, releases the phases characterizing the post-strike, beginning with re-approach. The transition from strike to post-strike is accompanied by a transition from an emphasis on radiation receptors to an emphasis on chemoreceptors, respectively. In particular, vomeronasal input is primary during most of post-strike. The vomodor cues appear to be processed in rank order, with cues related to envenomation receiving preference, followed by individual mouse scent, and finally cues related to fang penetration. The chemosensory image, used during the post-strike, is composed of two parts. One is learned during strike contact with the prey. The other part, induced by the process of envenomation itself, develops after release of the prey and must be innately recognized. These combined cues produce a unique chemosensory image in the central nervous system of the struck prey, and permit the rattlesnake to discriminate the scent trail of the struck prey from competing environmental odors. After a brief quies-

cent stage, this distinctive chemosensory image is used to locate, selectively trail, and recover, the envenomated prey. This distinctive chemosensory image is retained for hours or even a few days post-strike.

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