Ethology

Post-Strike Behavior of Timber Rattlesnakes (*Crotalus horridus*) During Natural Predation Events

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Abstract

The complexity of natural environments is an important component of animal behavior, and laboratory environments often cannot reproduce that complexity. Strike-induced chemosensory searching (SICS) is a robust phenomenon among venomous snakes that has been studied extensively in the laboratory. To date, observations of this behavior in the field have been limited largely to anecdotes; the extent to which post-strike behaviors in the laboratory accurately reflect what occurs in nature has not been examined. In this study, I use time-lapse video equipment in the field to record the predatory behavior of timber rattlesnakes (*Crotalus horridus*). This represents the first quantitative analysis of post-strike predatory behaviors associated with natural feeding events. As in the laboratory, stereotyped post-strike behaviors were only observed after successful strikes, and not after missed strikes. Snakes in the field were observed to proceed through the same basic behavioral stages that have been documented in the laboratory: striking prey, releasing prey immediately after strike, post-strike immobility, location of the chemosensory trail, trail following, and prey swallowing. However, the duration of post-strike immobility, trail location, and prey swallowing was substantially longer in field than in laboratory studies. Additionally, post-strike immobility was significantly longer when snakes struck large prey (prey over 100 g) than when they struck small prey. Overall, these results indicate that the behavioral challenges associated with SICS may be more robust than laboratory studies have indicated.

Introduction

Laboratory studies are invaluable in the field of animal behavior because they offer experimenters the ability to conduct manipulations that cannot be easily accomplished in the field. However, laboratory experiments can be limited in their relevance to natural history and evolution. Numerous examples exist of field studies that fail to validate results that are robust in laboratory (Mappes et al. 1998; Mahady & Wolff 2002; Wolff 2003, 2004). Whenever possible, behavioral paradigms that have been developed in the laboratory should be tested in the field.

Many venomous snakes feed by striking, injecting venom, and then immediately releasing prey, allowing prey items to flee until immobilized by venom. This strategy is thought to help snakes avoid retaliation by injured prey (Klauber 1972; Kardong 1986). Snakes subsequently locate prey by following the chemical trail left by the struck animal, a process known as strike-induced chemosensory searching (SICS). SICS is a robust phenomenon in many venomous and non-venomous snake species and has been the subject of numerous experimental investigations, making it a model system for predation behavior (reviewed by Chiszar et al. 1992; Withgott

1996; Kardong & Smith 2002; Greenbaum 2004). However, almost all studies of SICS have been conducted in captive or semi-captive conditions, often using snakes that are long-term captives themselves. Reports of SICS by free-ranging snakes under natural conditions are largely anecdotal and contain limited sample sizes (Klauber 1972; Diller 1990; Goode et al. 1990). Although it is clear that SICS occurs in the wild as well as in the laboratory, we do not know the degree to which basic behavior patterns expressed during SICS may vary under natural conditions.

Kardong & Smith (2002) organize post-strike behaviors into modular units consisting of three phases: re-approach (snake relocates envenomated prey), head searching (snake locates head of prey), and swallowing (snake swallows prey). The re-approach phase is further broken down into three stages: quiescence (snake remains immobile immediately following the strike), locate (snake identifies chemosensory prey trail), and trail (snake follows prey's chemical trail). This organizational scheme is based on laboratory studies, and has yet to be verified using natural predation events. By necessity, laboratory studies of SICS are conducted using a standardized set of conditions that may not accurately reflect most field conditions. For example, the laboratory environment is likely to be more thermally optimal, less physically complex, less chemically complex (i.e. less background chemosensory 'noise'), and less biologically complex (i.e. free from predators and competitors, and containing prey that are relatively small and invariant) than the natural environment.

A quantitative approach to post-strike behaviors under natural conditions could be used to estimate how the basic stages and patterns of post-strike behaviors may be altered in free-ranging snakes. In the past, this has not been accomplished because snakes feed so infrequently, direct observation of multiple predatory events is not feasible (Clark 2004a; Clark 2006). In this study, I analyzed the post-strike predation behaviors of radio-tagged timber rattlesnakes recorded in the field with unmanned, time-lapse video equipment.

Methods

Radio Telemetry

I tracked 17 individual timber rattlesnakes (11 females, six males, all adults) over the course of 2 yrs at a nature preserve in Chemung County, NY. Snakes were captured opportunistically throughout the study, and ranged in size from 104 to 137 cm total length and 650–2100 g (mean TL 21 ± 15 cm, mean wt 1405 ± 640 g). Miniature temperature-sensitive radio transmitters (Holohil Systems, models AI-2T and SI-2T) were surgically implanted in the peritoneal cavities of snakes under inhalation anesthesia, following the methods of Reinert & Cundall (1982). Transmitters weighed <5% of the snake's body mass. Snakes were returned to their point of capture within 24 h of recovering from anesthesia, and radio tracking began immediately. Individuals were located on a daily basis. Upon location, I recorded distance moved from last location, weather conditions, ambient temperature, locality, habitat use, body position, and body temperature. Distances less than 20 m were estimated visually to within 2 m, while distances greater than 20 m were estimated to within 5 m with the use of a handheld GPS unit.

Videography

To collect data on foraging behavior, I trained video cameras on snakes that were in ambush position (Reinert et al. 1984; Clark 2004b). Three different video units were used concurrently in the field. Each unit consisted of a security camera coupled to a time-lapse videocassette recorder (Mobile 12-V Time Lapse Recorder Model NCL3300) powered by a 12-V sealed lead-acid battery. Cameras (High Resolution Color CCD IR, model BC 1035) recorded in color when ambient light was available, and under low-light conditions automatically switched to black and white with infrared LEDs. Time-lapse VCRs were set to record continuously at 6.67 recording frames per second, with the date and time to the nearest second displayed on the tape.

Data Collection

Data on successful predation events were collected from videotapes. Tongue-flick rates could not be reliably obtained because of the relatively poor resolution of the tapes. The duration of strikes could only be recorded to the nearest 0.5 s because of the slow frame-recording rate. Struck prey were identified to as fine a taxonomic level as possible, but often could only be categorized as one of two to three possible species. Three post-strike stages of behavior noted in Kardong & Smith (2002) were apparent from the tapes (quiescent, locate, and trail). These stages were defined as follows: the quiescent phase was a period of post-strike immobility ending with mouth gaping or the beginning of head movements. The duration of this stage, from the end of the strike to the first lateral movements of the head, was recorded to the nearest second. The locate stage was characterized by side-to-side sweeping motion of the head and anterior body, concentrated around the area in which the struck prey was released. This stage ended after the snake had moved completely from its coil and begun to follow the trail left by the struck prey. Because this process takes place slowly and the transition to the trail stage was somewhat subjective, the duration of the locate stage was rounded off to the nearest minute. The trail stage was characterized by complete movement of the body out of the ambush coil and relatively rapid progression along the prey trail. The entire duration of this stage could not be recorded because the prey almost always fled outside the frame of the camera, but the rate of trail following, in m/s, was noted when possible. All values are given as mean ± SE.

Results

I recorded predatory strikes towards prey 22 times (n = 14 snakes). Snakes successfully struck prey 11 times (n = 8 snakes), and struck but missed prey 11 times (n = 9 snakes). All predatory strikes lasted less than 0.5 s. Stereotyped post-strike behaviors occurred after all 11 successful strikes, but did not occur after any of the missed strikes. After all 11 missed strikes, snakes did not abandon their sites, but resumed foraging in the same position.

In all 11 cases, there was a period of post-strike immobility (quiescent stage) lasting from 53 to 617 s (mean 201 ± 60 s) during which snakes neither moved their heads nor tongue-flicked (Table 1). There was a strong association between the size of prey struck and the duration of the quiescent phase. Snakes exhibited significantly longer post-strike immobility when striking large prey (estimated prey mass over 100 g, i.e. all sciurid rodents and mustelids, n = 4) than when striking smaller prey (prey mass under 50 g, i.e. all microtine rodents and *Peromyuscus* spp., n = 7) (74 ± 7, vs. 421 ± 88, Mann–Whitney U-test, p = 0.01, Fig. 1).

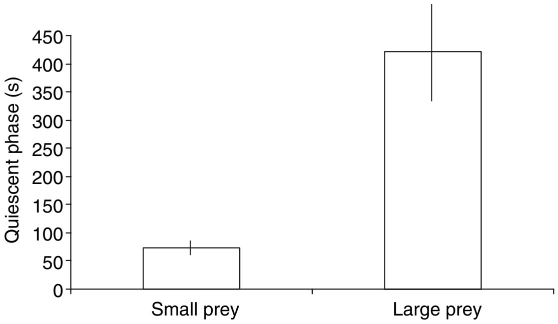

Fig 1: Duration of post-strike immobility for free-ranging timber rattlesnakes when striking large prey (prey mass over 100 g) vs. small prey (prey mass under 50 g)

Following post-strike immobility, snakes began stereotypical searching behaviors characteristic of the locate stage. This behavior lasted from 5 to 17 min (mean 9 ± 1.1 min). There was no difference in the length of the locate phase for snakes that had stuck large or small prey (8.8 ± 1.3 vs. 9.1 ± 4.3 min, Mann–Whitney U-test, p = 1.0).

After all 11 successful strikes, snakes located scent trails of struck prey and followed these trails out of the video frame. Once snakes had begun following scent trails, the average rate of movement was approximately 0.5 m/min. In two cases I was able to determine the distance that prey fled upon being struck, and the full amount of time that it took for snakes to locate and swallow their prey. In one case, a nocturnal rodent struck by the snake fled approximately 0.75 m before becoming immobile. The snake located this prey within 12 min of striking, and had

Table 1: Durations for each stage of post-strike scent trailing behaviors of rattlesnakes recorded under natural (n = 8 snakes) and laboratory conditions

Behavioral stage	Duration (this study)	Duration (laboratory or semi-natural studies)	Source
Strike	Less than 0.5 s	Less than 0.5 s	Kardong & Bels (1998) and Cundall & Beaupre (2001)
Quiescent	74 s (small prey) 421 s (large prey)	64–94 s (small prey)	Hayes (1992, 1993)
Locate	540 s	72–225 s	Golan et al. (1982), Chiszar et al. (1990), Goode et al. (1990), Kardong (1993), and Haverly & Kardong 1996
Trailing rate	~0.5 m/min	0.2–0.4 m/min	Golan et al. (1982), Chiszar et al. (1990), and Smith et al. (2000)
Swallowing	28.5 min (n = 2)	7–8 min	Kardong (1993) and Haverly & Kardong (1996)

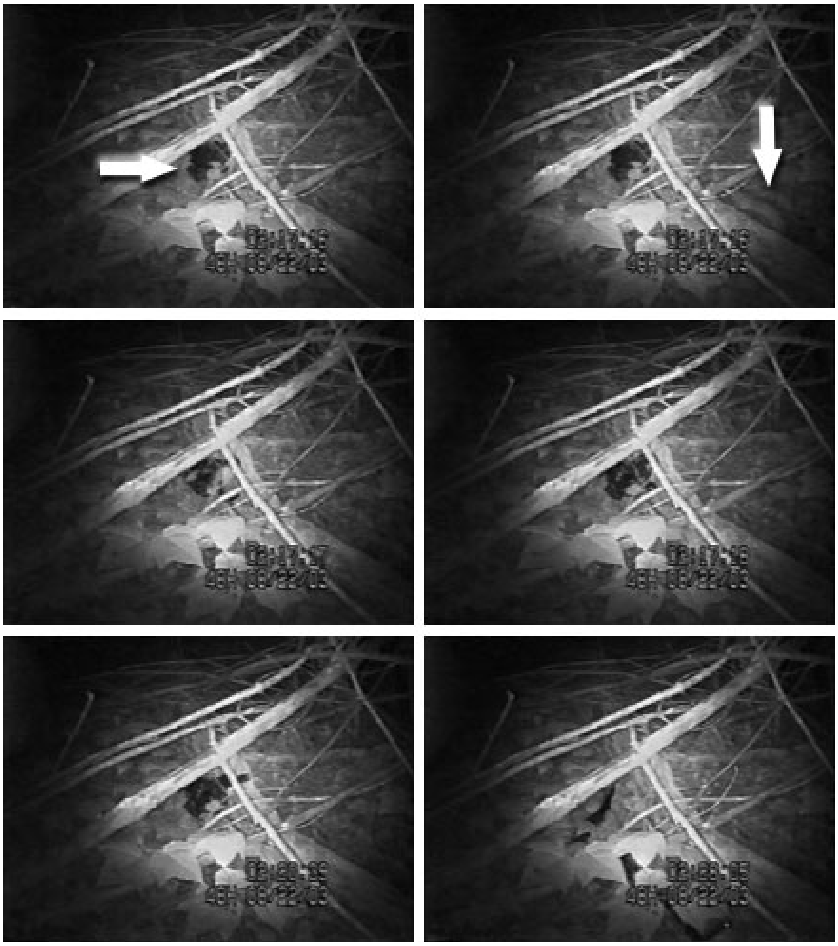

Fig 2: Still frames taken from time-lapse recordings illustrating the various stages of rattlesnake predatory behavior. (1) Pre-strike. Snake is coiled next to fallen log in ambush site, waiting for prey to come within strike range (white arrow next to snake). (2) Long-tailed weasel (*Mustela frenata*) approaches snake at 02:17:16 hours (white arrow next to weasel). (3) Snake strikes and realeses weasel at 02:17:17 hours. (4) Quiescent stage begins immediately post-strike at 02:17:18 hours. (5) Quiescent stage ends as snake begins to move head in lateral searching movements, beginning the locate stage at 02:20:39 hours. (6) Trailing stage begins as snake locates chemosensory trail, moves from coil, and begins following trail out of video frame at 02:28:05 hours

completed swallowing the prey within 51 min of striking. In another case, a red-backed vole (*Clethrionmys gapperi*) was struck and fled 7 m before becoming immobilized. The snake located this prey item within 41 min of striking, and had completed swallowing within 59 min of striking.

Snakes frequently appeared to resume foraging efforts immediately after feeding, often at the same site where the successful encounter occurred. After three of the 11 feeding events (n = 3 snakes), snakes returned to the exact same foraging position and adopted a stereotyped ambush position, where they remained for several hours before abandoning the site.

Discussion

Because recordings were made at a relatively slow frame rate under non-optimal lighting conditions, details of strike kinematics were difficult to see. However, these natural strikes did not appear to be qualitatively different from those seen in the laboratory (Kardong & Bels 1998), or from those seen in the field of snakes striking human-released prey (Cundall & Beaupre 2001). As has been noted in laboratory trials, all prey were released after striking and stereotyped post-strike behaviors only occurred after snakes successfully struck prey (never after missed strikes) (Chiszar et al. 1992; Kardong & Smith 2002).

The post-strike behaviors of free-ranging timber rattlesnakes followed the same pattern seen in laboratory studies on other *Crotalus* spp. (see Fig. 2 for illustration of behavioral stages). Although direct comparisons are difficult because laboratory studies often do not report the durations for the behavioral stages identified here, snakes in the present study appear to spend more time in the quiescent and locate stages (Table 1). It is unlikely that this difference is solely because of sub-optimal thermal conditions in the field, as the strike itself and the rate of trailing once the trail has been located are similar between laboratory trials and this study.

Hayes (1992, 1993) reports quiescent stages of 64 ± 11, 94 ± 18, and 82 ± 8 s for *Crotalus viridis*-fed deer mice in laboratory trials, while Kardong & Smith (2002) refer to the quiescent stage as 'refractory and short'. These values are similar to the 74 ± 7 s seen in this study when snakes struck items less than 100 g, but much shorter than the 421 ± 88 s for larger prey. Therefore, the discrepancy in the duration of the quiescent stage between this study and laboratory studies is probably because of the effect of prey size. It has been suggested that one function of the quiescent stage is to avoid retaliation by envenomated prey (Radcliffe et al. 1980; Kardong 1986; Hayes 1992). This hypothesis is supported by the fact that the quiescent stage lasts longer when snakes strike large prey, as larger prey may take longer to die (Russell 1980; Hayes 1995), and could potentially cause more severe injury than smaller prey. Although Hayes (1992, 1993) did not find a significantly longer quiescent stage for snakes striking larger prey, the prey used were large vs. small mice, which are more similar in size than the classes used in this study. Further experiments should be done to determine whether a prolonged quiescent stage is associated with striking larger prey in other viperids.

The duration of the locate stage seen in this study was longer than what has been reported in laboratory experiments (Table 1). The extended duration of the locate stage in the field may be because of the increased difficulty in locating scent trails made by live prey in a natural environment. Because of the need to reduce variability between trials, laboratory studies usually use scent trails created by dragging prey across a clean substrate in straight lines, thus creating a relatively continuous scent trail in a testing arena that is much less chemically complex than a field environment. Such a trail is likely to be easier to locate and follow than a discontinuous trail made by a wounded and fleeing mammal in an environment that is likely to contain many scent trails from a variety of other sources. This hypothesis is supported by Goode et al. (1990), who found that a free-ranging *Crotalus durissus unicolor* took only 3 min to locate and follow a 250-cm trail made by dragging a dead mouse over the substrate; much shorter than what is reported for *Crotalus horridus* in this study.

Although the rate of trail following estimated in this study is similar to, or faster, than what has been found in laboratory studies (Table 1), this estimate is based on the limited distance traveled while still in the camera frame (usually 1–2 m) and may not accurately reflect the length of time taken to fully locate immobilized prey. In two of the 11 recordings, snakes doubled back after initially leaving the recording frame and began following the prey scent trail from near the beginning again, a phenomenon that has not been reported in the laboratory. Additionally, in one case I directly observed a snake strike a red-backed vole, which subsequently ran 7 m before becoming immobilized. Even though the snake, when moving, moved approximately 0.5 m/min along this trail, it took 35 min for the snake to locate the prey because of frequent long pauses and non-linear searching movements.

Swallowing prey may also take substantially longer under field conditions than in the laboratory (Table 1). A snake in this study which took 39 min to swallow a nocturnal rodent looked as if it was having difficulty extracting the dead prey from under a rock. Thus, obstacles not present in the laboratory environment may make straightforward tasks more difficult in the field.

Overall, this study indicates that the process of trailing and swallowing envenomated prey may be more difficult and time-consuming for free-ranging snakes than previously realized. Although the laboratory environment is often more tractable for experimental studies, it is important to note that laboratory conditions may differ from natural conditions in ways that have important implications for behavior and selection.

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