



Field video recordings reveal factors influencing predatory strike success of free-ranging rattlesnakes (*Crotalus* spp.)

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Research on predator–prey interactions often focuses largely on prey behaviour, treating predators as static danger, rather than as active behavioural participants that can respond adaptively to prey choices. A complete understanding of the functional significance of both predator attack behaviours and prey escape behaviours can only come from examining the interaction between both parties. For example, although the predatory strike of venomous snakes has been studied extensively in the laboratory, we have little understanding of the proximate factors influencing snake strike behaviour under natural conditions. Here, we report details of the analysis of predatory strikes of free-ranging rattlesnakes (*Crotalus* spp.) towards their natural prey. We found that over half of strike attempts were unsuccessful, and the most significant factor influencing strike success was the ability of prey animals to initiate a rapid evasive dodge manoeuvre in the fraction of a second after snakes initiated strikes, but before snake strikes contacted them. Snakes, in turn, initiated strikes most frequently towards the flank of laterally moving prey, which is probably an attempt to counter the ability of prey to dodge strikes.

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Almost all animals have predators, and predation risk has long been appreciated as a major selective force in evolutionary biology. Consequently, a large body of research, both theoretical and empirical, has been devoted to how prey animals assess and respond to predation risk (reviewed in: Lima & Dill 1990; Caro 2005). Heightened vigilance and wariness come at a cost of increased physiological stress and decreased time and energy for other activities (Creel et al. 2009; Sansom et al. 2009; Sheriff et al. 2009). Such trade-offs are recognized as a necessary consequence of maximizing lifetime reproductive success (Clark 1994; Lind & Cresswell 2005), and the effect of these behavioural changes on trophic interactions can greatly influence the dynamics of ecological communities (Lima 1998; Werner & Peacor 2003). However, the outcome of any predation event depends on the interplay between both prey and predator behaviours, and much less attention has been given to how predators exhibit behavioural adaptations that may circumvent antipredator defences (Lima 2002). For example, because predators can attack prey quickly and without prior warning, prey have evolved antipredator

behaviours to detect attacks before they occur (Quenette 1990; Lima 1995) and to avoid attacks when they do occur (Weihs & Webb 1984; Yager et al. 1990; Watkins 1996). Predators, in turn, should alter the timing and orientation of their attacks in ways that minimize the probability of detection and avoidance by prey. The few empirical examples available do indicate that some predators actively target prey that are less likely to detect an oncoming attack (Fitzgibbon 1989; Krause & Godin 1996; Roth et al. 2006).

Despite the call to put predators back into research on predator–prey interactions (Lima 2002), predator-oriented studies are still lacking. It is inherently difficult to study both attack and escape behaviours in free-ranging animals because predators are often cryptic, and natural predation events are rare and unpredictable (Curio & Regelman 1986; Clark 2006a; Cresswell & Quinn 2010). Even when predation and escape are observed, they can occur too rapidly for observers to be able to see details of the attack and avoidance behaviours. Therefore, we have very little empirical data that contains quantifiable details of both predator and prey behaviour in situ.

Here, we present data accumulated from a large number of predatory attacks by free-ranging viperid snakes of the genus *Crotalus* (rattlesnakes). Viperid snakes are highly specialized predators found in habitats across the globe. All viperids rely on injection of venom to subdue their prey, which is usually employed

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via an ambush-foraging tactic (e.g. Reinert et al. 1984; Roth et al. 1999; Shine & Sun 2002; Tsairi & Bouskila 2004). Typically, the snake waits in ambush for unaware prey to come close enough for the snake to launch a rapid strike (Chiszar et al. 1992; Cundall & Greene 2001; Kardong & Smith 2002).

The strike behaviour of snakes has received a significant amount of attention from functional morphologists due to its kinematic intricacy (Janoo & Gasc 1992; Kardong & Bels 1998; Young 2001; Cundall 2009; Herrel et al. 2010). A typical viperid strike involves a snake starting from a coiled position and rapidly straightening the forefront of its body so that the head is extended forward towards the prey (reviewed in Kardong & Smith 2002). During this extension, the snake opens its mouth and rotates the maxillary bone so that the fangs are erected when it makes contact with the prey. Upon contact, the snake embeds its fangs into the prey, injects venom, then rapidly disengages its fangs from the prey. After envenomation, prey may flee some distance before being immobilized, at which point the snake uses chemosensory cues to follow the scent trail left by the envenomated animal (reviewed in Kardong & Smith 2002).

The entire strike sequence can occur in less than 0.2 s under laboratory conditions (Kardong & Bels 1998; Cundall 2009). Despite the rapidity of this attack, laboratory studies and anecdotal field observations indicate that some small mammals routinely preyed upon by rattlesnakes can use evasive movements to dodge the snake strike (Webster 1962; Hennessy & Owings 1988; Randall & King 2001). However, the frequency with which these attempts occur and their rate of success against free-ranging predators has not been previously investigated. We present the first systematic analysis of viperid predatory strikes towards natural prey recorded under field conditions. We hypothesized that the success of any given snake attack would depend on both predator and prey behaviours. Accordingly, we predicted that prey would attempt to detect snakes initiating ambush strikes, and engage in evasive movements that would take them out of the way of strikes before contact was made. We also predicted that snakes would perform strike behaviours that minimized the ability of prey to avoid strikes by striking at prey in close proximity and by striking towards the flank, rather than the head, of prey.

METHODS

We obtained video recordings of rattlesnake predatory strikes from two sources: (1) our own ongoing fieldwork using portable video surveillance cameras to record the foraging behaviour of radiotagged rattlesnakes (described in Clark 2006a, b) and (2) recordings from other sources, including USeeWildlife, and the British Broadcasting Company (BBC). All methods adhered to ASAB/ABS *Guidelines for the Use of Animals in Research* and were approved by the Institutional Animal Care and Use Committee at San Diego State University (APF 10-09-025C).

Radio Telemetry

We opportunistically captured all snakes and implanted miniature radiotransmitters (Holohil Systems Ltd, ON, Canada, models A1-2T and SI-2T) into the peritoneal cavities under inhalation anaesthesia, following the methods of Reinert & Cundall (1982). Transmitters weighed less than 5% of snake body mass, and snakes were returned to their site of capture within 24 h following surgery. Upon completion of the study, we removed transmitters and released snakes at the point of last capture after recovery from surgery. We relocated snakes daily and positioned video cameras within 1–3 m of coiled snakes to record foraging behaviours. We tracked four populations of snakes using radio telemetry: (1) 17

adult *Crotalus horridus* (timber rattlesnakes) from a mixed-hardwood eastern deciduous forest nature preserve in Chemung County, New York, U.S.A., during 2002 and 2003 (snakes were 104–137 cm in total length and weighed 650–2100 g); (2) 22 *Crotalus oreganus* (northern Pacific rattlesnakes) at a site of mixed oak-savannah habitat in the Sunol Regional Wilderness of Alameda County, California, U.S.A., during 2009 and 2010 (77–102 cm, 390–845 g); (3) six *Crotalus ruber* (red diamond rattlesnakes) from coastal sage scrub/chaparral habitat at the Santa Margarita Ecological Reserve, San Diego County, California during 2008 (80–131 cm, 230–1450 g); and (4) five *Crotalus scutulatus* (Mojave rattlesnakes) from a creosote-bajada Mojave desert habitat northwest of Victorville, San Bernardino County, California during 2008 (60–89 cm, 190–350 g).

Field Videography

For radiotagged snakes, we used portable video surveillance cameras focused on rattlesnakes in ambush coils (as defined by Reinert et al. 1984) to collect behavioural data. Each unit consisted of a security camera coupled to either a time-lapse Model NCL3300 VCR (*C. horridus* recordings), or a mini-digital video recorder (SVAT CVP800 DVR and Supercircuits MDVR14-3) powered by a 12 V sealed lead-acid battery (all other species). Cameras (Swann PNP-150, BC 1035 Color CCD IR, or SuperCircuit PC161IR-2) recorded in colour when ambient light was above 0.1 lx. Under low light conditions, cameras automatically switched to black and white recording with infrared light-emitting diodes. Frame rate of recordings varied from 6 to 30 frames per second (fps), with date and time (to the nearest second) displayed on the recording. Because condensation on camera lenses, obscuring vegetation, or other unanticipated events interfered with recordings, we only quantified behaviours where the image quality and clarity were sufficient for unambiguous measurements. In addition to recordings made with the above equipment, we included two recordings of *C. horridus* made by the BBC while they were filming the nature documentary *Life in Cold Blood* at our Chemung County, New York field site. The BBC used similar methods to locate and record snakes, except their higher resolution camera recording system was triggered by motion-detection devices rather than recording continuously.

We also analysed video recordings from a nature reserve consisting of mixed-hardwood deciduous forest in Independence County, Missouri, U.S.A. Wildlife feeders stocked with mixed grains are used to provision ungulates and other herbivores at the site, and several high-resolution cameras are placed around the reserve by the nonprofit organization USeeWildlife. Remote operators opportunistically view and record the behaviour of wildlife species that come within camera range. On several occasions, camera operators recorded predation behaviours of free-ranging timber rattlesnakes that occurred naturally at the site (viewable online at www.useewildlife.com). Although individual *C. horridus* are not marked at this site, some individuals could be distinguished in recordings through differences in size and colour pattern.

Video Analysis

We examined instances of snake strikes frame by frame to quantify the following variables. We follow the nomenclature of Kardong & Smith (2002) in their review of the different stages of the predatory snake strike.

Strike outcome

We categorized strikes as either hits or misses. Hits were defined as strikes in which the head of the snake could be seen contacting the prey item.

Strike range

We estimated strike range using the video frame prior to the frame that captured the first noticeable strike movement. We estimated the minimum distance between the head of the snake and the body of the prey item in that same frame. We estimated distances to the nearest centimetre by using the head of the snake as a reference. Klauber (1972) made detailed measurements of the correlation between body length and head length of a variety of rattlesnake species by measuring several hundred adult snakes of each species. Because we had measured the body length, but not head length, of all our snakes (except *C. horridus* from Missouri), we used Klauber's published correlations to estimate each individual's head length. We used the ImageJ software (Abramoff et al. 2004) to determine distances in digitized images from videos to the nearest centimetre, using snake head length to set the size scale in each image. For Missouri *C. horridus*, we used Klauber's average value of head length for adult *C. horridus* for all individuals because these snakes were not captured or measured (all individuals recorded were adults). Although we initially estimated distance to the nearest 1 cm, these estimates were subject to some imprecision, given the variation in camera angles and positions from site to site. Therefore, in our quantitative analyses we rounded measured distances to the nearest 5 cm to reflect a more realistic level of precision.

Extend stage

For hits, we estimated the duration of the extend portion of the strike by counting the number of frames between initiation of the strike movement (see strike range above) and the frame in which the snake made contact with the prey item (Fig. 1d). For misses, we estimated the extend stage by counting the number of frames between the initiation of the strike and the frame in which the head of the snake contacted the space that was occupied by the prey when the strike was initiated. In other words, we estimated the time at which the snake would have made contact if that prey had

not moved during the strike. To increase the accuracy of our estimates, we only estimated times from videos having frame rates of 10 fps or greater.

Contact stage

For hits, we estimated the duration of prey contact by counting the number of frames between initial prey contact and the first frame in which the snake's head was no longer in contact with the prey. Again, to increase the accuracy of our estimates, we estimated times from videos having frame rates of 10 fps or greater.

Prey trajectory

We classified prey as moving either laterally or anteroposteriorly to snakes. A prestrike movement vector was measured for each prey species as a line connecting the position of the prey 1 s before strike initiation to its position in the frame immediately preceding strike initiation. If prey did not exhibit movement in the 1 s prior to the strike, this time was extended to the nearest full second during which prey exhibited movement. Any prey whose movement vector was within 45° of the axis defined by this plane was classified as moving anteroposteriorly to snakes (i.e. they were moving head on, towards the snake), whereas prey whose movement vector was greater than 45° from the axis was classified as moving laterally to the snake (Fig. 2). For laterally moving prey, we categorized the position of the prey upon strike initiation as approaching or retreating. Prey were categorized as approaching if the head of the prey had not yet crossed the anteroposterior plane bisecting the snake's head upon strike initiation (Fig. 2). Additionally, we observed one unusual strike attempt on a prey that retreated while moving anteroposteriorly to the snake (described in Results).

Prey dodge

We categorized prey as either dodging or not dodging. To do this, we calculated a poststrike movement vector by



Figure 1. Video frames showing *Crotalus horridus* and *Peromyscus* prey (a) 1 s prior to strike initiation, (b) 0.04 s prior to strike initiation, (c) strike initiation, (d) contact with prey 0.08 s following strike initiation, (e) contact with prey just prior to release, (f) prey release 0.24 s following contact. In (a), snake and prey are outlined in white; dashed line indicates anteroposterior plane bisecting snake; white arrow represents vector of prey movement. In (b), the solid line indicates strike initiation distance; dashed line indicates anteroposterior plane.

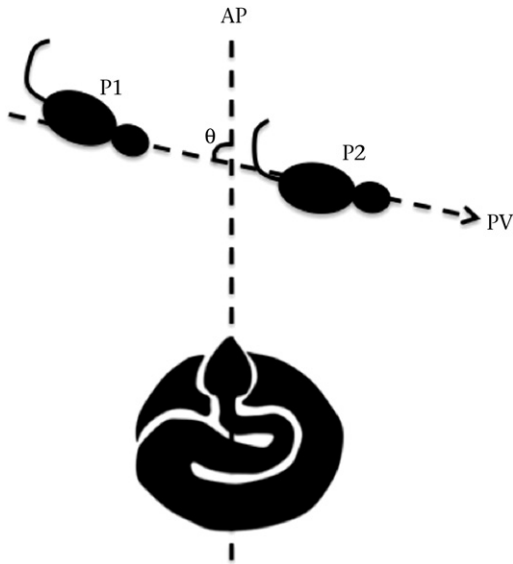


Figure 2. Trajectory of prey movement was categorized depending on the relative angle between the anteroposterior axis of the snake (AP) and the movement vector of the prey (PV). PV was calculated by connecting the position of the prey 1 s before strike initiation (P0) with the position of the prey when the strike was initiated (P2). If angle θ was greater than 45° , prey were categorized as moving laterally; if $\theta < 45^\circ$, prey were categorized as moving anteroposteriorly. The case shown would be categorized as lateral retreat, because $\theta > 45^\circ$ and the prey item had crossed the AP axis before the strike was initiated.

comparing the position of the prey immediately after strike initiation with the position of the prey at prey contact, or, in the case of misses, the position of the prey in the frame in which the snake's head contacted the area occupied by the prey at strike initiation (Fig. 3). We categorized prey as dodging if their post-strike movement vector was greater than 45° from their prestrike

movement vector (prey trajectory, above). Although this excludes some movements that could have been dodge movements (i.e. those dodges following the same trajectory as the prestrike movement), we thought it would be more conservative to categorize them as nondodges.

Prey identification

We identified prey to species or genus when possible. Because video resolution did not allow us to identify species accurately in many cases, we also placed prey into three broad categories: nocturnal rodents, diurnal rodents (in our study, squirrels and chipmunks), and lizards.

Data Analysis

All values are given as means \pm SD. We used multivariate logistic regression to explore the relationship between frequency of snake success, snake species and prey type. For many recordings we were unable to collect data on strike range, prey trajectory and prey dodging, leading to many missing values for these variables (see [Supplementary Table S1](#)). Thus, they were not included in the multivariate model, but were explored using univariate logistic regression. To explore the interaction between factors that showed a significant relationship with strike success, we tested for significant interaction terms ($P < 0.05$) in multivariate logistic regression models using only the subset of data with no missing values. We also used multivariate logistic regression to examine the effect of prey type and prey trajectory on prey dodging. Although we recorded multiple strike events for some individuals (the largest number of strikes recorded from any one individual was six), we treated all strikes as independent samples because they all involved independent prey items under a unique set of circumstances (i.e. strikes involved unique prey items and took place at different spatial locations and at different times during the active season). We used SYSTAT 12.0 software (2007, SPSS Inc., Chicago, IL, U.S.A.) to conduct all statistical analyses.

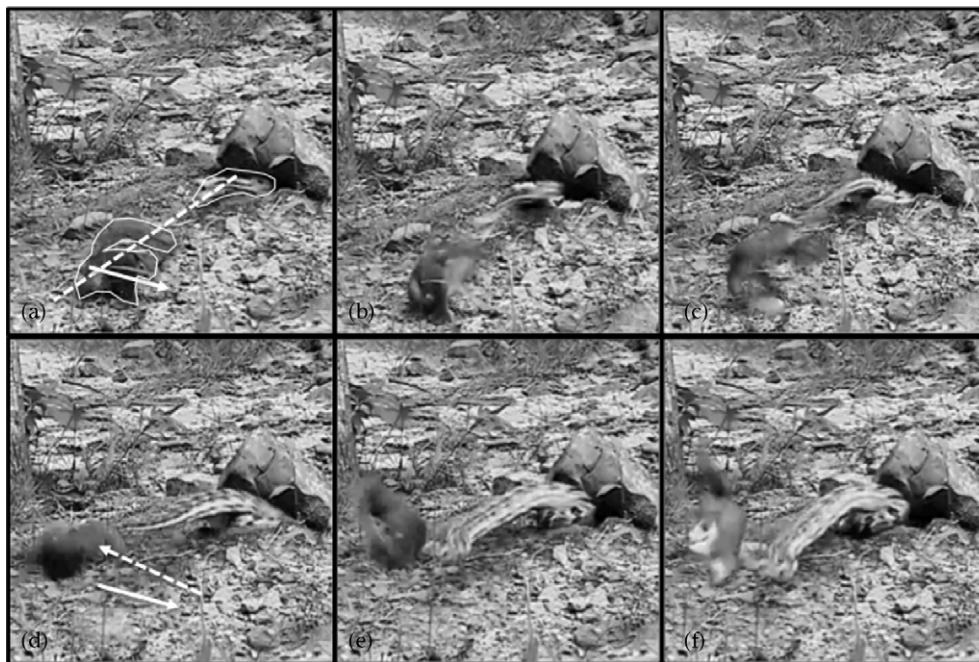


Figure 3. Video frames showing *Crotalus horridus* and *Sciurus carolinensis* (a) during strike initiation movement, (b) 0.03 s after strike initiation, prey turns its head towards snake, (c) 0.07 s after strike initiation the prey begins dodging movement, (d) 0.13 s after strike initiation, the snake contacts prey, (e) one frame prior to prey release, (f) 0.10 s after prey contact, the snake releases prey. In (a), the snake and prey are outlined in white; dashed line indicates anteroposterior plane bisecting snake; white arrow represents prestrike movement vector of prey. In (d), solid arrow indicates prestrike prey movement vector; dashed arrow indicates poststrike prey movement vector.

RESULTS

We obtained video recordings of 57 predatory strikes of free-ranging rattlesnakes (*Crotalus* spp.). Sample video recordings from this study are publicly viewable at the Clark laboratory website (<http://www.bio.sdsu.edu/pub/clark/>). Twenty-eight of these recordings were from 12 individual *C. horridus* (19 recordings from five telemetered individuals at our field site in New York, nine recordings from seven nontelemetered individuals at Missouri nature reserve), 19 from *C. oreganus* (nine individuals), eight from *C. ruber* (four individuals) and two from *C. scutulatus* (two individuals).

Attacked prey included a variety of small mammals and lizards typically found in the diet of these four snake species (see [Supplementary Table S1](#)). Of the 57 recorded strikes, 25 (44%) appeared to contact prey (hits) and 32 (56%) did not (misses).

Snakes initiated strikes at prey from distances of 5–50 cm (mean estimated distance between snake and prey upon initiation of strike = 17 ± 11 cm). Snake strikes lasted an average of 0.2 ± 0.1 s between the initiation of the strike and contact with prey. We were able to quantify the length of prey contact for 12 recordings. In all but one case, snakes released the prey immediately after it was struck. For the 11 cases where prey were released immediately, the average duration of prey contact was 0.5 ± 0.2 s. In the one exception, a *C. ruber* individual held a field mouse (*Peromyscus* sp.) until over 5 min had passed and the mouse was completely immobile.

We were able to categorize the trajectory of prey movement with respect to the orientation of the snake in 43 recordings. The majority of prey (32 of 43) were moving laterally in front of the coiled snake, as opposed to anteroposteriorly. In one unique case, a snake struck at a prey that was moving anteroposteriorly to the coiled snake, but from behind and to the side of the snake; in this strike, the snake reoriented its head and upper body as it initiated the strike movement so it was striking at the flank of the prey as the prey retreated. For 25 of the 32 cases of laterally moving prey (80%), snakes initiated strikes after the prey had passed the anteroposterior axis of the snake's head and was moving away from the snake ([Fig. 4](#)); this result differed significantly from the null expectation of strikes being equally likely before and after prey move past the snake (binomial test: $P < 0.001$).

We categorized prey movements during the extend phase of the strike in 37 recordings. In 18 of these 37 recordings (49%), prey attempted to dodge the strike. In only one of these 18 cases was a snake strike successful (6%). In contrast, 13 of the 19 strikes (68%) during which prey did not dodge were successful ([Fig. 5](#)).

There were no significant relationships between strike success and snake species or prey type ($\chi^2_2 = 0.1$, $N = 57$, $P = 0.94$), or between strike success and prey approach category (lateral approach, lateral retreat, or anteroposterior approach) ($\chi^2_1 = 0.02$, $N = 43$, $P = 0.87$). There was a highly significant relationship between strike success and strike range ($\chi^2_1 = 12.5$, $N = 44$, $P < 0.001$); the odds ratio of this test indicated that for every 10 cm of range, odds of a strike missing were 4.5 times greater (odds ratio 95% CI = 1.5–13.2). There was also a highly significant relationship between prey dodging and strike success ($\chi^2_1 = 17.7$, $N = 37$, $P < 0.001$); odds of a successful strike were 36.8 times higher if a dodge did not occur (odds ratio 95% CI = 3.9–344.8).

When we retained only the subset of data with no missing values for either prey dodging or strike range, there was still a significant relationship between strike success and both factors analysed separately (strike range: $\chi^2_1 = 11.6$, $N = 35$, $P = 0.001$; dodge: $\chi^2_1 = 15.7$, $N = 35$, $P < 0.001$), indicating that this subset of data still accurately captured the relationships seen with the full data set in each case. A multivariate logistic regression with this subset of data found a trend towards a significant interaction between dodge and strike range ($Z = 2.7$, $N = 35$, $P = 0.08$), indicating that these two factors may not be entirely independently of each other.

There was no significant relationship between prey dodging, prey type (categorized as diurnal rodent, nocturnal rodent, or lizard) and prey trajectory (categorized as lateral approach, lateral retreat, or anteroposterior approach) ($\chi^2_2 = 1.1$, $N = 33$, $P = 0.56$).

DISCUSSION

Our field recordings of *Crotalus* strikes showed that approximately half of snake strikes towards potential prey were unsuccessful. Two factors had a strong effect on whether snake strikes were successful: (1) the most significant factor affecting snake success was prey dodging, with snakes being much more likely to

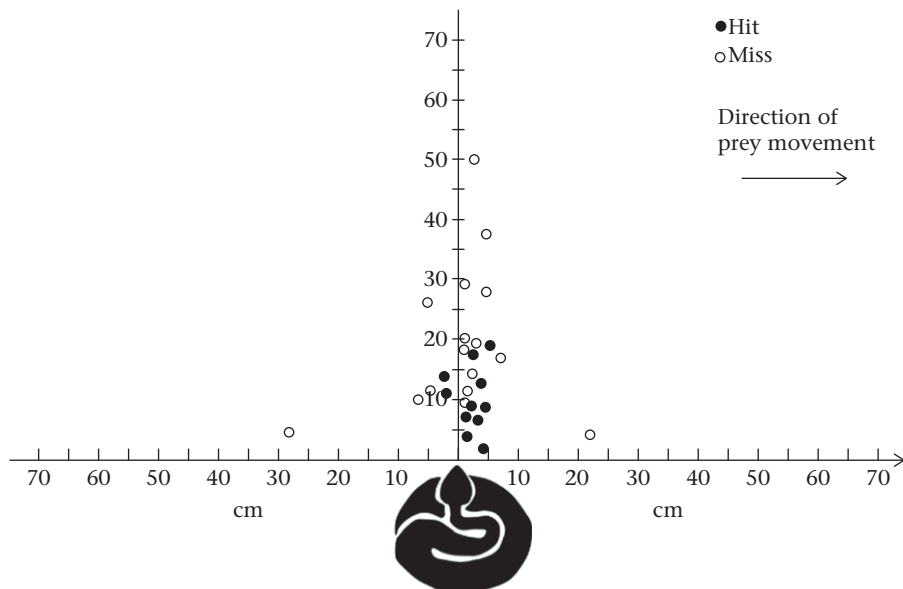


Figure 4. Approximate locations of laterally moving prey relative to snake upon strike initiation. All prey movements are standardized in the figure as moving from the left side of snake towards the right side of snake. Open circles indicate positions of prey that were missed by the snake; closed circles indicate positions of prey that were hit.

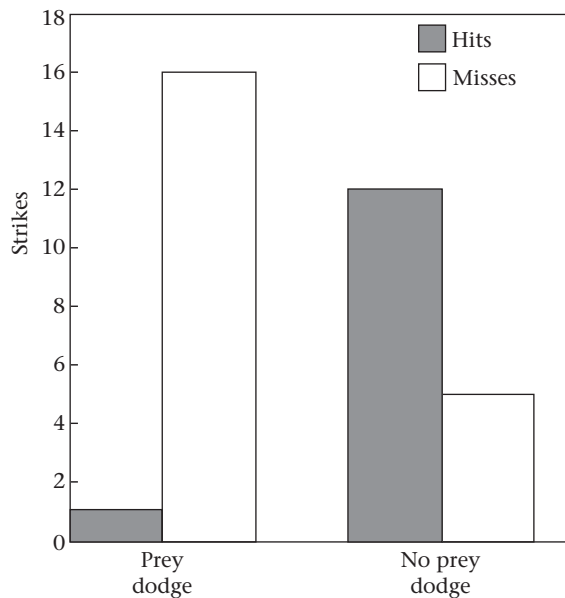


Figure 5. Number of strikes recorded in the field where snakes contacted prey (hits) or did not contact prey (misses), categorized separately for cases when prey made evasive movements after the strike was initiated (prey dodge) and for cases when prey did not make evasive movements after the strike was initiated (no prey dodge).

miss if prey were able to use an evasive manoeuvre during the extend phase of the strike (Fig. 5); (2) snakes were also more likely to strike successfully when prey were relatively close (typically less than 15 cm away; see Fig. 4).

Our data also revealed a significant tendency for snakes to initiate strikes towards the broadside of prey after prey had already passed the anteroposterior axis of the snake; thus, strikes were usually initiated when prey began retreating from snakes, rather than when prey were approaching snakes (Fig. 4). Striking towards the flank (i.e. after the prey has passed the head of the snake and is moving away) is likely to make it more difficult for prey to detect an oncoming strike in time to dodge. Taken as a whole, these results support our hypothesis that the outcome of a predation attempt is dependent on interacting behaviours of both predator and prey: prey attempt to detect and avoid snake strikes, and snakes attempt to minimize the ability of prey to do so by striking in close proximity towards the flank of retreating prey. This finding further illustrates the necessity for studies of predator/prey interactions to be conducted with both parties in situ (Lima 2002; Lind & Cresswell 2005).

We recorded dodging of snake strikes by a variety of prey species, including ground squirrels, *Spermophilus beecheyi*, tree squirrels, *Sciurus carolinensis*, chipmunks, *Tamias striatus*, woodrats, *Neotoma fuscipes*, kangaroo rats, *Dipodomys merriami*, and lizards (unidentified species). In the most extreme cases, prey were able to dodge successfully in less than 0.2 s and at distances as short as 5 cm. Although the ability to dodge snake strikes has been described anecdotally for a number of small mammals (Webster 1962; Loughry 1987; Randall & Stevens 1987; Hennessy & Owings 1988), it has rarely been investigated systematically. Additionally, our study is unique in that the dodging prey showed no awareness of the snake's position prior to the initiation of the strike (i.e. snakes were striking from ambush). Although we have observed snakes attempting to strike squirrels that have signalled snake awareness through tail flagging (Hersek & Owings 1993), in this study we only analysed videos of strikes towards nonsignalling prey.

Laboratory investigations of snake strike kinematics have mainly relied on recordings of captive individuals striking laboratory mice (Janoo & Gasc 1992; Kardong & Bels 1998; LaDuc 2002;

Vincent et al. 2005; Cundall 2009). Typically several hundred to several thousand frames/s can be recorded with high-speed video in the laboratory, whereas our field recording rates varied from 6 to 30 fps. Laboratory recordings also maximize the probability that strikes occur perpendicularly to camera angles and so engender more precise distance estimates than our field cameras. Thus, some of the behaviours from our videos were difficult to compare with laboratory studies because the precision was much lower. For example, with a video recorded from the field at 10 fps, a behaviour that actually takes only 60 ms would be rounded up to 0.1 s in our recordings. However, because our data set captures the full range of variability in prey behaviours encountered by snakes in their natural environment, we believe it is still useful to compare broad patterns from our study to those found in the laboratory.

Several of the broad patterns of strike behaviour of our snakes diverge from strike behaviour recorded under laboratory conditions. Snakes in the laboratory rarely miss strikes (Kardong & Bels 1998; Vincent et al. 2005; Cundall 2009), whereas snakes in our field study missed over half their strikes. A large portion of these misses can be attributed to prey dodging, as 15 of the 16 cases where prey dodged, snakes missed their prey. However, 29% of the strikes where prey did not dodge were still misses, indicating that factors other than prey dodging may affect strike success in the field. The duration and range of snake strikes in our data set show much greater variability than laboratory data. Data on laboratory strikes indicate a typical strike range of 3–20 cm, the extend stage lasts between 0.02 and 0.05 s, and prey contact lasts 0.05–0.25 s (Kardong & Bels 1998; Cundall & Beaupre 2001; Young 2001; LaDuc 2002; Vincent et al. 2005; Cundall 2009). Our recordings showed that the distance between prey and snake ranged from 5 to 50 cm, the extend stage lasted 0.05–0.5 s and contact with prey lasted 0.1–0.8 s.

Several factors probably contribute to the increased variability of snake strikes in the field. Free-ranging snakes may not be able to maintain optimal body temperatures at all times, and performance in ectotherms is generally lower at suboptimal temperatures. For example, free ranging hime-habu vipers with higher body temperatures struck more quickly at frogs that were offered to them by researchers (Vincent & Mori 2008). Free-ranging individuals may also be more motivated to feed compared to well-fed snakes maintained in captivity (e.g. Aubret & Bonnet 2005), causing them to increase the range at which they are willing to strike. Finally, captive-bred rodents typically used in laboratory studies probably do not show the effective snake-strike avoidance behaviours documented here in wild rodents.

In our study we combined predation events from four *Crotalus* species and 27 individuals of varying sex and size; pooling data allowed us to obtain a reasonable sample size for analysing broad patterns in this behavioural interaction. Although neither prey type nor predator species was a statistically significant factor affecting strike success in our analysis, our samples sizes for these factors were low, and factors such as species, age, size and sex may be important. As our fieldwork in this area is ongoing, additional studies in the future will provide a more detailed examination of these variables.

Our results also have implications for community dynamics in ecosystems where ambush-foraging snakes are major predators, given the influence that ambushing is likely to have on rodent vigilance. Nonconsumptive effects (e.g. reduced prey growth rates and fecundity) resulting from heightened vigilance are more pronounced in response to sedentary predators (Preisser et al. 2007), and these effects can strongly influence ecological communities (Preisser et al. 2005). To date, studies of rodent vigilance behaviour have focused mainly on predation risk from mammalian and avian predators (e.g. Kotler et al. 1991; Orrock et al. 2004; Eccard et al. 2008), while vigilance towards snakes has been largely

overlooked (but see Hersek & Owings 1993; Bouskila 1995). In a multiple-predator environment, prey should direct vigilance towards the predator type that imposes the highest predation risk (or encounter rate) (Lima 1992). Thus, rodent vigilance at many sites may be influenced mainly by ambushing snakes, since pit vipers can occur at much higher densities than endothermic predators (Nowak et al. 2008). The extent to which viperid snake predation influences rodent vigilance and the structure of ecological communities deserves more attention.

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Supplementary Material

Supplementary material for this article is available, in the online version, at doi:10.1016/j.anbehav.2012.04.029.

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