

DOES A QUICK OFFENSE EQUAL A QUICK DEFENSE? KINEMATIC COMPARISONS OF PREDATORY AND DEFENSIVE STRIKES IN THE WESTERN DIAMOND-BACKED RATTLESNAKE (*CROTALUS ATROX*)

TRAVIS J. LADUC

ABSTRACT: Rattlesnakes (*Crotalus* and *Sistrurus*) have a rapid envenomating strike which can be aimed toward either predators or prey. Previous researchers proposed that predatory and defensive strikes are differentiated by qualitative pre-strike features (e.g., presence of rattling or prolonged, arcing tongue flicks); quantitative kinematic differences between the two strike types have not been evaluated. To resolve this issue, four Western Diamond-backed Rattlesnakes (*C. atrox*) were filmed at 1000 fps striking at mice and at a large soft doll. The strikes aimed at mice were presumed to be predatory as the mice were subsequently ingested, whereas the strikes at the doll were interpreted as defensive. The maximum velocity and average velocity during the strike differed significantly between the strike types, as did distance from target upon initial forward movement. However, maximum and average accelerations varied only among individuals. Subjects initiated defensive strikes from distances twice those characteristic of predatory strikes, yet duration of the extension stage (time from initiation to primary target contact) did not differ between the strike types. This study indicates that defensive situations are characterized by an increase in strike velocity that derives from increased distances at strike initiation, yet rattlesnakes do not differ in their mean and maximum acceleration between strike types.

INTRODUCTION

The predatory strike of vipers (Viperidae) is a distinctive behavior in animals. In less than half a second, a snake lunges from a resting position, erects its elongated fangs, injects venom into its prey and returns to its original position, presumably to escape retaliation from its victim (Kardong, 1986a; Kardong and Bels, 1998). The elongated maxillary fangs rotate forward almost 90° during the strike (Cundall, this volume) and penetrate the prey, allowing primarily hemotoxic venom to be injected. The venom can subdue and predigest prey before ingestion, establishing an advantage to deep penetration of the fangs. Neuromuscular coordination must therefore be precise in the strike.

Defensive strikes, especially those of rattlesnakes (*Crotalus* and *Sistrurus*), often include a defensive display towards their attackers, particularly when the perceived threat is persistent and/or when the aggressor makes a sudden movement. Often the head of the snake is elevated between the body coils, and distinctive warning sounds are produced with the caudal rattle. These displays are typically followed by a rapid strike delivering an injurious and sub- or lethal-dose of venom upon fang contact.

Historically, predatory and defensive strikes in rattlesnakes were distinguished by a variety of qualitative pre-strike and strike behaviors. The snake rattles during defense (Minton, 1969; Klauber, 1972), the head is not flexed ventrally at contact with the target (Kardong, 1986b; Janoo and Gasc, 1992), and the

strikes proceed from elevated, vertical S-coils (Duvall et al., 1985). Slow-arcing tongue flicks studied in various colubrid species (Gove, 1979; Gove and Burghardt, 1983) were also proposed as a character potentially delineating defense strikes in rattlesnakes (Hayes and Duvall, 1991). Comparisons between the two strike types were further confused by general descriptions of rattlesnake strike variables and behavior that clearly include defensive strike situations (Vigne, 1833; Mitchell, 1861; Coues and Yarrow, 1878; Van Riper, 1954; Lester, 1955; Klauber, 1972; Russell, 1980). Although recent literature includes studies of such predatory strike variables as timing, behavior, and venom metering (Hayes et al., 1992; Hayes, 1993, 1995; Hayes et al., 1995; Kardong, 1986a, b; Kardong et al., 1986; Kardong and Bels, 1998), no study to date details quantitative differences between predatory and defensive strikes.

Are predatory strikes faster than defensive strikes to overcome the optimal escape behavior of potential prey items? Do maximal velocity and acceleration of the rattlesnake head prevent potential prey from eluding strikes? Conversely, might defensive strikes be faster than predatory strikes because startling or confrontational situations require maximal velocity and acceleration to deter predatory attack? For the two strike types, this study quantitatively evaluates velocity, acceleration, and timing variables of the rattlesnake head from the initial movement of the snake toward its target until the contact of jaws on the target.

MATERIALS AND METHODS

Four Western Diamond-backed Rattlesnakes (*Crotalus atrox*), ranging from 58.0 to 92.5 cm total

length, were collected from south-central Texas and used here. Animals were housed individually, kept on a 12L:12D light cycle and maintained over six months. Snakes were offered food (both live and dead laboratory mice) every two weeks and water was given ad libitum. Guidelines and safety features for the care of all rattlesnakes followed Gans and Taub (1964), Murphy and Armstrong (1978), and Altamari (1998), as well as guidelines established specifically for this study in conjunction with the University of Texas Animal Care and Welfare Committee.

The filming area consisted of a terrarium (L90 x W50 x H50 cm), bounded on three sides by glass and on the fourth by a sheet of pegboard with a small hole cut in the side; the floor was composed of white foam board. A 1-cm grid pattern traced onto film velum was placed onto the back glass pane to enable absolute distance measurements. A subject was placed unrestrained into a partitioned area (L50 x W50 x H50 cm) in the test arena 15–30 min before filming to allow for acclimatization. Two 15 W fluorescent bulbs were used to backlight the film velum placed on the back of the terrarium, and were left on during the acclimation period of each subject. The temperature during filming was kept at $27 \pm 0.5^\circ\text{C}$.

Each predatory strike sequence was recorded with a Redlake MotionScope 1000S video camera at 1000 fps. A Canon ES970 8 mm video camcorder was placed above the arena to quantify whether strikes were directed at 60° – 120° to the optical axis of the high-speed camera with strikes exceeding this range being excluded. A single 250 W incandescent flood lamp was used to illuminate the terrarium 15–20 sec before introduction of prey items. A single, freshly-euthanized mouse was introduced on the end of 62 cm forceps through the pegboard hole 10–20 sec following removal of the terrarium partition. The euthanized mouse was moved slowly toward and away from the snake in a plane perpendicular to the camera's optical axis until the snake struck. All subjects showed intense interest in the prey item, often characterized by a series of rapid tongue flicks and at times pursuit of the mouse, resulting in an off camera strike.

Laboratory mice were used to elicit predatory behavior in the subjects because they were previously found to produce predatory behaviors in snakes equivalent to those elicited by wild rodent prey (*Peromyscus*; Kardong, 1993). Dead mice were used in place of live mice in order to remove potentially confounding and unrepeatable kinematic effects of live mice when struck. Prey mass varied between 4.0

and 14.5% of snake mass ($\bar{x} = 7.02\%$). Hunger may heighten responsiveness to certain forms of stimuli (Hayes and Duvall, 1991; Hayes, 1993), so all snakes used in this portion of the analyses were offered laboratory mice (both live and dead) on a regular two-week basis.

Defensive strikes were filmed using the same camera configuration. Framing rate was reduced to 500 fps due to magnification constraints caused by the size of the defensive target (see below), with subsequent images blurred slightly. Because kingsnakes (*Lampropeltis*) are known to feed upon rattlesnakes, their visual or chemical presence would presumably enhance a defensive response, and in fact, rattlesnakes frequently strike kingsnakes during defensive encounters (Klauber, 1972). The Desert Kingsnake (*L. getula splendida*) is found sympatrically with *C. atrox* in south-central Texas. A small, stuffed, yellow doll (100 mm tall, 70 mm wide, 26.5 g) was housed with an adult *L. getula* for 30–60 min before it was used as a defensive target, and was introduced to rattlesnakes on the end of 62 cm forceps through the side of the terrarium. Presentation of the doll was in an erratic and confrontational manner. The subjects likely interpreted this doll as a threat because of its large size, its odor (acquired from *L. getula*), and its behavior. Further, subjects rattled during every presentation of the doll and performed long arcing tongue flicks prior to each strike, which were only seen during presentation of the doll. No flawed strikes (e.g., collision with obstacle or side of cage prior to target contact, only one fang driven into target, snake missed the target entirely; Kardong, 1986b) were included in the analysis.

The strike of rattlesnakes was previously divided into four stages: extension, contact, release, and retraction (Kardong and Bels, 1998). The extension stage is defined as the period between initiation of forward movement to target contact, and the contact stage is the entire period of prey contact. The release stage begins upon freeing of jaw contact from the target and ends with jaw closure. Retraction involves the period of movement away from the target. Using these definitions, the release and retraction stages overlap greatly with each other, although each deals with a slightly different head/jaw movement. Variables presented in this analysis are measured mostly from the extension and contact stages, with a single variable (maximum gape angle, release stage) taken from the release stage.

Filmed sequences were downloaded to videotape and analyzed using a MiroMotion frame grabber (Pinnacle Systems GmbH) and the software programs

Adobe Premiere 4.2 (Adobe Systems Inc.) and NIH Image 1.62 (developed at the U. S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). Analysis of films began at the frame of initiation of forward movement toward the target, and included the entire extension stage and up to 20–25 frames of the contact stage. Analysis of films ended at a maximum of five frames after secondary jaw contact, save calculation of maximum gape angle (release stage). Three distinct points on the snake head were used as landmarks (tip of snout, tip of lower jaw, angle of jaws [angle between jaws with the apex at the corner of the mouth]; Kardong and Bels, 1998). Maximum gape angle (MGA) was recorded for both the extension and release stages (Kardong and Bels, 1998). Distance from target was determined as the maximum straight-line distance between snake and target in the frame of initial movement toward the target. Time intervals, such as time to maximum gape angle (extension stage), time to contact of lower jaw with target, and time to contact of upper jaw (palatamaxillary complex) with target were also recorded. Percentage of the body kinematically active during the extension stage was obtained from the 8 mm video record. Duration of contact with target was initially recorded using the high-speed camera, but was not included in this study because many defensive strike sequences involved the snake moving both the target and itself off camera. Contact time could not be reliably estimated from the overhead (30 frames/sec) camera.

Velocities and accelerations were calculated using QuickSand.008 (Walker, 1997) using a smoothing algorithm (Kosarev-Pantos with odd extension algorithm) recommended by Walker (1998) for use with high-speed film. Cartesian coordinate data were analyzed separately in QuickSand.008, and were combined to yield velocities and accelerations; all acceleration values are absolute values. Instantaneous velocity is the distance traveled between frames divided by the time interval (predatory: 0.001 sec; defensive: 0.002 sec), and instantaneous acceleration is the change in velocity divided by the elapsed time. Velocity and acceleration values presented here are averages across the time intervals outlined below (Wainwright et al., 1991). Average velocity (V_{avg}) and absolute average acceleration (A_{avg}) values were calculated for the periods of movement of the tip of the snout from the frame of initial forward movement to the frame of target contact with both jaws (extension stage plus initial portion of contact). Average velocity ($V_{contactavg}$)

and absolute average acceleration ($A_{contactavg}$) values were also calculated for the time period between target contact of the first (often the lower) and second (usually the upper) snake jaw. Maximum velocity (V_{max}) and absolute maximum acceleration (A_{max}) values were determined for the each of these previous two time periods.

To address problems in measuring of velocity and acceleration from video data emphasized by Harper and Blake (1989a, b) and Walker (1998), a single predatory and a single defensive strike were each digitized 10 times by two individuals (Wainwright et al., 1991). Velocity and acceleration values were calculated for each of the 10 replicates. The coefficient of variation (CV) for V_{avg} was 1–6% for both data sets and both investigators. The CV for A_{avg} was 6–12% for both data sets and for both investigators. The CV's for V_{max} and A_{max} ranged from 2–4% and 13–20%, respectively, in the predatory strike and 10–30% and 30–40%, respectively, in the defensive strike. Measurement errors of displacement or velocity may increase with increased filming speed (Harper and Blake, 1989a, b; see also Walker, 1998), and V_{max} and A_{max} values may be underestimated. The CV's presented here indicate that my film analysis protocol provides an acceptable level of measurement error for average velocities and accelerations (Wainwright et al., 1991). Maximum instantaneous values for both variables, however, should be viewed as estimates, albeit comparable across individuals.

To test for kinematic differences between predatory and defensive strikes, 13 dependent variables were analyzed with a two-way ANOVA (factors of individuals and strike type). A one-way ANOVA was used to test the effects of both snake size (SVL < 700 mm or SVL > 700 mm, two snakes in each group) and strike initiation distance (> 4 cm and < 4 cm) on kinematic variables (Kardong and Bels, 1998). Multiple comparisons between kinematic variables were also examined using Pearson correlations. Pairs correlated at $r > 0.5$ were examined further using linear regression analysis at $P < 0.05$ (Sokal and Rohlf, 1995). All statistical tests performed using StatView 5.0.1 (Abacus Concepts Inc.).

RESULTS

A total of 26 strikes (13 predatory and 13 defensive) were analyzed. Four predatory strikes were analyzed for one snake, and three for the other three snakes. Four defensive strikes were analyzed for one snake (not the same snake with four predatory strikes), and

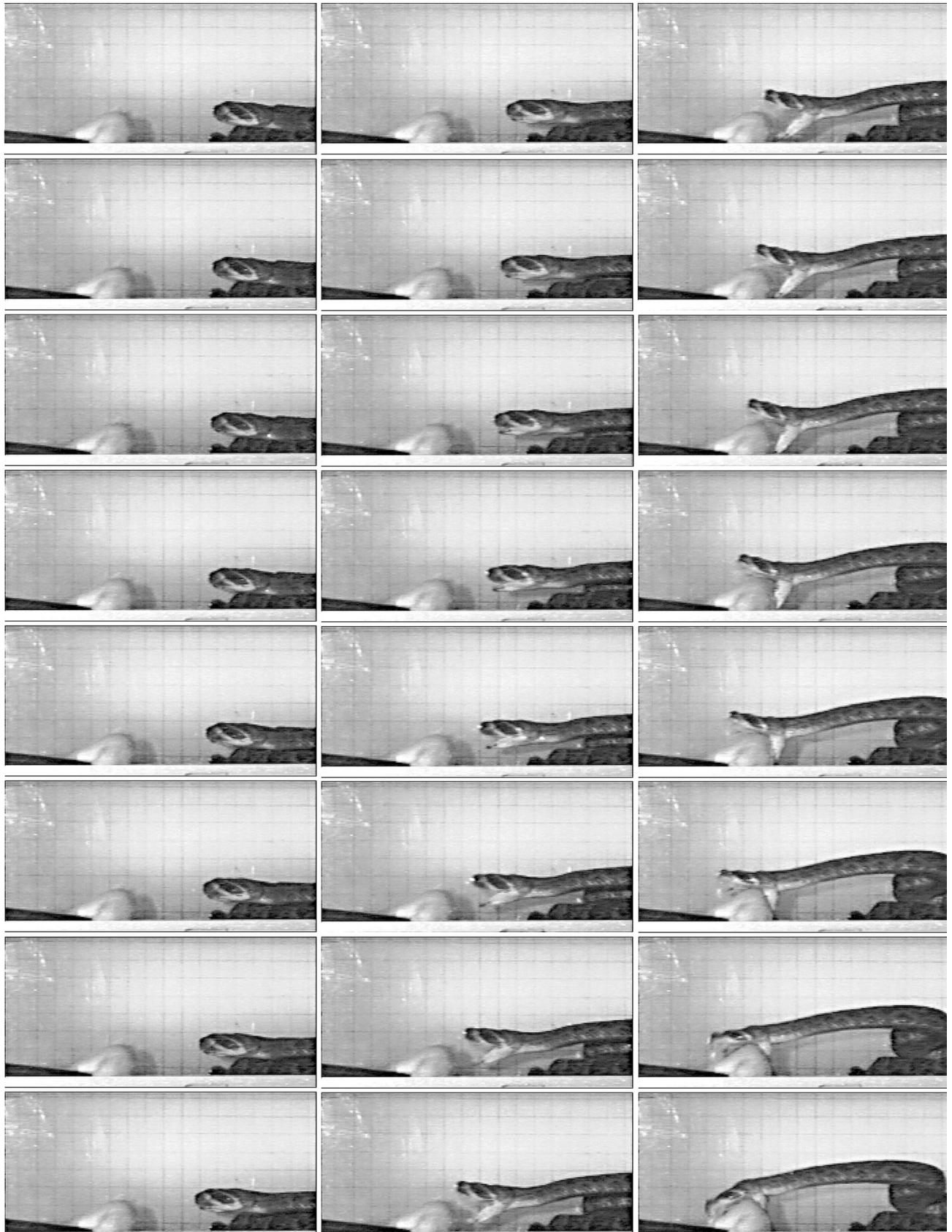


Fig. 1. Sequences of video stills filmed at 1/1000 sec intervals depicting the predatory strike of *Crotalus atrox* toward a pre-killed rodent. Video stills are consecutive, though every other frame in the sequence has been removed (interval between video stills shown = 2 msec). Sequences progress from top to bottom, left to right.

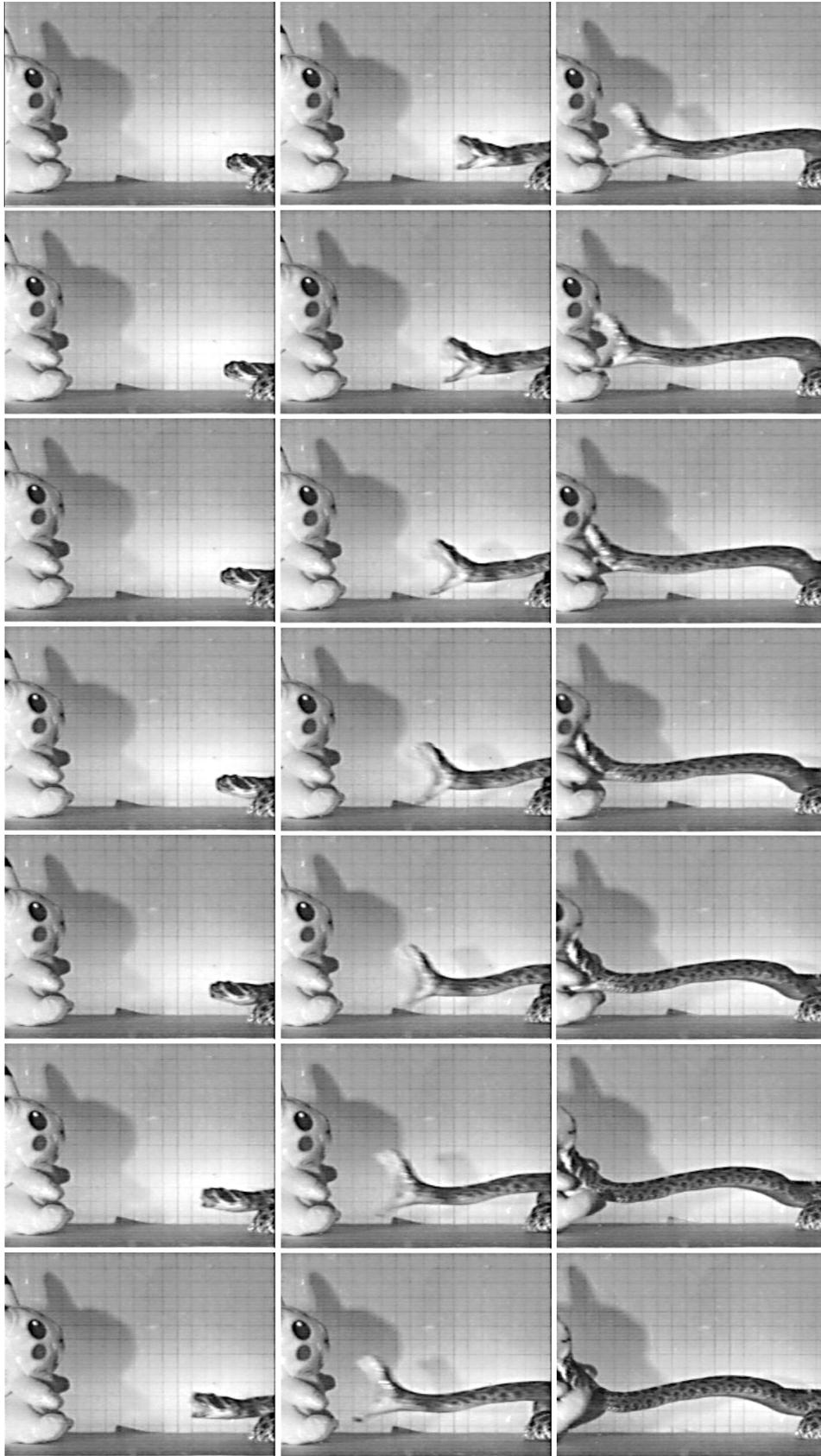


Fig. 2. Sequences of consecutive video stills filmed at 1/500 sec intervals depicting the defensive strike of *Crotalus atrox* toward a kingsnake scented doll. Video stills are consecutive, though every other frame in the sequence has been removed (interval between video stills shown = 4 msec). Sequences progress from top to bottom, left to right.

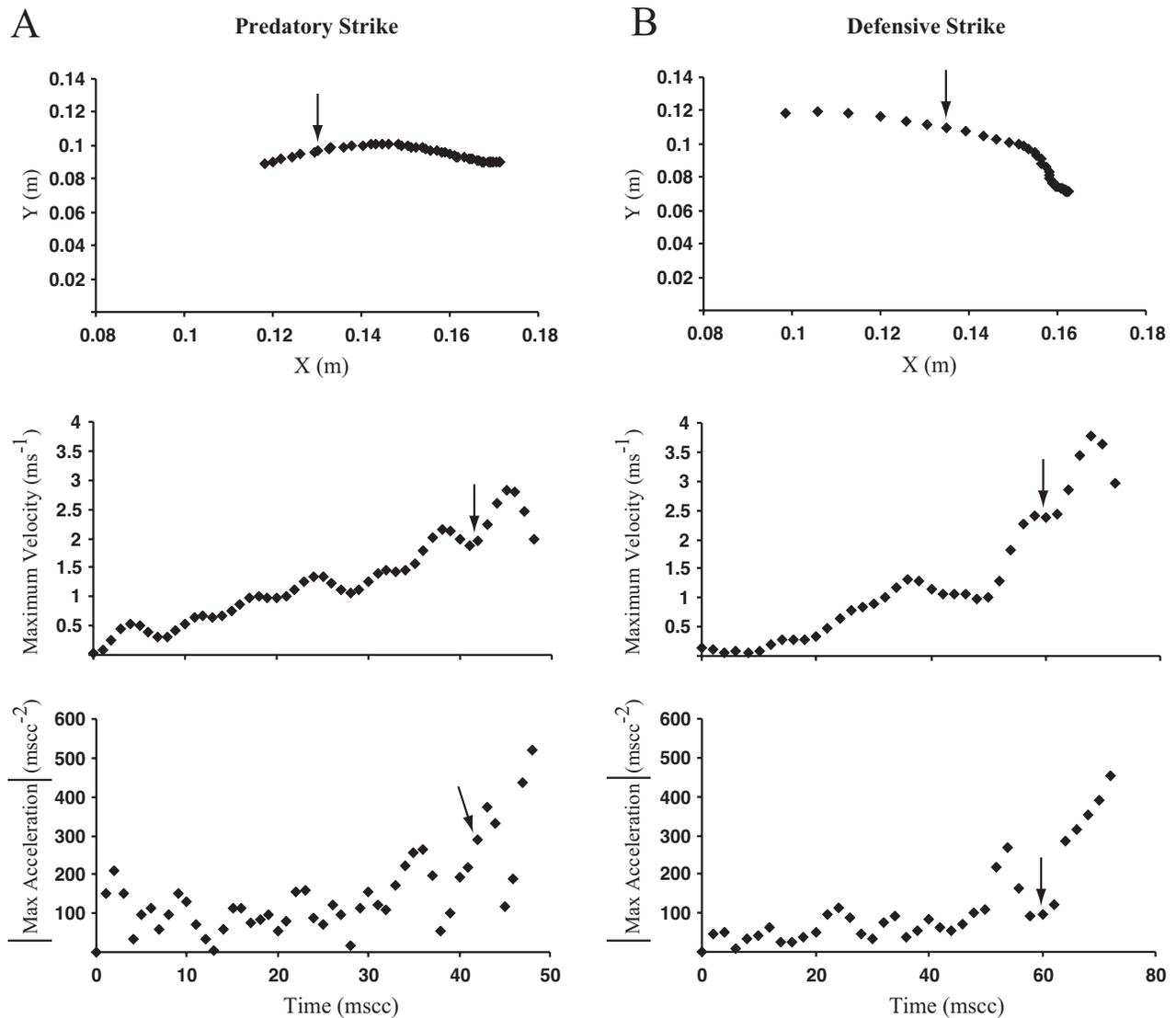


Fig. 3. Movement, velocity, and acceleration of the snout of a single *Crotalus atrox* during extension and initial contact with a target during (A) a predatory strike, and (B) a defensive strike. In X-Y plots, movement is from right to left. Arrows in all graphs indicate point of initial jaw contact with the target; last data point marks point of secondary jaw contact.

three analyzable defensive strikes were available for each of the remaining snakes. Representative video stills from a single snake for both a predatory and defensive strike sequence are presented in Figures 1 and 2. Representative values of velocity and acceleration for a single snake during each strike type (for the extension stage and first portion of the contact stage) are given in Figure 3.

Kinematics of the Predatory Strike

Predatory strikes were initiated at a variety of distances from the prey item (range 0.75–15 cm). Of the strikes in which both jaw contact times can be determined ($N = 12$), the lower jaw contacted the prey

item first in 11 times, and in a single strike both jaws contacted the prey item within the same millisecond. The entire extension stage lasted from 18 to 73 msec ($\bar{x} = 49$ msec), and the first jaw (typically the lower jaw) preceded contact of the second jaw (typically the palatomaxillary complex) on average by 9 msec (range 2–22 msec). On average, 28% of the rattlesnake's body was involved in the forward motion of the predatory strike (Table 1).

During the extension stage, maximum gape angle (MGA) typically occurred toward the latter portion of the stage, between 1–5 msec prior to contact in eight strikes ($\bar{x} = 6$ msec, $N = 12$ strikes). The MGA of the extension phase was always less than the MGA of the

jaws during the retraction stage in predatory strikes (Table 1). All strikes included a release and retraction stage; prey was never held during predatory strikes.

Maximum velocity and absolute maximum acceleration occurred at or between initial and secondary contact of the target by the snake jaws in 10 of 12 strikes and in 12 of 12 strikes, respectively. In the two strikes in which maximum velocity was achieved prior to prey contact, maximum velocity was reached 5 msec before contact. As a result, $V_{\text{contactavg}}$ and $A_{\text{contactavg}}$ were higher than throughout the entire extension stage in the majority of predatory strikes.

Kinematics of the Defensive Strike

Defensive strikes were initiated at a range of distances comparable to those of predatory strikes (range 2–17 cm). The lower jaw contacted the target first in 10 of 13 strikes, preceding contact of the upper jaw on average by 8 msec (range 2–22 msec). The upper jaw (palatamaxillary complex) contacted the target first on a single defensive strike (preceding lower jaw by 4 msec), and both jaws contacted the target within the same millisecond in two strikes. The entire extension stage lasted from 42 to 70 msec ($\bar{x} = 50$ msec).

During the extension stage, maximum gape angle (MGA) typically occurred toward the latter portion of the stage, between 1–5 msec prior to contact in seven strikes ($\bar{x} = 5$ msec, $N = 13$ strikes). The MGA of the extension phase again was always less than the MGA of the jaws during the retraction stage in defensive strikes (Table 1). All strikes included a release and retraction stage; prey was never held during defensive strikes. On average, 37% of the rattlesnake's body was involved in the forward motion of the defensive strike.

Maximum velocity and absolute maximum acceleration occurred at or between initial and secondary contact of the target by the snake jaws in four of 13 strikes and 10 of 13 strikes, respectively. In the nine strikes in which maximum velocity was achieved prior to target contact, V_{max} was reached 2 msec (1 frame) prior to contact in four strikes, 6 msec prior to contact in three strikes, 12 msec prior to contact in one strike, and 14 msec prior to contact in a single strike. Of the three strikes in which absolute maximum acceleration occurred prior to contact, A_{max} was reached at three different times (6, 20, and 36 msec).

Comparison of Predatory vs Defensive Strike Parameters

The distance from the target at the point of strike initiation differs significantly between the two treat-

ments as well as between individuals; defensive strikes were initiated at distances on average twice those of predatory strikes. Amount of the kinematically active body region also differed significantly between strike types, but not between individuals. However, time to initial contact and to secondary contact did not differ significantly either between strike types, or between individual rattlesnakes (Table 1). Time to MGA in the extension stage was also not significantly different between predatory and defensive strikes or between individuals. Gape angles were not statistically significant between the two treatments, and only the MGA in the extension stage was significant between individuals (Table 1).

All three acceleration values differed significantly among individuals, but not between strike treatments. Significant differences occurred between strike types for V_{max} and V_{avg} (Table 1). Individual V_{max} values were also significantly different (Table 1). No significant difference occurred between strike types for $V_{\text{contactavg}}$. The highest overall V_{max} (5.5 m/sec) and absolute A_{max} (878 m/sec²) occurred during defensive strikes; peak V_{max} and absolute A_{max} values obtained in predatory strikes were 4.28 m/sec, and 824 m/sec², respectively. No significant interactions occurred between strike type and individual for any variables, indicating effects of the two strike types were the same on all individuals for each variable (Table 1).

Effects of snake size and strike initiation distance on kinematic variables were analyzed using a one-way ANOVA. Snake size had a statistically significant effect for A_{avg} ($F_{1,20} = 4.95$, $P < 0.04$), and strike initiation distance had a statistically significant effect for V_{max} ($F_{1,20} = 6.31$, $P < 0.03$) and V_{avg} ($F_{1,20} = 5.73$, $P < 0.03$). Pearson correlations between strike variables showed significant correlations ($P < 0.05$) between strike initiation distance and the three velocity variables, but strike initiation distance was correlated with no acceleration variable. Ten of the 15 pairwise correlations between the six velocity and acceleration variables were significantly correlated. Time to upper jaw contact was significantly correlated with time to lower jaw contact, time to MGA, and V_{fastavg} . Time to MGA was also significantly correlated to both time to lower jaw contact and V_{fastavg} , and the amount of kinematically active body region was significantly correlated with both strike initiation distance and V_{avg} .

DISCUSSION

The significant differences found between velocity variables of both predatory and defensive strikes

Table 1. Summary statistics and F-ratios from two-way ANOVA results for 13 kinematic variables measured from profiles of two strike types in *Crotalus atrox*. Sample sizes for each individual and definitions of the variables are included in the text. Parenthetical values represent degrees of freedom. * = significance at $P < 0.05$.

Variable	Offensive			Defensive			ANOVA factors		
	N	Mean ± SE		N	Mean ± SE		Strike type	Individual	Interaction
Time to lower jaw contact (msec)	12	48.83 ± 5.535		13	50.15 ± 1.548		0.023 (1, 3)	0.283 (3, 17)	0.399 (3, 17)
Time to upper jaw contact (msec)	13	56.77 ± 5.177		13	56.15 ± 2.886		0.020 (1, 3)	0.973 (3, 18)	0.682 (3, 18)
Time to maximum gape: extend stage (msec)	12	43.25 ± 5.510		13	44.77 ± 2.769		0.021 (1, 3)	0.835 (3, 17)	0.601 (3, 17)
Distance from target at forward initiation (cm)	13	4.09 ± 1.243		13	9.43 ± 1.548		9.381 (1, 3)*	4.217 (3, 18)*	2.073 (3, 18)
Amount of body kinematically active (%)	9	28.33 ± 1.193		9	37.55 ± 2.151		13.038 (1, 3)*	1.759 (3, 14)	1.328 (3, 14)
Maximum gape angle: extend stage (degrees)	12	85.57 ± 3.992		13	98.37 ± 8.063		2.279 (1, 3)	4.092 (3, 17)*	0.982 (3, 17)
Maximum gape angle: retract stage (degrees)	13	146.93 ± 3.025		11	151.31 ± 3.501		2.123 (1, 3)	1.037 (3, 16)	1.755 (3, 16)
Maximum velocity of the snout (m/sec)	13	2.61 ± 0.267		13	3.71 ± 0.217		12.980 (1, 3)*	3.874 (3, 18)*	1.187 (3, 18)
Average velocity: initiation to primary contact (m/sec)	13	1.23 ± 0.148		13	2.27 ± 0.179		15.725 (1, 3)*	0.247 (3, 18)	0.267 (3, 18)
Average velocity: primary to secondary contact (m/sec)	11	2.36 ± 0.272		11	2.77 ± 0.290		0.906 (1, 3)	2.346 (3, 14)	0.136 (3, 14)
Absolute maximum acceleration of the snout (m/sec ²)	13	326.10 ± 63.561		13	333.77 ± 63.855		0.002 (1, 3)	6.498 (3, 18)*	0.260 (3, 18)
Absolute average acceleration: initiation to primary contact (m/sec ²)	13	88.94 ± 11.565		13	107.02 ± 9.948		1.617 (1, 3)	4.992 (3, 18)*	0.242 (3, 18)
Absolute average acceleration: primary to secondary contact(m/sec ²)	11	232.67 ± 45.434		11	235.68 ± 36.961		0.046 (1, 3)	5.137 (3, 14)*	0.725 (3, 14)

reflect differences in the distance from the target upon commencement of the extension stage. Defensive strikes start from roughly twice as far away as predatory strikes. However, total time spent in the extension stage does not vary significantly between strike types or individuals, nor do any other timing variables differ between strike types or between individuals, consistent with the significantly higher velocity values seen in defensive strikes. Strike type does not have a significant effect on accelerations. Instead, acceleration values only vary significantly between individual rattlesnakes, indicating that there is no difference in acceleration between predatory and defensive strikes in *C. atrox*. Rattlesnakes reach higher velocities in defensive strikes by covering greater distances over which a constant acceleration, maximized regardless of strike type, is applied.

Six of the 13 variables show significant differences among individuals, including individuals initiating strikes at significantly different distances (Table 1). This variability in individual performance has been noted in timing and velocity calculations in the kinematics of prey capture in other vertebrate studies (Shaffer and Lauder, 1988; Wainwright et al., 1991), including rattlesnake feeding (Kardong and Bels, 1998). Sources of kinematic variation within a species could be potentially attributed to geographical, ecological, anatomical, and/or ontogenetic differences affecting any given individual, but statistical analyses of these questions remain to be answered (e.g., ontogenetic effects related to size; T. LaDuc, unpublished).

Comparison with Previous Kinematic Studies

Velocity and acceleration.—High values of V_{\max} and A_{\max} indicate that a portion of the head is still moving quite rapidly after initial contact with target in predatory strikes (11 of 13 strikes). This contrasts with findings reported by Kardong and Bels (1998), who inferred that the head begins to decelerate just prior to target contact, perhaps in an effort to reduce jaw injuries from collision with the target. Although data for only a single point on the head are presented here, the data suggest that the snout reaches peak velocity and acceleration after primary contact of the lower jaw with the prey item.

The average V_{\max} values for predatory strikes in this study (2.61 m/sec) are greater than average values for predatory strikes in other solenoglyphs, *Vipera ammodytes* (1.47 m/sec), and *Bitis gabonica* (1.55 m/sec) (Janoo and Gasc, 1992; for a review of colubroid strike speeds, see Cundall and Greene, 2000).

The highest predatory V_{\max} calculated for *C. atrox* (4.3 m/sec, this study) also exceeds the highest V_{\max} reported by Janoo and Gasc (1992) for both *V. ammodytes* (2.2 m/sec) and *B. gabonica* (1.9 m/sec). Values of V_{\max} and A_{\max} in defensive strikes are reached prior to initial target contact in the majority (11 of 13) of strikes, consistent with findings reported by Kardong and Bels (1998) for predatory strikes. The head velocity of *Crotalus viridis* reported by Van Riper (1954) was between 1.6 and 3.5 m/sec during defensive strikes, comparable to the range found in *C. atrox* (2.5–5.0 m/sec; this study).

No acceleration strike data are available for other rattlesnake species or any other member of the Viperidae. Although absolute acceleration values (A_{\max} and A_{avg}) do not differ between strike types, those of *C. atrox* are some of the highest recorded for vertebrates (see Van Riper, 1953, 1954; Grobecker and Pietsch, 1979; Bergert and Wainwright, 1997).

Gape angles.—Maximum gape angles during the extension stage of the predatory strike are comparable to those presented by Kardong and Bels (1998) for *Crotalus v. oreganus* (85–90°), but are somewhat smaller than the maximum reported by Janoo and Gasc (1992) for *V. ammodytes* (108°). These values are likely equivalent to those presented for booid snakes (50–65°) by Cundall and Deufel (1999), who calculated the angle in a different manner (using the angle between the mandible and an axis parallel to the braincase at the quadrate-mandibular joint). Timing of the MGA just prior to initial jaw contact mirrors findings reported by Kardong (1975) for *Agkistrodon piscivorus*.

The slightly larger MGA seen in the extension stage of the defensive strike may be linked to the overall larger size of the stuffed animal target. Figure 2 illustrates the less frequent of two defensive strike behaviors seen in *C. atrox* with the strike directed at the doll's midbody. A majority of defensive strikes (11 of 13) were directed to the top of the doll's head and included a slight ventral flexion of the head after secondary contact (not pictured). Published figures of defensive strikes also illustrate a large MGA, up to 180°, especially at jaw contact (Van Riper, 1953, 1954; Lester, 1955; Russell, 1980; Kardong, 1986b). These figures, including Figure 2 of this study, also illustrate a potentially confounding factor in comparisons between the two strike types: targets used to elicit defensive strikes are often much larger than prey items. Many of these larger targets only offer a completely, or nearly completely, flat, vertical surface for

the rattlesnake to contact during its strike sequence, giving the strike an overall “stabbing” rather than “biting” appearance. A stabbing-type strike may be the direct result of a strike towards a large or awkwardly sized target (Dullemeijer, 1961). This difference in target size may additionally explain why behaviors seen in defensive strikes, such as a lack of dorsal neck arching, are seen when strikes are delivered to targets typically too large for the rattlesnake to consume.

A rapid withdrawal of its teeth by means of an exaggerated gape in the retraction stage leaves the snake better able to avoid potential retaliation by the target (Radcliffe et al., 1980; Kardong, 1986a; Kardong and Bels, 1998). Presentation of an even larger defensive target may further elucidate whether an increased MGA in the retraction stage is related to target size or strike type.

Timing of jaw contact.—The sequence of jaw contact with the target for predatory strikes follows that previously described for other solenoglyphs (Kardong, 1975, 1986b; Janoo and Gasc, 1992; Kardong and Bels, 1998). The snake’s mandibles make the initial contact with the prey item. Only once in the 13 predatory strikes did both upper and lower jaws arrive within 1 msec. Jaw contact sequences in defensive strikes also followed those described for predatory strikes, although both jaws arrive within the same 2 msec interval in three strikes, and the maxillary fang made contact before the mandible in a fourth strike. This last strike sequence may be a statistical outlier, caused by strike contact of the snout at the extreme concave angle of the doll’s head. Cundall and Deufel (1999) found differences between strike initiation distance and different strike categories, but no significant difference was found in this study ($F_{1,21} = 0.04$, $P > 0.84$), excluding the single defensive strike in which the maxillary fang contacts the target first.

Duration of extension.—The extension stage of the strike (as defined by Kardong and Bels, 1998) does not differ in duration between predatory and defensive strikes (Table 1). The mean duration of the extend stage for strikes presented here (49.5 msec) is similar to that for *V. ammodytes* (45 msec) (Janoo and Gasc 1992), but considerably larger than that for large (SVL 528–683 mm) *Crotalus v. oreganus* (33 msec) (Kardong and Bels, 1998).

Kinematically active body region.—Predatory strikes involved significantly less anterior body length than did defensive strikes (Table 1). Kardong and Bels (1998), who described a kinematically active anterior-

third portion of the body and a static region during their analysis of predatory strikes, found similar predatory strike values for this kinematically active body region. Klauber (1972) estimated that rattlesnakes used over half of their body during defensive strikes, whereas Janoo and Gasc (1992) suggested that strikes of *Bitis nasicornis* that exhibited little head displacement represented defensive strikes. Data presented here do not substantiate either claim, because the kinematically active body region for defensive strikes was significantly greater than that for predatory strikes, but never exceeded 46% of the rattlesnake’s total length. Before the advent of modern recording equipment, it is interesting to note that Mitchell (1861:21) was able to postulate that the rattlesnake “...is unable...to strike at a greater distance than one-half its length, while usually its projectile range does not exceed a third of its length.” Coues and Yarrow (1878: 268) mentioned a mere 17 years later, “...it is as well to remember that the utmost range of a rattlesnake’s blow is less than it’s own length.”

CONCLUSIONS

General descriptions of both predatory and defensive rattlesnake strikes are found throughout the literature, with many anecdotal descriptions perpetuating ideas and beliefs regarding comparisons of the two strike types. *Crotalus atrox* in this study initiated defensive strikes from distances twice those of predatory strikes, yet the extension stage (time from initiation of movement towards primary target contact) did not differ significantly between the strike types. Values of V_{\max} and V_{avg} were significantly different between the two strike types, defensive strikes were ~ 1 m/sec faster than predatory strikes (both V_{\max} and V_{avg}). Lack of significant differences between A_{\max} and A_{avg} for both predatory and defensive strikes may indicate that absolute acceleration is maximized, no matter the behavioral context of the strike. The significant correlation of distance with the two velocity values, V_{\max} and V_{avg} , identifies the dependence of velocity on strike initiation distance. Thus, the significant differences seen in the kinematics of these two strike types are caused by differences in strike initiation distance. By varying strike initiation distance, rattlesnakes interpret different targets based on size, individual experience, or ontogeny of rattlesnake body size. Additionally, shorter strike distances could improve fang placement whereas strikes from greater distances may reduce the chance of harmful interactions with aggressors: the precision of the predatory strike might

not be needed when trying to deter would-be attackers.

A recent study by Young et al. (2001) examined kinematic differences between predatory and defensive strikes in similarly sized (74–112 cm SVL) *Crotalus atrox*. Using filming techniques similar to those described in the present study, Young et al. (2001) found significant differences in strike distance and velocity between the two strike types, but determined values of maximum velocity and strike distance greater in predatory strikes than in defensive strikes, a result opposite to the findings reported in this study. Comparisons of predatory and defensive strikes between two different sets of rattlesnakes, as well as the treatment of every strike as an independent event (Young et al., 2001), may underlie some of the differences between this and the present study.

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