

Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophiine snakes

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Accepted 2 April 2003

Summary

The trunk plays an obvious and important role in the prey capture behavior of many species of snake, yet trunk function during predatory strikes is poorly understood. Axial kinematics of three thamnophiine snakes (*Thamnophis couchii*, *Thamnophis elegans* and *Nerodia rhombifer*) were studied to quantify differences between sideways-directed and forward-directed attacks and to investigate strike diversity at relatively low phylogenetic levels. Feeding strikes were filmed at 60 Hz, and 13 points along the head and body were digitized. These points were used to calculate body segment displacement, rotation and velocity during predatory strikes. Kinematic analysis revealed significant differences in the foraging modes of these aquatic-feeding species. *T. couchii* displayed a

stereotypical pre-strike posture in which the entire body was arranged in a series of loops directed towards the prey. Forward displacement of body segments sometimes occurred over the entire body in *T. couchii* but was restricted to the anterior one-third of the trunk in *T. elegans* and *N. rhombifer*. *T. couchii* and *N. rhombifer* both struck rapidly compared with *T. elegans*, although *N. rhombifer* typically had a short strike distance. *N. rhombifer* struck significantly faster than *T. elegans*. Aquatic prey capture diversity appears to reflect ecological diversity in thamnophiine snakes.

Key words: strike, functional morphology, snake, *Thamnophis*, *Nerodia*, axial kinematics, feeding, prey capture.

Introduction

The predatory strike of advanced snakes has been studied in boids (Cundall and Deufel, 1999; Deufel and Cundall, 1999; Frazzetta, 1966), colubrids (Greenwald, 1974, 1978; Jayne et al., 1988) and viperids (Janoo and Gasc, 1992; Kardong, 1986; Kardong and Bels, 1998). Much of this research has focused on cranial function (but see Kardong and Bels, 1998) and, as a result, the function of the trunk during predatory strikes remains poorly understood. Recently, it has been suggested that snake prey captures can be divided into two broad classes: slow systems, which involve head and trunk movements that are within the locomotor range of the animal and that lack a distinct pre-capture posture, and fast systems, which are faster than normal locomotor movements and involve distinct, often complex, preparatory postural changes (Cundall and Greene, 2000). However, there is little quantitative or comparative data available to evaluate this claim. Rigorous kinematic data on trunk function are also needed to answer broad biomechanical questions such as how the head is accelerated, what the relation of body posture to strike performance is, and what the musculoskeletal correlates of the trunk and striking behavior are.

Lineages from most major groups of snakes have reinvented aquatic habitats and become piscivores. Workers have noted

similarities in fishing behavior across a diversity of snake groups, including natricines (Alfaro, 1998; Braun and Cundall, 1995; Drummond, 1983; Halloy and Burghardt, 1990), homalopsines (Jayne et al., 1988; Smith et al., 1998), elapids (Voris et al., 1978) and viperids (Savitzky, 1992), the most notable being that aquatic prey are typically captured using a lateral sweep of the head. Although Cundall and Greene (2000) have suggested that fishing is a 'slow' behavior, some thamnophiines have recently been shown to strike as quickly as terrestrial colubrids (Alfaro, 2002).

The North American colubrid tribe Thamnophiini (garter snakes and water snakes) contains a number of highly specialized piscivores as well as generalists that include fish in their diet. Specialists and generalists have traditionally been thought to use lateral head sweeping to capture prey (e.g. Cundall and Greene, 2000), although recent work has shown that prey capture modes have diversified in homalopsines (Smith et al., 2002) and thamnophiines (Alfaro, 2002). Of particular note is the striking behavior of *Thamnophis couchii*, which uses a rapid, long-distance, forward attack to capture prey and appears to adopt a pre-strike posture (Alfaro, 2002; Drummond, 1983). Fast, forward striking has also evolved in at least one other garter snake species (Alfaro, 2002),

suggesting that aquatic prey capture strategies are far more diverse than previously recognized.

To examine the role of the trunk in aquatic prey capture and to begin to characterize the diversity of aquatic feeding modes in thamnophiines, a kinematic analysis of the strike in two garter snakes, *Thamnophis couchii* and *Thamnophis elegans*, and one water snake, *Nerodia rhombifer*, was undertaken. The species in this study are phylogenetically well differentiated from one another and represent at least two and possibly three independent evolutions of a piscivorous lifestyle (Fig. 1). *T. couchii* is an aquatic specialist on fishes and anuran larvae (Drummond, 1983; Rossman et al., 1996). *T. elegans* feeds on a broad range of aquatic and terrestrial prey (Rossman et al., 1996). *N. rhombifer* is a highly aquatic species that feeds mainly on fish and anurans (Mushinsky and Hebrard, 1977). As is typical for the genus, *N. rhombifer* is heavy-bodied compared with most garter snakes and thus provides a contrasting morphology to the other two species in this study. Digital sequences of trunk movement during 84 prey captures were analyzed to identify patterns associated with aquatic feeding. Univariate and multivariate statistical comparisons of kinematic variables were performed within and among species to determine levels of variation of this behavior and to identify species-specific characters of the strike.

Materials and methods

Specimens and data collection

Specimens for this study were collected during two field expeditions. Three *Nerodia rhombifer* Hallowell 1852 (standard length, 54.2–72.1 cm) were collected from fish hatcheries in Lonoke, AK, USA in July 1997, and three *Thamnophis elegans* Baird and Giroud 1853 (39.8–53.8 cm) and four *Thamnophis couchii* Kennicott 1889 (52.4–57.5 cm) were

collected near Eagle Lake, CA, USA in July 1999. Snakes were transported to the Field Museum of Natural History in Chicago, IL, USA and maintained in 37.91 aquaria. Animals were fed by placing fathead minnows (*Pimephales* sp.) in cage water bowls every 7–10 days. Room temperature was kept at 28–30°C and light cycle was seasonal.

Feeding trials occurred over a three-month period starting in August 1999. Animals were placed in a 113.61 aquarium filled with water to a depth of 8 cm. One end of the arena was filled

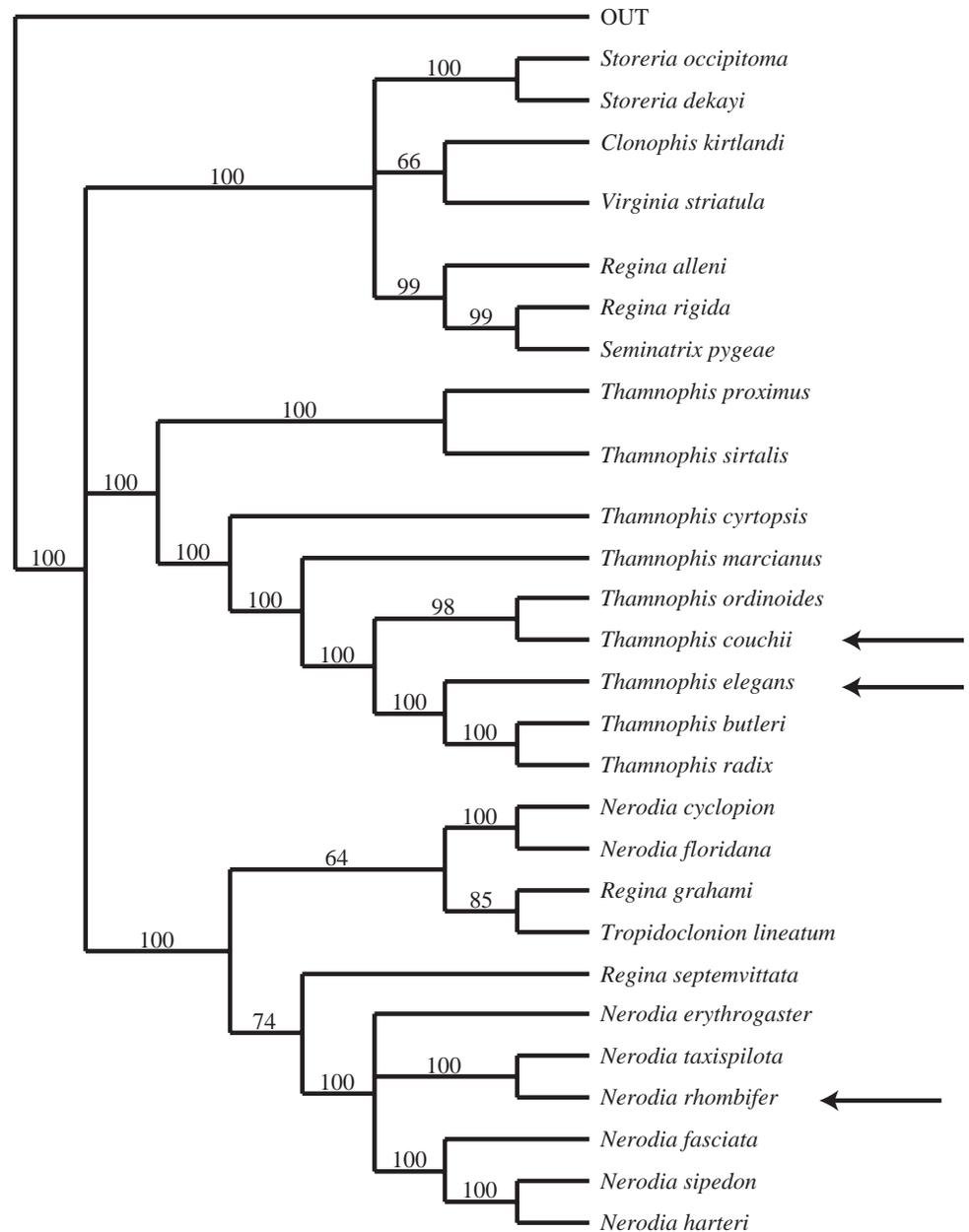


Fig. 1. Phylogenetic relationship of the tribe Thamnophiini (family Colubridae). Shown is the majority rules consensus of 90 000 post-burnin states visited by a million generation Bayesian Markov Monte Carlo reanalysis of previously published data (Alfaro and Arnold, 2001) performed using MrBayes (<http://morphbank.ebc.uu.se/mrbayes/info.php>). Taxa sampled in this study, indicated by arrows, represent two of the three major thamnophiine groups. Numbers above branches are the Bayesian posterior probabilities for the clade.

with gravel, providing a terrestrial refuge (23 cm long) for the animals. Water temperature ranged from 28°C to 30°C. To aid in locating the dorsal midline, snakes were marked with White Out® at approximately 1 cm intervals, beginning at the neck and ending at a point dorsal to the cloaca. Animals were placed in the arena at least two hours prior to the experiment to allow individuals to acclimate.

To initiate feeding trials, 15–20 fathead minnows, obtained from a local bait store, were added to the arena. Minnows ranged in size from approximately 4 cm to 6 cm standard length, although prey were not measured individually. Feeding bouts were recorded in dorsal view using a Sony TRV 900 digital video camera mounted on a tripod approximately 1.5 m above the tank. Prey density was maintained over the course

of the trial by adding minnows after successful captures. Trials were terminated when the snake stopped orienting to prey, typically after 4–7 successful captures. Experiments and animal care were performed in accordance with IACUC protocols (# 70401).

Digitization and analysis

Video sequences were transferred from the camera to a Macintosh G3 450 MHz computer *via* an IEEE-1394 interface (Firewire) using Adobe Premiere. Strike sequences were edited and previewed using Premiere. Sequences that reflected typical prey capture behaviors (subjectively assessed as being similar to behaviors observed in the field or during preliminary trials) and possessed high image quality and clarity of focus were exported as QuickTime movies for image analysis. The goal of the study was to examine species-level differences in behavior. Because qualitative observations of snake foraging behaviors suggested that the effects of success on strike kinematics were minor relative to differences between species, and since analysis of variances (ANOVAs) of starting segment angle, minimum path angle and minimum segment angle for the first three body segments revealed no significant effect of success on strike kinematics (analyses not shown), data from successful and unsuccessful strikes were pooled for subsequent analysis.

QuickTime movies were deinterlaced using a version of NIH Image (developed at the US National Institutes of Health and available on the internet at <http://www.usm.maine.edu/~walker/software.html>), customized by Jeffrey Walker. The resulting 60 Hz sequences were digitized frame-by-frame. The tip of the snout, the beginning of the neck, and points along the midline until the level of the cloaca were digitized at approximately 1–2 cm intervals. In cases where it was apparent that the snake had oriented to a particular prey item, prey position was also recorded at the prey's estimated center of mass. Snakes sometimes initiated strikes while crawling or swimming. The beginning of the strike was defined as the frame prior to the frame showing an obvious increase in head velocity. Sequences were digitized until the end of the strike, recognized by either the successful capture of the prey or the cessation of rapid forward head movement. Using QuicKurve (a custom-written PASCAL program by Jeffrey Walker, available at <http://www.usm.maine.edu/~walker/software.html>), a quintic spline was fit to the digitized points along the trunk (Fig. 2A). The smoothing parameter for this spline was based on the estimated error variance, which was calculated from a test series digitized three times. 100 points were interpolated along the midline spline, and coordinates for 11 equally spaced points were retained for analysis. The data set consisted of 13 points: the snout tip, 11 midline trunk points and prey position (Fig. 2B).

Strikes typically exhibited a high degree of variability in posture and direction. To permit comparisons, strikes were standardized by the strike vector. The starting point

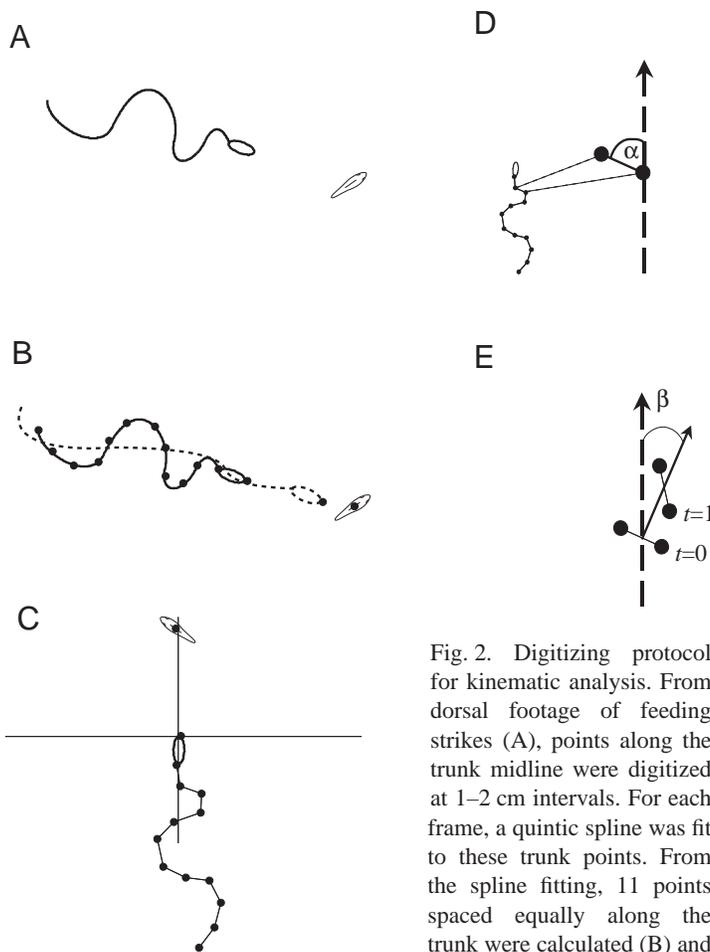


Fig. 2. Digitizing protocol for kinematic analysis. From dorsal footage of feeding strikes (A), points along the trunk midline were digitized at 1–2 cm intervals. For each frame, a quintic spline was fit to these trunk points. From the spline fitting, 11 points spaced equally along the trunk were calculated (B) and retained for analysis in

addition to the position of the tip of the snout and the center of mass of the prey item. To facilitate comparison, the strike vector was calculated. Strike vector was defined as the vector from the starting position of the snout to the position of maximum snout displacement during the strike. Digitized coordinates were then rotated so that the strike vector was parallel to the y-axis (C). Segment angle and path angle calculations treated the body as a series of segments. Segment angle (α) was the angle between each segment and the strike vector (D). Path angle (β) was the angle between a vector defined by the midpoint of a segment in successive frames and the strike vector (E).

of the snout and the point of maximum snout displacement defined this vector. A custom computer program transformed snake and prey coordinates so that the strike vector was parallel to the y -axis (Fig. 2C). These rotated coordinates were used to characterize the behavior of the head and trunk during prey capture. Throughout this paper, forward is defined as the direction that is parallel with this strike vector, and lateral is defined as the direction perpendicular to the strike vector.

To characterize the movement of the snake during the strike, I calculated the segment angle and the path angle (Gillis, 1997) of the 10 body segments defined by the 11 spline coordinates, and of the head segment, defined by the tip of the snout and the beginning of the neck (Fig. 2D). Segment angle was the orientation of the segment relative to the calculated strike vector. Path angle was the angle between a line connecting the midpoints of a segment in consecutive fields and the strike vector (Fig. 2E). Path angle reflected the displacement of the segment while segment angle reflected the rotation of the segment.

Finally, head velocity and acceleration, together with the parallel and perpendicular displacements of the 11 trunk points relative to the strike vector, were calculated. Velocity and acceleration were calculated using the raw data for the snout tip with QuickSand (Walker, 1998). Using this program, a quintic spline was fit to the snout coordinates over the course of the strike. Calculations of velocity and acceleration were based on the spline-fitted coordinates to mitigate against the effects of digitizing and sampling error on parameter estimation (Walker, 1998). Sample rate was potentially problematic for accurate calculation of accelerations, and reported values should be interpreted cautiously as they may be substantial underestimates of the truth. However, strike velocity and duration for the thamnophiines in this study was on the same scale (all peak velocities within an order of magnitude), so that error in estimated acceleration is expected to be roughly equal across species. Displacements, velocities and accelerations were standardized by head length to control for size variation in specimens.

Statistical analyses

Slow sweeping bouts in *T. elegans* and *N. rhombifer* were excluded from statistical analysis so that only fast prey capture behaviors were compared among species. Residual analysis revealed that the raw data met the necessary assumptions for parametric statistics. To determine if there was a difference in pre-strike posture among species, a two-way ANOVA on starting segment angle with species, body position, and body position \times species as fixed effects was performed. The effects of species and position on minimum path and segment angle were also tested using a two-way mixed-model ANOVA. For all ANOVAs, significant results were followed by Tukey *post hoc* tests to determine

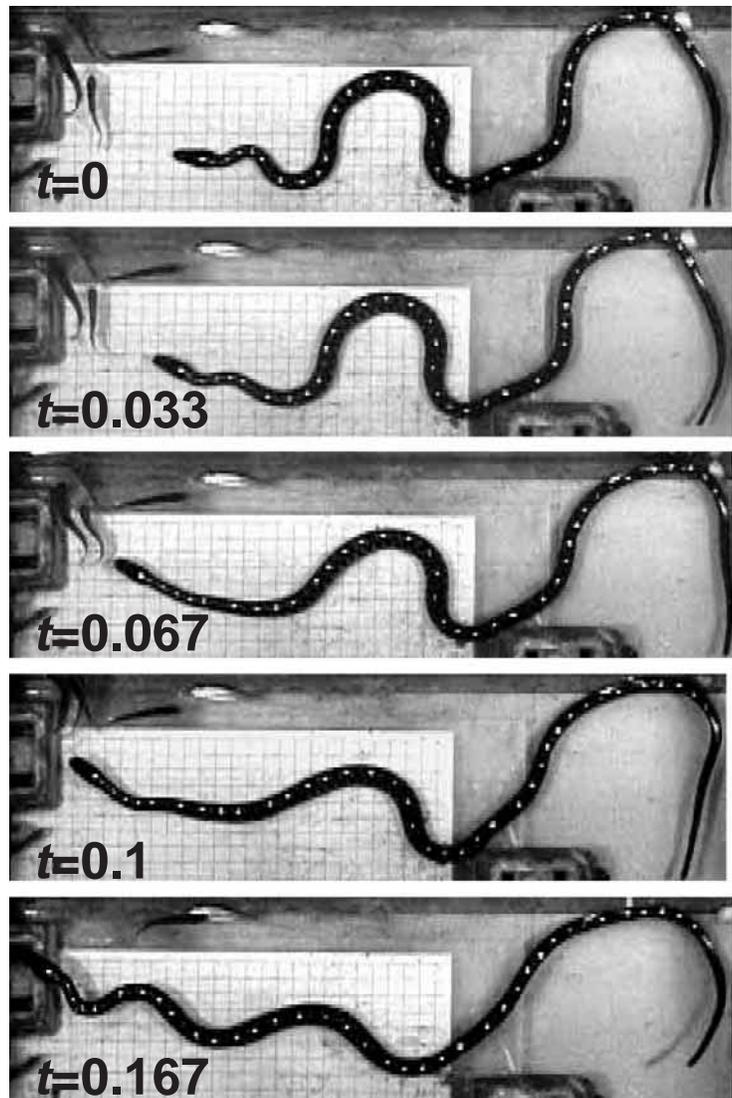


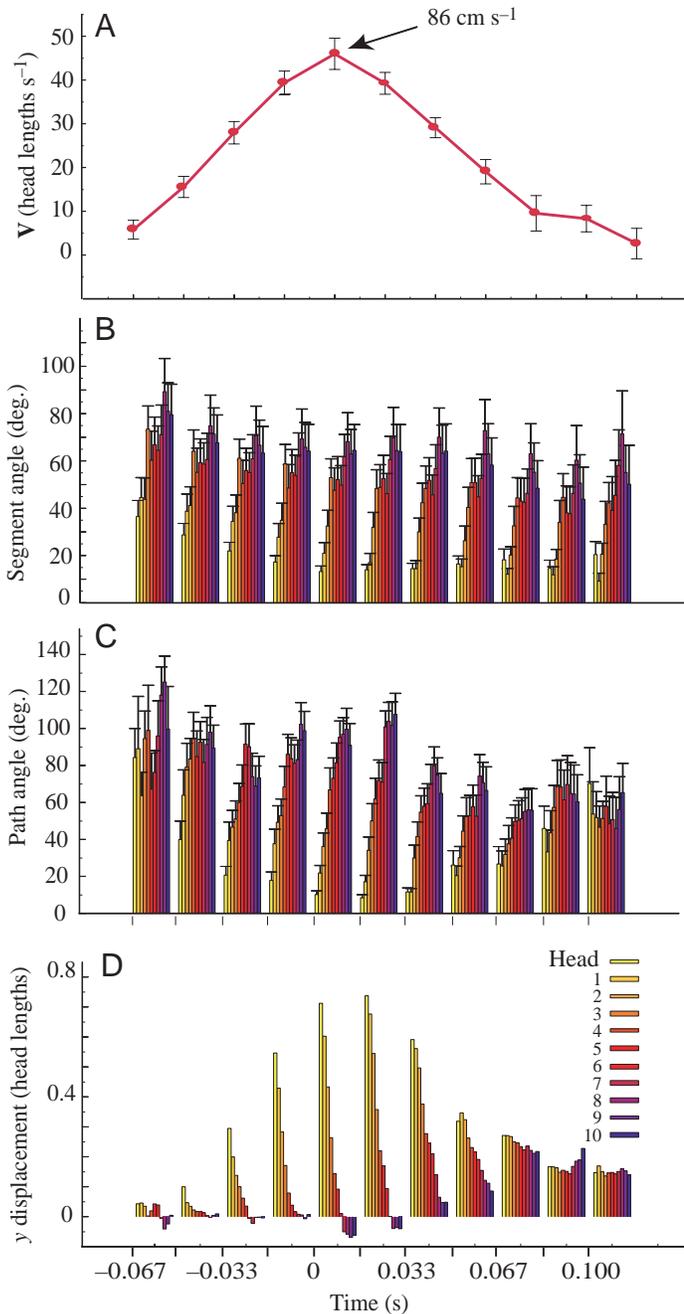
Fig. 3. *Thamnophis couchii* strike in dorsal view. t = time in seconds. At $t=0$, the typical prey-strike posture with a linear arrangement of body loops is evident. The strike proceeds as the anterior-most loops straighten, followed by straightening of the two larger posterior loops. *T. couchii* strikes were rapid and usually involved a large proportion of the trunk.

specifically which levels differed from each other. Finally, differences in strike performance were tested for with a multivariate ANOVA (MANOVA) of standardized head velocity and acceleration using species as a fixed effect and individuals within species as a random effect. Univariate one-way ANOVAs were then used to explore species-level differences in velocity and acceleration.

Results

The western aquatic garter snake Thamnophis couchii

This species captured prey *via* fast, forward-directed strikes (mean maximum velocity, 86 cm s^{-1} ; mean maximum acceleration, 19 m s^{-2}) that could be initiated either



terrestrially, in midwater or from rest underwater. Snakes visually oriented to specific prey items and almost always exhibited a preparatory phase in which the body was pointed towards the prey with the trunk arranged in a series of half-loops (Fig. 3). Once this posture was attained, snakes typically struck from rest or while slowly moving towards the prey using the posterior trunk while maintaining the anterior loops. This species launched directed strikes at prey from relatively long distances: mean maximum prey distance was 6.8 cm (3.9 head lengths), and successful strikes just over 8.8 cm (5 head lengths) were observed. Strikes launched without a brace point, usually from mid- or underwater, exhibited straightening and forward displacement of the

Fig. 4. Head velocity (A), segment angle (B), path angle (C) and forward displacement (D) profiles for *Thamnophis couchii*. Graphs have been standardized to the time of peak velocity so that maximum velocity is reached at $t=0$. Error bars represent 1 s.e.m. Anterior body points are yellow, posterior points are blue. *T. couchii* strikes showed the highest velocities of the three species measured. Segment straightening was apparent for most positions along the trunk. Segment angles generally did not exceed 90°, indicating that the anterior ends of all segments along the trunk were pointed in the direction of the strike. Head acceleration was accompanied by substantial angular rotation in segments 1–4. Path angles for most anterior segments were under 90° and decreased with increasing velocity, indicating that these segments traveled close to the calculated strike vector. Path angles exceeded 90° for posterior segments shortly before maximum velocity was achieved. This may have been the result of backwards displacement of posterior body segments in reaction to head-accelerating forces generated by the anterior trunk. Rearwards displacement of the posterior segments was sometimes observed in video sequences. Forward displacement was substantial and decreased in an anterior to posterior direction.

anterior two-thirds of the trunk and straightening and backwards displacement of the posterior one-third. When the snake was able to brace a portion of its body against an object in the tank, backwards displacement of the posterior trunk was not observed.

Head acceleration was high (18.1 m s⁻²), and individuals typically reached peak velocity (86 cm s⁻¹) within 60 ms of strike initiation (Fig. 4). Segment angle was low in the anterior-most segments and decreased across all segments coincident with increasing velocity. Mean path angle dropped sharply in the anterior trunk as velocity increased. In the posterior half of the trunk, path angle decreased after peak velocity was attained. In addition, path angle in these posterior points continued to decrease as path angle slightly increased in the anterior points late in the strike cycle. Segment displacements in the direction of the strike were high for the first four segments. During head acceleration, the last three segments exhibited displacement away from the prey, suggesting that the posterior trunk plays a role in balancing strike forces.

The western terrestrial garter snake Thamnophis elegans

Two main modes of prey capture, distinguishable by overall trunk kinematic pattern and speed of the behavior, were observed in this species. Open-mouth sweeping (Fig. 5) occurred in all individuals. Essentially, the animal swam forward while using the anterior one-third of its trunk to sweep the head to either side. This behavior was usually elicited in response to rapid movement by a nearby prey item but also followed unsuccessful forward strikes and, occasionally, was initiated without any obvious prey stimulus.

A diagram of segment motion based on a representative sweep (Fig. 6) shows that the five most anterior points undergo the most kinematic activity, while the posterior portion of the

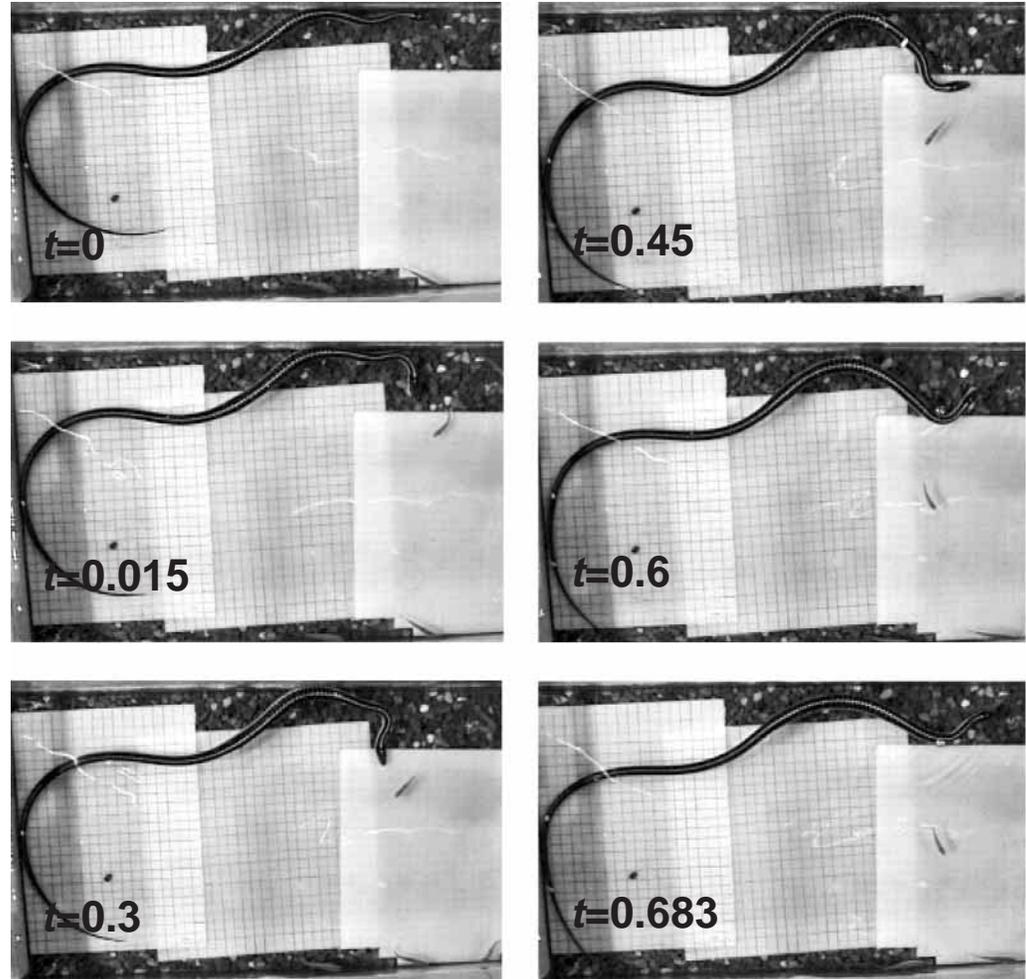


Fig. 5. Head sweeping by *Thamnophis elegans*. t = time in seconds. As the snake travels forward, the head is swung from side to side primarily by movements of the anterior trunk. Sweeping was the slowest of the behaviors observed in this study.

body largely maintains the same conformation during the bout. Head excursion is relatively slow, with peak forward velocities (velocity parallel to the calculated strike vector) generally below 33 cm s^{-1} . Sweeping bouts were also more sustained relative to strikes, typically lasting 1–3 s. The four anterior-most segments underwent large changes in path and segment angle. Forward velocity was greatest following periods of maximum lateral excursion.



Fig. 6. Diagrammatic view of point position along the trunk over the course of a sweep in *Thamnophis elegans*. t = time in seconds. The point of maximum head velocity is set as $t=0$. Colors distinguish various times. Head sweeping involves large lateral excursions of the anterior trunk while the posterior trunk remains relatively static.

T. elegans also captured prey by striking forward from rest or while swimming forward. Trunk recruitment was variable in this species: anterior loops were usually straightened during the initial phase of the strike (Fig. 7). In addition, large, posterior loops were sometimes straightened, especially when the strike covered a distance of four or more head lengths. In these instances, the forward strike transitioned into forward swimming and/or sideways sweeping. Prey appeared to be detected visually. Trunk looping was not as pronounced as that seen in *T. couchii*, and strikes were often initiated with only the anterior one-third of the trunk pointing towards the prey.

T. elegans strikes reached mean peak velocities of approximately 46 cm s^{-1} (35 head lengths s^{-1} ; Fig. 8), approximately half that of *T. couchii*. Accelerations were also relatively lower, reaching mean peak values of approximately 9 m s^{-2} (540 head lengths s^{-2}). Head acceleration was sustained for 80–100 ms before peak velocity was reached. Head segment angle decreased as velocity increased, although not to the same extent as in *T. couchii*. Segment angle also decreased in the first segment with increasing velocity, but showed little change in more-posterior segments. Path angles of the head and segments 1 and 2 decreased with increasing velocity. Forward displacement was largely restricted to the

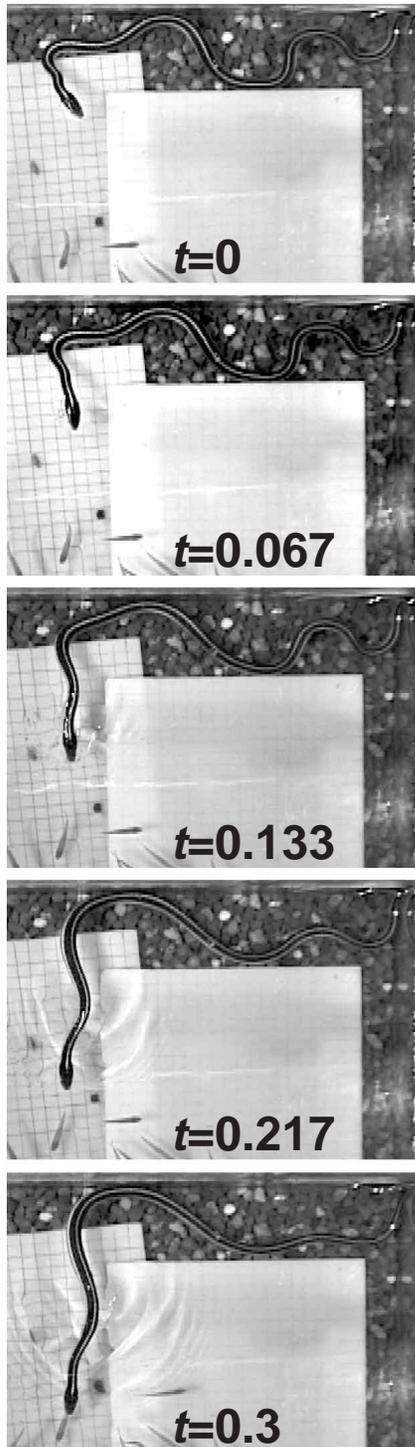


Fig. 7. *Thamnophis elegans* strike. Shown is a sequence from a predatory strike in dorsal view. t = time in seconds. At $t=0$, a strike is elicited from a motionless individual in an ambush position. Note the presence of small amplitude loops in the neck. Most of the long axis of the body is directed away from the direction of the strike. In the first 100 ms, head acceleration is accomplished by straightening of small loops in the anterior trunk as well as by the initial uncoiling of a large loop in the posterior trunk. As the strike proceeds, the large posterior coils continue to straighten, driving the largely straight anterior trunk towards the prey.

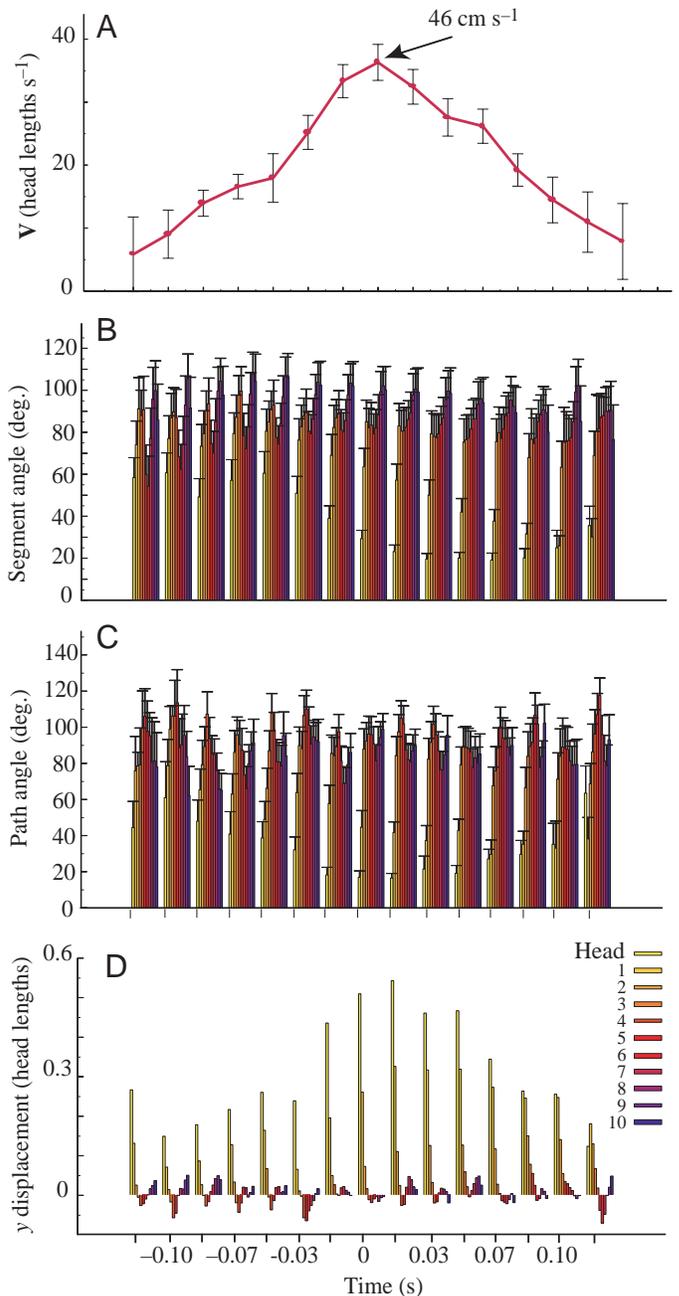


Fig. 8. Head velocity (A), segment angle (B), path angle (C) and forward displacement (D) profiles for *Thamnophis elegans*. Graphs have been standardized to time of peak velocity so that maximum velocity is reached at $t=0$. Error bars represent 1 S.E.M. Anterior body points are yellow, posterior points are blue. Head velocity during strikes was higher than in sweeps but still lower than in the other species examined. Segment straightening was apparent for positions 2 and 3 as the head approached peak velocity. Head segment angle was variable during the initial stages of head acceleration, decreasing shortly before the head reached peak velocity. Segment 1 segment angle decreased rapidly after peak velocity. More-posterior segment angles decreased slightly after peak velocity. Path angles for the three anterior-most positions dropped sharply as the head accelerated, while positions 4–8 showed little change from an initial path of 90° . Forward displacement was greatest at the snout and positions 1 and 2.

three anterior-most segments. More-posterior segments experienced a small amount of backwards displacement during the course of the strike.

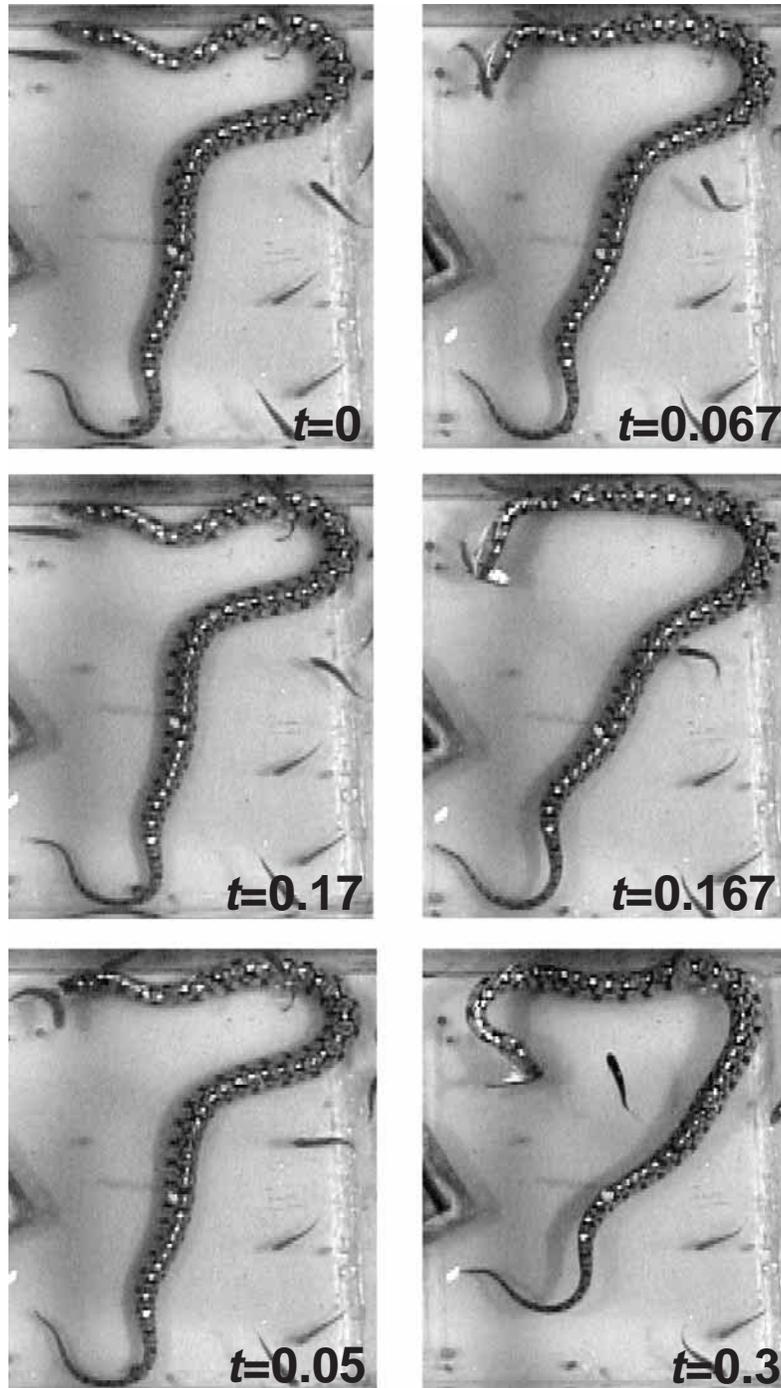


Fig. 9. Dorsal view of a predatory strike by *Nerodia rhombifer*. t = time in seconds. Prior to strike initiation, the snake is at rest on the bottom of the tank with the head out of the water in a typical ambush position ($t=0$). At $t=0.017$, the mouth is opened and the head is swung laterally towards the prey. As the strike proceeds, more-posterior portions of the trunk become involved in sweeping the head and prey laterally, although over two-thirds of the total length remains kinematically inactive.

The diamond-backed water snake Nerodia rhombifer

This species sometimes used a low-speed, high-amplitude, open-mouth sweeping behavior that resembled that found in *T. elegans*. More commonly, however, *N. rhombifer* displayed a high-speed strike from an ambush position (Fig. 9). During this behavior, the snake remained motionless, often with its head out of the water. Strikes were elicited by prey swimming close to the head or sometimes by prey contacting the anterior trunk. Often, these strikes showed a strong lateral component as the head was swung rapidly to the side to capture prey. *N. rhombifer* showed a remarkable ability to bend the neck and anterior trunk around to capture prey detected behind the head. In some of these instances, prey were trapped between the head and anterior trunk and corralled into the open jaws.

Strikes were relatively rapid, reaching a mean peak velocity of 84 cm s^{-1} (42 head lengths s^{-1} ; Fig. 10). Accelerations were also high relative to *T. elegans*, reaching mean peak values of 20 m s^{-2} (1027 head lengths s^{-2}). At the beginning of the strike, the head was oriented 90° relative to the prey item. Head angle and segment angle 1 decreased as the head was accelerated to roughly 20° . More-posterior segments decreased their segment angle to a much lesser degree than the head and segment 1. Path angles also dropped sharply for the head and segment 1 as velocity increased. More-posterior segments generally maintained path angles greater than 90° , indicating that these portions of the trunk were traveling away from the strike.

The head and segments 1 and 2 showed the greatest forward displacement. More-posterior segments experienced a minor amount of backwards displacement. Looping of the posterior segments resulted in segments with anterior ends pointing in the opposite direction to the strike. As the strike proceeded and the head was displaced forward, these backwards-facing segments were displaced in the opposite direction of the strike as they followed more anterior segments through a postural curve.

Statistical analysis

Species differed significantly in the mean starting segment angle at strike initiation (Table 1; Fig. 11). *Post hoc* contrasts revealed that *T. couchii* was significantly different from *T. elegans* + *N. rhombifer* ($F=120.72$, $P<0.0001$). *T. elegans* was not significantly different from *N. rhombifer* ($F=2.68$, $P=0.10$). Species and body position also had significant effects on minimum segment angle and minimum path angle. *Post hoc* contrasts revealed that *T. couchii* differed significantly in minimum segment angle from *T. elegans* + *N. rhombifer* ($F=129.59$, $P<0.0001$) and that *T.*

Fig. 10. Head velocity (A), segment angle (B), path angle (C) and forward displacement (D) profiles for *Nerodia rhombifer*. Graphs have been standardized to time of peak velocity so that maximum velocity is reached at $t=0$. Error bars represent 1 s.e.m. Anterior body points are yellow, posterior points are blue. The snake achieves peak velocity in approximately 50–60 ms. Starting head segment angle is approximately 90° , indicating that the head is not closely aligned to the direction of the strike at the onset of this behavior. The head and segment 1 show a sharp decrease in segment angle as the head is accelerated. Segment angle in these segments continues to decrease after peak velocity. More-posterior segments undergo relatively little angular change. Head and segment 1 path angle also markedly decrease with head velocity, while more-posterior segment angles are largely unchanged. Forward displacement is greatest at the snout, followed by body position 1. More-posterior positions experience minor displacement, with positions 5–10 undergoing periods of rearwards movement.

elegans was different from *N. rhombifer* ($F=3.36$, $P=0.07$). *T. couchii* differed significantly in minimum path angle from *T. elegans* + *N. rhombifer* ($F=80.5$, $P<0.0001$), and *T. elegans* was different from *N. rhombifer* ($F=18.55$, $P<0.0001$). MANOVA of acceleration and velocity revealed a significant species ($F=3.44$, $P=0.01$) and a nearly significant individual ($F=1.73$, $P=0.6$) effect. Univariate ANOVAs showed that species differed significantly in maximum head velocity, with both *T. couchii* and *N. rhombifer* attaining higher strike speeds than *T. elegans* (Table 2). Species also differed significantly in maximum head acceleration, with *T. couchii* and *N. rhombifer* achieving values roughly twice that of *T. elegans*.

Discussion

Strategies of aquatic prey capture

Snakes are unusual among squamates in that aquatic foraging has evolved numerous times throughout the group. A

Table 1. Results from a two-way ANOVA of the effects of position along the body, species, and position \times species on starting segment angle, minimum segment angle and minimum path angle

Variable	Stats	Species	Position	Position \times species
Start. seg. angle	P	<0.0001	0.02	0.62
	F	62.1	2.1	0.9
	SS, d.f.	15.97, 2	2.68, 10	2.25, 20
Min. seg. angle	P	<0.0001	<0.0001	0.74
	F	66.9	27.9	0.6
	SS, d.f.	19.2, 2	40.0, 10	1.73, 20
Min. path angle	P	<0.0001	<0.0001	0.73
	F	50.2	14.0	1.2
	SS, d.f.	7.5, 2	10.4, 10	0.79, 20

Species had a highly significant effect on all four variables, and position had a significant effect on minimum segment angle and minimum path angle. SS, sum of squares; d.f., degrees of freedom.

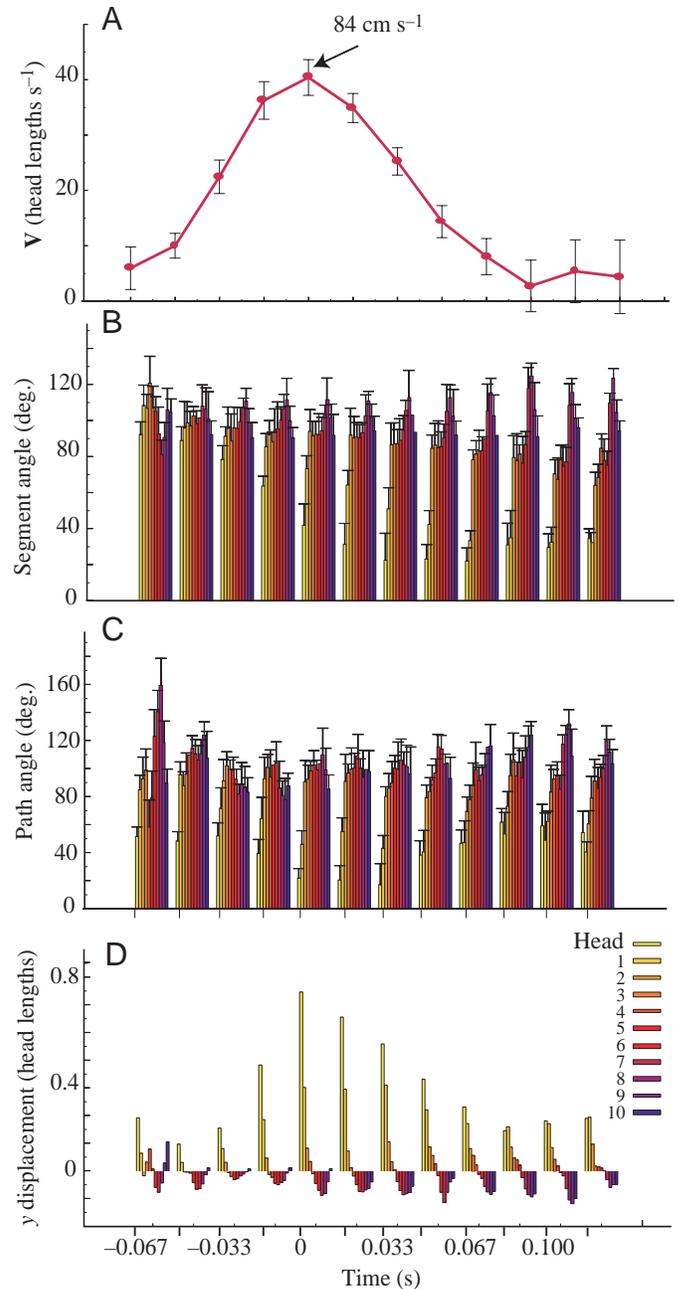


Table 2. Results of univariate ANOVAs on the effects of species on maximum velocity and maximum acceleration

Species	Max. velocity (head lengths s^{-1})	Max. acceleration (head lengths s^{-2})
	3.78* (2, 76)	5.80** (2, 76)
<i>T. couchii</i>	46.46 \pm 3.13	1027.7 \pm 120.11
<i>T. elegans</i>	34.57 \pm 3.07	537.99 \pm 117.78
<i>N. rhombifer</i>	42.10 \pm 2.96	1027.58 \pm 113.49

Numbers in bold are F ratios; numbers in parentheses are degrees of freedom. Table entries are species means \pm s.e.m. * $P<0.05$; ** $P<0.01$.

diversity of taxa, including natricines (Alfaro, 1998; Drummond, 1983; Halloy and Burghardt, 1990), homalopsines (Jayne et al., 1988; Mori, 1998; Smith et al., 1998), elapids

(Kropach, 1975; Voris et al., 1978) and viperids (Bothner, 1974; Savitzky, 1992), have been reported to sweep the head sideways to capture fish. Thus, despite the lack of detailed study of snake aquatic feeding, sideways sweeping has been recognized as a major aquatic foraging mode for snakes. Functional reasons for a sideways attack mode have rarely been elaborated, although the behavior is usually considered to be a strategy for reducing the drag profile and acceleration reaction forces associated with moving the head through water (Taylor, 1987; Young, 1991).

Results from this study demonstrate that sideways sweeping is an inadequate term to describe the diversity of feeding modes present within snakes at even a relatively low phylogenetic level. Sideways sweeping best describes the bouts of low-velocity, open-mouth, lateral attacks exhibited by *T. elegans* and *N. rhombifer*. However, both of these species displayed faster attack behaviors that could be distinguished from slow sweeping by the velocity of the head and duration of the bout.

Predatory strikes in *T. couchii* have been recognized as qualitatively distinct from those of generalist garter snakes (Drummond, 1983) and have been shown to have unique cranial kinematic characters (Alfaro, 2002). This study reveals that trunk kinematics in this species also differ significantly from other aquatic-feeding thamnophiines. *T. couchii* typically lines its entire body up with the prey prior to striking. By contrast, *Thamnophis rufipunctatus*, an independently evolved forward striker, appears to loop only the anterior half of the body, while the posterior portion is braced against a rock or other refuge (M. E. Alfaro, unpublished data). Non-thamnophiines, such as booids (Cundall and Deufel, 1999; Frazzetta, 1966), rattlesnakes (Kardong and Bels, 1998), vipers (Janoo and Gasc, 1992) and gopher snakes (Greenwald, 1974, 1978), strike by straightening tight loops in the anterior one-third or so of the trunk. The less-active posterior trunk may be directed away from the prey.

Linear arrangement of the trunk may partially explain the ability of *T. couchii* to generate strikes that are both rapid and long. Although mean maximum strike distances in *T. couchii* and *T. elegans* were very similar (6.8 cm vs 5.3 cm), maximum head displacement occurred over a shorter interval in *T. couchii* compared with *T. elegans* (100 ms vs 150 ms; Figs 4, 8). Although *N. rhombifer* achieved peak strike velocities and accelerations that were close to those of *T. couchii*, the mean maximum strike distance of *T. couchii* was relatively greater (3.9 head lengths vs 3.0 head lengths). Linear pre-strike looping may also increase the distance of midwater strikes by increasing the ability of the animal to use the posterior trunk to resist rearward-directed forces generated by the anterior trunk. This ability is likely to be important in a species that forages in fast-moving streams and rivers (Drummond, 1983; Rossman et al., 1996). Finally, selective pressures for rapid, long-distance aquatic strikes may explain the increased length and number of vertebrae found in this species relative to other garter snakes (Rossman et al., 1996).

Although *T. elegans* takes a wide range of prey, local

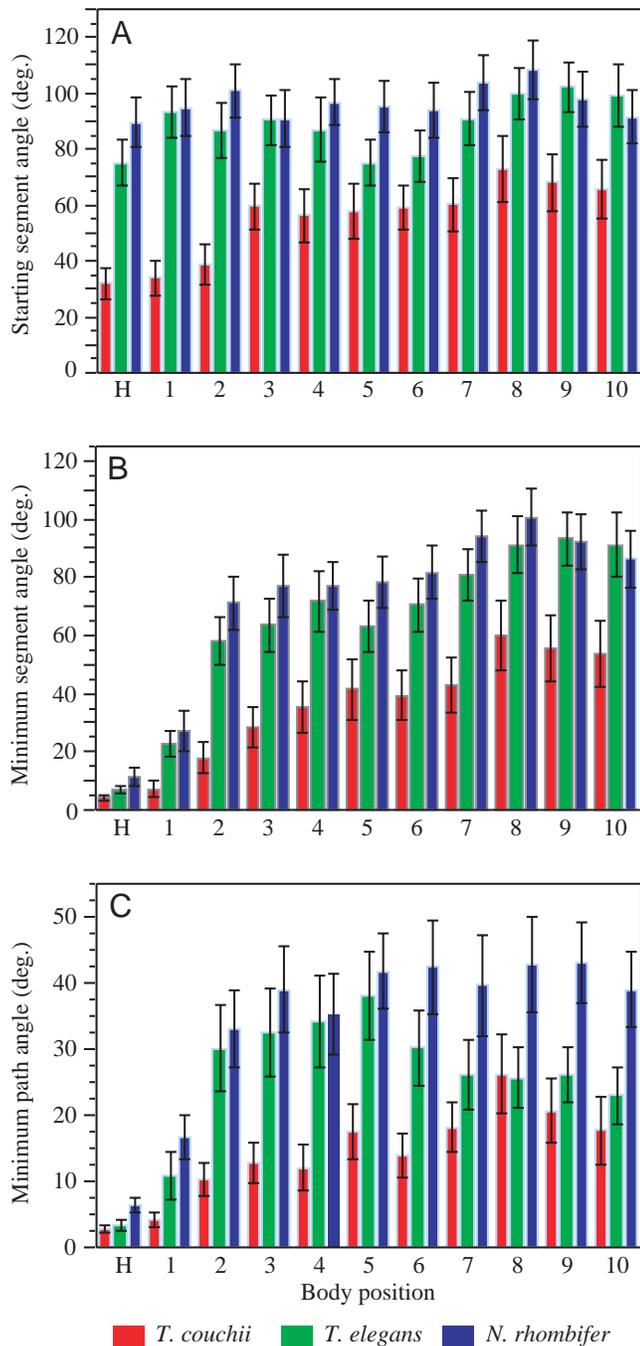


Fig. 11. Summary of mean species differences in three kinematic variables. (A) Starting segment was high in *N. rhombifer* and *T. elegans*, suggesting that these species struck at prey from a greater range of positions than did *T. couchii*. (B) Minimum segment angle over the course of a strike was lowest for all species at the head (H). *T. couchii* had significantly lower segment angles than did the other two species. (C) Minimum path angle was also lowest at the head for all three species and was significantly lower in *T. couchii* than in either of the other two species.

populations may be relatively specialized (Arnold, 1981). Populations of *T. elegans* in this study regularly capture minnows and tadpoles while swimming in lakes and ponds (Arnold, 1981; Rossman et al., 1996). In contrast to *Thamnophis sirtalis*, another generalist garter snake capable of capturing aquatic prey, *T. elegans* appeared comfortable when fully immersed (i.e. it did not avoid complete submersion and regularly engaged in sustained bouts of swimming) and appeared to have greater buoyancy control (Alfaro, 2002; Arnold, 1981). Although peak head velocities and accelerations were lower in *T. elegans* than in *T. couchii* or *N. rhombifer*, *T. elegans* showed substantially higher strike performance than that reported for *T. sirtalis* capturing fish (mean peak head velocity, 34.57 head lengths s^{-1} vs 11.04 head lengths s^{-1} ; mean peak head acceleration, 539.99 head lengths s^{-2} vs 227.92 head lengths s^{-2} ; Alfaro, 2002). Although comparative data on *T. sirtalis* trunk kinematics are not available, this study suggests that *T. elegans* is a more specialized fish-catcher than other generalist species of garter snake.

The anterior 20–30% of the trunk is most active during the strike of *T. elegans*. This portion of the body is generally aligned to the direction of the strike, although not to the same degree as in *T. couchii*. More posteriorly, the trunk may be coiled circularly or looped irregularly, but it is generally not aligned with the strike direction. Head displacement is accomplished by straightening the curves in the anterior part of the trunk and, during longer strikes, by straightening of posterior loops. The long axis of the head becomes nearly parallel with the strike vector as the head is displaced. Thus, while strikes may initially appear to involve a lateral sweep of the head, prey capture is usually accomplished by a frontal attack. The posterior trunk appears to contribute to head displacement by flowing through postural curves rather than by straightening.

Foraging mode and feeding ecology

The differences in axial kinematics observed here clarify our understanding of the foraging ecology of the three species examined. *T. couchii* is recognized as an aquatic specialist on fish (Alfaro, 2002; Drummond, 1980, 1985). The trunk kinematic behaviors I observed in this species appear to be related to the high-velocity, high-acceleration, long-distance strike that *T. couchii* uses to capture prey. *T. couchii* also possesses modifications that enhance its underwater vision (Schaeffel and De Queiroz, 1990). Together, these traits suggest that *T. couchii* is primarily a diurnal predator that has evolved a foraging mode for exploiting prey in deep water and at relatively low densities.

T. elegans does not show extreme trunk recruitment patterns and has a low-performance strike compared with that of *T. couchii*. Furthermore, this species does not possess especially acute underwater vision relative to other garter snakes (Schaeffel and De Queiroz, 1990). However, compared with *T. sirtalis*, another generalist species, *T. elegans* shows a greater capacity for aquatic foraging behavior (Arnold, 1981) and possesses a fast, forward-directed strike (Alfaro, 2002). These traits suggest that *T. elegans* is an intermediate aquatic specialist that may be

less able than *T. couchii* to exploit prey at low densities but is nevertheless adept at capturing fish in the water.

Nerodia have relatively poor underwater vision (Schaeffel and De Queiroz, 1990) and appear to rely heavily on tactile cues to direct strikes (Brown, 1958). Interestingly, and as an alternative to some hydrodynamic hypotheses that have been proposed to explain fishing behavior in *Nerodia* (Young, 1991), lateral striking may simply reflect the reliance of this species on tactile cues, since neck bending would be required to capture most prey that contacted the animal's body. That *N. rhombifer* is capable of high-velocity and high-acceleration strikes relative to generalist garter snake species suggests that prey capture in *Nerodia* is specialized. Unlike *T. couchii*, which relies on acute underwater vision and a long-distance strike to exploit prey at low densities, *N. rhombifer*, and probably also other *Nerodia* species, utilize tactile cues and a rapid, short-distance strike. This may allow this genus to efficiently exploit prey at high densities and may explain the ability of many *Nerodia* to become nearly entirely nocturnal (e.g. Drummond, 1983).

Models of trunk activity during the strike: open gate vs tractor-tread model

Two simple models have been proposed to describe the trunk displacement and head acceleration of the rattlesnake strike (Kardong and Bels, 1998). In the open gate model, acute body bends are straightened. In the tractor-tread model, the body flows through postural curves. The aquatic snakes in this study appear to make differential use of these modes during feeding. *T. couchii* may provide the best example of a species that uses the open gate mode to strike: straightening of pre-strike coils usually occurs over the entire body (Fig. 3). This mechanism may be the most advantageous way to generate high speeds for snakes able to recruit large portions of the trunk into the strike, since additional bends should sum to increase resultant head velocity.

T. elegans strikes generally fit the tractor-tread model well, especially in the posterior trunk, where more-posterior points followed the paths of anterior points (Fig. 7). These posterior curves were often in contact with the sides or bottom of the tank and are probably the site of active pushing. Furthermore, force may be generated by pressing trunk segments against the water. It is unclear whether this water reaction force is sufficient to account for the relatively rapid strikes characterized here, although it is almost certainly the means by which forces are generated during sideways sweeping (Figs 5, 6).

N. rhombifer usually struck opportunistically at prey as they passed near the head rather than orienting its head and body towards a specific prey. Prey were often captured lateral to the head, exhibiting a pattern of displacement that does not fit either the tractor-tread or open gate model. In this behavior (Fig. 9), a strong bend develops in the anterior portion of the trunk that was initially relatively straight. Displacement in the kinematically active region follows the direction of the bend. Although initial bending occurs at a localized point, regions around this bend also become more curved as the head

continues to swing laterally. The posterior trunk is held relatively static and probably serves as an anchor for the kinematically active region. This pattern of displacement appears similar to that exhibited by homalopsines (Jayne et al., 1988; Smith et al., 2002).

The results of this study challenge many popular preconceptions regarding aquatic prey capture in snakes. Snakes don't all fish in the same way. Sideways sweeping actually encompasses two distinct behaviors: a slow, open-mouthed search, apparently undirected and typically lasting several seconds, and a more rapid strike that is directed at specific prey items. Furthermore, as suggested by differences in the two lateral-striking species examined in this study, diversification within this mode can occur at relatively low phylogenetic levels. This result shows that 'fast' (Cundall and Greene, 2000) strike systems have evolved within natricine snakes a number of times and suggests that other piscivorous lineages might also have evolved rapid strikes.

In addition to quantifying the diversity of trunk function in aquatic and terrestrial species, future studies should focus on the skeletal and muscular mechanisms of head acceleration during the strike so that kinematic differences can be understood in a biomechanical context. The combined approach of kinematics and biomechanics has the potential to provide functional explanations of the morphology and behaviors that underlie 'fast' and 'slow' strikes, thus greatly improving our understanding of this complex and important behavior.

I thank Stevan Arnold for assistance in collecting snakes, and Mark Westneat for helpful advice. This manuscript was greatly improved through the comments of my committee members, Mark Westneat, Stevan Arnold and Michael LaBarbera, and two anonymous referees.

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