

Forward attack modes of aquatic feeding garter snakes

M. E. ALFARO*†

Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA and Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th Street, Chicago, IL 60637, USA

Summary

1. Previous studies have suggested that piscivorous snakes generally use sideways head sweeping to capture prey in order to minimize drag on the skull and/or to avoid pushing prey items away from the mouth. However, some aquatic species of garter snakes (genus *Thamnophis*) have been reported to use fast forward strikes to capture fish and amphibians. To characterize fast forward striking as a mode of piscivory in snakes and compare its use among specialist and generalist species, the aquatic specialists *Thamnophis couchii* and *T. rufipunctatus*, and a terrestrial generalist, *T. sirtalis*, were filmed at 250 fps (frames per second) while preying on minnows.
2. Both *T. couchii* and *T. rufipunctatus* oriented visually toward prey items and struck forward rapidly with peak head velocities that approached speeds attained by fast striking booid, colubrid and viperid species on land. In contrast, *T. sirtalis* did not orient visually toward specific prey items and displayed strikes that were four to six times slower than those of specialist species.
3. Aquatic specialists used moderate amounts of cranial rotation during jaw opening and achieved maximum gape within 20 ms of jaw opening. In the generalist *T. sirtalis*, jaw opening took 40–60 ms and was due almost entirely to mandibular rotation.
4. Significant differences in the prey capture kinematics of the two aquatic specialists are consistent with the hypothesis that *T. couchii* is an open water hunter, whereas *T. rufipunctatus* is an ambush predator. Thamnophiine snakes display a diversity of aquatic prey capture styles that reflect different behavioral and mechanical solutions to the problem of feeding in water.

Key-words: Colubrid, functional morphology, kinematics, *Thamnophis*

Functional Ecology (2002) **16**, 204–215

Introduction

Piscivory is a common feeding mode among snakes and has evolved multiple times independently in boas, pythons, elapids, viperids and colubrids (Young 1991). These independent acquisitions of a piscivorous lifestyle represent repeated evolutionary experiments of how to catch a fish and, thus, afford an excellent opportunity to study the evolution of behaviour and morphology in vertebrate feeding systems. In an apparent evolutionary convergence of predatory strike behaviours, lateral head sweeping has been observed as a common mode of aquatic prey capture in a diverse range of taxa, including natricines (Drummond 1983; Halloy & Burghardt 1990), homalopsines (Jayne, Voris & Heang 1988), elapids (Voris, Voris & Liat 1978) and viperids (Savitzky 1992).

*Current address: Section of Ecology and Evolution, One Shields Avenue, University of California, Davis, CA 95616, USA.

†Author to whom correspondence should be addressed. E-mail: malfaro@ucdavis.edu

It is thought that sideways sweeping reduces drag forces on the head (Taylor 1987). Despite the prevalence of this behaviour, it has not been explicitly examined in living animals although in experiments with disembodied heads drag forces were lower for sideways profiles than for frontal profiles (Young 1991; Braun & Cundall 1995). Sideways attacks are also thought to mitigate the effects of water displaced by the predator upon the prey item. Taylor (1987) suggested that forward attack strategies in vertebrates, which are primitive for most terrestrial snakes, would be ineffective underwater because the bow wave produced by the approaching head would tend to push prey away, or at least alert it to the incoming strike. Although there have been no studies that have quantified the bow wave in front of a snake's head, the prevalence of sideways sweeping in aquatic feeding snakes would seem to add support to this hypothesis. Turtles, which are the only other amniotes in which aquatic forward striking has been studied, are thought to overcome the effects of the bow wave by generating compensatory suction, largely via the robust hyoid apparatus (Lauder &

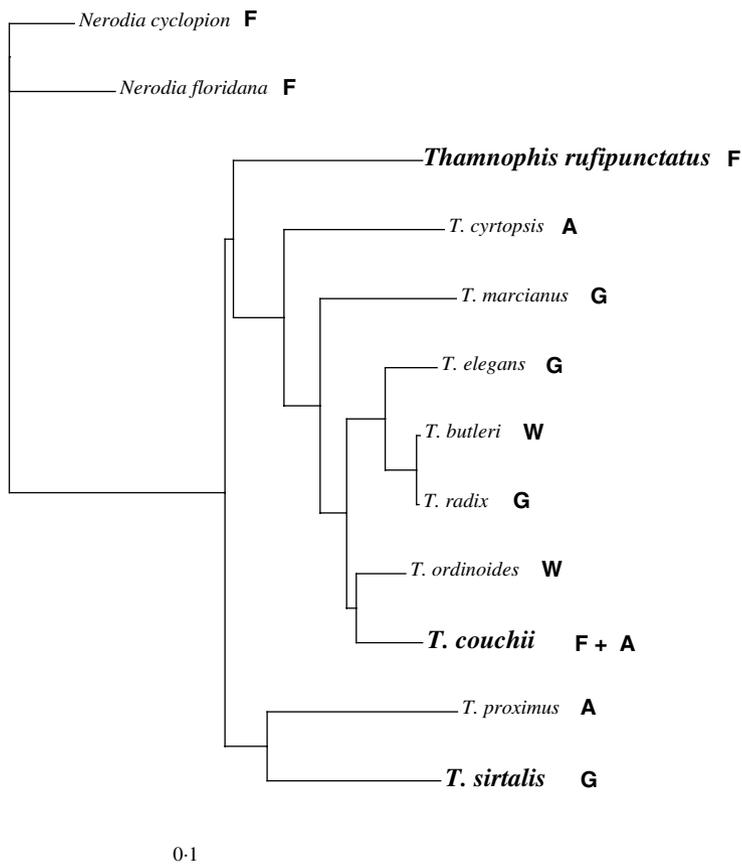


Fig. 1. Maximum likelihood tree of garter snake relationships showing dietary preference of terminal taxa. Phylogram shown is based on three mitochondrial genes (*12S*, *ND2*, *CytB*, Alfaro & Arnold 2001) with two *Nerodia* species serving as the outgroup. Considerable genetic differentiation has occurred within the genus *Thamnophis*. The three taxa examined in this study were relatively distantly related to each other (uncorrected genetic distances for each pair ranged from 7 to 7.5%). *Thamnophis couchii* has evolved a highly aquatic, piscivorous lifestyle independently from *Nerodia*. While reconstruction of the ancestral feeding type of *T. rufipunctatus* is ambiguous, this study suggests that *T. rufipunctatus* captures prey in a fundamentally different manner from *Nerodia*. Thus, novel aquatic feeding modes have arisen at least twice within the garter snakes. F = fish, A = amphibians, G = generalist, W = worms. Dietary data from Rossman *et al.* (1996). Scale = number of expected substitutions per site for unit branch length.

Prendergast 1992; Van Damme & Aerts 1997; Summers *et al.* 1998). Snakes lack a well-developed hyoid apparatus and, presumably, the ability to generate substantial suction. Thus, if displaced fluid from head acceleration is a major impediment to successful underwater prey capture (Young 1991), then aquatic feeding snakes, as well as other vertebrates that lack the capacity to generate suction, might be functionally constrained to use lateral strikes to capture evasive prey. However, in an ecological study (Drummond 1983), two species of garter snake (*Thamnophis couchii* and *Thamnophis melanogaster*) were reported to use a fast forward strike under water. This foraging mode is thought to be an adaptation for capturing widely dispersed prey (Drummond 1983). In contrast, terrestrial generalist species were found to use the sideways attack strategy typical of aquatic snakes (Drummond 1983).

The ability of some *Thamnophis* to execute a high-speed, forward directed attack under water suggests that bow waves do not impose a universal constraint on the aquatic feeding behaviour of snakes. However, there has been little recognition of this unusual predatory mode in the feeding literature and its implications for our understanding of trends in amniote aquatic prey capture have gone largely unexplored. This neglect may be due in part to limitations of the original study: standard video (30 Hz) was used to record prey captures and cranial movements, and velocities were not measured. Thus, despite the qualitative description of the behaviour as fast and covering distances of up to 6–8 cm, prey capture in *T. couchii* has been classified as a ‘slow capture strategy’ (Cundall & Greene 2000).

The purpose of the current study was to compare forward striking performance between aquatic specialists, which rely on forward strikes to capture the majority of their prey, and terrestrial generalists, which typically use sideways head sweeping to capture fish, but which occasionally lunge forward. Specifically, the hypothesis that aquatic specialist garter snakes strike forward faster under water than terrestrial generalists was tested. The kinematics and performance of forward-directed strikes were measured in three species of garter snake, including two highly aquatic specialists: the Western Aquatic Garter Snake, *T. couchii* (Kennicott), and the Narrow Headed Garter Snake, *T. rufipunctatus* (Cope), and a less aquatic generalist, *T. sirtalis* (Linnaeus). A second goal of this study was to evaluate the diversity of aquatic feeding modes in garter snakes. Available phylogenetic data strongly support the conclusion that specializations for aquatic feeding evolved independently in *T. couchii* and *T. rufipunctatus* (Fig. 1). How convergent are prey capture kinematics in these species, and to what extent do they differ from those of generalists such as *T. sirtalis*?

Methods and materials

Three *T. rufipunctatus* were collected from upper Oak Creek, Coconino Co., AZ, and five *T. couchii* were collected from the eastern Sierra Nevada (Lassen Co., CA) in July 1999. Five *T. sirtalis* (two from Cook Co., IL, one from Macon Co., NC, and two animals from wholesalers in Chicago) were obtained over a three-year period. An attempt was made to collect snakes that were similar in size (Table 1). *Thamnophis rufipunctatus* is found in river drainages in Arizona, New Mexico, and northern Chihuahua to northern Durango in Mexico (Rossman, Ford & Siegel 1996) and feeds primarily on fish (Flehart 1967). *Thamnophis couchii* is found associated with streams and rivers across much of the Sierra Nevada in California (Rossman *et al.* 1996). Its diet consists primarily of fish and larval and adult amphibians (Fitch 1949; Rossman *et al.* 1996). *Thamnophis sirtalis* is widely distributed across much of the USA and Canada and is a terrestrial,

Table 1. Species and individuals examined in this study. Strikes is the number of strikes analysed for each individual. Head length was measured from the tip of the snout to the mid-dorsal, posterior extent of the parietal scales. SVL = snout-vent length in centimetres

Species	Strikes	Head length (cm)	SVL (cm)
<i>T. couchii</i> (C1)	10	1.9	57.2
<i>T. couchii</i> (C2)	4	1.9	57.7
<i>T. couchii</i> (C3)	4	1.7	47
<i>T. couchii</i> (Da)	3	1.8	52.4
<i>T. couchii</i> (D1)	10	2.0	57.5
<i>T. couchii</i> (D2)	3	1.8	55.0
<i>T. rufipunctatus</i> (1)	6	2.1	58.2
<i>T. rufipunctatus</i> (2)	5	2.3	72.8
<i>T. rufipunctatus</i> (3)	6	1.8	52.3
<i>T. sirtalis</i> (b)	3	1.8	48.2
<i>T. sirtalis</i> (H1)	4	1.8	46.3
<i>T. sirtalis</i> (P1)	5	2.0	68.2
<i>T. sirtalis</i> (P2)	5	2.0	67.5

riparian forager that feeds primarily on anurans and annelids and only occasionally on fish (Rossman *et al.* 1996). Although field and laboratory studies have been conducted on feeding in *T. couchii* and *T. sirtalis* (Drummond 1983), there have been no detailed kinematic analyses of aquatic prey capture in these species. Besides brief observational accounts of *T. rufipunctatus* foraging in the field (Tanner 1988), its feeding behaviour is almost completely unknown. Animals were maintained in 10-gallon (38-l) aquaria with corn-cob bedding, and water and fed live minnows (*Pimephales promelas*) weekly. Room temperature was kept at 27–30 °C and light cycle was seasonal.

Observed prey captures were classified as belonging to one of three types of behaviour. *Aerial attacks* (Drummond 1983) were initiated from terrestrial perches and involved the head and some of the trunk crossing from air into water. *Fast forward strikes* were initiated under water and involved the rapid acceleration of the head in a straight line towards the prey item. *Sideways sweeps* involved the swinging of the head with open mouth at low speeds. Fast forward strikes and aerial attacks were the behaviours of interest in this study; sideways sweeping was noted when performed, but not subject to kinematic analysis.

Strikes were recorded in a 30-gallon (135-l) aquarium fitted with a Plexiglas wall, which reduced the

front to back width of the tank to 10 cm and restricted the direction of strikes. This step was taken to encourage snakes to strike in a plane perpendicular to the camera so that strikes could be seen in lateral view. Restriction of tank area did not appear to alter striking behaviour. *Thamnophis sirtalis* individuals refused to feed when they were placed into a completely aquatic filming arena. To elicit aquatic foraging, filming trials for *T. sirtalis* occurred in the same arena as described for *T. rufipunctatus* and *T. couchii*, but with bricks placed to provide a terrestrial perch and restrict the aquatic portion of the tank to an 18-cm long window. Aerial attacks from *T. couchii* also were filmed in this arena. Prey items for all filming trials were minnows approximately 3–5 cm long. For *T. couchii* and *T. rufipunctatus*, from one to three prey items were placed into the tank at a time. *Thamnophis sirtalis* apparently had difficulty detecting prey at low densities, so this species was usually presented with three to five fish at a time. Experiments and animal care were performed in accordance with IACUC protocols (no. 70401).

FILMING AND DIGITIZING PROTOCOL

Strikes were filmed using a Redlake MotionScope PCI high-speed digital imaging system (Motion Engineering Co., Indianapolis, IN, USA) at 250 fps with a shutter speed of 1/750 s. To reduce the effects of striking angle on the calculation of kinematics only sequences in which the strike path was approximately perpendicular to the camera were analysed. Thus, all strikes were analysed in lateral view. The following points on the head and neck were digitized: the tip of the snout, the tip of the mandible, the jaw (quadrate/articular) joint, the centre of the eye, a landmark along the neck within approximately 2 cm of the jaw joint (this point was not homologous among individuals) and a point at the estimated centre of mass of the prey item (Fig. 2). These points were digitized using a modified version of NIH Image (National Institutes of Health, Bethesda, Maryland, USA).

The following variables were calculated across all sequences: gape angle, the angle from the maxillary and mandibular tips to the jaw joint; prey distance, the distance from the eye to the prey item; strike velocity; and strike acceleration. Velocity and acceleration were calculated along a straight-line trajectory towards the initial position of the prey. For the purposes of this paper these are referred to as the performance variables. Furthermore, when the head and trunk were visible over the entire strike, three additional variables were calculated (Fig. 2): head rotation, the angle from the neck landmark to the jaw joint to the tip of the snout; mandibular rotation; the angle from the neck landmark to the corner of the mouth to the tip of the mandible; and gape distance, the distance from the tip of the snout to the tip of the mandible. It was only possible to calculate these variables for a subset of the strikes in Table 1 (*T. couchii*, three individuals, 4–5

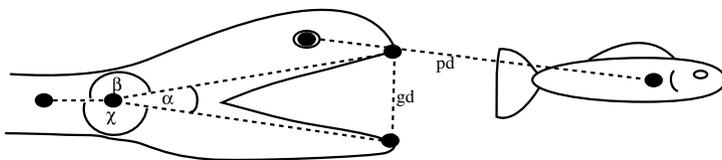


Fig. 2. Digitizing protocol. Points were digitized frame-by-frame and used to calculate the following parameters: α = gape angle, β = head rotation, χ = mandibular rotation, pd = prey distance, gd = gape distance. In addition, a point on the eye was used to track changes in acceleration and velocity of the head. Raw linear measurements were also reported in units of head length to account for differences in snake size.

strikes/individual; *T. rufipunctatus* three individuals, 3–6 strikes/individual; *T. sirtalis* four individuals, 3–5 strikes/individual).

Velocity and acceleration were calculated for the eye landmark with QuickSand (Walker 1998). Using this program, a quintic spline was fit to the coordinate data. Calculations of velocity and acceleration were based on the spline-fitted coordinates to mitigate the effects of digitizing and sampling error on parameter estimation (Walker 1998). Velocities and accelerations were standardized by head length to control for size variation in specimens. Head and mandibular rotation were also calculated as the angle between a vector parallel to the neck and a vector parallel to the braincase or mandible at the level of the quadrate–articular joint (similar to Cundall & Deufel 1999). However, angles calculated in this manner displayed a high degree of variability, possibly due to the flexibility of the anterior trunk and the high variation in attack angle exhibited during aquatic striking. Angles calculated using a landmark on the neck were not susceptible to this problem. However, because neck landmarks generally were not homologous among individuals, rotations of the head and mandible relative to their starting positions were calculated and these values were used for statistical analysis.

The beginning of the strike was defined as the frame preceding noticeable head movement. For *T. couchii* and *T. rufipunctatus*, the end of the strike was defined as the frame after prey contact or, in the case of a miss, the frame in which the head reached the furthest point of its initial trajectory. In frames beyond this point the animal's head frequently moved out of frame or became obscured by the prey. *Thamnophis sirtalis* exhibited a longer, slower striking behaviour that generally ended with the head being swept laterally out of the field of view of the camera. Since *T. sirtalis* rarely encountered prey and generally did not reach a point in which its forward trajectory clearly stopped, the end of the strike in this species was arbitrarily defined as 40 frames following mouth opening. This ensured that the animal remained in the same plane of the strike over the entire sequence.

ANALYSIS

The data sets used in this study included both successful and unsuccessful strikes. Kinematics have been shown to vary with strike success (Kardong 1986). A MANOVA performed on each aquatic specialist in this study (all forward strikes in *T. sirtalis* were unsuccessful) with individuals and success nested within individuals as effects revealed no significant effect of success on the measured variables (*T. couchii* $P = 0.54$, $F = 0.98$, $df = 12, 6$; *T. rufipunctatus* $P = 0.08$, $F = 5.39$, $df = 18, 3$). Therefore, successful and unsuccessful strikes were combined for subsequent analysis.

The data set was subjected to several analyses. To test the hypothesis that species differed significantly in

strike performance, a MANOVA was performed on the four performance variables it was possible to calculate across all strikes (maximum gape angle, maximum velocity, maximum acceleration and maximum prey distance) with species as a fixed effect, and individual nested within species as a random effect. Aerial attacks from *T. couchii* were excluded from this analysis. To determine if medium (air or water) affected strike performance within a species, ANOVAs were performed on *T. couchii* performance variables with environment as a fixed effect and individuals nested within environment as a random effect. Finally, to test for the effect of species on aerial strikes, *T. sirtalis* and *T. couchii* aerial strikes were used in a MANOVA with species as a fixed effect, and individuals nested within species as a random effect. For all MANOVAs of performance data, univariate ANOVAs were subsequently performed to identify variables contributing to significant effects.

To determine if species differed significantly in their strike kinematics, a MANOVA was performed with peak head rotation, maximum gape distance, maximum gape angle, maximum prey distance, maximum head acceleration and maximum head velocity as dependent variables, species as a fixed effect and individual nested within species as a random effect. Univariate ANOVAs also were performed to identify variables that contributed to significant effects in the MANOVA.

Results

Thamnophis couchii and *T. rufipunctatus* captured prey underwater using fast forward strikes. While forward directed attacks appeared to be the dominant mode of successful prey capture for both specialist species, *T. sirtalis* forward aerial attacks were rarely successful. Instead, nearly all prey were taken during subsequent bouts of sideways head sweeping with captured prey usually less than 1–2 cm from the head. Although a more appropriate test of fishing performance might have been between *T. sirtalis* sideways sweeping and specialist fast forward striking, forward attacks for all three species were compared to highlight differences in a kinematically similar behaviour.

PREY CAPTURE STRATEGY

Thamnophis couchii demonstrated remarkable control of buoyancy and usually initiated strikes while completely submerged. *Thamnophis couchii* individuals also oriented visually toward prey items at a distance from 2 to 12 cm. During underwater foraging bouts, snakes would alternate motionless waiting with short intervals of crawling along the bottom. Upon detecting a fish, individuals would turn their heads towards prey items and slowly organize most of the trunk into high-amplitude coils (Fig. 3). The plane of the strike was often parallel with the tank bottom, although upwards and downwards strikes were also observed. Strike initiation involved a rapid acceleration of the

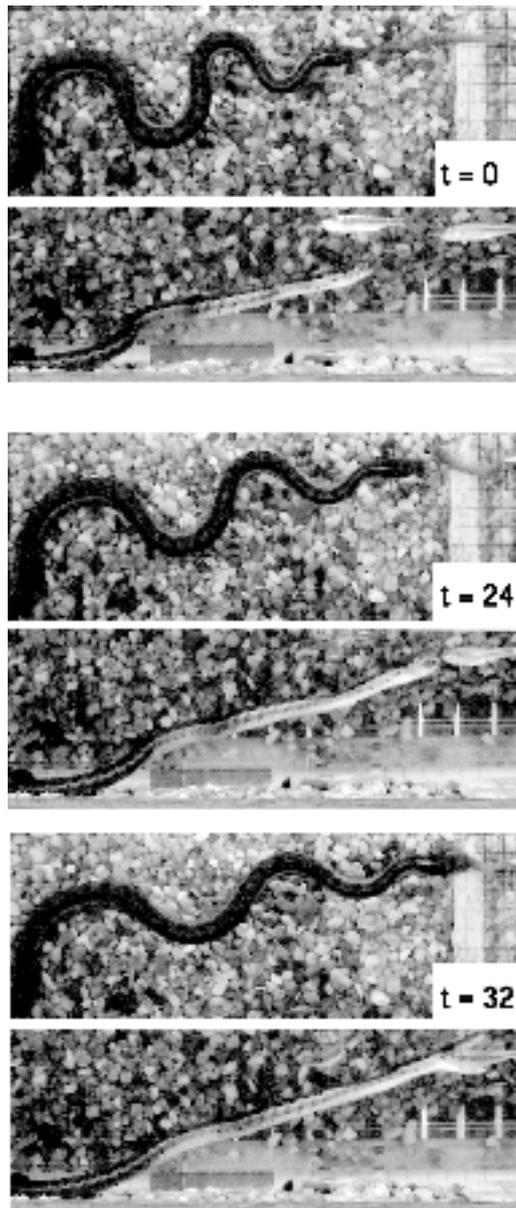


Fig. 3. *Thamnophis couchii* executing a fast forward strike. Shown are video images from a feeding sequence filmed at 250 fps. For this sequence, a mirror was placed in the tank at 45° to the tank floor to show both lateral and dorsal views of the strike. For this figure, $t = 0$ indicates the frame in which movement of the snake towards the prey was observed. At $t = 0$ ms the snake has visually oriented to the prey item approximately 4–5 cm away. The entire trunk is arranged in a series of loose coils. At $t = 24$ ms the jaws are opened as the head reaches the prey. At $t = 32$ ms, peak gape is observed as the jaws are passed over the prey item. The passing of the jaws over the prey so that both the upper and lower jaw contact the prey simultaneously is similar to the driving scissors attack exhibited by booids (Cundall & Deufel 1999).

head in a straight line towards the prey item. In some instances, this rapid acceleration was preceded by a short period of slow movement of the head towards the prey. Approximately one-third of all strikes ended in successful captures.

Jaw opening occurred over a period of approximately 25 ms, with mandibular rotation responsible for

over twice the amount of gape angle as head rotation (Fig. 4). Head and mandibular rotation began nearly synchronously, although head rotation ended slightly before mandibular rotation. Peak head acceleration occurred prior to the start of mouth opening; however, maximum gape occurred 12–20 ms (one to two head lengths) before prey contact and the head reached maximum velocity nearly simultaneous with maximum gape.

During successful captures, the jaws were passed over the prey item before jaw closing was initiated; thus the upper and lower jaws usually came into contact with the prey simultaneously in a behaviour that resembled the driving scissors strike of some booid snakes (Cundall & Deufel 1999). As the jaws closed, snakes often ventroflexed the head so that the head and prey moved forward and down in a manner similar to that reported for pythons and boas (Frazzetta 1966; Cundall & Deufel 1999). Consistent with observations by Drummond (1983), missed strikes were often followed by a recoiling and subsequent forward strike.

Thamnophis rufipunctatus individuals easily achieved negative buoyancy and usually kept the entire body in contact with the bottom of the tank. Snakes visually oriented to prey from a distance of 2–6 cm. When individuals became aware of prey items, they would sometimes remain still while waiting for fish to approach. In this position, the anterior trunk nearly always formed one or two loose coils. Individuals would also forage slowly along the bottom of the tank, frequently stopping and waiting. During these bouts of slow foraging, loose loops were maintained in the anterior trunk. Prior to strike initiation, these coils would be tightened as the head was oriented towards the prey item. Snakes struck forward and generally upward (Fig. 5). Jaw opening usually occurred after the head was accelerated towards the prey although, in some strikes, these activities occurred simultaneously. Like *T. couchii*, *T. rufipunctatus* frequently reached maximum gape at a distance of one or two head lengths from the prey. Jaw opening lasted approximately 30–35 ms in *T. rufipunctatus* and head rotation accounted for almost half of the total gape angle (Fig. 6). In contrast to *T. couchii*, peak head acceleration occurred after jaw opening. Head velocity prior to jaw opening was low. Like *T. couchii*, the jaws were passed over the body of the prey before jaw closing was initiated so that upper and lower jaws made near simultaneous contact with the prey. Ventroflexion of the neck occasionally accompanied the end of jaw closing. Like *T. couchii*, approximately one-third of all strikes in *T. rufipunctatus* ended in successful captures.

In contrast to the other two species examined, *T. sirtalis* appeared to have difficulty developing negative buoyancy. Individuals placed in an entirely aquatic filming arena rarely submerged completely and were never observed resting on or crawling along the bottom of the tank. Drummond (1983) noted a similar lack of buoyancy control for *T. sirtalis* in both field and

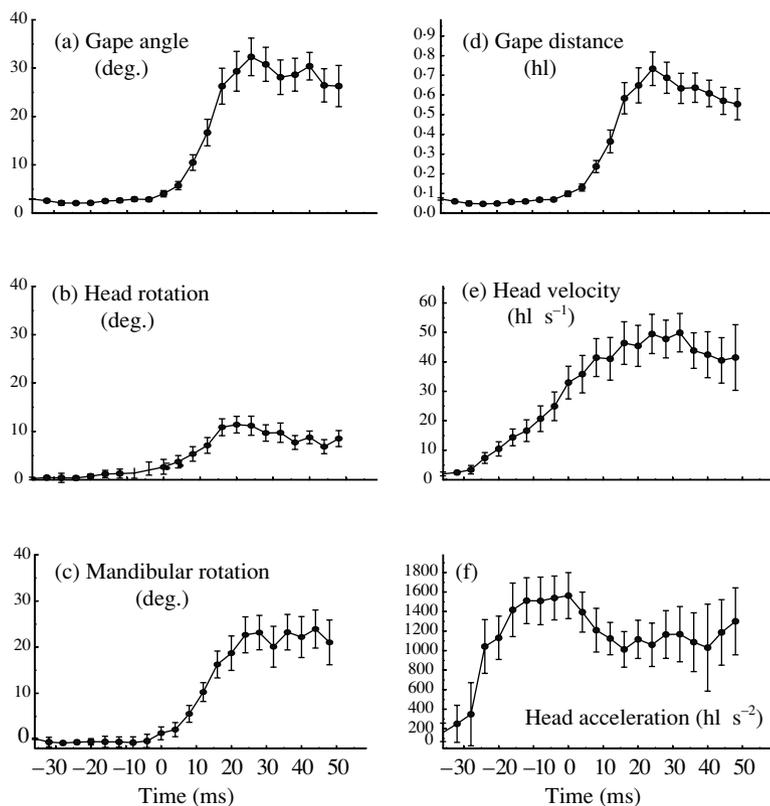


Fig. 4. Summary kinematic plot for *Thamnophis couchii*. Shown are 13 fast forward strikes from three individuals standardized by the time of jaw opening. Error bars indicate one standard error of the mean. Mean gape angle was achieved approximately 25 ms after the start of mouth opening. Head and mandibular rotation began at nearly the same time though jaw rotation continued approximately 10 ms after head rotation had ceased. Head rotation was responsible for approximately one-third of the total gape. Peak gape distance approached 70% of head length (1.73 cm). Head acceleration occurred up to 30 ms before jaw opening began, and peak velocity was maintained for approximately 10–15 ms after peak gape. Mean peak head velocity across all strikes was approximately 112 cm s⁻¹.

laboratory settings. In the terrestrial/aquatic arena, prey strikes were initiated with the head and body out of the water. Individuals approached the pool and extended their head and a short length of trunk over

the water surface. From this position, snakes would wait until they detected the prey. Unlike *T. couchii* and *T. rufipunctatus*, which oriented visually to specific prey items, *T. sirtalis* did not reorient the head prior to striking. Instead, turns or other rapid movement by the prey would trigger a sudden forward lunge by the snake. These initial lunges were almost never successful and usually were followed by a bout of apparently undirected sideways head sweeping. Lateral head sweeps accounted for most successful prey captures although the kinematics of this behaviour were not analysed in this study.

Gape angles in *T. sirtalis* were similar to those seen in *T. couchii* and *T. rufipunctatus* (Fig. 7). However, nearly all of the gape was achieved through mandibular rotation – head rotation was negligible. Jaw opening duration was much longer in *T. sirtalis* than in *T. couchii* or *T. rufipunctatus*, lasting approximately 50 ms. Head acceleration and velocity were markedly lower in *T. sirtalis* than in the other two species. Like *T. couchii*, peak acceleration was reached before the start of jaw opening.

STATISTICAL ANALYSES

MANOVA of kinematic and performance variables revealed a highly significant species effect as well as a significant individual effect on kinematic variables (for species $P = <0.001$, $F = 9.49$, $df = 14, 46$ for individual $P = 0.022$, $F = 1.58$, $df = 49, 121.19$) indicating that, while substantial intraspecific variation exists, these three species employ distinct feeding behaviours. *Post hoc* contrasts showed that the specialists were significantly different from *T. sirtalis* ($P < 0.0001$) and that *T. couchii* and *T. rufipunctatus* also differed significantly from each other ($P = 0.0046$). Univariate ANOVAS showed that species differed significantly in the degree of head or mandibular rotation but did not differ in total gape angle or gape distance (Table 2). The two aquatic species displayed greater head rotation (*T. couchii*, 12°; *T. rufipunctatus*, 19°) than *T. sirtalis* (7°).

Table 2. Results from univariate ANOVAS on performance and kinematic variables for three garter snake species. Table entries show mean and one standard error (based on number of strikes) of kinematic variables. $F = F$ -ratio, ind. = individual, hl = head length

Variable	<i>T. couchii</i>	<i>T. rufipunctatus</i>	<i>T. sirtalis</i>	F species	F ind.
Mean max. gape angle (degrees)	39.32 (2.1)	38.81 (2.3)	37.70 (2.2)	0.1	1.2
Max. gape – head rotation (%)	32.1 (2.7)	47.8 (2.8)	19.5 (2.5)	28.9**	0.5
Max. gape – mandibular rotation (%)	67.9 (2.7)	52.2 (2.8)	80.5 (2.5)	28.9**	0.5
Mean max. gape distance (hl)	0.90 (0.1)	0.93 (0.1)	0.81 (5.8)	1.8	0.4
Mean max. gape distance (cm)	1.73 (0.1)	1.90 (0.1)	1.55 (0.1)	3.4	0.55
Mean max. head velocity (hl s ⁻¹)	60.85 (5.2)	41.64 (5.5)	11.03 (5.5)	12.5**	2.2
Mean max. head velocity (cm s ⁻¹)	114.49 (11.0)	79.22 (11.5)	20.4 (10.9)	19.0**	1.4
Mean max. head acceleration (hl s ⁻²)	2096.7 (202.8)	1515.4 (212.3)	227.9 (211.1)	21.5**	1.6
Mean max. head acceleration (m s ⁻²)	39.40 (3.5)	30.05 (3.6)	4.00 (3.5)	27.8**	1.3
Mean max. prey distance (hl)	2.66 (0.5)	1.38 (0.5)	4.90 (0.5)	12.4**	2.6*
Mean max. prey distance (cm)	4.87 (0.9)	2.81 (1.2)	10.07 (1.1)	11.1**	3.3**

* $P < 0.05$, ** $P < 0.01$.

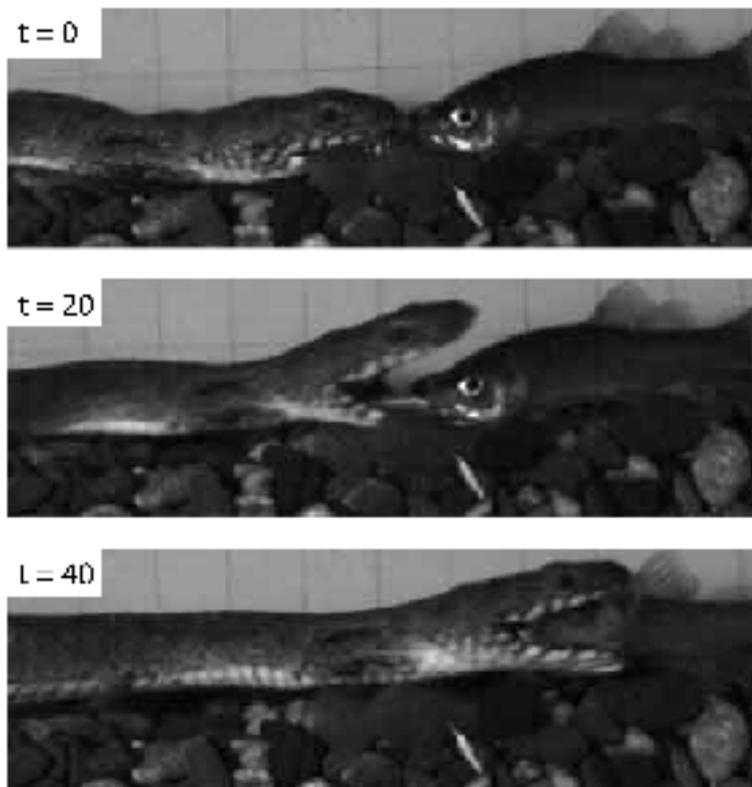


Fig. 5. *Thamnophis rufipunctatus* executing a fast forward strike. Shown are video images from a feeding sequence filmed at 250 fps in lateral view. For this figure, $t = 0$ indicates the frame in which movement of the snake towards the prey was observed. Prior to this, the snake has visually oriented to the prey and remained motionless with the anterior portion of the trunk arranged in loose coils. At $t = 20$ ms, peak gape is achieved as the head is accelerated towards the prey. At $t = 40$ ms, the jaws are closed onto the prey. The passing of the jaws over the prey so that both the upper and lower jaw contact the prey simultaneously is similar to the driving scissors attack exhibited by booids (Cundall & Deuffel 1999).

The aquatic species also struck at velocities 4 to 6 times greater than *T. sirtalis* and accelerated 6 to 10 times faster. Species also differed significantly in head velocity, head acceleration and prey distance (Table 2). Surprisingly, *T. sirtalis* struck at prey from a much greater distance than either of the aquatic species. However, this result reflects a fundamental difference in the predatory mode of these species rather than greater performance in the generalist. Both *T. couchii* and *T. rufipunctatus* visually identified specific prey items prior to striking and spent a noticeable amount of time in a prestrike preparatory phase in which slight postural changes of the head and trunk were made. In

contrast, *T. sirtalis* did not appear to target specific prey from its terrestrial perch or to perform prestrike preparation. Instead, individuals usually responded to a turn or start by the prey from almost anywhere within the pool with a forward strike. Although this resulted in a greater prey distance for this species, it appeared to correlate negatively with capture success, as nearly all observed successful strikes occurred during lateral sweeps at prey items less than 2 cm from the head.

For *T. couchii*, strikes initiated terrestrially differed significantly from strikes initiated under water (Table 3). This difference was driven primarily by head acceleration and velocity. Surprisingly, fully aquatic strikes were faster than strikes that originated terrestrially. This result was possibly due to the prestrike conformation of the body during aerial attacks. Individuals were relatively compactly looped on the terrestrial substrate and aerial attacks appeared to recruit only one to two large loops in the anterior trunk. In contrast, during aquatic strikes the body was less compact and more linearly arranged, allowing greater trunk recruitment during the strike. Thus, the amount of trunk recruitment might play an important role in determining final head velocity.

A MANOVA of strike performance comparing terrestrial-to-aquatic strikes in *T. couchii* and *T. sirtalis* revealed a significant species effect (for species $P = <0.001$, $F = 20.69$, $df = 4, 12$; for individual $P = 0.009$, $F = 2.40$, $df = 20, 40.75$). Univariate ANOVAs showed that prey distance, head velocity and head acceleration differed significantly between species, but gape angle did not (Table 4).

Discussion

The results of this study point to three major conclusions regarding the evolution of aquatic prey capture modes in snakes. First, fast forward striking is a high-performance foraging strategy for aquatic snakes. Since these snakes lack a well-developed hyoid apparatus and do not exhibit the obvious signs of buccal cavity expansion that are typically associated with the development of negative intra-oral pressures (Figs 3 and 5), this suggests that the role of the bow wave as a factor in alerting prey or pushing prey away from the predator may have been overstated in previous studies. Second, an aquatic medium may impose design

Table 3. Results of univariate ANOVAs of mode (aquatic vs aerial) on four performance variables in *Thamnophis couchii*. Table entries are group means and one standard error. $F = F$ -ratio, hl = head length

Effect	Aerial	Aquatic	F
Mean maximum gape angle (degrees)	38.37 (1.8)	39.32 (1.5)	0.2
Mean maximum velocity (hl s^{-1})	27.99 (6.0)	60.85 (5.6)	16.1**
Mean maximum acceleration (hl s^{-2})	1273.19 (181.5)	2096.70 (170.5)	10.9*
Mean maximum prey distance (hl)	2.88 (0.4)	2.66 (0.4)	0.2

* $P < 0.05$, ** $P < 0.01$.

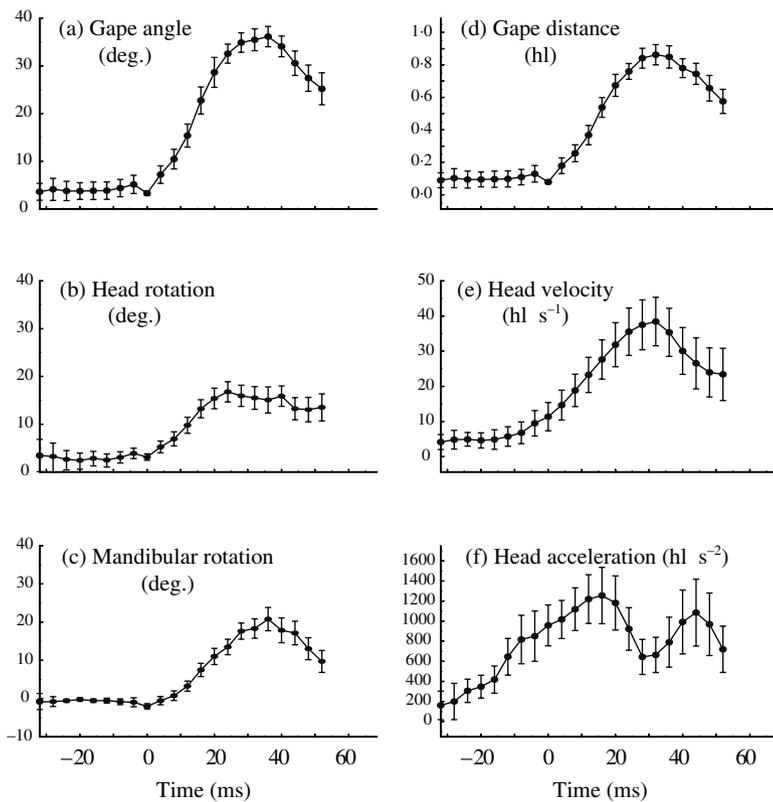


Fig. 6. Summary kinematic plot for *Thamnophis rufipunctatus*. Shown are 14 fast forward strikes from three individuals standardized by time of jaw opening. Error bars indicate one standard error of the mean. Mean gape angle was achieved approximately 30–35 ms after the start of mouth opening. Head and mandibular rotation began at nearly the same time though jaw rotation continued approximately 10 ms after head rotation had ceased. Head rotation was responsible for approximately one-half of the total gape. Peak gape distance approached 90% of head length (1.89 cm). Head acceleration occurred during jaw opening, and peak velocity coincided with peak gape. Mean peak head velocity across all strikes was approximately 82 cm s⁻¹.

constraints on fast forward striking as the two independently evolved forward strikers examined in this study shared some elements of their predatory strike. Third, the significant variation in kinematic pattern found among all three species in this study suggests that aquatic prey capture modes in thamnophiine snakes are diverse and vary at low phylogenetic levels.

AQUATIC FORWARD STRIKING: A HIGH-PERFORMANCE FEEDING BEHAVIOUR

Aquatic specialists use a high-performance, forward directed strike to capture prey underwater. High accel-

eration, high velocity and moderate to large amounts of cranial rotation characterized strikes of both aquatic species. In contrast, *T. sirtalis* strikes exhibited low acceleration and velocity and negligible amounts of cranial rotation. In addition, the specialists appeared to carefully aim strikes at specific prey items in contrast to the undirected strikes of *T. sirtalis*. Comparative data on strike success were not collected in this study, but *T. couchii* has been shown to catch significantly more fish than *T. sirtalis* under controlled conditions (Drummond 1983). This study supports an earlier suggestion that *T. sirtalis* probably depends on high prey density to capture prey with short lunges and sideways sweeps (Drummond 1983). In contrast, both *T. couchii* and *T. rufipunctatus* have evolved prey capture mechanisms that can successfully overcome a fast-starting prey in open water. Significantly, these species possess improved underwater visual acuity relative to other garter snakes (Schaeffel & De Queiroz 1990). The ability to orient to specific prey items at a distance underwater would appear to be a necessary prerequisite to long-distance forward directed attacks. An alternative to the bow wave hypothesis as an explanation for the predominance of sideways attack modes in aquatic snakes may simply be that most snakes have extremely poor abilities to visually select specific prey underwater. As a result, the majority of snakes may be incapable of detecting underwater prey without tactile cues. Thus lateral head sweeping might properly be regarded as a behaviour that maximizes the number of prey contacts when prey densities are high rather than as a behaviour that reduces the effects of predator-induced flow upon the prey.

If an open mouth significantly increases the drag of an aquatically striking snake, one might expect aquatic specialists to show reduced maximum gape angles relative to generalists. However, both aquatic and terrestrial species attained similar gape angles during the strike, suggesting that other factors, such as prey size, may have a stronger influence than hydrodynamics on optimal gape size. Alternatively, specialist taxa could be compensating for high drag on the head during forward strikes through morphological or behavioural mechanisms. The bullet-shaped heads of *T. couchii* and *T. rufipunctatus* seem likely to reduce overall head drag during the strike, potentially incurring lower drag during mouth opening and/or at maximum gape than the heads of generalist taxa. Specialists also showed a

Table 4. Results of univariate ANOVAs testing the effects of species on aerial attack performance in *Thamnophis couchii* and *T. sirtalis*. Table entries are group means and one standard error of the mean. *F* = *F*-ratio, hl = head length

Effect	<i>T. couchii</i>	<i>T. sirtalis</i>	<i>F</i>
Mean maximum gape angle (degrees)	38.37 (1.5)	37.70 (1.5)	0.1
Mean maximum velocity (hl s ⁻¹)	27.99 (3.2)	11.04 (3.2)	14.2*
Mean maximum acceleration (hl s ⁻²)	1273.19 (181.5)	227.92 (143.9)	14.2**
Mean maximum prey distance (hl)	2.88 (0.4)	4.90 (0.4)	9.8*

P* < 0.05, *P* < 0.01.

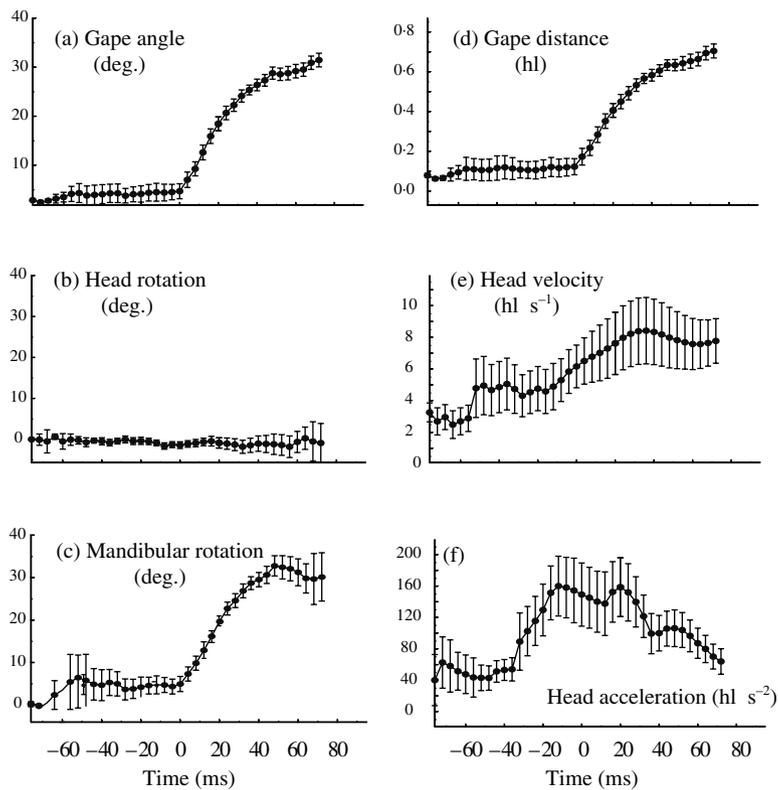


Fig. 7. Summary kinematic plot for *Thamnophis sirtalis*. Shown are 15 aerial attacks from four individuals standardized by the time of jaw opening. Error bars indicate one standard error of the mean. Mean gape angle was achieved approximately 50–70 ms after the start of mouth opening. Head rotation was negligible. Peak gape distance approached 70% of head length (1.56 cm). Head acceleration occurred during jaw opening, and peak velocity coincided with peak gape. Aerial attacks were much slower than the fast forward strikes observed in the specialist species. Mean peak head velocity across all strikes was approximately 11 cm s⁻¹.

shortened jaw-opening phase that might also help reduce head drag during aquatic strikes. In addition, the simultaneous rotation of the head and lower jaw to produce total gape might be a mechanism to balance drag forces on the skull during jaw opening. Flow visualization experiments would be useful to confirm effects of head shape and behaviour on skull hydrodynamics.

PARADIGMS, BOW WAVES AND COMPENSATORY SUCTION

This study does not conclusively demonstrate that *T. couchii* and *T. rufipunctatus* are not generating compensatory suction during feeding. However, kinematic and morphological evidence suggests that any suction generated in these species is likely to be negligible relative to that produced by true suction-feeding vertebrates. For example, some cryptodire turtles which are thought to generate only enough suction to overcome the bow wave (Summers *et al.* 1998), yet display remarkable excursion of the hyoid and expansion of the buccal cavity. Hyoid excursion was not quantified in this study but qualitative evidence

from feeding sequences suggests that buccal expansion is minor and passively associated with the initial phases of jaw opening. That garter snakes are capable of capturing fish underwater with forward-directed attacks suggests at least three possibilities with regard to the influence of the bow wave on prey capture in snakes. First, that snakes are capable of generating compensatory suction adequate to avoid displacing their prey simply through the opening of the mouth. Qualitative assessment of the strikes in this study suggests that this is unlikely to be true. Peak gape in both species often occurred at a distance of more than two head lengths from the prey, especially when total strike distance was long. As a result, mouth opening would seem to be an inadequate mechanism for mitigating bow wave effects in these species since the pressure differential between the intra-oral cavity and the water in front of the jaws would be expected to disappear well before prey contact. A second possibility is that garter snakes have developed behaviours or morphologies that mitigate the effects of predator-induced motion on the prey. The driving scissors strike that is characteristic of the specialists examined in this study may effectively move the point of contact of any bow wave from in front of the snout to a point inside the mouth. In other words, as a consequence of the long jaws of the predator, prey items may not encounter any predator-induced flow until they are well inside the oral cavity, at which point frictional forces from the teeth and jaws are sufficient to overcome hydrodynamic forces associated with bow waves or water displacement from the oral cavity during jaw closing. The third possibility is that for garter snakes, the inertia of the prey is sufficiently large to resist the bow wave created by the predator. This would imply that under some conditions, namely when a relatively small predator is feeding on relatively large prey at a relatively high velocity, bow wave effects might become irrelevant to feeding success. This last possibility is perhaps the most intriguing of the three as it would suggest that factors such as prey size, prey evasiveness, predator size, predator attack speed, head morphology and fluid dynamics interact to produce two very different kinds of prey capture environments for animals on the same order of size (aquatic turtles and garter snakes). Additional experiments focused on measuring pressure and fluid flow around the head will be helpful in determining which, if any, of these hypotheses are correct.

MODES OF PISCIVORY IN SPECIALIST SNAKES

Although *T. couchii* and *T. rufipunctatus* shared many gross features of strike kinematic pattern and performance, finer scale differences between these species suggest that they have evolved different prey capture strategies. *Thamnophis rufipunctatus* achieved slightly higher gape angle, and used more head rotation during mouth opening than *T. couchii*. While *T. rufipunctatus* generally struck at prey within 3 cm of the head, *T.*

couchii were observed to successfully catch prey from over 10 cm away and regularly struck at prey 4–6 cm distant. In addition to kinematic and performance differences, laboratory observations revealed differences in feeding behaviour between these species. *Thamnophis rufipunctatus* would frequently strike at prey from a submerged refuge, recruiting a third or less of the anterior trunk and almost always struck from beneath the prey. In contrast, *T. couchii* rarely struck from refugia, and would launch attacks from above or below the prey item, depending on the position of the snake in the water column. A notable characteristic of *T. couchii* prey capture was pronounced looping and compression of most of the trunk prior to strike initiation. Drummond (1983) also reported this behaviour during substrate crawling and found that attacks from the substrate or from midwater were the two most commonly observed predatory behaviours for this species.

Many behavioural characteristics of *T. rufipunctatus* suggest that it is an ambush predator. Relative to *T. couchii*, this species showed a shorter strike distance, lower amount of trunk recruitment and readiness to strike from refugia. Anecdotal field observations also support this interpretation of *T. rufipunctatus* ecology: this species generally forages in slow-moving streams and ponds (S. Arnold, unpublished data) and is often found submerged beneath or near rock refugia (Flehart 1967). In contrast, *T. couchii* often forages in fast-moving streams and rivers (S. Arnold, unpublished data.). It seems likely that long distance striking in *T. couchii* depends on the recruitment of most of the body into prestrike loops. This necessity might preclude long distance striking from a refuge, as hiding and striking would appear to place competing demands on trunk arrangement. A preference for long distance striking by *T. couchii* is suggested by both the low incidence of ambush predation from a refuge in this study and the relatively low frequency of rock crevice attacks reported by Drummond (1983) and is consistent with the classification of this species as an active, open water hunter.

AERIAL ATTACKS IN SPECIALISTS AND GENERALISTS

Aerial attacks by *T. couchii* exhibited higher velocity and acceleration than those of *T. sirtalis* (Table 4). This difference could reflect an increased morphological or physiological capacity for fast strikes in this species. *Thamnophis couchii* is the longest species of garter snake and also contains the most vertebrae (Rossman *et al.* 1996). If vertebral number is an important determinant of maximum strike speed, higher strike speeds in *T. couchii* than *T. sirtalis* may reflect this morphological difference. Alternatively, the increased visual acuity of *T. couchii* (Drummond 1985; Schaeffel & De Queiroz 1990) relative to *T. sirtalis* could result in regular, directed strikes at prey in *T. couchii* vs blind

or near-blind strikes at disturbances generated by darting prey in *T. sirtalis*. *Thamnophis sirtalis* may never exhibit a fast forward strike because it lacks the visual acuity necessary to orient to specific prey. With this constraint, it may not be energetically efficient to invest in high-energy strikes that have a low success rate. The preferred mode of prey capture in *T. sirtalis*, sideways sweeping, does not appear to depend on especially rapid movements for success at high prey densities.

STRIKING IN OTHER SNAKES: AQUATIC PREY CAPTURE VS 'FAST' TERRESTRIAL MODES

Peak velocities for fast terrestrial striking species (Cundall & Greene 2000) range from 1.6 to 3.5 m s⁻¹ for *Crotalus* (Van Riper 1954), 1.22–2.85 m s⁻¹ for *Pituophis* (Greenwald 1974), 1.5 m s⁻¹ for vipers (Janoo & Gasc 1992), and 0.6–2.1 m s⁻¹ for *Elaphe obsoleta* (M. Alfaro, unpublished data). On the basis of these and other studies, Cundall & Greene (2000) proposed that snake prey capture modes could be divided into two broad classes: slow captures (characterized by a lack of a prestrike preparatory phase and strike velocities within the range of normal movement) and fast captures (characterized by a prestrike preparatory phase and high strike velocities). Remarkably, *T. couchii* was routinely able to reach velocities comparable to those of terrestrial species (mean peak velocity = 1.12 m s⁻¹, maximum recorded velocity = 1.73 m s⁻¹) striking through water with an open mouth. Given the difference in density between air and water, *T. rufipunctatus* strikes also reached impressive speeds (mean peak strike velocity = 0.82 m s⁻¹, maximum recorded velocity = 1.2 m s⁻¹). These high speeds, combined with the observation that both species adjusted head and body orientation prior to striking (complex preparatory postural changes, Cundall & Greene 2000), reveal that fast capture strategies have evolved in aquatic environments as well as in terrestrial environments. Furthermore, it appears that morphological and physiological traits associated with fast prey capture in snakes are evolutionarily labile, as this behaviour has almost certainly evolved independently in *T. couchii* and *T. rufipunctatus* and possibly in *T. melanogaster* as well (De Queiroz & Lawson 1994). Only the generalist, *T. sirtalis*, exhibits a feeding strike that could be characterized as slow capture, i.e. low velocity and no preparatory phase. However, more studies will be needed to fully evaluate the hypothesis of divergence between slow and fast systems because prey type may have an important effect on strike performance (Wainwright 1989). For example, *T. sirtalis* striking terrestrially on highly evasive prey (*Hyla cinerea*) can reach peak velocities of 1.17 m s⁻¹ (M. Alfaro, unpublished data), which approaches values for other fast-striking species.

The ability of snakes to achieve fast or slow strike speeds depends critically on a component of prey

capture that has received very little attention: the kinematics and function of the anterior trunk. Almost nothing is known of how trunk loops, coils, and kinematic behaviour influence strike speed (but see Kardong & Bels 1998). While preparatory behaviour of the trunk may indeed be correlated with increased strike speeds, we presently lack a biomechanical model that relates trunk straightening to head acceleration as well as the comparative data on trunk kinematics. As a result, Cundall & Greene's (2000) characterization of strikes as fast or slow is almost certainly an oversimplification of what is likely to be a complex character system.

PISCIVORY IN SNAKES: A MODEL SYSTEM FOR EXAMINING FUNCTIONAL DIVERSIFICATION

In contrast to other squamates, piscivory is a primary feeding mode for a diversity of snake species. The first attempt to characterize aquatic feeding in terrestrial vertebrates predicted that hydrodynamic considerations would dictate a narrow range of solutions to the problem of feeding by secondarily aquatic vertebrates (Taylor 1987). However, the evidence from snake feeding rejects this paradigmatic view: forward striking is indeed a viable mode of underwater prey capture for amniotes, at least for snakes. In addition to the two species examined in this study, forward striking behaviour has been reported in *T. melanogaster* (Drummond 1983), *T. validus* (A. De Quieroz, unpublished data) and in the Old World natricines genus *Natrix* (A. Herrel, unpublished data). Thus, forward striking has probably evolved multiple times within natricine snakes, and quite possibly in other snake lineages as well. In addition, the specialists in this study may have evolved different prey capture strategies, suggesting that diversification of predatory mode occurs within the broad category of forward striking. Evidence suggests that there is high diversity in the prey capture modes of sideways sweeping taxa as well. For example, *Erpeton tentaculum* holds the anterior trunk nearly straight and ambushes prey that wander into a 'sweet spot' lateral to the head with an extremely rapid strike ($>180 \text{ cm s}^{-1}$) (Smith, Povel & Kardong 1998), whereas *Nerodia rhombifer* uses an open-mouthed sweeping behaviour that is very similar to that used by *T. sirtalis* (Drummond 1983). Yet *Nerodia* is also capable of faster ($60\text{--}70 \text{ cm s}^{-1}$) lateral strikes in which the neck and anterior trunk display remarkably high curvature (M. Alfaro, unpublished data). By recognizing that diversification has occurred within the predatory modes of aquatic snakes, the factors responsible for morphological, physiological and behavioural shifts in the feeding mechanism during the transition from terrestrial to aquatic feeding modes may be better studied. Given the diversity of behaviour and morphology in these animals, future study of aquatic foraging in snakes would seem to offer a rich system for the study of ecological, functional and behavioural evolution.

Acknowledgements

I would like to thank the following people for their help in various phases of this project. Anthony Herrel, Jay Meyer, Jim O'Reilly, Stevan Arnold and Michael Pfrender helped with snake collecting and provided stimulating discussion about aquatic prey capture in snakes. Mark Westneat generously provided facilities for data capture and analysis. Mark Westneat, Steve Arnold, Michael LaBarbera, Amy Driskell and two anonymous reviewers provided helpful criticism of several versions of this manuscript. Snakes were collected under scientific collecting permits to Stevan Arnold (CA) and Jay Meyer (AZ). This project was partially supported by grants from the American Society of Ichthyology and Herpetology, the Society for Integrative and Comparative Biology, and the University of Chicago. In addition, NSF DEB 9903934 to SJA and MP provided support for field collecting.

References

- Alfaro, M.E. & Arnold, S.J. (2001) Molecular systematics and evolution of *Regina* and the thamnophiine snakes. *Molecular Phylogenetics and Evolution* **21**, 408–423.
- Braun, T.B. & Cundall, D. (1995) Hydrodynamics of fishing in snakes (*Nerodia*). *American Zoologist* **35**, 105A.
- Cundall, D. & Deufel, A. (1999) Striking patterns in booid snakes. *Copeia* **1999**, 868–883.
- Cundall, D. & Greene, H.W. (2000) Feeding in snakes. *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates* (ed. K. Schwenk), pp. 293–333. Academic Press, San Diego, CA.
- De Quieroz, A. & Lawson, R. (1994) Phylogenetic relationships of the garter snakes based on DNA sequence and allozyme variation. *Biological Journal of the Linnean Society* **53**, 209–229.
- Drummond, H. (1983) Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Behaviour* **86**, 1–30.
- Drummond, H. (1985) The role of vision in the predatory behavior of natricine snakes. *Animal Behaviour* **33**, 206–215.
- Fitch, H.S. (1949) Study of snake populations in central California. *American Midland Naturalist* **41**, 513–579.
- Fleahy, E.D. (1967) Comparative ecology of *Thamnophis elegans*, *T. cyrtopsis*, and *T. rufipunctatus* in New Mexico. *Southwestern Naturalist* **12**, 207–230.
- Frazzetta, T.H. (1966) Studies on the morphology and function of the skull in the Boidae (Serpentes). II. Morphology and function of the jaw apparatus in *Python sebae* and *Python molurus*. *Journal of Morphology* **118**, 217–295.
- Greenwald, O.E. (1974) Thermal dependence of striking and prey capture by gopher snakes. *Copeia* **1974**, 141–148.
- Halloy, M. & Burghardt, G.M. (1990) Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*). *Behaviour* **112**, 299–318.
- Janoo, A. & Gasc, J.-P. (1992) High speed motion analysis of the predatory strike and fluorographic study of oesophageal deglutition in *Vipera ammodytes*: More than meets the eye. *Amphibia Reptilia* **13**, 315–325.
- Jayne, B.C., Voris, H.K. & Heang, K.B. (1988) Diet, feeding behavior, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homolopsinae) in Malaysia. *Fieldiana: Zoology* **50**, 1–15.

- Kardong, K.V. (1986) The predatory strike of rattlesnakes: when things go amiss. *Copeia* **1986**, 816–820.
- Kardong, K.V. & Bels, V.L. (1998) Rattlesnake strike behaviour: kinematics. *Journal of Experimental Biology* **201**, 837–850.
- Lauder, G.V. & Prendergast, T. (1992) Kinematics of aquatic prey capture in the snapping turtle *Chelydra serpentina*. *Journal of Experimental Biology* **164**, 55–78.
- Rossmann, D.A., Ford, N.B. & Siegel, R.A. (1996) *The Garter Snakes: Evolution and Ecology*. University of Oklahoma Press, Norman, OK.
- Savitzky, B.A.C. (1992) Laboratory studies on piscivory in an opportunistic predator. *Biology of the Pitvipers* (eds J. A. Campbell & E. D. J. Brodie), pp. 347–368. Selva, Tyler, TX.
- Schaeffel, F. & De Queiroz, A. (1990) Alternative mechanisms of enhanced underwater vision in the garter snakes *Thamnophis melanogaster* and *Thamnophis couchii*. *Copeia* **1990**, 50–58.
- Smith, T.L., Povel, G.D.E. & Kardong, K.V. (1998) Predatory strike of the aquatic tentacled snake: getting a mouth full. *American Zoologist* **38**, 202A.
- Summers, A.P., Darouian, K.F., Richmond, A.M. & Brainerd, E.L. (1998) Kinematics of aquatic and terrestrial prey capture in *Terrapene carolina*, with implications for the evolution of feeding in cryptodire turtles. *Journal of Experimental Zoology* **281**, 280–287.
- Tanner, W.W. (1988) Status of *Thamnophis sirtalis* in Chihuahua Mexico (Reptilia: Colubridae). *Great Basin Naturalist* **48**, 499–507.
- Taylor, M.A. (1987) How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society* **91**, 171–195.
- Van Damme, J. & Aerts, P. (1997) Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira: *Chelodina*). *Journal of Morphology* **233**, 113–125.
- Van Riper, W. (1954) Measuring the speed of a rattlesnake strike. *Animal Kingdom* **57**, 50–53.
- Voris, H.K., Voris, H.H. & Liat, L.B. (1978) The food and feeding behavior of a marine snake, *Enhydrina schistosa* (Hydrophiidae). *Copeia* **1978**, 134–146.
- Wainwright, P.C. (1989) Prey processing in haemulid fishes: patterns of variation in pharyngeal jaw muscle activity. *Journal of Experimental Biology* **141**, 359–376.
- Walker, J.A. (1998) Estimating velocities and accelerations of animal locomotion: a simulation experiment comparing numerical differentiation algorithms. *Journal of Experimental Biology* **201**, 981–995.
- Young, B.A. (1991) The influences of the aquatic medium on the prey capture system of snakes. *Journal of Natural History* **25**, 519–531.

Received 7 February 2001; revised 18 August 2001; accepted 29 August 2001