Comparisons of Aquatic Versus Terrestrial Predatory Strikes in the Pitviper, *Agkistrodon piscivorus*

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ABSTRACT   Recent studies comparing terrestrial versus aquatic locomotion in animals have shown that changes in kinematics, muscular activation patterns, and performance across media are often dramatic. Surprisingly, however, despite the importance of feeding to the survival of most animals, few studies have compared differences in feeding behaviour between media. The present study compares prey-capture behaviour, strike success, strike velocity and acceleration, and prey-capture kinematics in a semi-aquatic pitviper (*Agkistrodon piscivorus*) when capturing both terrestrial (mice) and aquatic (fish) prey in a standardized laboratory setting. Strike velocity and acceleration did not differ significantly between media, but instead were positively correlated with initial prey distance. By contrast, the kinematics of terrestrial and aquatic strikes differed significantly in several aspects: max gape angle during the retraction phase, angular velocity of mouth closing during the strike, and the initial head angle before the strike. Terrestrial strikes were associated with higher gape angles during the retraction phase, higher angular velocities of mouth closure, and a more inclined head angle at the onset of the strike. Finally, strike success differed significantly between strike types, with terrestrial strikes being considerably more successful than aquatic strikes. Strike success likely differed due to the relatively slow mouth-closing velocity of aquatic strikes. *J. Exp. Zool. 303A:476–488*, 2005.   © 2005 Wiley-Liss, Inc.

INTRODUCTION

Recent studies on animals moving in different environments have demonstrated significant changes in locomotor behaviour in response to the differences in the physical properties of the medium through which they move. For instance, anguillid eels undulating through water or across land alter the relative timing of the activation of their axial musculature between environments (Gillis, '98). Additionally, studies comparing terrestrial versus aquatic locomotion in birds, amphibians, and lizards show that changes in kinematics, muscular activation patterns, and performance across media can be dramatic (e.g., Biewener and Gillis, '99; Gillis and Biewener, 2000; Biewener and Corning, 2001; Ashley-Ross and Bechtel, 2004). Differences in locomotor patterns between water and land are largely believed to be a consequence of the difference in physical properties between the two media. Water is forty times more viscous and eight hundred times denser than air, so considerable drag forces will be generated when animals move through water, thereby strongly influencing how animals move within the aquatic medium (see e.g., Vogel, '81).

Although an increasing number of studies have examined differences in the kinematics of locomotion in water versus on land, fewer studies have examined differences in the feeding behaviour of animals feeding in different media (but see Lauder and Shaffer, '85, '88; Reilly and Lauder, '88; Shaffer and Lauder, '88). This lack of data comparing how individuals feed on land versus within water is surprising given the documented differences in locomotor behaviour, and the obvious importance of feeding ability to the fitness of an organism. Whereas a diversity of terrestrial

prey-capture behaviours has evolved amongst tetrapods in general (see Schwenk, 2000 for an overview), the vast majority of aquatically feeding tetrapods rely on suction feeding or filtration mechanisms (Lauder, '85; Bramble and Wake, '85; Van Damme and Aerts, '97; Herrel and Aerts, 2003). Suction feeding in tetrapods is generally achieved via a robust hyoid apparatus that, when depressed, acts to increase the volume of the buccal cavity, thereby increasing the pressure differential between the buccal cavity and the surrounding water. In snakes, however, the hyoid apparatus is largely reduced as a consequence of its specialization for chemoreception (McDowell, '72; Schwenk, '94), and hence cannot be used to expand the oral cavity and generate suction. Consequently, snakes must strike at aquatic prey in a manner similar to that used in terrestrial environments. As snakes are unable to generate suction, aquatic strikes will likely involve high drag forces and will be subject to substantial bow-wave generation. These hydrodynamic constraints may in turn result in decreased strike speed and displacement of the prey item away from the predator as a result of bow-wave generation (Drummond, '83; Taylor, '87; Young, '91).

Aquatic snakes capture prey by striking either frontally (as observed for terrestrial snakes), or by using an open mouthed, lateral side-sweeping motion (Drummond, '83; Taylor, '87; Smith et al., 2002; Alfaro, 2002, 2003). Based on considerations of the physical properties of the medium, previous authors have suggested that lateral side-sweeping may be more effective in circumventing hydro-dynamic constraints, especially in animals, such as snakes, that are unable to generate suction (Taylor, '87; Young, '91). This argument is largely based on the fact that drag forces will increase proportional to the shape (i.e., whether the shape is streamlined or not) and the area of the surface moving in the direction of the strike (Vogel, '81). Thus, animals unable to generate suction could be expected to employ rapid lateral head motions (minimizing surface area) to capture elusive prey such as fish (e.g. Alfaro, 2002, 2003; Smith et al., 2002). Yet, fast frontal strikes have independently evolved multiple times in highly specialized lineages of aquatically feeding natricine snakes (Alfaro, 2002, 2003; see Cundall and Greene, 2000 for a discussion of fast versus slow snake strikes). The ability of these snakes to feed effectively in the aquatic medium has been attributed to their relatively small, bullet-shaped heads (Hibbits, 2001; Alfaro, 2002), which are thought to stream-

line the flow around the snake's head and body, thereby enabling fast aquatic strikes. Additionally, fast strikes are likely essential to capture evasive aquatic prey such as fish. Surprisingly, even though vipers have one of the fastest known strikes among snakes (Van Riper, '54; Janoo and Gasc, '92; Kardong and Bels, '98; Young et al., 2001; LaDuc, 2002), the cottonmouth (*Agkistrodon piscivorus*) is the only viper known to actively feed on fish. The paucity of aquatically feeding snakes among vipers is believed to be due to the relatively large triangularly-shaped head typical of vipers (Young, '91). Not only may the absolutely large head of a viper generate substantial bow-waves and induce considerable drag, but the *shape* of the head also appears to be poorly designed for aquatic feeding. Experimental studies using preserved specimens have demonstrated that the head shape of *A. piscivorus* tends to create turbulent flow around the head during simulated underwater strikes, leading Young ('91) to predict that these animals should employ a lateral head motion when capturing aquatic prey. By contrast, previous authors have reported observing *A. piscivorus* using frontal strikes to capture fish (Burkett, '66; Savitzky, '92). Nonetheless, these studies did not employ high-speed cinematography, making it difficult to definitively characterize the aquatic strike behaviour of *A. piscivorus*.

Cottonmouths will strike at both aquatic and terrestrial prey, making these snakes particularly good subjects for testing the prediction that aquatic strikes are constrained by the aquatic medium (i.e. have lower maximum speeds compared to terrestrial strikes; Young, '91). Although the cottonmouth is a generalist forager that will consume terrestrial prey such as rodents and reptiles, dietary studies have shown that up to 44% of its diet by volume is composed of fish (Vincent et al., 2004a, b). Moreover, cottonmouths are known to actively forage aquatically for fish in nature (Savitzky, '89). Whereas some basic prey capture kinematics have been quantified for terrestrial strikes in the cottonmouth (Kardong, '74, '75, '82), no studies have examined the kinematics and strike velocity/acceleration of the cottonmouth strike during both aquatic and terrestrial feeding to evaluate the effect of the differences in medium on prey capture behaviour.

To examine this issue, various behaviors were quantified: prey-capture, strike success, strike velocity and acceleration, and prey-capture kinematics for adult cottonmouths capturing both terrestrial (mice) and aquatic (fish) prey in a

standardized laboratory setting. These data prompted two related questions: (1) Does strike success differ between media? (2) If so, are these differences in strike success associated with differences in strike kinematics and/or strike velocity/acceleration? Finally, these data are compared to other published studies on snake strike behaviour and kinematics.

MATERIALS AND METHODS

Collection, housing, and feeding trials

The experimental procedures outlined here were approved by IACUC prior to the start of the investigation. Cottonmouths (*Agkistrodon piscivorus*) were collected from the Hebert Research Center in Belle Chasse, Louisiana. Snakes of similar sizes were used ($N=4$, snout-vent length$=55\pm14.1$ cm [SD]), because velocity and acceleration often differ among differently sized animals. Snakes were housed in aquaria specifically designed for feeding trials. Each aquarium was composed of a raised dry platform (35 cm $\times$ 25 cm $\times$ 20 cm; length $\times$ width $\times$ height) and a water-filled feeding arena (21 cm $\times$ 15 cm $\times$ 35 cm). The living area was separated from the feeding arena by a removable piece of Plexiglas. In this manner, the prey could be placed inside the feeding arena without the researcher having any direct contact with the snake. The floor of the platform was 15 cm above the floor of the feeding arena. Thus, during feeding trials, the snake was initially looking down into the feeding arena. This design was used because cottonmouths have been reported as orienting towards fish prey from above the water column and subsequently striking in a forward manner at the fish (Savitzky, '92).

Although not entirely reflecting natural terrestrial strike behaviour, the standardized design for both aquatic and terrestrial strikes ensured that any kinematic or velocity/acceleration differences would be the result of the properties of the medium, rather than differences in strike position. To facilitate kinematic analyses a mirror (19.5 cm $\times$ 19.5 cm) was placed at exactly 45° above the feeding arena.

Feeding trials

Cottonmouths were not fed for a period of three weeks prior to feeding trials to facilitate feeding. For aquatic strikes, water was poured into the feeding arena until the water line was just below the floor of the snake's living area. A single fish (*Fundulus grandis*; mean length from snout tip to the start of the caudal fin 4.3 ± 0.7 cm) was then placed inside the feeding arena. This fish species was used because it has been previously reported in the diet of cottonmouths (Vincent et al., 2004b). Next, the Plexiglas separator was removed, allowing the snake to strike at the fish. For terrestrial strikes, a single three-week-old mouse (mean snout-vent length 4.1 ± 0.8 cm) was placed inside the feeding arena, and the Plexiglas separator was removed. Strikes were filmed using a Redlake MotionScope PCI camera and Redlake strobe lights (Motion engineering Co. Indianapolis, IN) set at 250 fps. Terrestrial strikes were recorded for four individuals, and aquatic strikes were recorded for three of these same individuals (Table 1).

Kinematics and velocity/acceleration

Strike kinematics and velocity/acceleration were analyzed by digitizing homologous externally-visible landmarks on the heads of snakes and prey for each frame of the predatory sequence using PEAK Motus 6.1 (PEAK Inc., Englewood, CO USA). The landmarks used were the tip of the upper jaw, tip of the lower jaw, corner of the mouth, tip of the upper jaw in dorsal view, tip of the fang, eye of the prey, and the anterior most point of the prey in dorsal view. All landmarks were placed on the right side of either the snake or prey. For scaling purposes, the beginning and the end of the feeding arena were digitized. Horizontal

TABLE 1. *The numbers of strikes recorded for each individual snake and for each data set (performance vs. kinematic data). The relevant morphological variables for each individual are also reported*

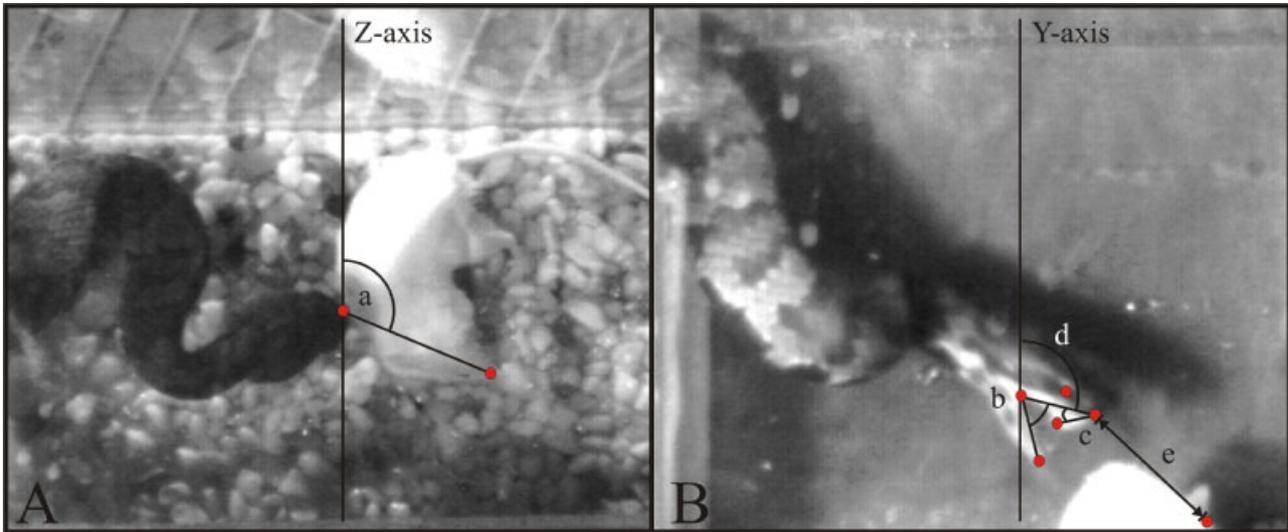| Individual	# terrestrial strikes performance	# terrestrial strikes kinematics	# aquatic strikes performance	# aquatic strikes kinematics	Head length (cm)	SVL (cm)
Ap-1	4	4	0	0	3.72	68.4
Ap-2	9	5	5	4	2.73	45.3
Ap-3	9	5	14	9	2.52	42.0
Ap-5	5	5	5	5	3.62	67.5

Fig. 1. Figure illustrating the points digitized on the head of the snake and on the prey as well as the angular variables determined. A) Dorsal view of the snake at the onset of prey capture. The head orientation angle (a) was calculated as the angle subtended by the line interconnecting the tip of the prey and the tip of the snake and the Z-axis. B) Lateral view of the snake about halfway through the strike. The gape angle (b) was calculated as the angle subtended by the lines interconnecting the tip of the lower jaw and the corner of the mouth, and the tip of the upper jaw and the jaw vertex. The fang angle (c) was calculated as the angle subtended by the line interconnecting the tip of the fang and the tip of the upper jaw, and the line interconnecting the corner of the mouth and the tip of the upper jaw. The head angle (d) was calculated as the angle between the line interconnecting the corner of the mouth and the tip of the upper jaw and the Y-axis. Prey distance was calculated as the rectilinear distance between the tip of the upper jaw and the eye of the prey (e).

(x) and vertical (y) coordinates were recorded for each landmark for every frame of the sequence.

Several kinematic variables (see Fig. 1) were calculated from these landmarks: the gape angle (the angle between the tip of the upper jaw, the corner of the mouth, and the tip of the lower jaw); the head angle (the angle between the y-axis, the corner of the mouth, and the upper jaw); the fang angle (angle between the corner of the mouth, the tip of the upper jaw, and the fang tip); and orientation of the head in dorsal view (angle between the z-axis, the dorsal tip of the head, and the dorsal tip of the prey). Strike velocity and acceleration were calculated by filtering the raw coordinates of the snout tip using a quintic-spline procedure, after which velocities and accelerations were calculated by numerical differentiation. To determine the maximum angular velocity of the mouth during opening and closing, the gape profile was smoothed using a quintic-spline procedure (see Walker, '98) and the angular jaw velocity calculated as previously mentioned. The following timing variables were extracted from the kinematic data set: time to max gape angle, time to max fang angle, time to prey contact, and time to contact with water for aquatic strikes. The initial distance of the prey relative to the snake's head, the orientation of the head in dorsal view at the onset of the strike, and the orientation of the head in lateral view at the onset of the strike and at its alignment with prey were also calculated for all strikes.

For analytical purposes, strikes were subsequently divided into a strike and a retraction phase (Fig. 2). The strike phase was defined as beginning with the first movement of the snake and ending at the maximal forward displacement of the snout tip. The retraction phase started at the time of maximal forward displacement of the snout tip and lasted until the snake had returned to its resting position. Several kinematic and performance variables were calculated for the strike and retraction phases separately. Peak and average velocity and acceleration of the head during the strike were both calculated. For aquatic strikes, average velocity of the head before (aerial phase) and after water contact (aquatic phase) was calculated. Maximum gape angle and fang angle during the strike phase was also calculated. Peak and average head retraction velocity were calculated for the retraction phase, as well as the maximal gape and fang angles.

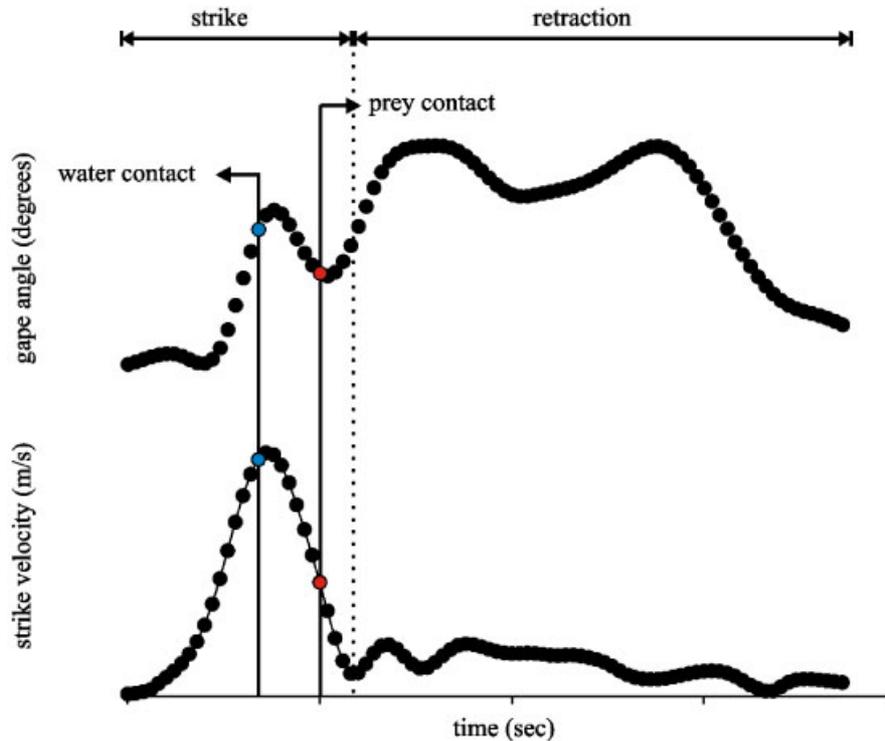In addition to the aforementioned kinematic variables, strike success was quantified by calcu-

Fig. 2. Representative strike and gape profile of an aquatic strike illustrating the kinematic phases as defined within the strike. The actual strike phase comprises the phase starting from the first movement of the snake until the end of the forward movement of the head in the direction of the prey. The retraction phase begins at the initiation of head retraction and ends when the head has returned to its resting position. In this case, the strike is unsuccessful and is followed by a second slow strike associated with an additional irregular double-humped gape cycle. Also indicated are the point of water contact and prey contact. The aerial phase of the strike is defined as beginning at the onset of the strike until water contact. The aquatic phase of the strike is defined as beginning at water contact and ending at the onset of head retraction.

lating the total number of successful and unsuccessful strikes in each environment for each snake. The part of the head that first contacted the prey in both aquatic and terrestrial strikes (i.e., upper and/or lower jaw) was recorded.

Statistical analysis

All variables were Log_{10} transformed prior to statistical analyses. Strike kinematics and velocities/accelerations have been shown to differ between successful and unsuccessful strikes in other snake species (Kardong and Bels, '98), therefore a MANOVA was used to test for differences between successful and unsuccessful strikes. No differences were detected in kinematics, strike velocity, and acceleration between successful and unsuccessful strikes (Wilk's Lambda=0.051; P=0.54), and therefore all strikes were pooled for further analysis. To explore whether prey distance may affect strike velocity and/or strike acceleration, these variables were

regressed against initial prey distance using a least-squares regression. As strike velocity and acceleration were both significantly related to initial prey distance, a MANCOVA was used, with prey distance as the covariate to test for differences between aquatic and terrestrial strikes in their velocity and acceleration. Subsequent univariate ANCOVAs with the individual introduced as a random factor into the analysis were used to explore whether velocity and/or acceleration differed between the two media. For all univariate tests, significance levels were adjusted using the sequential Bonferroni correction procedure (Rice, '89).

As no effect of prey distance was detected on the kinematic variables aquatic and terrestrial strike kinematics were compared using a MANOVA on the data from the three individuals that fed in both environments. To test which specific variables differentiated between aquatic and terrestrial strikes, a one-way ANOVAs was used, with individual introduced as a random factor and

corrected the significance level using sequential Bonferroni corrections (Rice, '89).

To examine if strike success differed significantly between aquatic and terrestrial strikes, the proportion of successful strikes (i.e., number of successful strikes divided by the total number of strikes) was calculated for both aquatic and terrestrial strikes. A Kolmogorov-Smirnov test (KS) was then used to test for differences in the proportion of successful strikes (relative to the total number of each strike type) between aquatic and terrestrial strikes. Chi-square tests were performed to examine if snakes contacted aquatic versus terrestrial prey differently, and whether strike success differed in the two media. All statistical analyses were performed on SPSS (V. 11.5; SPSS Inc.).

RESULTS

In the feeding trials, forty terrestrial strikes, and fifty-four aquatic strikes were observed, and scored as successful or not. A total of thirty-five terrestrial strikes and fifty aquatic strikes were filmed. Estimates were made of strike velocity, strike acceleration, and the contact point of the snake's head with the prey for twenty-four aquatic strikes and twenty-seven terrestrial strikes (Table 1). A full kinematic data set was recorded for eighteen aquatic strikes and nineteen terrestrial strikes. It was not possible to obtain a full kinematic data set for some videos, due to the snake's head being obscured by the prey. Therefore, only videos in which the entire head could be viewed throughout the feeding trial were used.

Strike success differed significantly between aquatic and terrestrial strikes (D_{max}=0.97, P=0.001), with terrestrial strikes being more successful. Specifically, of the 40 terrestrial strikes visually observed here, 38 were successful (95%), whereas only seven of the fifty-four aquatic strikes were successful (13%). Prey contact also differed between aquatic and terrestrial strikes, with prey contact occurring almost exclusively at the lower jaw for aquatic strikes (χ^2=10.28, d.f.=23, P=0.001), and the upper jaw for terrestrial strikes (χ^2=12.56, d.f.=26, P=0.0001).

GENERAL DESCRIPTION OF PREY-CAPTURE

Terrestrial prey-capture

As is typical of vipers in general (see Kardong and Smith, 2002 for an overview), *A. piscivorus*
began its predatory sequence by tongue flicking before orienting towards the mouse. Once the snake detected the mouse, the snake would move closer to the mouse until the tip of the snake's lower jaw was 5.8–18.0 cm from the snout tip of the mouse (4.8 cm on average). At this point the snake's head was oriented horizontally to the mouse's snout tip at an average angle of 186.5 ± 20.0 degrees indicating that the mouse was oriented perpendicular to the long axis of the head of the snake (see Table 2), and relative to the Y-axis at an average angle of 152.0 ± 22.1 degrees (i.e., pointing down at the mouse). Thus, before the strike, the head was both relatively close to the mouse and at a relatively steep angle to the Y-axis. As noted by Kardong ('75), before striking at a mouse, *A. piscivorus* bends its trunk into high amplitude S-shaped curves, and subsequently waits for the mouse to move before initiating a fast frontal strike. Once the strike was initiated, both mouth opening and fang erection occurred within the first 0.03–0.07 seconds of the strike. During the strike phase, the average max gape and fang angles were 73.3 ± 4.90 degrees and 76.8 ± 3.39 degrees respectively. Jaw opening resulted from the simultaneous depression of the mandibles and the dorsal flexion of the braincase and snout (see Kardong, '74 and Cundall, '87 for an overview of jaw opening mechanics in *Agkistrodon*). The point of contact with the mouse during terrestrial strikes was typically the fangs and upper jaws. However, it could not be determined from these videos whether both fangs or only one fang penetrated the prey initially. Within a few milliseconds of the upper jaws contacting the mouse, the lower jaw would rapidly close around the mouse. In only two strikes did both the upper and lower jaws contact the prey simultaneously, similar to the driving scissors action in *Pythons* (Deufel and Cundall, '99). During terrestrial strikes, *A. piscivorus* typically released its prey shortly after mouth closure. Specifically, *A. piscivorus* would rapidly lift its head while simultaneously opening its mouth and disengaging its fangs, thereby distancing the mouse from the snake's head. During the release of the mouse, the snake erected its fangs a second time to an average angle of 74.4 ± 4.50 degrees for a period ranging from 0.03–0.10 seconds. Finally, as the snake moved back to its initial resting position, it would close its mouth and retract its fangs. Thus, both the strike and retraction phases were characterized by a single gape cycle (i.e., one mouth opening and closing cycle for each).

TABLE 2. Mean ± 1 SEM of aquatic and terrestrial strike variables

Variable	Aquatic strikes	Terrestrial strikes
	Performance variables	
Max velocity (m/s)	1.62 ± 0.09	1.53 ± 0.08
Max acceleration (m/s^2)	75.5 ± 9.35	74.7 ± 9.32
Avg. velocity to contact (m/s)	0.81 ± 0.07	0.90 ± 0.07
Avg. acceleration to contact (m/s^2)	33.9 ± 3.58	48.0 ± 8.30
Avg. retraction velocity (m/s)	0.42 ± 0.04	0.54 ± 0.04
Avg. retraction acceleration (m/s^2)	16.2 ± 2.04	37.6 ± 9.43
Avg. aerial strike velocity (m/s)	0.66 ± 0.06	NA
Avg. strike velocity after contact w/water (m/s)	1.22 ± 0.12	NA
	Kinemactic variables	
Max gape angle (degrees)	66.4 ± 3.64	73.3 ± 4.90
Max fang (degrees)	64.6 ± 6.48	76.8 ± 3.39
Max gape angle during retraction (degrees)	69.7 ± 5.24	89.0 ± 5.29
Max fang angle during retraction (degrees)	65.2 ± 4.95	74.4 ± 4.50
Max angular jaw opening velocity (degrees/s)	2920 ± 150	3570 ± 190
Max angular jaw closing velocity (degrees/s)	360.0 ± 40.0	1280 ± 160
Initial head orientation (degrees)	150.4 ± 17.5	186.5 ± 20.0
Head orientation at prey alignment (degrees)	203.7 ± 20.9	180.0 ± 19.0
Head orientation at contact w/water (degrees)	204.4 ± 18.3	NA
Initial head angle (degrees)	12.3 ± 1.34	152.0 ± 22.1
Time to max gape (s)	0.08 ± 0.03	0.05 ± 0.01
Time to max fang (s)	0.06 ± 0.01	0.05 ± 0.01
Distance to prey (cm)	9.77 ± 1.11	4.84 ± 0.675

Bold variables were significantly different between aquatic and terrestrial strikes after sequential Bonferoni correction. Italicized variables were no longer significant after Bonferroni correction.

Aquatic prey-capture

Once the researcher placed a fish inside the feeding arena, the snake would begin tongue flicking and soon thereafter, orient towards the fish. Upon the snake detecting the fish, the snake would typically bend its trunk into high-amplitude S-shaped curves. At this point, the head in dorsal view was oriented relative to the snout tip of the fish at an average angle of 150.4 ± 17.5 degrees (see Table 2) indicating that the fish was oriented approximately perpendicular to the long axis of the head of the snake. The head angle at the onset of the strike was 12.3 ± 1.34 degrees on average indicating a markedly less inclined position than that observed during terrestrial strikes. The distance to the prey ranged from 2.4–17.3 cm (on average 9.8 cm). Thus, the snake's head before the strike was both relatively far from the fish, and nearly perpendicular to the Y-axis. Once the strike was initiated, both mouth opening and fang erection occurred within the first 0.03–0.07 seconds of the strike. The average max gape and fang angles were slightly smaller than those for terrestrial strikes (Table 2), although these angles did not differ significantly between terrestrial and aquatic strikes (see below). Interestingly, mouth opening occurred prior to water contact (Fig. 2). Unlike terrestrial strikes, the point of contact with the prey was almost exclusively the lower jaw. Additionally, the jaw-closing phase of aquatic strikes was significantly slower than in terrestrial strikes (Table 2), and as a result, the fish usually escaped before the mouth could be fully closed. During both the strike and retraction phases, *A. piscivorus* often opened and closed its mouth multiple times, and thus, the aquatic strike of *A. piscivorus* can be characterized as having multiple gape cycles. All strikes recorded were fast frontal strikes.

Strike velocity and acceleration

For both aquatic and terrestrial strikes, max velocity and the average velocity to prey contact showed significant correlations with initial prey distance (all $P < 0.001$; see Fig. 4). In other words, longer strikes-for both aquatic and terrestrial strikes-were associated with higher velocities. For aquatic strikes, max acceleration was weakly, but significantly, correlated with the initial prey distance ($r^2 = 0.18$; d.f. ^{2} 23, P ^{2} 0.038). Analysis of

covariance demonstrated significant effects of the medium on the average velocity ($F_{1, 4.68}^2$ 11.81; P^2 0.021) and average acceleration ($F_{1, 3.38}^2$ 9.02; P^2 0.049) during the strike phase. Terrestrial strikes were on average faster and associated with higher average accelerations (Table 2). However, none of these differences remained significant after Bonferroni correction. Individual effects and 'individual by medium' interaction effects were non-significant.

Prey-capture kinematics

A multivariate analysis of variance showed significant overall effects of the medium on the prey capture kinematics in *A. piscivorus* (Wilks' Lambda $F_{10,18}^2$ 12.14; $P < 0.001$). Individual effects (F^2 1.73) and 'individual by medium' effects (F^2 1.18) were non-significant ($P > 0.05$). Subsequent univariate F-tests showed that the difference between aquatic and terrestrial strikes was associated with differences in the maximal gape angle during retraction, the maximal angular velocity of mouth closing and the initial head angle (all $P < 0.005$; see Table 2). Differences remained significant after sequential Bonferroni correction. Terrestrial strikes were associated with higher gape angles during the retraction phase, higher angular velocities of mouth closing and a more inclined head angle at the onset of the strike.

DISCUSSION

Comparative strike speeds, success, and kinematics

Strike velocity and acceleration

In this study, peak velocity and acceleration were generally achieved a few milliseconds prior to prey contact, for both aquatic and terrestrial strikes (Fig. 3). Kardong and Bels ('98), Smith et al. (2002), and Alfaro (2002) found similar patterns for peak velocity and acceleration relative to prey contact in a terrestrially feeding viper (*Crotalus viridis*), an aquatic specialist homolapsine (*Erpeton tentaculatum*), and three species of garter snakes (*Thamnophis sp.*), respectively. By contrast, LaDuc (2002) found that the predatory strike of the viper *Crotalus atrox* reaches its peak velocity and acceleration either at, or just after initial prey contact. Previous authors have suggested that fast frontal predatory strikes-as seen here-should reach their peak velocities and accelerations prior to prey contact, thereby reducing the potential for mechanical damage from a head-on collision with the prey (Kardong and Bels, '98; Cundall and Greene, 2000; Cundall, 2002).

Among solenoglyphs (i.e., snakes with retractable fangs), the average maximal velocity for terrestrial strikes reported here (1.53 m/s) was similar to those reported for *Vipera ammodytes* (1.47 m/s), and *Bitis gabonica* (1.55 m/s) (Janoo and Gasc, '92). On the other hand, the average maximal velocity reported here was substantially slower than that reported for *Crotalus atrox* (3.48 m/s, Young et al., 2001; 2.61 m/s, LaDuc, 2002). The average maximal acceleration of the terrestrial strike in *A. piscivorus* (74.7 m/s^2) was also lower than that reported for *C. atrox* (326 m/s^2, LaDuc, 2002). Therefore, *A. piscivorus's* terrestrial strike velocity and acceleration are comparable to most other solenoglyphs for which strike data exists, but it is not an extreme for this group.

The aquatic strike of *A. piscivorus* has both a higher average maximal velocity (1.62 m/s) and maximal acceleration (75.5 m/s^2) than the average maximal velocity (1.14 m/s) and maximal acceleration (39.4 m/s^2) of the fastest known aquatically-feeding garter snake, *Thamnophis couchii* (Alfaro, 2002). This finding is particularly interesting because one would expect *A. piscivorus*, with its bulky triangular head to be easily outperformed by a garter snake with a relatively small, bullet-shaped head (Alfaro, 2002). This difference might be associated with the starting point of the strike. *Agkistrodon piscivorus* always began its aquatic predatory strike from above the water (termed *aerial* strike, see Drummond, '83), whereas *T. couchii* was fully submerged while striking aquatically. Thus, the lack of resistance present at the beginning of *A. piscivorus's* semi-aquatic aerial strike may enable it to reach much higher peak velocities and accelerations than the fully underwater strike of *T. couchii*. Indeed, Young ('91) suggested that aerial strikes should be much less affected by hydrodynamic constraints than fully submerged strikes, although aerial strikes should still encounter considerable resistance once the snake's head has entered the water. Furthermore, cottonmouths typically struck at fish 7–10 cm below the surface of the water (not simply at the surface of the water where hydrodynamic constraints would be minimized), indicating that hydrodynamic constraints are functionally relevant during aquatic predation by cottonmouths.

Within *A. piscivorus*, it is interesting that strike velocity/acceleration does not differ significantly between aquatic and terrestrial strikes (Table 2).
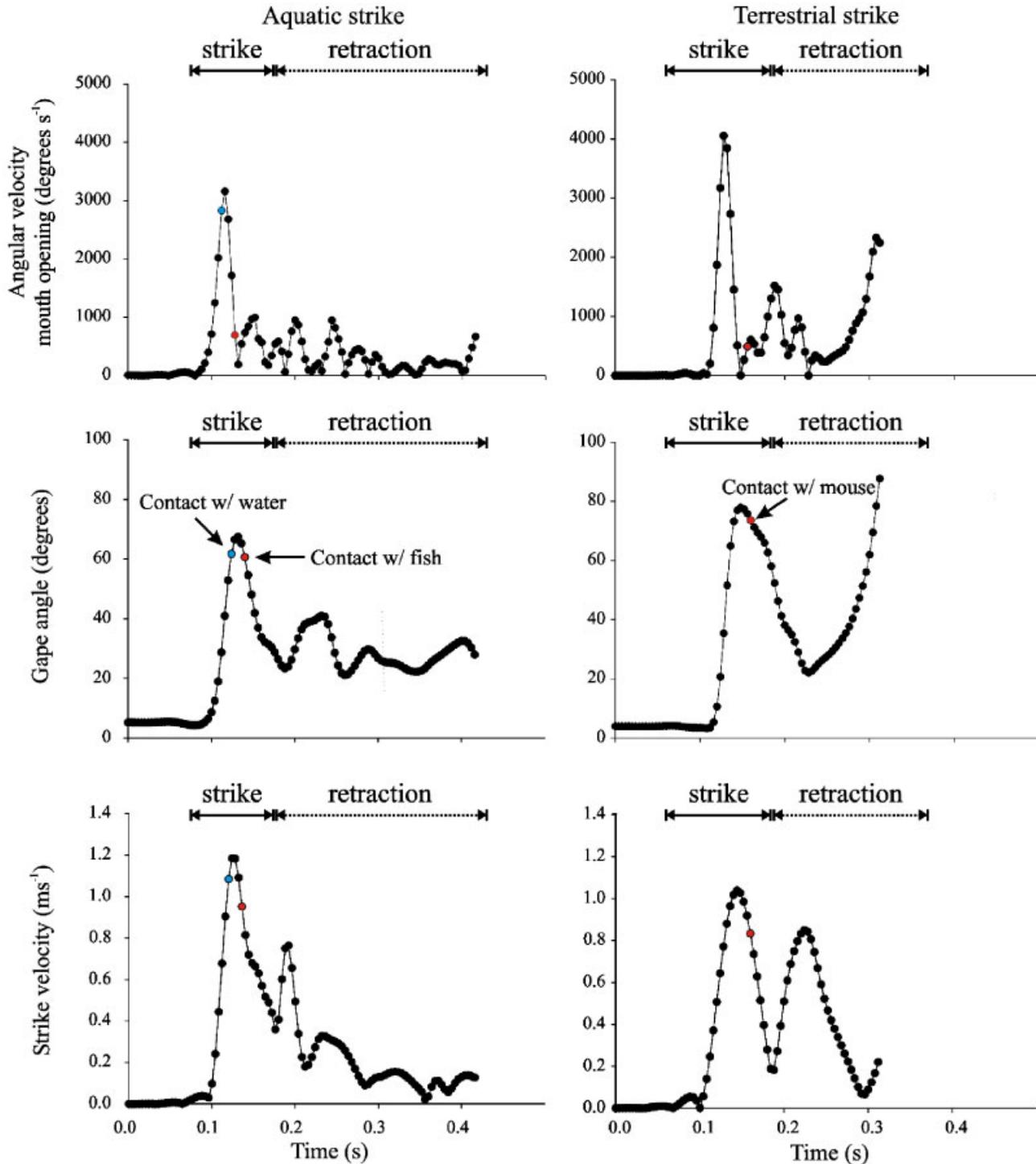
Fig. 3. Representative kinematic profiles illustrating aquatic (left) and terrestrial (right) strikes from a single individual of *A. piscivorus*. Note the similarity in overall kinematics between aquatic and terrestrial strikes. Also note the second, pronounced jaw opening phase occurring during terrestrial strikes during which the mouse is released. Unexpectedly, aquatic strikes are slightly faster in maximum velocity than terrestrial strikes. Water contact is indicated in blue; prey contact in red. Also indicated are the 'strike' and the 'retraction' phases.

Even more striking, peak velocities and accelerations are slightly higher (but not significant) for aquatic strikes. Due to the difference in physical properties of water and air, one would predict that the peak strike velocity of aquatic strikes should be markedly slower than for terrestrial strikes
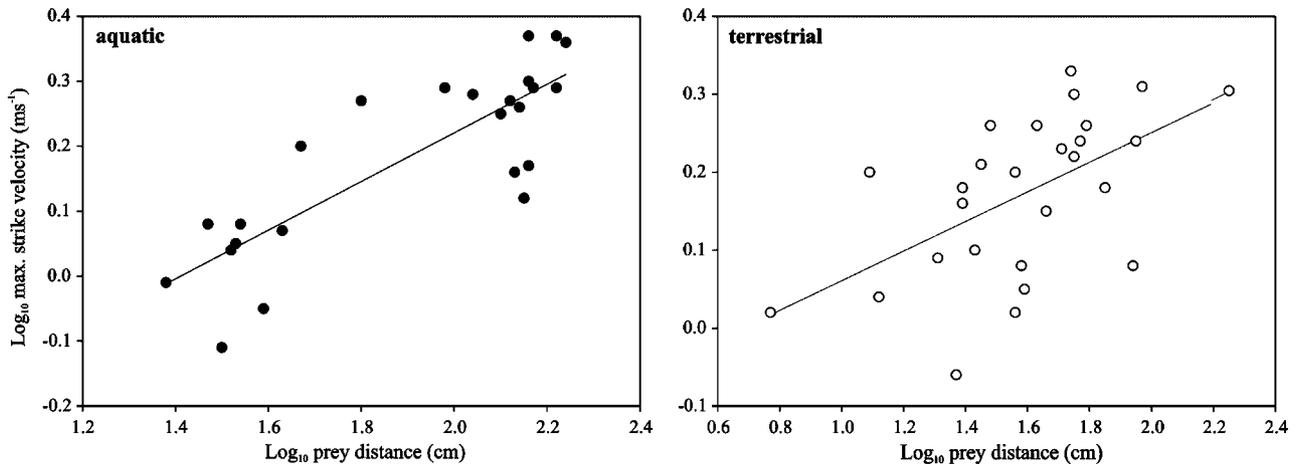
Fig. 4. Graph illustrating the strong correlation between prey distance and strike performance (instantaneous velocity) during both aquatic (left) and terrestrial (right) strikes. Strikes elicited from longer distances are associated with higher strike velocities.

(Taylor, '87; Young, '91). However, one would predict that if the velocities of the two strike types do not differ, the acceleration profiles certainly should. Aquatic strikes will require more force to overcome inertial forces in order to yield velocity profiles similar to terrestrial strikes (Vogel, '81). Nonetheless, neither scenario could be confirmed here. Therefore, a relevant question is why does neither strike velocity nor acceleration differ between media? One possibility may be that because much of the aquatic strike occurred above water, momentum loss due to inertial forces may not be an issue until the snake is already close to the prey. Indeed, whereas *peak* velocity and acceleration were higher for aquatic strikes, the *average* velocity and acceleration were lower than those of terrestrial strikes (see Table 2). Although these differences were not significant after Bonferroni correction, they do suggest that 1) snakes try to maximize their velocity and acceleration while striking aquatically and 2) that once the head comes into contact with the water the velocity and acceleration of the strike decrease dramatically. Alternatively, pressure drag may have been grossly overestimated for aquatic snake strikes (Taylor, '87; Young, '91; Braun and Cundall, '95), and therefore, quantitative measures of drag on the head and trunk of differently shaped snakes are needed to shed light on this issue.

Even though strike velocity and acceleration did not differ significantly between media, strike success did. This difference could be attributed to several factors. First, the angular gape velocity was slower in aquatic strikes than terrestrial strikes (Table 2). This result is expected because water's relatively high density should present sizeable resistance to the mandibular adductor muscles during mouth closure. As a result, *A. piscivorus* was not able to rapidly close its mouth once it contacted a fish. Additionally, Savtizky ('92) found that strike success was particularly poor when *A. piscivorus* struck at fish in open water. Moreover, the relatively poor aquatic strike performance was attributed to the inability of *A. piscivorus* to rapidly close its mouth once it contacted a fish. Therefore, the ability to rapidly close the mouth during underwater foraging in snakes may be a key functional trait determining prey capture success. Future studies examining mouth closure speed in a phylogenetically diverse sample of aquatically-feeding species may shed light on this issue. In this way, one could directly examine the importance of this functional trait to the evolution of aquatic feeding within enlarged-gape (macrostomatan) snakes. Additionally, it would be particularly interesting to examine if generalist and specialist aquatic feeders differ in mouth closing velocity, especially since specialists are considerably more successful at aquatic prey capture than generalists (Drummond, '83; Halloy and Burghardt, '90; Alfaro, 2002, 2003).

Second, the turbulent flow generated by the aquatic strike of *A. piscivorus* could negatively affect prey capture success as well. Videos clearly showed that bow waves were produced during aquatic strikes (i.e., the water became very

turbulent once the snake's head entered the water). Even so, there is no quantitative data to further explore this possibility here, and therefore, future studies should employ visualization techniques such as digital particle image velocimetry (DPIV) to examine the potential for bow wave generation during aquatic feeding in snakes.

Finally, initial prey distance is likely critical to strike success. Although it is not possible to directly test for the effect of distance on prey capture success with these data, two other studies by Drummond ('83) and de Queiroz (2003) found that for aquatically-feeding garter and water snakes (*Thamnophis* and *Nerodia sp.*), initial prey distance strongly determined prey capture success (i.e., longer distances equate to lower capture rates for fish prey). De Queiroz (2003) suggested that longer distances give fish more time to sense the predator and thus escape. However, strike velocity/acceleration was positively correlated with prey distance (Fig. 4), and as a result there was no detectable difference in the duration of long versus short distance strikes in either aquatic or terrestrial strikes. Additionally, a similar pattern was demonstrated for *C. atrox* striking at mice (Young et al., 2001; LaDuc, 2002). Consequently, prey items that are farther away do not have significantly more time to react due to the considerable strike speeds of *A. piscivorus* and *C. atrox*. Nevertheless, because bow waves scale as the square of velocity (Vogel, '81), the larger bow waves generated by *A. piscivorus,* compared to slower striking garter snakes, may trigger the lateral line system of fish faster, allowing fish to respond earlier to the predatory threat.

Alternatively, longer distances to the fish prey likely reduce the accuracy of visual orientation to the fish once underwater, because *A. piscivorus* is not visually adapted to counteract the dispersion effects of water, as are some garter snakes (Schaeffel and de Queiroz, '90). Indeed, several long aquatic strikes (>5 cm) by *A. piscivorus* in this study missed the fish prey by several centimeters. Ecologically, the inability to clearly focus on fish prey in deep water may explain why *A. piscivorus* forages predominantly in shallow drying pools (Savitzky, '92). Nevertheless, *A. piscivorus* has been reported as striking at fish in open water in the wild (Burkett, '66; S.E. Vincent, personal observation) and thus it is particularly puzzling how this snake can energetically afford to engage in a task that it performs so poorly. Indeed, *A. piscivorus* may only hunt for fish over open water when fish are particularly abundant or during times when other prey are rare. Further studies examining how fish density affects strike performance would shed significant light on this issue.

Kinematics and timing variables

These kinematic and timing variables for the terrestrial strikes of *A. piscivorus* were overall very similar to those reported in other kinematic studies on vipers (Kardong, '75, '86b; Janoo and Gasc, '92; Kardong and Bels, '98; LaDuc, 2002), as well as some colubrids (see Cundall and Greene, 2000 for a review of colubrid strike kinematics). However, the contact point with terrestrial prey was not the same as reported in other studies (see Cundall and Greene, 2000 for an overview). Typically, vipers have been reported as contacting prey with their lower jaw for predatory strikes and the upper jaw for defensive strikes (e.g., Kardong, '86a; Kardong and Bels, '98; Cundall, 2002; LaDuc, 2002). Of the thirty-five terrestrial strikes filmed here, only two were recorded where initial prey contact occurred at the lower jaw. Nonetheless, these thirty-five strikes were predatory strikes, not defensive strikes, as indicated by the fact that the snakes ate all the mice that were initially attacked. Moreover, defensive strikes in vipers are characterized by having a relatively large pre-strike distance, and typically lack a prey retention period (LaDuc, 2002; Cundall and Greene, 2000). In this study, however, terrestrial strikes were generally initiated at short distances from the mouse and always contained a prey retention period (Table 2). This discrepancy in the prey contact point may be due to the experimental design. Generally, kinematic studies have filmed snakes striking in a horizontal plane as would typically occur during natural strikes (e.g., Deufel and Cundall, '99; LaDuc, 2002). By contrast, snakes here were striking at a mouse from above, in an inclined plane. Although this may have affected the contact point of the snake with the prey, all other kinematic variables examined here were highly similar to other studies on this species (e.g., Kardong, '82), and other other vipers (e.g., LaDuc, 2002).

In summary, the main findings were the following: 1) *A. piscivorus* employs a fast forward strike when feeding aquatically, not a lateral side-sweep as predicted previously. 2) Strike success differed significantly between strike types, with terrestrial strikes being considerably more successful than aquatic strikes. 3) Strike velocity/acceleration did

not differ significantly between terrestrial and aquatic strikes. Maximum velocity and acceleration in both aquatic and terrestrial strikes were, however, significantly correlated with initial prey distance (Fig. 4). Aquatic strikes were undertaken from a significantly further distance than terrestrial strikes ($F_{1,49}=13.22$; $P<0.01$; see Table 2). 4) Terrestrial and aquatic strikes differ in several aspects of their kinematics: max gape angle during the retraction phase, angular velocity of mouth closing during the strike, the initial head angle before the strike, and the contact point of the head with the prey. Terrestrial strikes were associated with higher gape angles during the retraction phase, higher angular velocities of mouth closing, and a more inclined head angle at the onset of the strike.

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LITERATURE CITED

Alfaro ME. 2002. Forward attack modes of aquatic feeding garter snakes. Func Ecol 16: 204–215.

Alfaro ME. 2003. Sweeping and striking: a kinematic study of the trunk during prey capture in three thamnophine snakes. J Exp Biol 206:2381–2392.

Ashley-Ross MA, Bechtel BF. 2004. Kinematics of the transition between aquatic and terrestrial locomotion in the newt *Taricha torosa*. J Exp Biol 207:461–474.

Braun TB, Cundall D. 1995. Hydrodynamics of fishing in snakes (*Nerodia*). Am Zool 35:105A.

Biewener AA, Gillis GB. 1999. Dynamics of muscle function during locomotion: accommodating variable conditions. J Exp Biol 202:3387–3396.

Biewener AA, Corning WR. 2001. Dynamics of mallard (*Anas platyrhynchos*) gastrocnemius during swimming versus terrestrial locomotion. J Exp Biol 204:1745–1756.

Bramble DM, Wake DB. 1985. Feeding mechanisms of the lower tetrapods. In: Hildebrande M, Bramble DM, Liem KF, Wake DB, editors. Functional Vertebrate Morphology. Cambridge, MA: Harvard University Press.

Burkett RD. 1966. Natural history of the cottonmouth moccasin, *Agkistrodon piscivorus* (Reptilia). Lawrence, KS: University of Kansas.

Cundall D. 1987. Functional Morphology. In: Seigel RA, Collins JT, Novak SS, editors. Snakes: Ecology and Evolutionary Biology. New York: MacMillian. p 106–140.

Cundall D. 2002. Envenomation strategies, head form, and feeding ecology in vipers. In: Schuett GW, Höggren M,

Douglas ME, Greene HW, editors. Biology of the Vipers. Eagle Mountain, UT: Eagle Mountain Publishing. p 149–161.

Cundall D, Greene HW. 2000. Feeding in snakes. In: Schwenk K, editor. Feeding: form, function, and evolution in tetrapod vertebrates. London: Academic Press. p 293–333.

de Queiroz A. 2003. Testing an adaptive hypothesis through context-dependence: effects of water depth on foraging behavior in three species of garter snakes. Ethology 109:369–384.

Deufel A, Cundall D. 1999. Do booids stab prey? Copeia 4:1102–1107.

Drummond H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. Behaviour 86:1–30.

Gillis GB. 1998. Environmental effects on undulatory locomotion in the American eel *Anguilla rostrata*: Kinematics in water and land. J Exp Biol 201:949–961.

Gillis GB, Biewener AA. 2000. Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). J Exp Biol 203:3547–3563.

Halloy M, Burghardt GM. 1990. Ontogeny of fish capture and ingestion in four species of garter snakes (*Thamnophis*). Behaviour 112:299–318.

Herrel A, Aerts P. 2003. Biomechanical Studies of Food and Diet Selection. Nature Encyclopedia of Life Sciences. London: Nature Publishing Group. http://www.els.net/ [doi:10.1038/npg.els.0003213].

Hibbits T. 2001. Morphological and ecological convergence in two natricine snakes. Unpublished master's thesis. Texas A&M University.

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. Amphib Reptil 13:315–325.

Kardong KV. 1974. Kinesis of the jaw apparatus during the strike in the cottonmouth snake, *Agkistrodon piscivorus*. Forma et Functio 7:327–354.

Kardong KV. 1975. Prey capture in the cottonmouth snake (*Agkistrodon piscivorus*). J Herpetol 9:169–175.

Kardong KV. 1982. Comparative study of changes in the prey capture behavior of the cottonmouth snake (*Agkistrodon piscivorus*) and Egyptian cobra (*Naja haje*). Copeia 1982:337–343.

Kardong KV. 1986a. The predatory strike of the rattlesnake: when things go amiss. Copeia 1986:816–820.

Kardong KV. 1986b. Predatory strike behavior of the rattlesnake, *Crotalus viridus oreganos*. J Comp Psychol 100:304–314.

Kardong KV, Bels VL. 1998. Rattlesnake strike behavior: kinematics. J Exp Biol 201:837–850.

Kardong K, Smith TL. 2002. Proximate factors involved in rattlesnake predatory behavior: a review. In: Schuett GW, Höggren M, Douglas ME, Greene HW, editors. Biology of the Vipers. Eagle Mountain, UT: Eagle Mountain Publishing. p. 253–266.

LaDuc TJ. 2002. Does a quick offense equal a quick defense? Kinematic comparisons of predatory and defensive strikes in the western diamond-backed rattlesnake (*Crotalus atrox*). In: Schuett GW, Höggren M, Douglas ME, Greene HW, editors. Biology of the Vipers. Eagle Mountain, UT: Eagle Mountain Publishing. p 267–278.

Lauder G. 1985. Aquatic feeding in lower vertebrates. In: Hildebrande M, Bramble DM, Liem KF, Wake DB, editors.

Functional Vertebrate Morphology. Cambridge, MA: Harvard University Press. p. 210–229.

Lauder GV, Shaffer HB. 1985. Functional morphology of the feeding mechanism in aquatic ambystomtid salamanders. J Morph 185:297–326.

Lauder GV, Shaffer HB. 1988. Ontogeny of functional design in tiger salamanders (*Ambystoma tigrinum*): are motor patterns conserved during major morphological transformations? J Morph 197:249–268.

McDowell SB. 1972. The evolution of the tongue in snakes, and its bearing on snake origins. In: Dobzhansky T, Hecht MK., Sterre WC, editors. Evolutionary Biology, Vol. 6 New York: Appleton-Century-Crofts. p. 191–273.

Reilly SM, Lauder GV. 1988. Ontogeny of aquatic feeding performance in the eastern newt, *Notophtalmus viridescens* (Salamandridae). Copeia 1988:87–91.

Rice WR. 1989. Analyzing tables of statistical tests. Evol 43:223–225.

Savitzky BAC. 1989. Aquatic foraging in two independently evolved species of snake: *Nerodia rhombifer* (Colubridae) and *Agkistrodon piscivorus* (Viperidae). Unpublished D. Phil. Thesis, University of Tennessee, Knoxville.

Savitzky BAC. 1992. Laboratory studies on piscivory in an opportunistic predator, the cottonmouth, *Agkistrodon piscivorus*. In: Campbell JA, Brodie Jr., ED, editors. Biology of the pitvipers. The University of Texas at Arlington Press. p 347–368.

Schaeffel F, de Queiroz A. 1990. Alternative mechanisms of enhanced underwater vision in the garter snakes *Thamnophis melanogaster* and *T. couchii*. Copeia 1990:50–58.

Schwenk K. 1994. Why do snakes have forked tongues? Science 263:1573–1577.

Schwenk K. 2000. Feeding: Form, Function, and Evolution in Tetrapod Vertebrates. London: Academic Press.

Shaffer HB, Lauder GV. 1988. The ontogeny of functional design: metamorphosis feeding behavior in the tiger salamander (*Ambystoma tigrinum*). J Zool Lond 216:437–454.

Smith TL, Povel GDE, Kardong KV. 2002. Predatory strike of the tentacled snake (*Erpeton tentaculatum*). J Zool Lond 256:233–242.

Taylor MA. 1987. How tetrapods feed in water: a functional analysis by paradigm. Zool J Linn Soc 91:171–195.

Van Damme J, Aerts P. 1997. Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; Chelonia). J Morph 233:113–125.

Van Riper W. 1954. Measuring the speed of a rattlesnake's strike. Anim King 57:50–53.

Vincent SE, Herrel A, Irschick DJ. 2004a. Ontogeny of intersexual head shape and diet in the pitviper, *Agkistrodon piscivorus*. Biol J Linn Soc 81:151–159.

Vincent SE, Herrel A, Irschick DJ. 2004b. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). J Zool Lond 264:53–59.

Vogel S. 1981. Life in moving fluids. Boston: Willard Grant Press.

Walker JA. 1998. Estimating velocities and accelerations in animal locomotion: a simulation experiment comparing numerical differentiation algorithms. J Exp Biol 201:981–995.

Young BA. 1991. The influences of the aquatic medium on the prey capture system of snakes. J Nat Hist 25:519–531.

Young BA, Phelan M, Jaggers J, Nejman N. 2001. Kinematic modulation of the strike of the western diamondback rattlesnake (*Crotalus atrox*). Hamadryad 26:316–349.