KINEMATICS OF AQUATIC PREY CAPTURE IN THE SNAPPING TURTLE *CHELYDRA SERPENTINA*

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Summary

The kinematics of feeding on two prey types is studied quantitatively in the common snapping turtle, *Chelydra serpentina*, to provide a description of prey capture mechanisms and to determine whether kinematic patterns can be altered in response to prey that vary in escape capability. High-speed video recordings of prey capture (200 fields s^{-1}) provide data for field-by-field analysis of 12 kinematic variables characterizing head and neck movement. Feedings on fish were accomplished in 78 ms, with peak head extension velocities of 152.5 cm s^{-1}. Worm feedings lasted 98 ms with maximum head extension velocities of 54 cm s^{-1}. Both univariate and multivariate statistical analyses demonstrate significant differences in kinematic patterns between fish and earthworm feedings: *Chelydra serpentina* possesses the ability to modulate its kinematic pattern depending on the prey. The pattern of bone movement during the fast opening phase of the gape cycle is similar to that found in ray-finned fishes, lungfishes and aquatic salamanders. However, movements of the cranium and lower jaw during the closing phase are markedly different. Our data show *Chelydra* to be predominantly a ram-feeder, with any intraoral negative pressures generated during the strike having a negligible effect on the prey, which remains largely stationary relative to a fixed background. Hyoid and esophageal expansion during the closing phase may function to allow a unidirectional flow of water and prey into the mouth until the gape closes and to delay reverse flow until the prey has been trapped inside the mouth. The independent evolutionary acquisition of aquatic feeding in fishes and turtles reveals some kinematic similarities that may be the result of hydrodynamic constraints on aquatic prey capture systems, as well as kinematic differences that result from the fundamentally different morphological design of the prey capture apparatus.

Introduction

One of the major conclusions to emerge from comparative analyses of feeding kinematics in aquatic vertebrates over the last ten years is that even taxa that differ substantially in cranial morphology may exhibit considerable similarity in kinematic patterns. For example, the kinematics of aquatic prey capture in both fishes and salamanders (both larval and metamorphosed) show many similarities, such as the

relative timing of gape, hyoid and gill bar cycles (Bemis and Lauder, 1986; Lauder, 1985; Lauder and Shaffer, 1991; Shaffer and Lauder, 1985; Westneat and Wainwright, 1989). One potential reason for this is hydrodynamic constraints placed on capturing prey in an aquatic medium nine hundred times more dense, and eighty times more viscous, than air (Lauder, 1985). Prey items have nearly the same density as the medium and perhaps only one general pattern of jaw bone movement is effective at moving prey of near neutral buoyancy into the mouth.

The hypothesis of kinematic similarity as a result of hydrodynamic constraints (Lauder, 1985; Lauder and Shaffer, 1991) has been based primarily on studies of fishes (Alexander, 1970; Elshoud-Oldenhave, 1979; Lauder, 1980a,b, 1983, 1985; Liem, 1970; Muller, 1983; Westneat and Wainwright, 1989) and amphibians (Lauder and Shaffer, 1985; Matthes, 1934; Reilly and Lauder, 1989a; Shaffer and Lauder, 1988). Few studies, however, have analyzed feeding mechanics in aquatic turtles, although several workers have discussed some aspects of aquatic turtle feeding (Bramble, 1973, 1978; Burghardt and Hess, 1966; Gans, 1969; Mahmoud, 1968; Mahmoud and Klicka, 1979; Shafland, 1968; Winokur, 1974; Weisgram, 1982, 1985). No descriptions have been published of basic kinematic patterns nor have quantitative comparisons been made with aquatic feeding in fishes and salamanders.

Turtles are of special interest for investigations of the functional morphology and evolution of aquatic feeding for two reasons. First, paleontological evidence strongly suggests that modern cryptodiran and pleurodiran turtles are derived from a primitive stock of shelled terrestrial anapsids (Gaffney and Meeker, 1983; Carroll, 1988). Gaffney et al. (1987) suggested that, although aquatic habits evolved very early in the evolution of chelonians, the ancestors of all modern turtles were probably terrestrial in habit. The existence of many modern genera of aquatic-feeding turtles provides functional morphologists with a group of vertebrates that have evolved aquatic feeding convergently with anamniote feeding systems. Therefore, turtles permit the testing of hypotheses and generalizations regarding morphological and functional patterns associated with aquatic feeding in lower vertebrates. Given that the kinematics of prey capture used by fishes and salamanders are remarkably similar (Lauder, 1985; Lauder and Shaffer, 1991), turtles possess a different feeding morphology which permits a comparative test of the extent of kinematic conservatism when the aquatic habitat is reinvaded during vertebrate evolution.

Second, it is often stated that aquatic turtles use a suction mechanism during feeding in which negative pressures are generated in the buccal cavity by rapid depression of the hyoid, causing water *and prey* to be drawn towards, and then into, the mouth. Specifically, *Chelus*, *Deirochelys*, *Claudius* and *Chelydra* are modern genera of aquatic turtles believed to utilize this method of prey capture (Hartline, 1967; Shafland, 1968; Gans, 1969; Bramble, 1973, 1978; Jackson, 1978; Weisgram, 1982, 1985; Lauder, 1985; Ernst and Barbour, 1989). The belief that suction feeding is used by several species of aquatic turtles is based primarily on comparative studies of the oral mucosa, hyolingual complex, the cervical musculo-

skeletal features of terrestrial and aquatic species and preliminary kinematic investigations (Shafland, 1968; Bramble, 1973, 1978; Weisgram, 1982, 1985; Winokur, 1974; Bramble and Wake, 1985). However, specific kinematic analyses to examine methods of prey capture, movement of the prey and variability in feeding dynamics are lacking.

This paper has three main goals. First, we characterize quantitatively the kinematics of prey capture in the aquatic chelonian *Chelydra serpentina* in order to provide a basic description of the process of prey capture. This is accomplished through an analysis of high-speed videos of the feeding of *Chelydra* on fish and earthworms. Second, we compare statistically the kinematics of prey capture on these two prey items to determine whether kinematic patterns can be altered in response to prey that vary in escape capability. Third, we discuss the above findings in the light of existing models of suction feeding and hypotheses of feeding mechanics in aquatic vertebrates.

Materials and methods

Animals

Five individuals of the aquatic turtle species *Chelydra serpentina* (Linnaeus), the common snapping turtle, were studied. Data from the three specimens most similar in size were selected for detailed analysis, and these animals ranged in carapace length from 13.0 to 15.5 cm (mean=14.2 cm; s.D.=1.3 cm). The turtles were collected in Tennessee, USA, by a commercial supplier. The snapping turtles were maintained in separate fifteen gallon aquaria with filtered dechlorinated water. Water temperature was maintained at $19.5 \pm 1.5\,°C$ and a photoperiod of approximately 12 h daylight and 12 h darkness was established.

Snapping turtles are omnivores and consume almost anything edible in or near their aquatic habitat (Hammer, 1975). A list of known prey items includes fish, various freshwater invertebrate species, frogs, waterfowl, carrion and large amounts of vegetation (Hammer, 1975; Pritchard, 1979; Ernst and Barbour, 1989). The two experimental prey types chosen were fish (goldfish, *Carassius*) and earthworms (*Lumbricus*) in order to provide prey that would possess substantially different visual stimuli, as in previous studies (Reilly and Lauder, 1989b; Sanford and Lauder, 1990; Wainwright and Lauder, 1986). Goldfish often exhibit a rapid startle response when stalked by snapping turtles and constitute an elusive prey, while earthworms fall to the bottom and move slowly. These two prey types also differ in shape (and usually also in their location in the experimental aquarium) and these characteristics serve to distinguish the prey as stimuli to the turtle.

Anatomical observations of the cranial and cervical musculo-skeletal complex were made on two preserved individuals of *Chelydra serpentina* obtained from the Field Museum of Natural History in Chicago (FMNH numbers 8811 and 11016).

Video data analysis

High-speed video recordings of *Chelydra* feeding on earthworms and goldfish

were obtained on VHS videotape using a NAC HSV-400 high-speed video system running at 200 fields s^{-1} (5 ms per field). Two strobes were synchronized with the video camera shutter and provided 400 W of illumination for 20 μs during each video field. Only successful prey captures that occurred nearly parallel to the film plane were used for kinematic analysis.

An earthworm segment was dropped from forceps about 5 cm anterior to the snout of the turtle, and fell slowly towards the bottom. Strikes occurred both at the falling earthworm and at worm segments that had fallen to the bottom. A new segment of worm was offered in the same manner only after the captured prey had been fully swallowed. Goldfish were often held by the caudal fin with forceps and offered to the turtle at a distance approximately 8 cm anterior to the snout and 6 cm above the bottom of the aquarium. The goldfish were released when the turtle began stalking the prey. This method was employed in order to increase the chance of obtaining feedings parallel to the plane of the film.

Because the two prey types often differed in location at the time the strike began, detection of a prey-type effect may also indicate that strike kinematics are influenced by prey location. However, each prey item elicited a very similar pattern of turtle head movement that did not depend on prey position, indicating that the location of the prey did not grossly affect the kinematic pattern. In addition, the goal of presenting prey that differ in overall stimulus to test the null hypothesis of kinematic stereotypy is actually furthered if prey are located at different positions. Finding no kinematic difference between prey types would provide a strong indication of a stereotyped strike.

Neck, body and cranial movements of the turtles during feeding, as well as relative movements of the prey item with respect to the turtle's shell and a background grid, were analyzed field by field using a custom video digitizing system. Thirty feedings from three individuals were used for detailed analysis: for each individual, five goldfish feedings and five worm feedings were chosen. The sequences selected exhibited the least transverse movement of the turtle relative to the plane of the camera. Each feeding sequence consisted of approximately thirty-five video fields and 1050 video fields were digitized for this study. Video sequences of two more turtles were compared to those digitized to ensure that the conclusions reached from the digitized fields matched patterns seen for all five turtles.

A video field defined as 'time zero' was selected for each of the sequences by locating the field immediately before rapid mouth opening. The following video fields were digitized for each sequence (times are in ms relative to time zero): −500, −200, −100, −15, −10, −5, 0, 5–125 (in 5 ms increments), 200, 300, 500 and 1000.

Several days before a filming session, the experimental animal was anesthetized with halothane. Landmarks to be used during video analysis were painted on the head, neck and shell of the turtle using white and black paint.

From each video field, the following twelve kinematic variables were measured (Fig. 1). Gape distance is defined as the distance (in cm) between the ventral-most
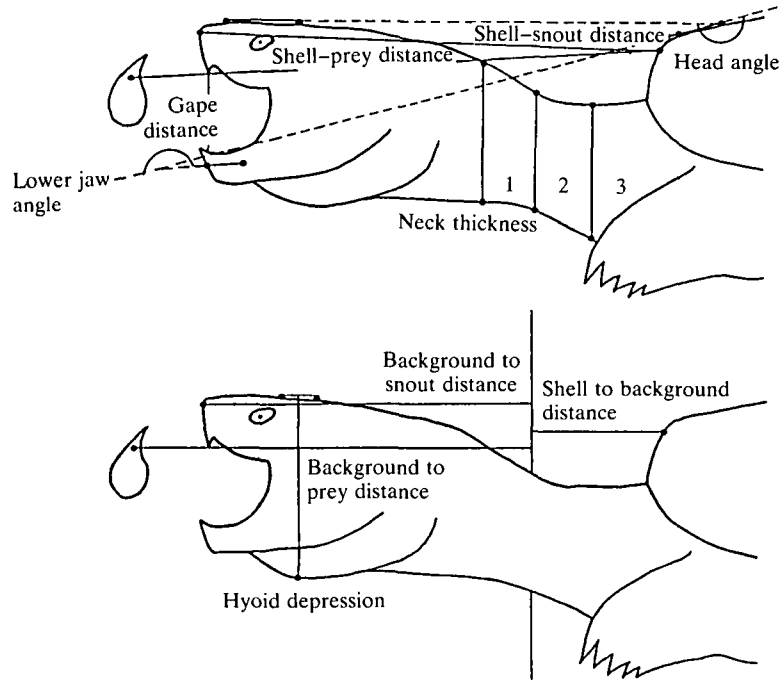
Fig. 1. Lateral view of the head, neck and anterior body of *Chelydra serpentina* to illustrate the kinematic variables measured from high-speed video fields of prey capture. Different variables are shown in two panels for clarity but all were measured from each video field. A detailed discussion of each measurement is presented in the Materials and methods. The prey item, a goldfish, is shown in typical mid-strike position, perpendicular to the plane of neck movement.

point of the anterior surface of the premaxilla and the dorsal-most point of the anterior surface of the mandibular symphysis. Gape distance measures change in gape, which may be accomplished by a combination of skull and lower jaw movements.

Head angle is measured as the angle (in degrees) between two lines (Fig. 1). One line is defined by two points along the dorsal border of the cranium. The other line is defined by two points along the dorsal, anterior border of the carapace. This obtuse angle reflects the elevation of the head produced both by neck movements and by movements between the head and cervical vertebrae. An increase in head angle indicates elevation or lifting of the head.

Lower jaw angle is measured as the angle (in degrees) between two lines (Fig. 1). One line is defined by two points along the mid-border of the dentary and the other by two points along the dorsal, anterior border of the carapace. A decrease in lower jaw angle represents depression of the lower jaw around the jaw joint and/or ventral bending of the neck.

Because neck movements may confound interpretation of the head and lower

jaw angle variables considered alone, it is useful to compare simultaneously the change in gape distance, head angle and lower jaw angle. Changes in any one of these variables can be separated from those due only to elevation and depression movements of the entire head as a result of neck movement. For example, a decrease in lower jaw angle might merely indicate that the whole head is being moved towards the substratum and might not represent an opening of the lower jaw. However, if head angle stays constant and gape distance increases, then the lower jaw must be opening and causing the increase in gape.

Hyoid depression (Fig. 1) is defined as the perpendicular distance (in cm) between a line along the dorsal border of the cranium and the ventral-most point visible externally on the hyoid apparatus. An increase in this distance signifies ventral–posterior motion of the hyoid since the center of hyoid rotation lies posterior to the skull.

Three neck thickness measurements were made (Fig. 1). The first measurement indicates neck thickness anteriorly, behind the second branchial horn of the hyoid, while the second measures the thickness of the central region of the neck. The third neck thickness measurement is defined as the distance (in cm) between a landmark point on the dorsal border of the neck near the shell and a landmark point on the ventral border, immediately below the dorsal point.

The extension of the head and neck from their pre-strike condition, the shell to tip of snout distance (Fig. 1), is defined as the distance (in cm) from a point on the anterior-most dorsal border of the first nucal scute of the carapace and a point on the anterior-most tip of the snout. Background to snout distance is defined as the perpendicular distance (in cm) between a fixed reference line on the background grid and a point on the anterior-most tip of the snout (Fig. 1). The horizontal position of the body during feeding, shell to background, is defined as the perpendicular distance (in cm) between a fixed reference line on the background grid and a point on the anterior-most dorsal border of the first nucal scute.

The predator–prey distance, shell to prey, is defined as the distance (in cm) from a point on the anterior-most border of the first nucal scute to a point at the base of the dorsal fin of the goldfish or to a point on the midlateral side of an earthworm segment. A related variable, background to prey (Fig. 1), is defined as the perpendicular distance (in cm) between a fixed vertical reference line on the background grid and the same points on the two prey items previously discussed.

Three additional variables were calculated from these kinematic data: the velocity of the change in gape distance, the velocity of the head and neck extension during the strike, and the velocity of the hyoid during depression. Velocity was calculated as the distance travelled between two video fields divided by the time interval between fields.

For all individuals, the kinematic variables measured or calculated from each video field were plotted *versus* time on a Tektronix 4107 graphics terminal, and twelve new variables for statistical analysis were measured from each profile (Table 1). These twelve statistical variables were: (1) maximum gape distance during the strike, in cm; (2) time elapsed to maximum gape as measured from time

Table 1. *Summary statistics of the mean and standard error of 12 statistical variables digitized from the kinematic profiles of* Chelydra serpentina *feeding on two prey types*

Variable	Prey type	Mean ($N=15$)	S.E.M. ($N=15$)
Maximum gape distance (cm)	Fish	2.2	0.07
	Worm	1.1	0.05
Time to maximum gape distance (ms)	Fish	33.4	1.68
	Worm	59.1	2.52
Gape cycle time (ms)	Fish	78.1	2.19
	Worm	98.4	2.84
Maximum velocity of the gape ($cm\,s^{-1}$)	Fish	119.9	4.61
	Worm	47.9	2.81
Maximum head extension from the body (cm)	Fish	5.1	0.23
	Worm	1.8	0.08
Maximum velocity of head extension from the body ($cm\,s^{-1}$)	Fish	152.5	6.33
	Worm	53.6	3.17
Maximum head angle (degrees)	Fish	15.1	0.97
	Worm	9.4	0.67
Maximum lower jaw angle (degrees)	Fish	39.6	2.07
	Worm	24.2	1.17
Maximum hyoid depression (cm)	Fish	2.2	0.13
	Worm	1.4	0.11
Maximum velocity of hyoid depression ($cm\,s^{-1}$)	Fish	119.2	5.78
	Worm	51.1	4.09
Time to maximum hyoid depression (ms)	Fish	58.9	3.73
	Worm	112.6	3.12
Maximum second measure of neck extension (cm)	Fish	1.2	0.08
	Worm	0.6	0.09

zero, in ms; (3) duration of the gape cycle, in ms; (4) maximum velocity of gape increase, in $cm\,s^{-1}$; (5) maximum extension of the head from the body during a strike, in cm; (6) maximum velocity of head extension from the body during the strike, in $cm\,s^{-1}$; (7) maximum elevation of the cranium during gape opening, in degrees; (8) maximum depression of the mandible during gape opening, in degrees; (9) maximum distance attained by ventro-posterior movement of the hyoid during feeding, in cm; (10) maximum velocity of hyoid depression, in $cm\,s^{-1}$; (11) time elapsed to maximum hyoid depression, in ms; and (12) maximum second neck extension distance, in cm.

Statistical analysis

Three types of statistical analysis were performed on the data. First, basic descriptive statistics were calculated; these consisted of the means, standard errors and variances for each of the twelve statistical variables. Second, a two-way

analysis of variance (ANOVA) was performed to determine whether the mean values for each of the twelve statistical variables differed among the three individuals or between prey types (Sokal and Rohlf, 1981). Individuals were treated as a random effect and prey type as a fixed effect, as in previous research (Wainwright and Lauder, 1986; Reilly and Lauder, 1989b; Sanford and Lauder, 1990). Statistical significance was accepted at the $P < 0.01$ level because multiple ANOVA comparisons were being conducted.

Third, a principal components analysis (PCA) was performed (using the microcomputer statistics package SYSTAT) on the correlation matrix of the twelve statistical variables. This provided an indication of the major axes of multivariate variation in feeding kinematics, as well as a multivariate summation of patterns of variation in the data set.

Terminology

The terminology used to describe prey capture is based on that presented in Lauder (1985) and Reilly and Lauder (1990). The term 'gape cycle' refers to opening and closing of the mouth and is divided into two phases. The fast opening phase of the gape cycle is characterized by rapidly increasing gape distance and this phase extends from the start of mouth opening to peak gape (e.g. Fig. 4: time zero to 35 ms for solid symbols, gape distance curve). The closing phase, during which the gape distance decreases, extends from peak gape to mouth closure (e.g. Fig. 4: 35 ms to 100 ms for solid symbols, gape distance curve). The gape cycle is preceded by a preparatory phase during which the prey item is being slowly stalked by the turtle and before the initiation of mouth opening at time zero. During this time the head and neck may be slowly extended towards the prey in preparation for the strike. The recovery phase begins at the end of the closing phase and lasts until the head, neck and hyoid have returned to their initial positions.

Results

Overview of strike kinematics

Fig. 2 shows high-speed video fields of *Chelydra serpentina* striking at a goldfish

Fig. 2. Ten fields from high-speed video sequences of the feeding in *Chelydra* on two different prey types. The numbers in the upper right-hand corner of each field indicate the sequence number and the time in milliseconds. The column on the left shows five fields from sequence number 015 of *Chelydra* feeding on a goldfish (from 04:910 at time zero in the upper left-hand field to 05:000 at gape closure in the lower left-hand field, a total duration of 90 ms). The column on the right depicts five fields from sequence number 021 of *Chelydra* feeding on an earthworm segment (from 40:420 at time zero in the upper right field to 40:550 at gape closure in the lower right-hand field, a total duration of 130 ms). Note that, although the head often starts at a different position in feedings on the two prey types, the kinematic measurements used for statistical analysis represent the excursions from time zero when the mouth first starts to open (see Materials and methods). A cross placed on each print shows a fixed background position. Grid size is 1 cm².
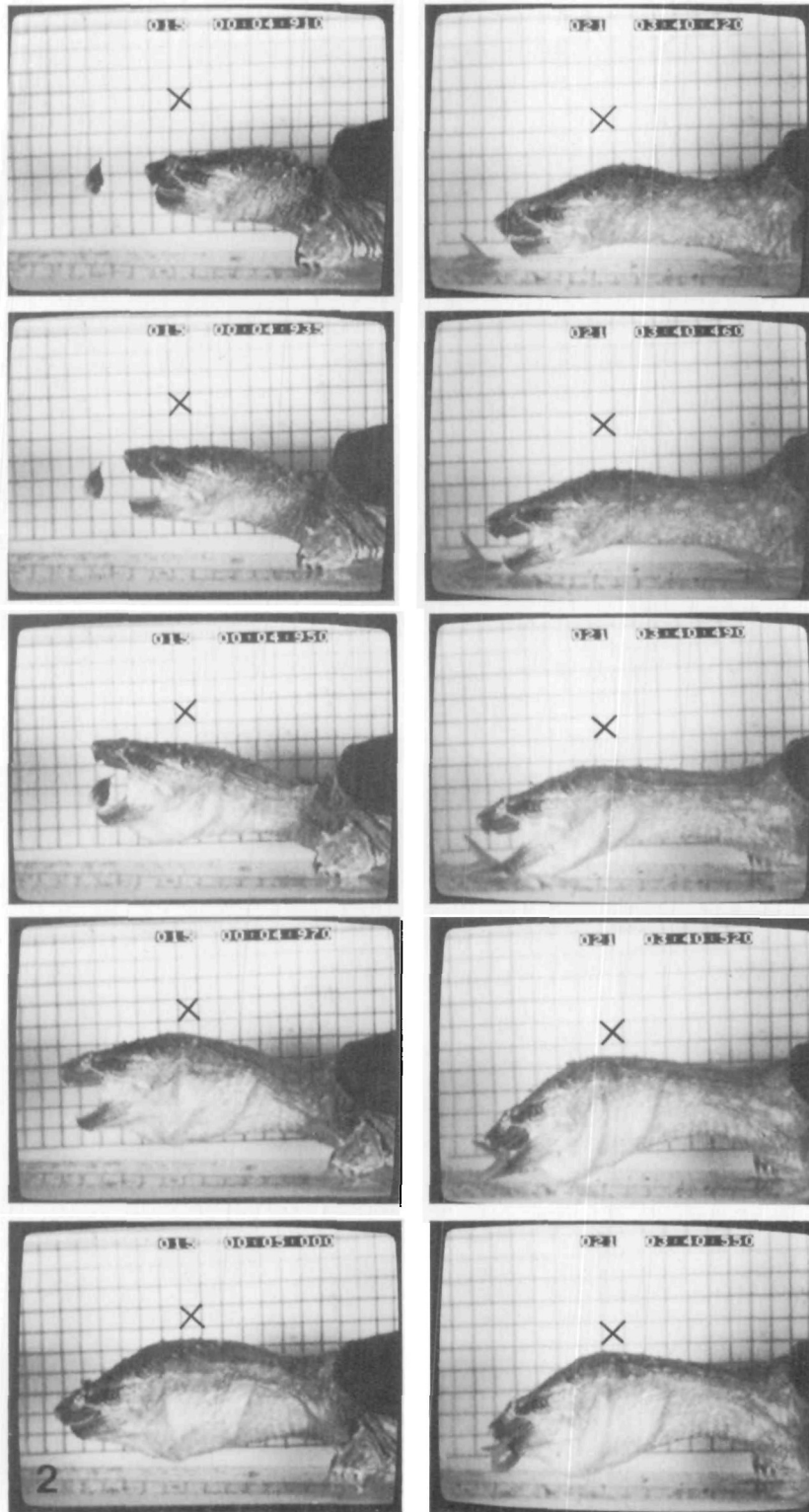
(on the left) and an earthworm (on the right). When prey are introduced into the experimental aquarium, a slow, stalking motion is often initiated by *Chelydra* until the tip of the snout is about 2 cm from the prey item. During this preparatory phase of prey capture, there is little horizontal or vertical motion of the head and neck with respect to the shell (Fig. 3). This pre-strike behavior is present in virtually all observed feedings on both prey types.

All successful strikes are characterized by rapid opening of the mouth due to elevation of the cranium and depression of the lower jaw (Fig. 2). The neck and head are accelerated forward in a trajectory aimed near the center of mass of the prey. Peak gape coincides with about 50 % of maximum shell to snout distance and mouth closure occurs just after the head is fully extended (Figs 2 and 3). The hyoid is moved posteriorly and ventrally during the fast opening phase and reaches full depression during the closing phase. The hyoid remains almost fully depressed for about 400 ms after mouth closure (Figs 2 and 3).

Figs 2 and 3 show that there are only small movements of the shell with respect to the background during the entire gape cycle. There is some slight backward movement of the body (about 0.15 cm) that occurs before peak gape in fish feedings. Horizontal body position is held nearly constant until gape closure and full head extension from the shell. The head begins to retract after gape closure and retracts nearly 4.5 cm or 40 % of its full extension length (7.5 cm) by 500 ms after time zero. As the head retracts, the body begins to move forward, and at 500 ms after time zero it has moved forward almost 1.3 cm (Figs 2 and 3).

It is important to note that in both worm and goldfish feedings there is very little (about 1 mm) movement of the prey with respect to the background before peak gape (Figs 2 and 3). The goldfish are within the mouth cavity at the time of peak gape and disappear from view about 10–15 ms after the beginning of mouth closure (Figs 2 and 3). The earthworm segments are not engulfed by the turtle but are caught between the jaws 5–10 ms after peak gape and remain there well after gape closure and during neck retraction (Fig. 2).

Feeding kinematics

Strikes on fish and worms are both accomplished within a similar overall time of 78–98 ms. Worm strikes tend to have longer gape cycle times but the difference is not significant in our statistical comparison (Tables 1, 2). Maximum gape is significantly greater in amplitude and is achieved more rapidly in fish feedings than in worm feedings, and the jaws of the turtle open with significantly greater velocity when feeding on fish (Tables 1, 2; Fig. 4).

Gape opening, for both worm and fish feedings, is achieved by the simultaneous elevation of the cranium and depression of the lower jaw. Head angle increases and lower jaw angle decreases during fast opening for both fish and worm feedings.

The closing phase of the gape cycle may be divided into two distinct components that are especially noticeable during strikes on fish. First, the cranium begins to rotate ventrally about 5 ms before peak gape is reached and continues to descend for 25–30 ms after peak gape. During this same time interval, lower jaw depression
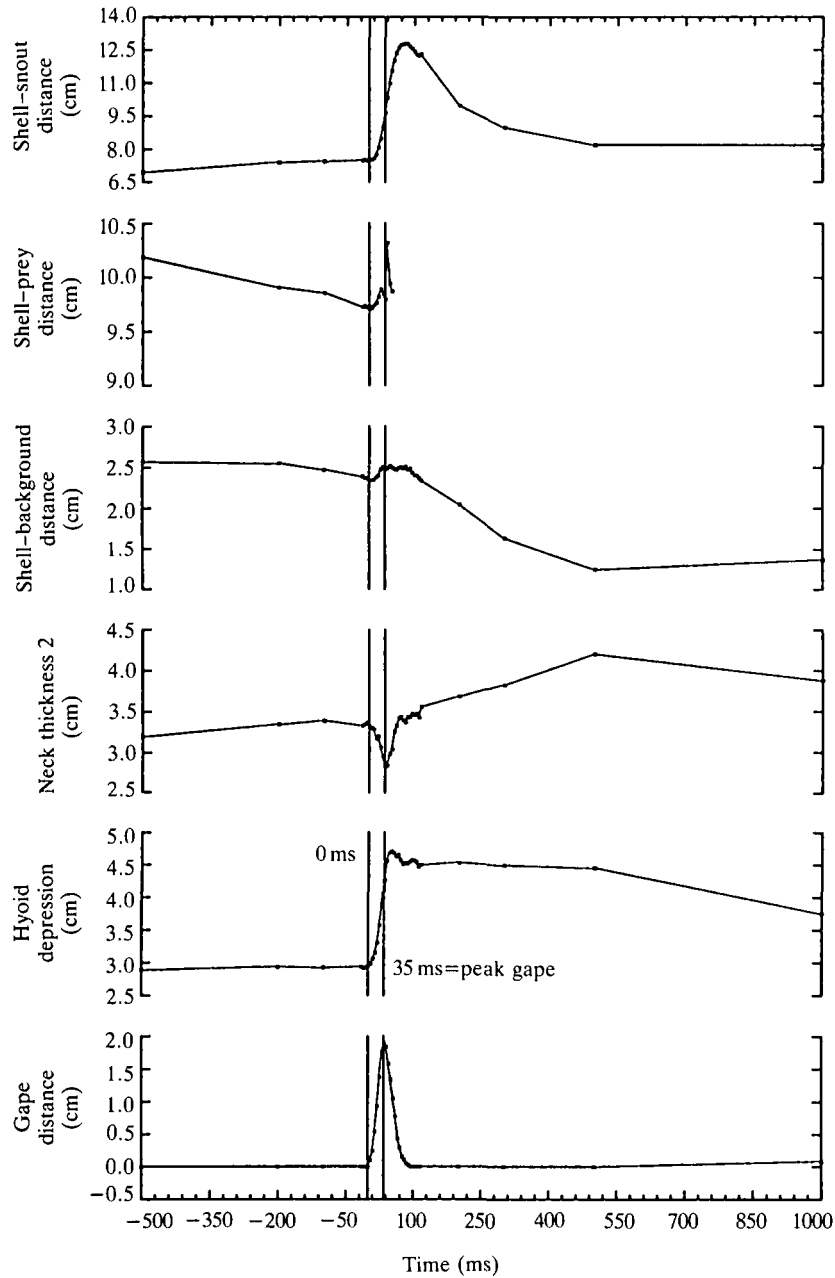
Fig. 3. Kinematic overview of successful goldfish captures by one individual snapping turtle; each point represents the average for five feedings from one individual. Time zero (labelled 0 ms, and demarked by vertical lines) indicates the onset of the fast opening phase of the gape cycle. The vertical lines labelled 35 ms indicate the mean time of maximum gape amplitude (peak gape). The preparatory phase is the time prior to time zero (−500 to 0 ms), the fast opening phase is from time zero to 35 ms, the closing phase is from 35 ms to 100 ms, and the recovery phase lasts from 100 ms to beyond 1000 ms. On the shell to prey distance trace, the prey disappears into the mouth at 50 ms.

Table 2. *Univariate two-way ANOVA* F-*statistics for the 12 statistical variables digitized from the kinematic profiles of feedings by* Chelydra serpentina *on two prey types*

Variable	Prey type (d.f.=1,2)	Individual (d.f.=2,24)	Individual× prey type (d.f.=2,24)
Maximum gape distance (cm)	140.7*	3.2	1.9
Time to maximum gape distance (ms)	26.2	13.5*	6.0*
Gape cycle time (ms)	10.9	4.7	3.7
Maximum velocity of the gape (cm s⁻¹)	758.4*	1.1	0.3
Maximum head extension from the body (cm)	1025.5*	0.6	0.26
Maximum velocity of head extension from the body (cm s⁻¹)	146.7*	1.7	1.4
Maximum head angle (degrees)	6.1	2.6	6.3*
Maximum lower jaw angle (degrees)	22.1	0.6	2.8
Maximum hyoid depression (cm)	4.2	16.1*	23.6*
Maximum velocity of hyoid depression (cm s⁻¹)	16.2	7.3*	10.7*
Time to maximum hyoid depression (ms)	284.4*	2.8	0.5
Maximum second measure of neck extension (cm)	5.3	6.7*	8.2*

* Significant at $P<0.01$.

continues (Fig. 4). The rate of cranial depression exceeds the rate of lower jaw depression for this part of the closing cycle and is the major factor responsible for initially closing the gape. Second, ventral cranial rotation ceases about 30–35 ms after peak gape, at which point cranial elevation begins and continues until gape closure. Lower jaw depression stops about 20–25 ms after peak gape and the lower jaw then begins to elevate to gape closure (Fig. 4). The rate of lower jaw ascension exceeds the rate of cranial elevation during this second part of the closing phase and results in final closure of the gape.

As with the fish feedings, the maximum gape distance in the worm feedings is achieved when head extension from the shell is approximately 50 % of maximum. However, the actual length of the head extension as well as the velocity of the head during the strike are significantly greater in fish feedings than in worm feedings (Tables 1, 2; Fig. 4). For example, in fish feedings, peak gape occurs at a mean velocity of head extension of 126.3 cm s⁻¹, 5 ms before maximal velocity of 140 cm s⁻¹ is achieved (Fig. 5). In worm feedings, peak gape occurs at a mean velocity of head extension of 34.5 cm s⁻¹, 10 ms after the maximal velocity of 45.3 cm s⁻¹ is attained (Fig. 5). Thus, one difference between fish and worm
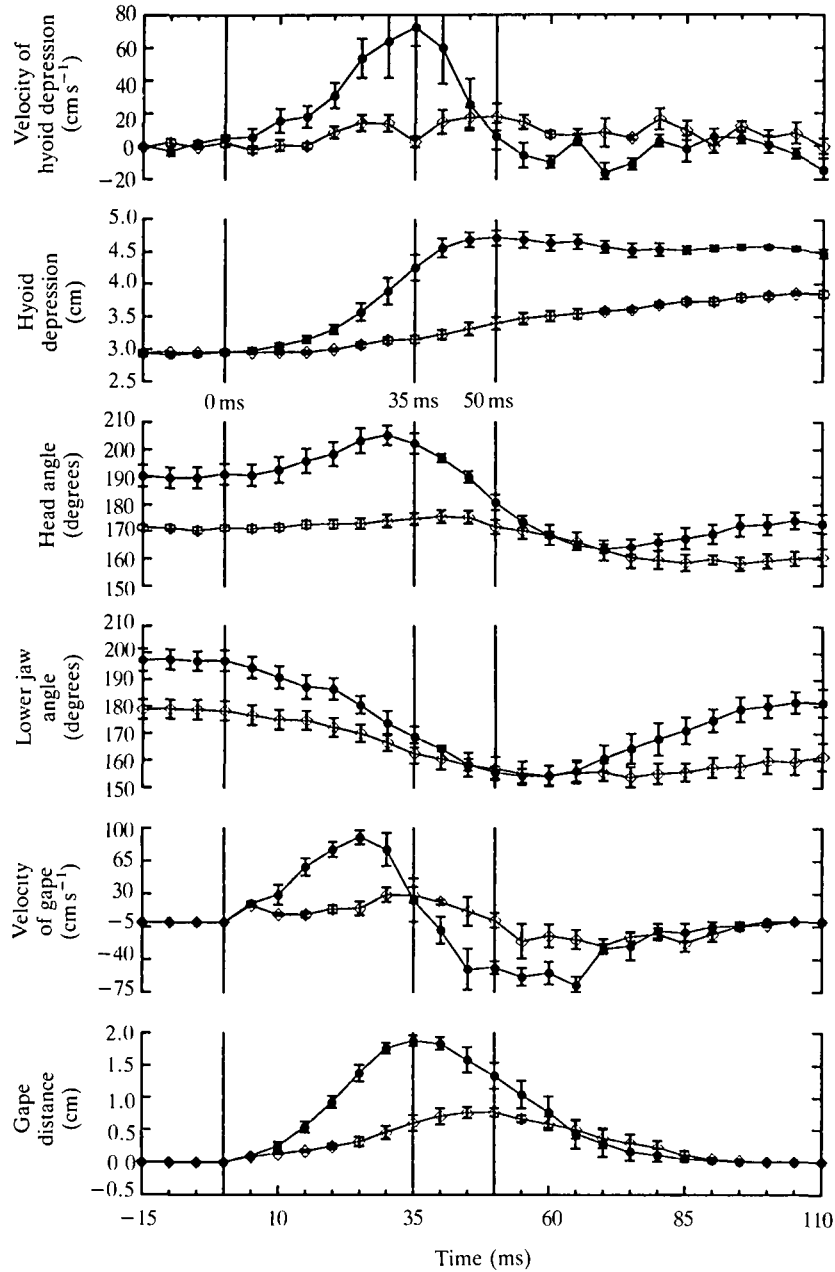
Fig. 4. Kinematic summary of capture by an individual snapping turtle of fish (filled symbols) and worms (open symbols). Variables are plotted as a function of time in milliseconds with the standard error for the mean in each 5 ms interval indicated by a vertical bar. Each mean value is the average of five points. Time zero (labelled 0 ms, and demarked by vertical lines) indicates the onset of the fast opening phase of the gape cycle. The vertical lines labelled 35 and 50 ms indicate the mean time of maximum gape amplitude (peak gape) for fish and worm captures, respectively.
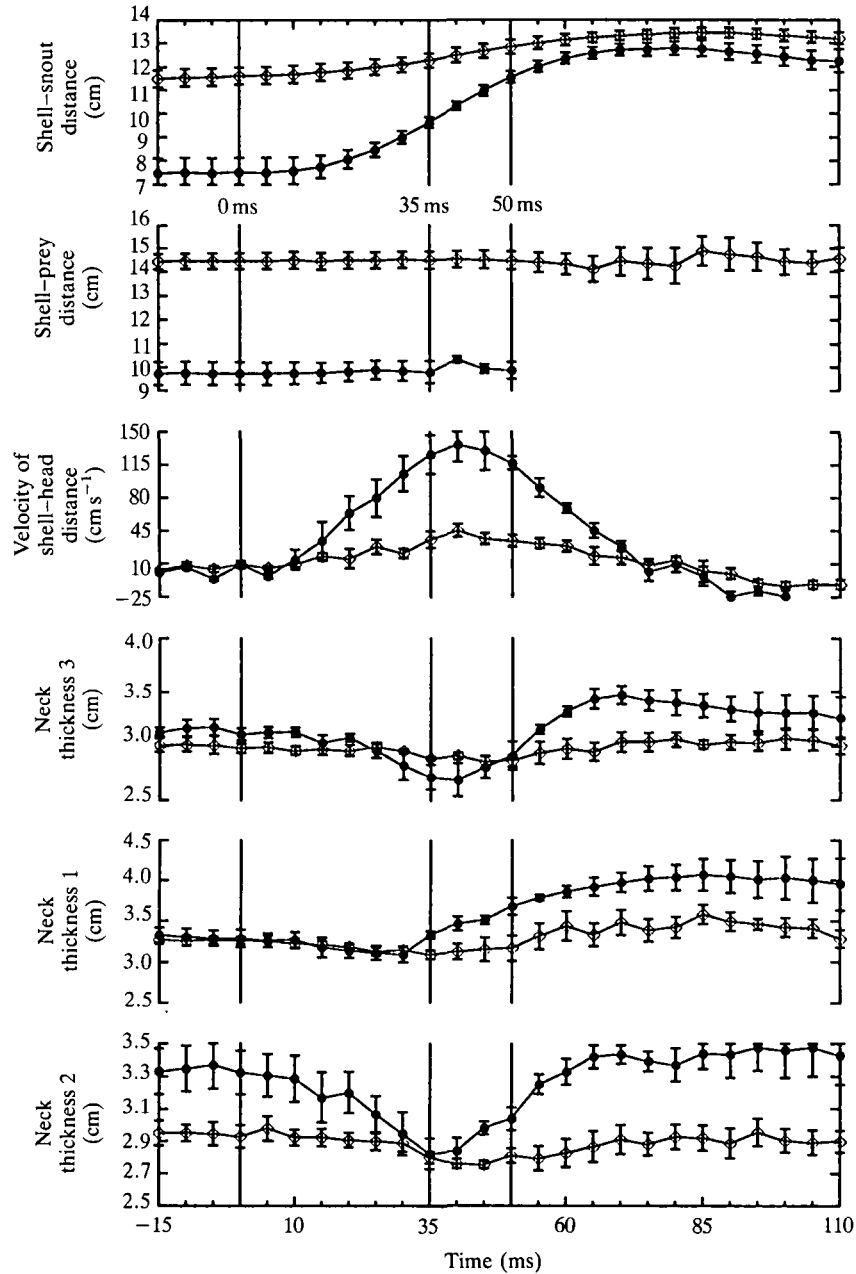
Fig. 5. Kinematic summary of prey capture by an individual snapping turtle on fish (filled symbols) and worms (open symbols). Variables are plotted as a function of time in milliseconds with the standard error for the mean in each 5 ms interval indicated by a vertical bar. Each mean value is the average of five points. Note the small size of the vertical standard error bar for the mean value of the shell to prey distance at 40 ms, 5 ms after peak gape.

feedings is that peak gape shifts from occurring before maximum velocity of head extension is attained to occurring after maximum head extension velocity.

The maximal extent of hyoid depression, caused by the posteroventral movement of the hyoid, is not significantly different between fish and worm feedings (Table 2). Note that this is due in part to the fact that maximum hyoid depression during worm strikes occurs much later than the last time shown in Fig. 4 (110 ms). Maximum hyoid depression is accomplished significantly more rapidly when *Chelydra* feeds on fish. Also, the maximum velocity of the hyoid depression is greater for fish feedings than for worm feedings but the difference is not statistically significant (Tables 1, 2). Maximum hyoid depression is achieved later than maximum gape for both fish and worm feedings (Fig. 4): during fish feedings, hyoid depression peaks, on average, 25 ms later than maximum gape as opposed to 54 ms during worm feedings (Table 1).

During the fast opening phase of the gape cycle, the overall thickness of the neck in both fish and worm feedings decreases from time zero to peak gape (Fig. 5). For fish feedings, the thickness of the neck posterior to the second branchial hyoid horn (Fig. 5, position 1) begins to increase 5 ms before peak gape, from 3.0 cm to 3.9 cm at gape closure. This increase begins at peak gape in worm feedings but the overall increase in neck thickness is only about 0.25 cm (Fig. 5). At 10 ms after peak gape the thickness of both the central neck region (position 2) and the neck region near the shell (position 3) begin to increase. For fish feedings, these overall increases are 0.6 cm and 0.75 cm for the second and third neck thickness measures, respectively, while the corresponding increases for worm feedings are about 0.2 cm and 0.3 cm (Fig. 5).

There is little movement of either type of prey before the fish or worm are within the plane of the gape. Both the fish and worm curves for shell to prey distance (Fig. 5) are nearly flat until after peak gape. It is important to note that there is a small sudden increase in the prey to shell distance at 40 ms, 5 ms after peak gape for fish feedings that reflects a consistent movement of the prey away from the turtle (Fig. 5: shell to prey distance). This pattern of prey movement was not seen for worm feedings.

The results of the univariate ANOVAs for the statistical variables are presented in Table 2. There is a significant prey-type effect for five of the twelve variables at the 0.01 level of significance. Large F-values for three of the variables (Table 2: time to maximum gape distance, maximum lower jaw angle, maximum velocity of hyoid depression) indicate that the low degrees of freedom may be making it difficult to detect a significant effect that in fact exists. Caution should thus be exercised in interpreting these three variables as showing no difference between prey types. Four variables show signs of significant individual variation (at $P < 0.01$) while the interaction term is significant in five of the variables ($P < 0.01$). Four variables display both significant individual and interaction terms.

Principal components analysis

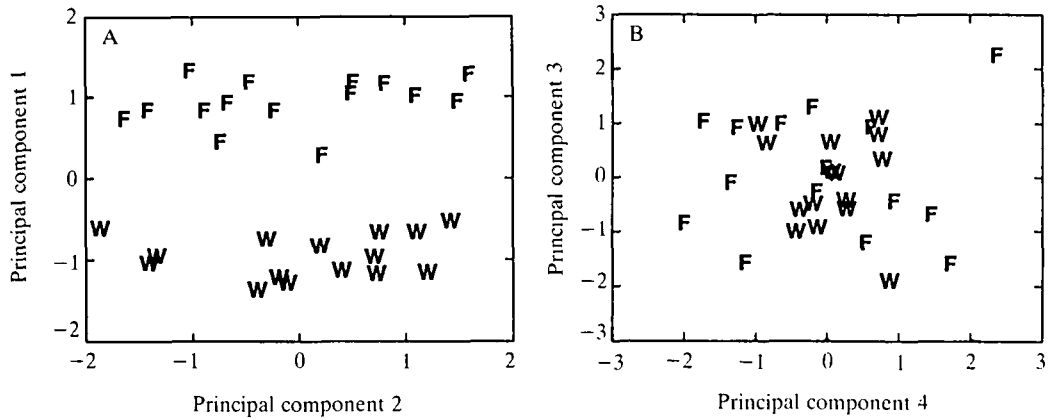Patterns of kinematic variation during feeding on two prey types are summar-

Fig. 6. Principal components (PC) analysis of 12 statistical variables of *Chelydra* feeding on fish (F) and worms (W) plotted as PC1 *versus* PC2 (A) and PC3 *versus* PC4 (B). Each letter represents one feeding. Loadings for each of the 12 variables are presented in Table 3. Note that PC1 separates the two prey types.

ized in a principal components analysis illustrated in Fig. 6A,B. The loadings of twelve variables are presented in Table 3. Components 1 and 2 account for 75.1 % and 11.6 % (respectively) of the variation in the data set and, when plotted, demonstrate the large difference between the fish and worm strikes of *Chelydra serpentina* in multivariate kinematic space: fish and worm feedings are completely distinct on principal component 1. High scores on principal component 1 reflect a greater amplitude of peak gape distance due to a greater extent of cranial elevation and lower jaw depression, as well as greater gape velocity, hyoid depression, velocity of the hyoid, head and neck extension, velocity of head and neck extension, and neck thickness. High scores on principal component 1 also reflect a shorter time to peak gape, gape cycle, and time to peak hyoid depression. All of the above are attributes in which fish feedings differ from worm feedings in *Chelydra*. High scores on principal component 2 reflect primarily differences in hyoid depression, gape cycle time and the second measure of neck thickness, variables that did not show significant differences among prey types. The nearly equal variation in both fish and worm feedings along this PC axis indicates that both prey types elicited feedings that exhibited nearly equal variation in neck expansion, gape cycle time and in the extent of hyoid depression.

A plot of principal components 3 and 4 shows that, while there is extensive overlap between fish and worm feedings (Fig. 6B), worm feedings occupy a central area of the fish feeding polygon along principal component 4, showing less variation in the extent of hyoid depression.

Discussion

Prey-type effects

The results of this study demonstrate that *Chelydra serpentina* possesses the

Table 3. *Factor loadings (for principal components 1-4, PC1-4) for the 12 statistical variables digitized from kinematic profiles of feedings by* Chelydra serpentina

	Factor loadings			
Variable	PC1	PC2	PC3	PC4
Maximum gape distance (cm)	0.95	0.14	0.01	−0.03
Time to maximum gape distance (ms)	−0.85	0.42	0.16	0.16
Gape cycle time (ms)	−0.75	0.48	0.32	0.27
Maximum velocity of the gape (cm s^{-1})	0.96	0.08	0.01	0.13
Maximum head extension from the body (cm)	0.95	−0.15	0.10	0.08
Maximum velocity of head extension from the body (cm s^{-1})	0.96	−0.09	0.06	0.17
Maximum head angle (degrees)	0.69	0.42	0.39	−0.43
Maximum lower jaw angle (degrees)	0.80	−0.39	0.35	0.22
Maximum hyoid depression (cm)	0.79	0.50	−0.25	0.01
Maximum velocity of hyoid depression (cm s^{-1})	0.94	0.28	−0.01	0.04
Time to maximum hyoid depression (ms)	−0.92	0.27	−0.02	0.04
Maximum second measure of neck extension (cm)	0.78	0.44	−0.22	0.15
Proportion of total variance explained	75.1 %	11.6 %	4.4 %	3.4 %

ability to modulate feeding kinematics based on prey type. Both the principal components analysis (Table 3; Fig. 6) and the univariate analyses (Table 2) illustrate a change in the overall kinematic pattern when feeding on the two prey types. Despite low degrees of freedom for testing the prey-type effect, the high *F*-values and the complete separation of feedings for worms and fish on principal component 1 demonstrate significant differences in kinematics used when feeding on these two prey. Since *Chelydra* naturally feeds on many different types of prey items (Ernst and Barbour, 1989; Hammer, 1975; Pritchard, 1979) that vary greatly in agility, size and elusiveness, more than the two basic kinematic patterns found in this study are almost certainly utilized in the wild. While the two prey types used differ in shape, size, elusiveness and occasionally location, the data show that the prey presented stimuli sufficiently different to the turtle to elicit considerable variation in feeding kinematics.

This result is significant because of the lack of variation that has been noted previously during aquatic prey capture by salamanders and some fish species (Reilly and Lauder, 1989b; Wainwright and Lauder, 1986) and shows that vertebrate mechanisms for capturing prey in the water using rapid movements of

the head need not be highly stereotyped. The study of Reilly and Lauder (1989*b*) on ambystomatid salamanders used fish and worm prey (and similar methods of data analysis to this study) and found no differences in the pattern of muscle activity used to capture these prey. Several of the fish studied by Wainwright and Lauder (1986) had a similar skull size to the turtles analyzed in this paper, and size alone seems unlikely to explain differences in strike modulation. Rather, the flexible response to different prey by snapping turtles would appear to reflect a fundamentally variable strike motor output that depends on prey type and position, something not found in aquatic ambystomatid salamanders.

Feeding kinematics in aquatic vertebrates

Four phases of prey capture in *Chelydra* may be defined by the movement of the cranial bones and cervical vertebrae: a preparatory phase, a fast opening phase, a closing phase and a recovery phase.

The preparatory phase in *Chelydra* for feedings on both prey types consists of slow, deliberate stalking with little horizontal body and neck movement prior to fast opening. Some percomorph fishes display a pronounced preparatory phase in which buccal cavity volume is decreased just prior to mouth opening by medial compression of the suspensorium, protraction of the hyoid apparatus and adduction of the lower jaw (Elshoud-Oldenhave, 1979; Lauder, 1985; Liem, 1978). Lauder (1985) cites preliminary studies of the kinematics of prey capture in *Chelydra* that describe a preparatory phase similar to that found in these percomorph teleosts (Bramble, 1978). The proposed function of this phase is to reduce the volume of the mouth cavity prior to fast opening by slightly depressing the mandible, protracting the hyoid and tongue and compressing the esophagus. However, the kinematic profile (Fig. 3) displays neither gape opening 500 ms before mouth opening nor any significant protraction of the hyoid, suggesting a lack of buccal compression. Our results also showed no decrease in overall neck thickness during this time; in fact, a slight increase often occurred (Fig. 3). A review of the feedings by all turtles on both prey types revealed that on many occasions the mouth was slightly open during the preparatory phase and immediately before fast opening, but no evidence of hyoid protraction was seen.

However, buccal compression during the preparatory phase is difficult to demonstrate from kinematic analyses alone. This problem was also noted when the feeding kinematics of aquatic salamanders was studied (Lauder, 1985; Shaffer and Lauder, 1985). It may be possible for snapping turtles to protract the tongue slightly and compress the esophagus, while keeping the gape virtually closed. Water could be forced out of the nostrils, thereby causing some reduction in buccal volume. These actions may be difficult to detect with superficial kinematic measurements, and simultaneous intraoral pressure and hyoid muscle electromyograms will be necessary to quantify preparatory phase function.

In fishes and aquatic salamanders, the fast opening phase is typically very rapid with a shorter duration than the closing phase. In *Chelydra*, the fast opening phase lasts 33 ms on average for fish feedings. Salamanders exhibit a similar duration,

34–47 ms, while fishes show much more variation and this phase can last from 5 to 40 ms, depending on the species (Liem, 1978; Grobecker and Pietsch, 1979; Lauder, 1980*b*, 1983, 1985; Lauder and Shaffer, 1985). For fishes, salamanders and *Chelydra*, the fast opening phase is characterized by similar kinematic attributes: rapid opening of the mouth and posteroventral movement of the hyoid. It is important to note that these kinematic features occur regardless of whether suction feeding is occurring. Thus, fishes that utilize ram-feeding (in which body velocity is used to overtake prey) exhibit similar fast opening kinematics to suction-feeding fishes (Lauder and Liem, 1981).

During the fast opening phase, three key similarities in aquatic prey capture among fishes, salamanders and *Chelydra* are (1) posteroventral hyoid movement beginning at the start of fast opening, (2) the peak in hyoid depression following peak gape, and (3) the contribution of both cranial elevation and lower jaw depression to the increase in gape.

The compressive or closing phase in *Chelydra* lasts, on average, 45 ms and is at least 10 ms longer than the fast opening phase. This situation is similar to that found in three species of aquatic salamanders in which the fast opening phase varied from 34 to 47 ms and the closing phase lasted 35–40 ms (Lauder and Shaffer, 1985). The fast opening phase in fishes varies greatly in duration, but the closing phase is typically longer than the opening phase (Lauder, 1983, 1985).

The closing phase in *Chelydra* may be divided into two kinematic components, especially evident during fish strikes. During the first component of the closing phase, the gape is decreasing while both the cranium and the lower jaw are rotating ventrally. In fact, cranial depression is responsible for causing most of the decrease in gape amplitude during the first half of the closing phase (Fig. 4). The decrease in the lower jaw angle during this first component of the closing phase is due primarily to the downward movement of the head and neck relative to the shell.

The remaining decrease in gape amplitude occurs during the second component of the closing phase, when the lower jaw rotates dorsally, and results in the final closure of the gape. The small increase in the head angle during this time is due to the elevation of the head and neck relative to the shell (Fig. 4).

One of the major differences between the closing phase in *Chelydra* and that in fishes and salamanders involves the movement of the cranium. In fishes and salamanders, cranial elevation peaks near peak gape and has nearly returned to its initial position by the end of the compressive phase. Gape closure is achieved by nearly equal contributions from cranial depression and lower jaw elevation. In *Chelydra*, initial gape closure is due to depression of the cranium while the lower jaw continues to rotate ventrally (visible in Fig. 2, fields 04:970 and 05:000 and fields 40:490 and 40:550). Final gape closure occurs when the absolute position of the cranium is stabilized, presumably by the spinalis-cervico capitis muscles, and the lower jaw is elevated, presumably by the adductor mandibulae muscle. This asynchronous movement of the cranium and lower jaw during the closing phase is a phenomenon not observed in any previous study of aquatic feeding in fishes and

salamanders (Bemis and Lauder, 1986; Lauder, 1983, 1985; Lauder and Shaffer, 1985; Liem, 1978, 1979; Reilly and Lauder, 1989*a*; Shaffer and Lauder, 1988).

The recovery phase in *Chelydra* is extremely long. If the recovery phase is defined as the time from gape closure to the return of the neck, hyoid and jaws to their initial positions, then this phase in *Chelydra* lasts for more than 1 s. This contrasts with the recovery phase times seen in fishes and salamanders, which last around 0.5 s for large prey items. In *Chelydra*, the hyoid remains just below maximum depression levels for about 0.45 s after peak gape and is coupled with an overall increase in the thickness of the neck that lasts for at least 1 s after time zero. During the recovery phase, water in the mouth may exit anteriorly through the small gape opening (note the small gape increase between 500 and 1000 ms in Fig. 3).

Suction feeding in Chelydra serpentina

Chelydra, like several species of aquatic turtles, has been thought to use fluid suction as a means of prey capture (Shafland, 1968; Gans, 1969; Bramble 1973, 1978; Jackson, 1978; Lauder, 1985). Suction feeding is a mechanism of aquatic prey capture in which a reduction in pressure within the mouth cavity (with respect to the ambient fluid) generates a flow of water into the mouth (Lauder, 1985). It is important to clarify two possible phenomena associated with suction feeding. First, suction feeding may refer to the reduction in pressure within the mouth cavity of a predator that necessarily occurs as mouth cavity volume increases (Muller, 1983). Second, suction may refer to the pattern of prey movement: is the prey drawn into the mouth of a predator or does it remain stationary relative to a fixed background?

These two aspects of suction feeding are quite distinct: as mouth cavity expansion (with the accompanying hydrodynamically obligatory pressure decrease) may occur far away from a prey item and the predator may then use body velocity to overtake the prey with an open mouth. If a prey item is observed to remain stationary relative to the background, then any suction pressure generated by the predator during mouth opening does not move the prey towards the predator (this is the case in *Luciocephalus pulcher*, Lauder and Liem, 1981).

Previous studies have examined the morphology of the buccal cavity in *Chelydra* and have found features associated with known suction feeders, such as a well-ossified and robust hyoid, poorly developed tongue musculature, a non-papillose tongue and oral mucosa, and a low vaulted palate (Bramble, 1973; Bramble and Wake, 1985; Winokur, 1974). Also, preliminary kinematic investigations suggested that posteroventral movement of the hyoid in *Chelydra* is responsible for both mandibular depression and a volume change in the mouth cavity often associated with suction-feeding vertebrates (Bramble, 1973, 1978; Lauder, 1985). However, the findings in this paper suggest a re-evaluation of the role of suction during prey capture in *Chelydra* and perhaps in several other species of aquatic turtles.

As pointed out by Muller (1983), expansion of mouth cavity volume will

necessarily be accompanied by an intraoral pressure reduction. In the case of *Chelydra*, the substantial expansion of the mouth and neck during prey capture (as documented by kinematic measurements, Figs 4, 5) necessitates a pressure reduction within the mouth and esophagus. To determine if this affects the position of the prey, the relative positions of the predator and prey with respect to a fixed background may be compared (Lauder and Liem, 1981). If the predator-to-prey distance decreases while prey position remains fixed relative to the background, then suction is not being used to draw prey into the mouth, and has no effect *on the prey*. The data on *Chelydra* show that the prey only begins to move into the mouth after the plane of the gape has been crossed, not before, and that the decrease in predator-to-prey distance prior to peak gape is entirely due to movement of the head towards the prey. Liem (1980) has named this pattern of feeding 'ram feeding' by analogy with ram ventilation during locomotion, and the data on *Chelydra* match exactly those expected for a ram-feeding predator (Lauder and Liem, 1981). Once the prey has crossed the plane of the gape, then the negative pressures generated by neck expansion and hyoid depression in *Chelydra* do appear to produce a posteriorly directed flow of water that carries the prey into the mouth.

Rapid acceleration of the head and neck towards prey does produce a hydrodynamic pressure gradient that could be detected by the Mauthner neurons of the fish and cause a startle escape response. Fig. 5 shows that the position of the prey relative to the shell remains virtually constant until the fish is within the plane of the open gape at peak gape (also see Fig. 2: field 04:950). Hyoid depression at peak gape is 4.3 cm, while maximum hyoid depression is 4.7 cm and is achieved 15 ms later. Also at peak gape, neck thickness (Fig. 5), and presumably the esophagus too, begins to expand. These results suggest that one role of ventral hyoid excursion and enlargement of the esophagus after peak gape may be to eliminate a pressure gradient in front of the head by creating a reservoir for the column of water to occupy as the head and rapidly opening gape accelerate towards the prey. Thus, one role of intraoral suction may be to reduce near-field effects of head motion on prey movement-detection systems (such as the lateral line). However, the data of Fig. 5 also indicate that the prey may still experience small effects of turtle head movement and be pushed slightly away for a brief period as it passes the plane of the gape.

These observations agree with a report by Bramble (1978) in which he described successful strikes on fish as showing no evidence of suction effects (on the prey) until the jaws intersected the prey item. Our data show that in *Chelydra* the effect of fluid suction *on the prey* is minimal, and that *Chelydra* relies heavily upon the acceleration of the head and rapidly opening jaws to overtake and surround the prey in the mouth cavity (ram-feeding). Pressure transducer recordings of buccal pressures would enable a determination of the negative pressures generated during prey capture and an estimation of the effect of pressure differentials on water flow into the mouth.

Lauder (1985) and Lauder and Shaffer (1986) defined two major classes of

aquatic feeding mechanisms: unidirectional and bidirectional designs. *Chelydra* is a bidirectional aquatic feeder, as opposed to fishes and larval aquatic salamanders, which are unidirectional. In unidirectional feeders, water swallowed during the strike exits *via* a posterior openings (gill slits). In bidirectional feeders, water entering the mouth during the fast open and closing phases must also exit through the mouth during the recovery phase. Esophageal expansion, however, may function to allow unidirectional flow of water and prey until the gape closes and may serve to delay reverse flow until the recovery phase has begun.

Films of all five turtles feeding show a significant decrease in neck thickness, a decrease in hyoid protraction and slight mouth opening about 1000 ms after peak gape. Water that was swallowed during prey capture can be seen to be expelled anteriorly during this time. The role of the esophagus as a store for water entering the mouth during prey capture may be critical to feeding by *Chelydra*. Previous analyses of bidirectional feeding in salamanders (Lauder and Shaffer, 1986; Lauder and Reilly, 1988), in which no site of water storage exists within the mouth cavity, showed that bidirectional feeding was much less effective in capturing prey than unidirectional feeding systems in the same animal.

It is interesting to note that the most consistent kinematic components in fish and worm feedings were the extent of hyoid depression and the overall thickness of the second neck distance. These two variables have the least prey-type variation, as reflected by the lowest F-values in Table 2. In contrast, the time to maximum hyoid depression was significantly faster for fish feedings than for worm feedings. Consequently, the *volumes* of the buccal and esophageal cavities attained during feeding on both prey types appear to be similar but the *rate of volume change* is faster for fish feedings. When feeding on elusive prey items, *Chelydra* combines greater head accelerations, greater neck extensions, larger and more rapid gape openings, and more rapid posteroventral hyoid movement to produce a significantly greater rate of volume change than in worm feedings. This may be necessary to reduce the pressure gradient in front of the head and overtake the elusive prey item which might otherwise escape the strike.

Finally, these data show that evolutionary convergence of a feeding mechanism for the rapid capture of aquatic prey in turtles (on the one hand) and fishes and salamanders (on the other hand) has produced both kinematic similarities and differences. The relative timing of gape and hyoid profiles are very similar between fishes and turtles, suggesting that these kinematic components of the strike may be necessary hydrodynamic consequences of having a large volume of water enter the mouth during feeding. The necessity of reducing any near-field effects of head movement at the prey may dictate that throat expansion follow peak gape and reach maximum velocity synchronously with maximum gape (as in Fig. 4 on fish strikes). However, fundamental differences from salamanders and fishes in the morphological design of the turtle head (such as the long and flexible neck) may result in differences in prey capture kinematics. The striking dissimilarities between closing-phase kinematics in fishes and *Chelydra* may reflect the effect of the neck on the pattern of head movement.

References

ALEXANDER, R. McN. (1970). Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* **162**, 145–156.

BEMIS, W. AND LAUDER, G. V. (1986). Morphology and function of the feeding apparatus of the lungfish *Lepidosiren paradoxa* (Dipnoi). *J. Morph.* **187**, 81–108.

BRAMBLE, D. M. (1973). Media dependent feeding in turtles. *Am. Zool.* **13**, 1342.

BRAMBLE, D. M. (1978). Functional analysis of underwater feeding in the snapping turtle. *Am. Zool.* **18**, 623.

BRAMBLE, D. M. AND WAKE, D. B. (1985). Feeding mechanisms of lower tetrapods. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake), pp. 230–261. Cambridge: Harvard University Press.

BURGHARDT, G. M. AND HESS, E. H. (1966). Food imprinting in the snapping turtle. *Science* **151**, 108–109.

CARROLL, R. L. (1988). *Vertebrate Paleontology and Evolution*. New York: W. H. Freeman and Co.

ELSHOUD-OLDENHAVE, M. J. W. (1979). Prey capture in the pike perch, *Stizostedion lucioperca* (Teleostei, Percidae): a structural and functional analysis. *Zoomorphology* **93**, 1–32.

ERNST, C. H. AND BARBOUR, R. W. (1989). *Turtles of the World*. Washington, DC: Smithsonian Institution Press.

GAFFNEY, E. S. (1979). Comparative cranial morphology of recent and fossil turtles. *Bull. Am. Mus. nat. Hist.* **164**, 65–376.

GAFFNEY, E. S., HUTCHINSON, J. H., JENKINS, F. A. AND MEEKER, L. J. (1987). Modern turtle origins: the oldest known cryptodire. *Science* **237**, 289–291.

GAFFNEY, E. S. AND MEEKER, L. J. (1983). Skull morphology of the oldest turtles: A preliminary description of *Proganochelys quenstedti*. *J. Vert. Paleont.* **3**, 25–28.

GANS, C. (1969). Comments on inertial feeding. *Copeia* **1969**, 855–857.

GROBECKER, D. B. AND PIETSCH, T. W. (1979). High-speed cinematographic evidence for ultrafast feeding in antennariid anglerfishes. *Science* **205**, 1161–1162.

HAMMER, D. A. (1975). Soft sell on the hard-shell: exploring waterfowl predation pressure – ducks, coons and snappers. *Ducks Unlimited* Sept/Oct, 46–71.

HARTLINE, P. H. (1967). The unbelievable fringed turtle. *Int. Turtle Tortoise Soc. J.* **1967**, 24–29.

JACKSON, D. J. (1978). Evolution and fossil record of the chicken turtle *Deirochelys*, with a re-evaluation of the genus. *Tulane Stud. Zool. Bot.* **20**, 35–55.

LAUDER, G. V. (1980a). Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morph.* **163**, 283–317.

LAUDER, G. V. (1980b). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. exp. Biol.* **88**, 49–72.

LAUDER, G. V. (1983). Food capture. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 280–311. New York: Praeger Publishers.

LAUDER, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake), pp. 210–229. Cambridge: Harvard University Press.

LAUDER, G. V. AND LIEM, K. F. (1981). Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes. *Env. Biol. Fish.* **6**, 257–268.

LAUDER, G. V. AND REILLY, S. M. (1988). Functional design of the feeding mechanism in salamanders: causal bases of ontogenetic changes in function. *J. exp. Biol.* **134**, 219–233.

LAUDER, G. V. AND SHAFFER, H. B. (1985). Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J. Morph.* **185**, 297–326.

LAUDER, G. V. AND SHAFFER, H. B. (1986). Functional design of the feeding mechanism in lower vertebrates: unidirectional and bidirectional flow systems in the tiger salamander. *J. Linn. Soc. (Zool.)* **88**, 277–290.

LAUDER, G. V. AND SHAFFER, H. B. (1991). Design of the aquatic vertebrate skull: major patterns and their evolutionary interpretations. In *The Vertebrate Skull* (ed. J. Hanken and B. Hall). Chicago: University of Chicago Press. (in press).

LIEM, K. F. (1970). Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana Zoology* **56**, 1–166.

LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morph.* **158**, 323–360.

LIEM, K. F. (1979). Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool., Lond.* **189**, 93–125.

LIEM, K. F. (1980). Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns. In *Environmental Physiology of Fishes* (ed. M. A. Ali), pp. 299–334. New York: Plenum Press.

MAHMOUD, I. Y. (1968). Feeding behavior in kinosternid turtles. *Herpetologica* **24**, 300–305.

MAHMOUD, I. Y. AND KLICKA, J. (1979). Feeding, drinking, and excretion. In *Turtles: Perspectives and Research* (ed. M. Harless and H. Morlock), pp. 229–243. New York: John Wiley.

MATTHES, E. (1934). Bau und Function der Lippensaume wasserlebender Urodelen. *Z. Morph. Ökol. Tiere* **28**, 155–169.

MULLER, M. (1983). *Hydrodynamics of Suction Feeding in Fish.* Wageningen: Veenman and Zonen.

PRITCHARD, P. C. H. (1979). *Encyclopedia of Turtles.* Neptune: T. F. H. Publications, Inc. Ltd.

REILLY, S. M. AND LAUDER, G. V. (1989a). Kinetics of tongue projection in *Ambystoma tigrinum*: quantitative kinematics, muscle function, and evolutionary hypotheses. *J. Morph.* **199**, 223–243.

REILLY, S. M. AND LAUDER, G. V. (1989b). Physiological bases of feeding behavior in salamanders: do motor patterns vary with prey type? *J. exp. Biol.* **141**, 343–358.

REILLY, S. M. AND LAUDER, G. V. (1990). The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution* **44**, 1542–1557.

SANFORD, C. P. J. AND LAUDER, G. V. (1990). Kinematics of the tongue-bite apparatus in osteoglossomorph fishes. *J. exp. Biol.* **154**, 137–162.

SHAFFER, H. B. AND LAUDER, G. V. (1985). Patterns of variation in aquatic ambystomatid salamanders: kinematics of the feeding mechanism. *Evolution* **39**, 83–92.

SHAFFER, H. B. AND LAUDER, G. V. (1988). The ontogeny of functional design: metamorphosis of feeding behavior in the tiger salamander (*Ambystoma tigrinum*). *J. Zool., Lond.* **216**, 437–454.

SHAFLAND, J. L. (1968). Functional and anatomical convergence in body form and feeding behavior in three diverse species of freshwater bottom dwelling vertebrates. PhD. dissertation, University of Chicago.

SOKAL, R. R. AND ROHLF, F. J. (1981). *Biometry* (2nd edn). New York: W. H. Freeman and Co.

WAINWRIGHT, P. C. AND LAUDER, G. V. (1986). Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *J. Linn. Soc. (Zool.)* **88**, 217–228.

WEISGRAM, J. (1982). *Claudius angustatus* (Kinosternidae) – Nahrungsaufnahme. *Wiss. Film Fr.* **28**, 28–35.

WEISGRAM, J. (1985). Feeding mechanics of *Claudius angustatus* COPE 1865. *Fortschr. Zool.* **30**, 257–260.

WESTNEAT, M. AND WAINWRIGHT, P. C. (1989). The feeding mechanism of the sling-jaw wrasse, *Epibulus insidiator* (Labridae; Teleostei): evolution of a novel functional system. *J. Morph.* **202**, 129–150.

WINOKUR, R. M. (1974). Adaptive modifications of the buccal mucosa in turtles. *Am. Zool.* **13**, 1347–1348.