

AQUATIC PREY TRANSPORT AND THE COMPARATIVE KINEMATICS OF *AMBYSTOMA TIGRINUM* FEEDING BEHAVIORS

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Summary

Four definable feeding behaviors used during the metamorphic life history of tiger salamanders are terrestrial prey capture and transport (as adults) and aquatic prey capture and transport (as larvae). Previous studies have focused primarily on the first three of these behaviors and thus aquatic prey transport is poorly understood. These studies have indicated that terrestrial prey capture has unique kinematic and motor patterns, whereas the other behaviors are quite similar to one another. Using high-speed video analysis, the kinematics of aquatic prey transport in larval *Ambystoma tigrinum* are described using both lateral and ventral views. These kinematic patterns are statistically compared with the kinematic patterns of aquatic prey capture, terrestrial prey capture and terrestrial prey transport. Statistical analyses allow us to assess the similarities and differences among the four behaviors and to determine the effect of the metamorphic environmental transition (water to land) and morphological changes of the feeding mechanism (suction- to lingual-based) on feeding kinematics. Our data do not support the notion that lingual-based terrestrial prey capture uses unique kinematic patterns compared with the other three behaviors, which consist of similar movements. Rather, each of the feeding behaviors has unique kinematic features that distinguish it from the others. In addition, variation in tiger salamander feeding kinematics is more a function of the feeding event (whether it is capture or transport) than of the environment in which the feeding takes place or the morphology of the feeding mechanism. Finally, we encourage the use of parsimony-based methods of phylogenetic analysis to analyze shared traits (such as kinematic and/or electromyographic variables) in comparative studies of behavior within a single species.

Introduction

Environmental transitions may pose formidable problems which organisms must solve in order to survive and reproduce. One such transition faced by many animal taxa is the aquatic to terrestrial transition. The different physical properties of air and water (e.g. density, viscosity, heat capacity, molecular diffusivity) have been well described (Vogel,

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1983; Schmidt-Nielsen, 1990), and comparative physiologists have approached the problems involved in a transition between these two media from many perspectives (Little, 1983; Dejours *et al.* 1987; Schmidt-Nielsen, 1990; Feder and Burggren, 1992). However, the issue of how the aquatic to terrestrial transition affects the feeding system of an organism has received little quantitative attention (exceptions are Lauder and Shaffer, 1988; Shaffer and Lauder, 1988). Understanding these effects will allow a greater appreciation of the biophysical constraints underlying feeding behaviors in water and air (Bramble and Wake, 1985).

Many salamanders undergo such an environmental transition when they metamorphose from aquatic larvae into terrestrial adults. During metamorphosis, many morphological changes take place that are associated with the change in environment, including changes in locomotor, sensory, respiratory and feeding structures (Duellman and Trueb, 1986). Changes in skull and feeding morphology during metamorphosis include a reduction in head size, acquisition of a tongue, closing of gill slits and a change in hyobranchial structure (Lauder and Shaffer, 1988; Lauder and Reilly, 1990). These morphological changes lead to concomitant changes in the feeding mechanism of the salamander, from one which is suction-based in the larva to one which is primarily lingual-based in the adult, although post-metamorphic tiger salamanders do return to the water and suction feed (Miller and Larsen, 1986) less effectively (Lauder and Shaffer, 1986). Such different morphological designs have presumably evolved to accommodate the increased prominence of gravitational forces relative to drag forces that act on food items after the transition to land (Bramble and Wake, 1985).

Ignoring swallowing, salamander feedings can be divided into at least two distinct phases: prey capture and prey transport. Prey capture is defined as the initial acquisition of a prey item, while prey transport refers to the movement of captured prey closer to the esophagus where it can then be swallowed. As the term 'transport' has been used previously to encompass a diverse array of behaviors, including buccal and pharyngeal jaw manipulations in fishes (Sibbing, 1982; Lauder, 1983; Sibbing *et al.* 1986; Drucker and Jensen, 1991), and a diversity of transport-like behaviors also occur in aquatic salamanders, we restrict our definition of transport to movement of prey, which has been captured but not completely engulfed, further or entirely into the buccal cavity. In other words, transport, as we are defining it in this paper, can take place only if part of the prey remains outside the mouth after prey capture is complete.

Therefore, at least four different feeding behaviors can be defined for a salamander which undergoes metamorphosis as part of its life history: aquatic prey capture and aquatic prey transport as larvae, as well as terrestrial prey capture and terrestrial prey transport as adults. Comparing these four behaviors in terms of their kinematics and/or muscle function allows one to address the effects of different morphologies and different physical properties of the fluid medium on salamander feeding behaviors.

The kinematics and motor patterns associated with salamander feeding have been studied most extensively in *Ambystoma tigrinum* and include aquatic prey capture (Lauder and Shaffer, 1985, 1988; Shaffer and Lauder, 1988), terrestrial prey capture (Larsen and Guthrie, 1975; Lauder and Shaffer, 1988; Shaffer and Lauder, 1988; Reilly and Lauder, 1989, 1990a) and terrestrial prey transport (Reilly and Lauder, 1990b, 1991).

Larval aquatic prey capture consists of a rapid increase in volume and decrease in pressure within the buccal cavity, resulting in a unidirectional flow of water and prey into the mouth. Terrestrial prey capture involves protraction of the tongue beyond the plane of the gape, contact and adhesion to the prey, and retraction of both the tongue and prey into the mouth. Terrestrial prey transport consists of repeated cyclical movements of the jaws, hyoid and tongue with attached prey, which move the prey posteriorly; see Lauder and Reilly (1993) for a more detailed account of these three behaviors. Aquatic prey transport, or hydraulic transport (Bemis and Lauder, 1986), on the other hand, has not been examined quantitatively in any taxon despite its widespread use among aquatic vertebrates. Therefore, we chose to examine aquatic prey transport in *A. tigrinum* in order to gain insight into a common, but poorly understood, feeding behavior and to make a quantitative comparison among the four behaviors within the same species.

Previous studies have shown that lingual-based terrestrial prey capture is kinematically unique relative to aquatic prey capture and terrestrial prey transport, because of a plateau in the gape cycle correlated with tongue protrusion and longer-duration movements (Reilly and Lauder, 1989). In addition, general kinematic and motor pattern similarities have been found between aquatic prey capture and terrestrial prey transport in *A. tigrinum* (Reilly and Lauder, 1990b) and aquatic prey transport in fishes (Reilly and Lauder, 1991). These studies led Lauder and Reilly (1993) to propose that kinematic and motor patterns used during aquatic prey capture, aquatic prey transport and terrestrial prey transport are more similar to each other than to those used during terrestrial prey capture. An explicit quantitative test of this hypothesis has not been made.

One goal of this paper is therefore to describe and quantify the kinematics of aquatic prey transport in *A. tigrinum* using high-speed video analysis. A second aim is to compare statistically the four different feeding behaviors naturally found within the life history of *A. tigrinum* and test the hypothesis that terrestrial prey capture is distinct from other feeding behaviors. Finally, we discuss the relationship between prey capture and prey transport behaviors as they change across environments and metamorphosis, and we introduce a new method for the comparative intraspecific analysis of kinematic patterns.

Materials and methods

Feeding kinematics of aquatic prey transport

Kinematic data were collected from five similarly sized *Ambystoma tigrinum* (Green) larvae [2.8–3.1 cm HW (head width at jaw), mean=2.9 cm], obtained from a commercial supplier. Larvae were individually housed in 40 l aquaria and were maintained on a diet of earthworms (*Lumbricus*). Water temperature was kept at 19.5 ± 1.5 °C and a photoperiod of 12 h light:12 h dark was established.

Salamanders were trained to feed under bright lights in a 40 l aquarium with a white 1 cm² grid background and a clear 4 cm² grid false bottom for scale. Videos of transport sequences were recorded at 200 fields s⁻¹ onto VHS videotape using a NAC HSV-400 high-speed video system. Animals were filmed from both ventral and lateral views simultaneously using two cameras, one aimed directly at a front surface mirror positioned

at a 45° angle underneath the aquarium (ventral view), the other aimed directly at the side of the aquarium (lateral view). Two strobe lights (400 W), synchronized with the shutters of the video cameras, and two bright tungsten halogen lights (1200 W), were used to provide illumination during filming. Cameras were adjusted and aligned prior to filming so that both cameras were parallel, and both ventral and lateral video images were at identical (or very similar) magnifications and showed the same area of the filming tank.

To elicit feedings parallel to the plane of the film, 3–4 cm pieces of earthworm were held with forceps several centimeters anterodorsal to a salamander's jaws in order to attract the salamander into a position in view of, and perpendicular to, the long axes of both cameras. Worms were then released from the forceps just prior to or during the strike, to facilitate a successful capture of the prey. Although this method ensured that prey capture was parallel to the plane of film, the salamander often turned its head or entire body out of the proper plane prior to or during the first prey transport. Therefore, many repeated feedings were necessary in order to film an adequate number of prey transports in the proper orientation relative to the cameras. Pieces of worm 3–4 cm long were used so that, after initial prey capture, some portion of the worm (usually about 1–2 cm) remained outside the buccal cavity. These longer pieces of worm permitted quantification of prey movements during transport.

The kinematics of prey transport were analyzed field by field using a custom video digitizing system. Six feedings from each of five different individuals were analyzed. All transport sequences chosen for analysis were parallel to the plane of the film or very nearly so. The analyzed portion of a transport sequence usually consisted of 26 video fields encompassing 360 ms. One video field, designated as time zero, was selected for each transport sequence as a reference point and represented the field just prior to gape opening. Video fields -10, -5, 0–75 (in 5 ms increments), 100, 125, 150, 175, 200, 250, 300 and 350 were always used for digitizing and analysis.

For most transport sequences, six kinematic variables were digitized from each of the 26 video fields. Gape distance was measured (in cm) from a lateral view as the linear distance between the anteriormost points of the upper and lower jaws. Gape distance increases as the mouth opens and decreases to zero when the mouth is closed.

Head angle was measured (in degrees) from a lateral view as the angle between two lines. One line was defined by two points along the dorsal border of the skull and the second by two points along the dorsal margin of the body, anterior to where the tail fin begins. At time zero, head angle is defined as 0°, and all other head angle measurements are made relative to this angle. Head angle increases when the head is lifted and decreases when it is lowered.

Lower jaw angle was also measured from a lateral view as the angle between two lines. One line was defined by a point at the anterior edge of the lower jaw and a second point at the vertex of the jaw angle. The other line was defined by the same two points along the dorsal margin of the body as those used for head angle. Again, at time zero, lower jaw angle is defined as 0°. Lower jaw angle decreases as the lower jaw is depressed and increases when it is raised. When the mouth is closed, changes in lower jaw angle can reflect movements of the head rather than of the lower jaw exclusively.

Hyoid distance was measured (in cm) from a lateral view as the linear distance from a

point on the dorsal border of the skull, 1 cm posterior to the eye, to the ventral border of the gular region. An increase in hyoid distance reflects posteroventral retraction of the hyoid apparatus, while a decrease represents the recycling of the hyoid anterodorsally. Since one of the points defining hyoid distance was located on the skull, changes in head angle could affect the hyoid distance. However, because the point was located quite close to the vertex of the head angle, errors were minimized. For an illustration of how gape distance, head angle and hyoid depression were measured, see Fig. 1 in Shaffer and Lauder (1985).

Lateral head expansion was measured (in cm) from a ventral view as the largest linear distance connecting two points anterior to the origin of the external gills. An increase in this variable indicates lateral expansion of the head.

Worm length was measured (in cm) as the distance from the point on the worm farthest from the mouth of the salamander to the anteriormost portion of the jaws. Either a lateral or a ventral view was used for the measurement, depending upon the orientation of the worm. If the worm was close to perpendicular, relative to the longitudinal axes of the cameras, the lateral view was used, and if it was approximately parallel to a horizontal grid line on the background grid, the ventral view was used. As worm length decreased, more of the worm was entering the salamander's mouth. Because no inertial movement of the salamander occurred during transport, this variable was used to calculate worm velocity by measuring the distance the worm moved between fields and dividing by 5 ms.

In addition, for each individual, average values of kinematic variables from all six feedings were plotted against time (in ms). This created individual mean profiles for kinematic variables and associated standard errors for each time interval in order to illustrate quantitatively patterns and variation associated with aquatic transport kinematics (Figs 2 and 3).

The following 14 statistical variables were then derived from the data used to make the kinematic profiles and were calculated for each feeding (all timing variables were measured relative to time zero and are accurate to the nearest 5 ms): (1) maximum gape distance during prey transport (cm); (2) time to maximum gape (ms); (3) gape cycle duration (elapsed time from the start of gape opening until gape closure) (ms); (4) maximum head elevation (degrees); (5) time to maximum head elevation (ms); (6) maximum lower jaw depression (degrees); (7) time to maximum lower jaw depression (ms); (8) maximum hyoid depression (cm); (9) time to maximum hyoid depression (ms); (10) time to minimum hyoid depression (ms) (further explained below); (11) maximum lateral head expansion (cm); (12) time to maximum lateral head expansion (ms); (13) maximum worm velocity (cm s^{-1}) and (14) time to maximum worm velocity (ms) (means and standard errors are listed in Table 1).

Comparative kinematic data

The data obtained on larval aquatic prey transport from this study were compared with previous data collected on larval aquatic prey capture, adult terrestrial prey capture (both from Lauder and Shaffer, 1988) and adult terrestrial prey transport (from Reilly and Lauder, 1990*b*). Data for aquatic prey capture came from four individual larvae (mean head width 2.7 cm), 7, 6, 11 and 6 feedings; for terrestrial prey capture, data came from

Table 1. *Summary statistics of 14 statistical variables digitized during aquatic prey transport in Ambystoma tigrinum larvae*

Variable	<i>N</i>	Mean (standard deviation)
Maximum gape (cm)	30	0.92 (0.19)
Time to maximum gape (ms)	30	18.67 (3.92)
Gape cycle time (ms)	30	44.0 (7.59)
Maximum head elevation (degrees)	30	15.99 (5.25)
Time to maximum head elevation (ms)	30	29.0 (5.93)
Maximum lower jaw depression (degrees)	29	12.13 (6.22)
Time to maximum lower jaw depression (ms)	29	16.21 (4.94)
Maximum hyoid depression (cm)	27	2.82 (0.13)
Time to maximum hyoid depression (ms)	27	59.44 (10.59)
Time to minimum hyoid depression (ms)	29	6.21 (2.53)
Maximum lateral head expansion (cm)	23	3.5 (0.14)
Time to maximum lateral head expansion (ms)	23	37.61 (14.76)
Maximum worm velocity (cm s ⁻¹)	18	117.9 (44.02)
Time to maximum worm velocity (ms)	18	25.0 (5.42)

five adults (mean head width 2.0 cm), 3, 3, 4, 7 and 7 feedings; for terrestrial prey transport, data came from four adults (mean head width 2.25 cm), 6, 7, 4 and 5 feedings. Statistical variables used for the comparison were the seven variables commonly collected in the two studies mentioned above and in this study: (1) maximum gape, (2) time to maximum gape, (3) gape cycle duration, (4) time to maximum hyoid depression, (5) time to minimum hyoid depression, (6) maximum head angle and (7) time to maximum head angle.

The fifth statistical variable (time to minimum hyoid depression) has not been used previously in kinematic studies of *A. tigrinum* feeding behaviors. However, after reviewing video tapes, it was clear that measuring maximal hyoid excursions and their associated durations did not capture the extent to which hyoid movements varied among the different feeding behaviors. By measuring the time to minimum hyoid depression in addition to the time to maximum hyoid depression, the strikingly different pattern of hyoid movement observed during terrestrial prey capture could be characterized and included in our analyses. This novel variable was obtained from the original digitized data used by Lauder and Shaffer (1988) and Reilly and Lauder (1990b).

Statistical analyses

Comparative kinematic data were collected from different studies which used different sets of individuals. This necessitated using a nested experimental design for statistical analyses, with different individuals nested within each of the four behaviors (aquatic capture, aquatic transport, terrestrial capture and terrestrial transport). Variation in kinematic variables could be attributed to (1) differences among the four behaviors (behavioral level), (2) differences among individuals nested within each of the four behaviors (individual level) and (3) differences within individuals (used as the error term).

Basic statistics were calculated for all 14 statistical variables associated with aquatic prey transport, and for the seven statistical variables obtained from the remaining three behaviors. A nested analysis of variance (ANOVA) (Sokal and Rohlf, 1981) was performed on each of the seven statistical variables collected for all four behaviors. These analyses were designed to indicate to what extent variation in feeding kinematics could be attributed to the three different levels in our nested design. Significance levels for these ANOVAs were corrected for multiple tests using the sequential Bonferroni method (Rice, 1989). In cases where the nested ANOVA revealed a significant difference among behaviors for a particular statistical variable, a *post-hoc* multiple comparison Tukey test (Zar, 1984) was employed to pinpoint which behaviors were significantly different from one another and which were not. Statistical contrasts (Sokal and Rohlf, 1981) were used to test specific, *a priori* hypotheses by determining whether there were mean differences between particular combinations of behaviors, such as testing whether terrestrial prey capture is significantly different from aquatic prey capture, aquatic prey transport and terrestrial prey transport considered together (as proposed by Lauder and Reilly, 1993).

In order to provide a multivariate description of comparative feeding kinematics, two different techniques were used. First, to determine whether significant differences existed among the four behaviors when all seven variables (and their particular correlations) were taken into account simultaneously, a nested multivariate analysis of variance (MANOVA) was performed. Second, to visualize multivariate patterns of dispersion and to illustrate the similarities and differences among the different feeding behaviors in terms of all seven statistical variables, a principal components analysis (PCA) was performed. PCA analysis has proved to be a useful tool for examining multivariate patterns of feeding kinematics (e.g. Lauder and Shaffer, 1988; Shaffer and Lauder, 1988; Reilly and Lauder, 1992), and the procedures followed here were similar. Seven principal components were extracted from the correlation matrix, their component loadings were examined, and factor scores of the four components which explained the most variation were plotted against one another.

Comparative behavioral analysis using phylogenetic methods

To summarize our comparative results on the different behaviors, a phylogenetic analysis program (PAUP v.3.1.1 for Macintosh; Swofford, 1993) was used on a Macintosh Quadra 700. The four behaviors were entered as taxa and the seven statistical variables as characters. The original statistical variables were continuous rather than discrete, and so to define particular character states, univariate nested ANOVA or Tukey results were used. For any particular variable, behaviors which were not significantly different from one another (as defined by nested ANOVAs or Tukey tests) were assigned the same character state, while those that were significantly different were assigned different character states. Character states were defined as unordered, and an unrooted network was constructed using the exhaustive search option of PAUP without imposed topological constraints. All seven kinematic characters were included for completeness, although two of them (characters 4 and 6) are phylogenetically uninformative. This resulted in one unrooted network of nine steps. Note that PAUP typically keeps 'trees' in

computer memory as unrooted, and roots them for display (Swofford, 1993: p. 24). Thus, the displayed tree must be unrooted to visualize the network shown in Fig. 5.

This procedure is distinct from using statistical contrasts which test for *mean* differences among groups, in that it allows the grouping of behaviors based exclusively on *shared* characters. The implications of this novel use of phylogenetic analysis to study kinematic variation are presented in the Discussion.

Results

Aquatic prey transport kinematics

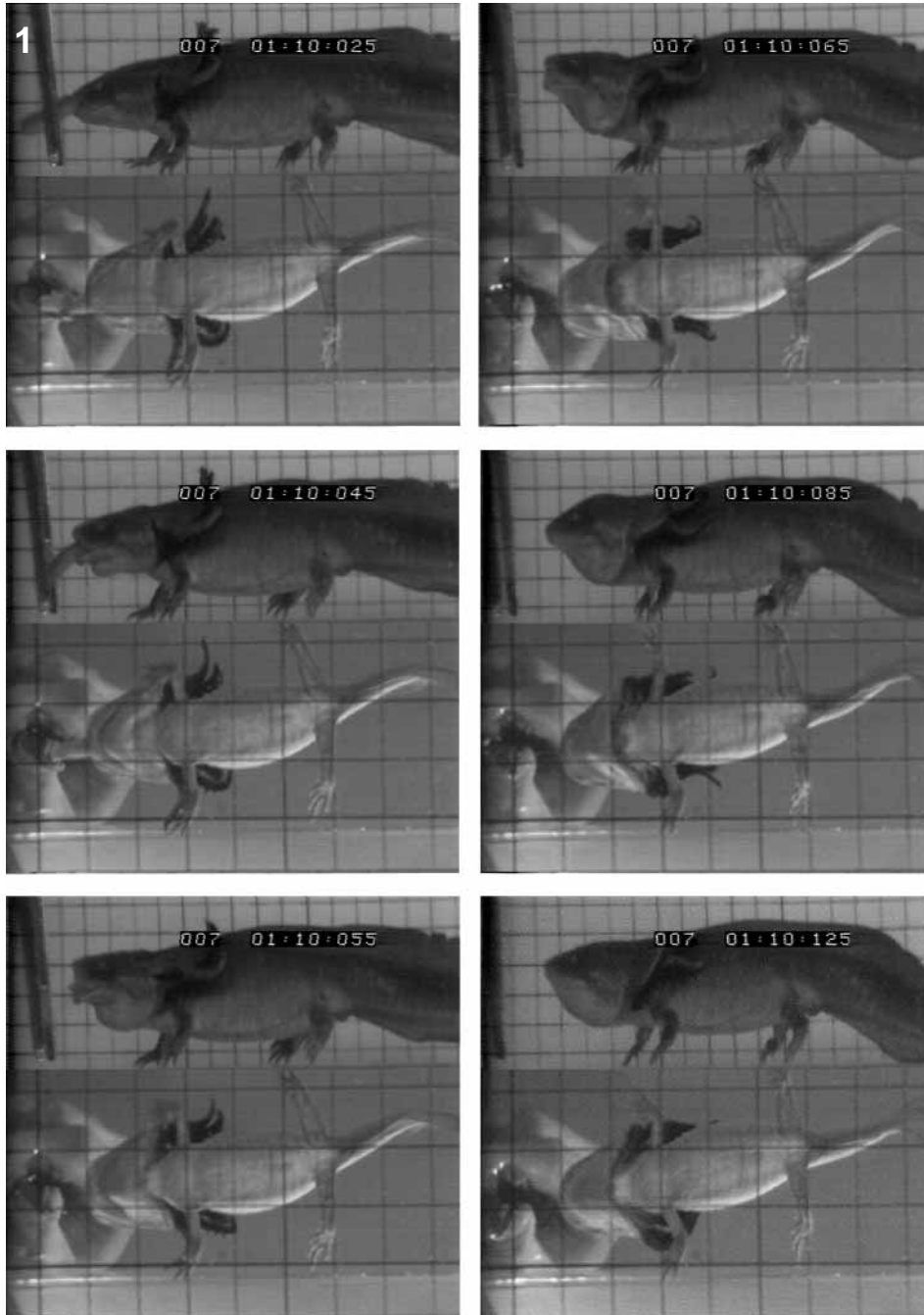
Fig. 1 shows six video fields taken from a single transport sequence. The six fields span 100 ms and provide a representative example of the general movements associated with aquatic prey transport in *A. tigrinum*. Mean profiles of five kinematic variables digitized from six transports by one individual are shown in Fig. 2 to illustrate, quantitatively, the kinematics of aquatic transport.

Gape distance at time zero is substantial because the worm is held between the jaws just prior to transport (Figs 1 and 2). The gape cycle lasts 44 ms on average, with maximum gape occurring at 19 ms (Table 1). Gape opening and gape closing require similar times, with opening occurring slightly faster, on average, than closing (Table 1). Changes in gape distance are brought about by movements of both the head and lower jaw. Lower jaw depression occurs rapidly, its maximum nearly coinciding with maximum gape, whereas head elevation occurs much more slowly, taking almost twice as long to reach its maximum (Table 1). Gape distance begins to decrease after about 20 ms, despite continuing cranial elevation as a result of the faster rate of lower jaw elevation. A second peak in head elevation occurs at about 100 ms (Fig. 2). A similar peak is seen for lower jaw angle because the jaws are closed and, as a result, moving in concert.

Changes in the volume of the buccal cavity are brought about by movements of the hyoid apparatus and lateral expansion and contraction of the head. Head expansion and hyoid retraction increase the volume of the buccal cavity, whereas head contraction and hyoid protraction decrease its volume. During aquatic prey transport, both lateral head expansion and hyoid retraction increase at a similar rate (enlarging the buccal cavity), reaching their maxima at about 40 and 60 ms, respectively, before slowly returning back to normal (Fig. 2).

Fig. 1. Six fields spanning 100 ms from a high-speed video sequence (taken at 200 fields per second) of aquatic prey transport in *Ambystoma tigrinum*. Each panel shows one full field as recorded during an experiment. Note that the lateral and ventral views were obtained using two different cameras taking their respective images simultaneously. The numbers at the top of each field indicate the sequence number (on the left) and time: minutes: seconds: milliseconds (on the right). At time zero (01:10:025), gape distance is already substantial because the worm is being held between the jaws prior to the transport. The majority of worm transport takes place between 01:10:045 and 01:10:055, and the gape cycle ends 60 ms after time zero (01:10:085). Note the second elevation of the head starting to be seen in field 01:10:125; maximum head elevation was reached at 01:10:065, then by 01:10:085 the neurocranium had been significantly depressed, only to begin to be lifted again in the last field.

Fig. 3 shows the mean profile of worm (prey) velocity, digitized from six transports by one individual, to indicate the rate and pattern of movement of prey during aquatic transport. Prey transport, on average, begins 10–15 ms after time zero, which is prior to maximum gape (Fig. 3). A maximum worm velocity of 118 cm s^{-1} , on average, is



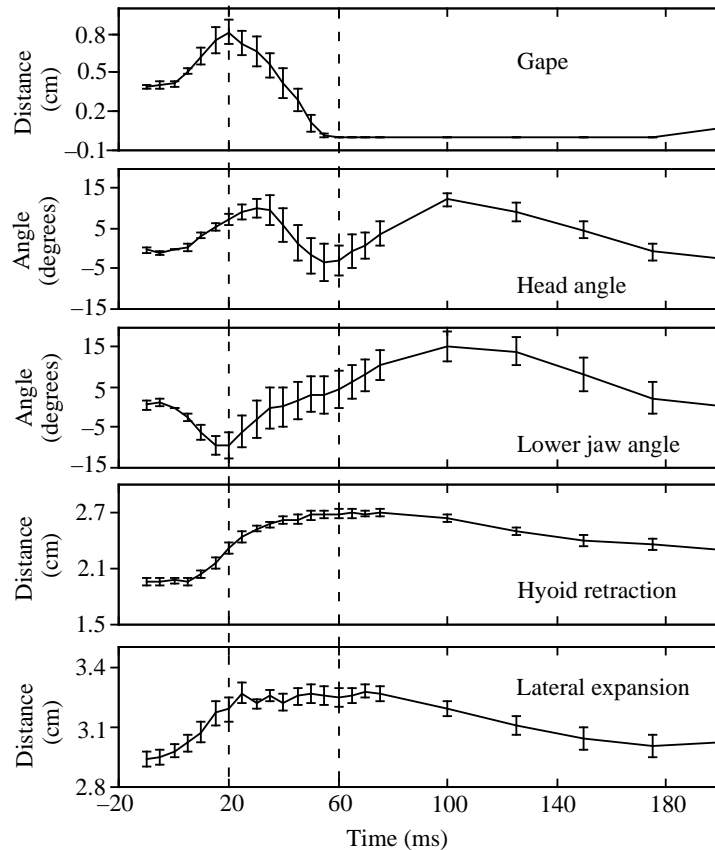


Fig. 2. Mean kinematic profiles (with standard error bars) of five variables during aquatic prey transport (from 1 individual, 6 transports). Angle variables have been scaled to equal zero at time zero to allow comparisons among transports in which initial head or lower jaw angles were not identical. Vertical dashed lines represent time at maximum gape (left) and the end of the gape cycle (right). Note the second elevation of the head which reaches its maximum at approximately 100 ms on average.

attained rapidly during the transport about 25 ms after the start of the gape cycle (Table 1).

Comparative feeding kinematics

The means and standard errors of seven statistical variables comparing feeding kinematics are shown in Table 2 for all four behaviors. Maximum gape distance, time to maximum gape, gape cycle time and time to maximum head angle all tend to be greater during prey capture than prey transport and also tend to be greater during terrestrial feedings than during aquatic feedings. Maximum head angle, on the other hand, while also tending to be greater during prey capture, tends to be smaller during terrestrial feedings. Time to maximum hyoid depression showed great variability, with no obvious trends, while time to minimum hyoid depression was much greater during terrestrial prey capture than during the other three behaviors.

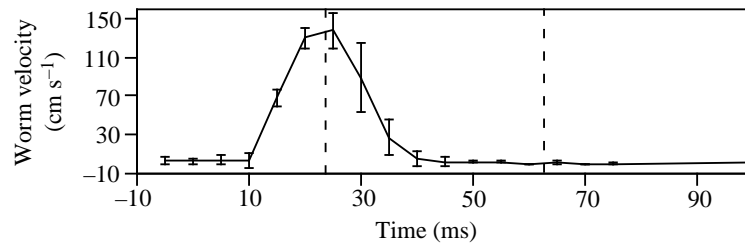


Fig. 3. Mean profile (with standard error bars) of worm velocity during aquatic prey transport (from 1 individual, 6 transports). Vertical dashed lines represent time at maximum gape (left) and the end of the gape cycle (right). Note that prey begins to be transported 10–15 ms into the gape cycle and that maximum velocity is reached just after maximum gape.

The results of the univariate nested ANOVAs for the seven statistical variables are shown in Table 3. There is a significant difference among behaviors ($P < 0.01$) for all variables except time to maximum hyoid depression. Individual variation is also apparent, with four of the seven variables showing a significant difference among individuals nested within behaviors. The results of the nested MANOVA, which took into account all seven statistical variables simultaneously, showed a highly significant behavior effect (Wilks' lambda=0.001; $P < 0.001$).

Results from the *post-hoc* Tukey tests are presented schematically in Table 4 for the six statistical variables which showed a significant difference among behaviors in the

Table 2. Mean, standard error and (sample size) for seven statistical variables and one morphometric variable digitized from prey capture and prey transport events in aquatic and terrestrial environments

Variables	Aquatic transport	Terrestrial transport	Aquatic capture	Terrestrial capture
Head width (cm)	2.9, 0.03 (5)	2.2* (4)	2.7* (4)	2.0* (5)
Maximum gape (cm)	0.9, 0.03 (30)	1.1, 0.07 (22)	1.3, 0.03 (30)	1.4, 0.04 (23)
Time to maximum gape (ms)	18.7, 0.72 (30)	20.2, 1.06 (22)	44.0, 1.95 (30)	54.6, 2.72 (23)
Gape cycle time (ms)	44.0, 1.38 (30)	57.4, 3.96 (21)	80.8, 3.66 (30)	89.8, 4.60 (23)
Time to maximum hyoid depression (ms)	59.4, 2.04 (27)	53.0, 6.67 (20)	48.7, 2.34 (30)	63.0, 7.86 (23)
Time to minimum hyoid depression (ms)	6.2, 0.47 (29)	12.6, 3.34 (21)	11.0, 1.03 (30)	41.7, 5.32 (20)
Maximum head angle (degrees)	16.0, 0.94 (30)	12.1, 1.46 (22)	29.9, 2.11 (30)	26.8, 2.03 (23)
Time to maximum head angle (ms)	29.0, 1.08 (30)	32.0, 2.50 (22)	47.0, 2.51 (30)	55.0, 3.75 (23)

*Data are taken from previous studies; individual variation is not known.

Table 3. *Univariate nested ANOVA results for the seven statistical variables measured during aquatic and terrestrial prey capture and transport*

Variable	Among behaviors d.f. = 3, (13–14)	Among individuals within behaviors d.f. = (13–14), (82–87)
Maximum gape	8.39 [†]	4.91 [‡]
Time to maximum gape	51.12 [‡]	2.06
Gape cycle time	22.15 [‡]	1.88
Time to maximum hyoid depression	0.75	4.13 [‡]
Time to minimum hyoid depression	7.50 [†]	4.30 [‡]
Maximum head angle	13.69 [‡]	1.97
Time to maximum head angle	10.11 [‡]	2.26*

Table entries are *F*-values.

Significant at **P* = 0.05, [†]*P* = 0.01, [‡]*P* = 0.001, using the sequential Bonferroni method described in Rice (1989).

univariate nested ANOVAs. Any behaviors which share similar symbols in the table (i.e. X, O or A) connected by a dashed line, are not significantly different from each other for that particular statistical variable (*P* > 0.05). Behaviors which do not share similar symbols, or have no symbols at all for a statistical variable, are significantly different from all other behaviors (*P* < 0.05). No significant differences were found between aquatic and terrestrial prey capture for four variables: maximum gape distance, gape cycle time, maximum head angle and time to maximum head angle. For terrestrial prey capture, time to maximum gape was significantly different from that for aquatic prey capture, and both types of prey capture were significantly different from each type of prey transport. For time to minimum hyoid depression, terrestrial capture was significantly different from the other three behaviors, which were not significantly different from each other.

Furthermore, no significant differences were found between aquatic and terrestrial prey transport for four variables: time to maximum gape, time to minimum hyoid depression,

Table 4. *Schematic diagram of results from post-hoc Tukey tests for each of the statistical variables which showed a significant difference among behaviors in the univariate nested ANOVAs*

Variable	Aquatic transport	Terrestrial transport	Aquatic capture	Terrestrial capture
Maximum gape			X-----X	
Time to maximum gape	O-----O			
Gape cycle time			X-----X	
Time to minimum hyoid depression	A-----A-----A			
Maximum head angle	O-----O		X-----X	
Time to maximum head angle	O-----O		X-----X	

Behaviors which share the same symbol, X, O or A, are not significantly different from one another. See text for further explanation of table.

maximum head angle and time to maximum head angle. For both maximum gape and gape cycle time, transport in one environment was significantly different from that in the other, and both types of transport were significantly different from each type of prey capture. In summary, prey capture behaviors showed no significant differences across environments for four of the statistical variables, and the same is true for prey transport behaviors. However, all variables except one (time to minimum hyoid), regardless of the environment, showed a significant difference between the different phases of the feeding cycle (prey capture and prey transport).

A statistical contrast corroborated the *a priori* hypothesis that terrestrial prey capture was significantly different from the other three behaviors considered together ($P=0.006$). However, caution should be exercised when interpreting this result, because when *any one behavior*, other than terrestrial prey capture, was contrasted against the remaining three behaviors considered together, a significant difference of $P=0.001$ was found. This indicates that each behavior is significantly different from all other behaviors considered together.

Multivariate patterns of dispersion found in the kinematics of the different feeding behaviors are presented in a principal components analysis shown in Fig. 4. The factor loadings of the statistical variables are shown (Table 5) for the two components which accounted for the most variation (52% and 16%, respectively, for PC1 and PC2). PC3

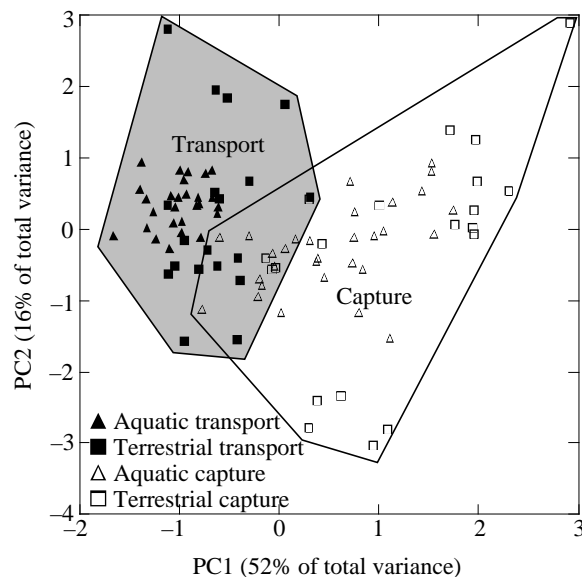


Fig. 4. Principal components analysis of four different feeding behaviors in *A. tigrinum*: aquatic prey capture, aquatic prey transport, terrestrial prey capture and terrestrial prey transport, based on seven statistical variables. Each symbol represents one feeding from one individual. Factor loadings for each variable are presented in Table 5. Note that, although there is a small region of overlap, capture and transport behaviors are largely separated along the PC1 axis.

Table 5. Factor loadings of the seven statistical variables used in the comparative analyses for the two principal components which explain the most variance (PC1 and PC2)

Variable	Factor loadings	
	PC1	PC2
Maximum gape	0.68	0.03
Time to maximum gape	0.95	-0.04
Gape cycle time	0.90	0.12
Time to maximum hyoid depression	0.33	0.87
Time to minimum hyoid depression	0.46	-0.50
Maximum head angle	0.60	-0.34
Time to maximum head angle	0.89	0.07

and PC4 accounted for 14% and 8% of the variation, respectively, and examination of PC3 and PC4 plots revealed no clear patterns of behavioral variation. Although there is a small region of overlap in the plot of PC1 *versus* PC2 (Fig. 4), PC1 distinguishes prey capture from prey transport behaviors, regardless of environment, with prey capture tending to have higher scores. Higher scores on PC1 reflect longer durations associated with timing kinematic variables during feedings, and also larger maximum gape and head angle displacements. The PC2 axis primarily reflects differences in the time to maximum hyoid depression. There is a great degree of overlap among the four behaviors along the

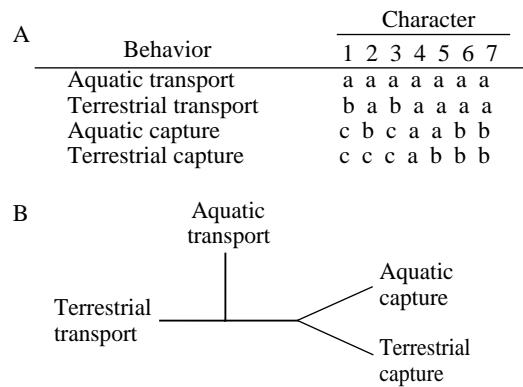


Fig. 5. Parsimony analysis of shared characteristics among the four feeding behaviors. Character matrix (A) was used to create the unrooted network (B) which shows that prey transport behaviors share more similarities with each other than either does with prey capture behaviors and that capture behaviors share more similarities with each other than either does with transport behaviors. Characters 1–7 are the seven statistical variables described in Materials and methods: (1) maximum gape, (2) time to maximum gape, (3) gape cycle duration, (4) time to maximum hyoid depression, (5) time to minimum hyoid depression, (6) maximum head angle and (7) time to maximum head angle. Note that the character states are unordered and are based upon Tukey results ($P < 0.05$). Character states imply nothing about the relatively primitive or derived state of the character. A state of 'a' was arbitrarily assigned to the smallest mean values (distance, duration or angle) while 'b' and 'c' were assigned to increasingly larger significant values respectively.

PC2 axis, indicating the extent to which the amount of variation found in the different behaviors for time to maximum hyoid depression was similar. The principal components analysis also shows the high degree of overlap found among feedings within prey capture or prey transport multivariate space. This indicates that the environment does not have a consistent, significant effect which differentiates aquatic from terrestrial prey capture or aquatic from terrestrial prey transport in terms of the kinematic variables used in this study.

Fig. 5 shows the data matrix used in the phylogenetic analysis and the most parsimonious network (nine steps) which could be constructed. Prey capture behaviors share more similarities with each other (characters 1, 3, 6 and 7) than with either of the prey transport behaviors, and the same is true of prey transport behaviors (which exclusively share the same state for characters 2, 6 and 7). Character 4 gives no information regarding the network since all behaviors share the same state. Character 5 could be considered an 'autapomorphy' of terrestrial prey capture. Note that the unrooted network shown in Fig. 5 does not allow a conclusion to be drawn as to which of the transport behaviors is most closely related to the capture behaviors. If the network is rooted, then treating either transport behavior as the sister behavior to both capture behaviors produces a tree length of nine steps. However, the unrooted network shows that captures and transports share separate unique kinematic traits.

Discussion

Aquatic prey transport

Traditional characterization of suction feeding in lower vertebrates involves terminology that was first used to define the different phases associated with prey capture in ray-finned fishes: preparation, expansion (fast opening), compression (closing) and recovery (Lauder, 1985). Aquatic prey transport in *Ambystoma tigrinum* larvae consists of at least the latter three phases; a preparatory phase could not be identified using our kinematic data alone. As Lauder (1985) suggested for aquatic prey capture in salamanders, electromyographic evidence is probably necessary to demonstrate clearly the reduction in buccal volume which characteristically defines the preparatory phase, if it exists.

The expansive phase is the shortest in duration, encompassing only 19 ms on average. Although expansion traditionally has been defined as beginning with the start of mouth opening, during prey transport the definition must be revised. Since prey is held between the jaws before prey transport, the mouth is open prior to the expansive phase, and hence expansion during transport must be defined as starting when the mouth begins to open wider than the distance needed to accommodate the prey. During the expansion phase, the jaws open, maximum gape is reached, and posteroventral hyoid retraction and lateral head expansion increase significantly, although they do not reach their maxima. This kinematic pattern of maximum gape being reached prior to maximum posteroventral hyoid displacement is common to aquatic prey capture events in a wide variety of lower

vertebrate taxa as well (Lauder, 1985), suggesting that this is a primitive characteristic of aquatic vertebrate feeding behaviors.

Hyoid retraction and lateral head expansion during aquatic prey capture in *A. tigrinum* create a reduction in pressure within the expanding buccal cavity, drawing or 'sucking' both water and prey into the mouth (Lauder and Shaffer, 1985). Kinematic patterns suggest that aquatic prey transport uses a similar suction-based mechanism. As Reilly and Lauder (1990*b*) found with terrestrial prey transport, no significant inertial movements of the salamander are used to help move prey further into the oral cavity during aquatic prey transport. During the latter half of the expansive phase, significant transport of the prey takes place (up to 1 cm) and velocities of prey moving into the mouth can exceed 100 cm s^{-1} .

Following the expansive phase is the compressive or closing phase, which usually lasts approximately 25 ms, slightly longer on average than expansion. This kinematic pattern, in which compression lasts longer than expansion, like maximum gape being reached prior to maximum hyoid depression, typically exists during aquatic prey capture in a variety of lower vertebrate taxa, such as fishes (Lauder, 1985), salamanders (Lauder and Shaffer, 1985; Reilly and Lauder, 1992) and turtles (Lauder and Prendergast, 1992), and may also be a primitive characteristic of aquatic vertebrate feeding behaviors. The compressive phase begins at the time of maximum gape and extends until the jaws either close together or close down onto prey remaining outside the buccal cavity. Closing of the jaws occurs primarily as a result of simultaneous lower jaw elevation and neurocranial depression. However, for a short period near the start of the phase, rapid lower jaw elevation is exclusively responsible for the decrease in gape distance while the neurocranium actually continues to elevate at a slow rate.

Hyoid retraction and head expansion plateau very near their maxima during this phase. On average, head expansion reaches its maximum prior to hyoid retraction, which is inconsistent with the anterior-to-posterior sequence of maximal kinematic excursions observed during prey capture in fishes (Lauder, 1985). However, because lateral expansion was occurring on such a small scale relative to hyoid depression, and since both variables plateau near their peak for a significant period, it was quite difficult to determine when the actual maximum head expansion took place. It is only possible to say that both variables reach their maxima at a similar time after maximum gape. In addition, it is during this phase when the majority of prey transport (1–2 cm) occurs and maximum prey velocities (sometimes over 200 cm s^{-1}) into the mouth are reached.

The recovery phase extends from the end of the compressive phase until kinematic variables return to their original values prior to expansion. This phase clearly lasts the longest, 300–500 ms, and usually it is the hyoid apparatus which takes the most time in returning to its initial position. Interestingly, during the first portion of the recovery phase there is a fairly consistent, distinct increase in head elevation, sometimes even beyond the angle reached during the gape cycle itself. To our knowledge, such an event has not been documented previously during any suction-feeding behavior, and the functional significance of this second head elevation during transport is not known.

Aquatic prey transport in *A. tigrinum* usually follows 200–400 ms after a successful prey capture event. Each cycle of transport is capable of moving up to 3 cm of worm into

the mouth of the salamander, and typically only one or sometimes two transport cycles occur per prey captured. The nature of terrestrial prey transport is quite different in that only 4–8 mm of worm is typically moved into the salamander's mouth per transport cycle, requiring 5–10 transport cycles to engulf a similarly sized piece of prey (Reilly and Lauder, 1990*b*). As a larval salamander becomes satiated, aquatic prey transport events are indistinguishable from those transports prior to satiation. However, the time between prey capture and prey transport and the time between prey transport events tend to increase. Eventually, when the salamander can swallow no more, a captured item of prey will simply be spat out after several unsuccessful transport attempts.

Feeding behavior, morphology and environment

The most readily observable distinction among the four different feeding behaviors examined in this paper is the obvious protrusion of the tongue during terrestrial prey capture. Kinematic and electromyographic novelties correlated with, and presumably related to, tongue protrusion during terrestrial prey capture have been documented (Lauder and Shaffer, 1988; Shaffer and Lauder, 1988; Reilly and Lauder, 1991). These novelties led Reilly and Lauder (1991) to suggest that terrestrial prey capture is a unique behavior composed of derived kinematic and motor patterns, whereas the other three behaviors (as well as aquatic feeding by post-metamorphic individuals) are quite similar. Lauder and Reilly (1993) proposed an explicit test to examine the unique nature of terrestrial prey capture, by hypothesizing that the kinematic and motor patterns of a lingual-based strike would be significantly different from those patterns of the other three behaviors which, in addition, would be more similar to each other than any is to a terrestrial strike.

The data presented here do not support this view. Statistical evidence from four different contrasts revealed that each behavior, when tested against the other three considered together, showed a significant difference ($P < 0.01$). Furthermore, the test contrasting terrestrial prey capture against the other three behaviors had the smallest F -statistic (8.2 relative to 15.8, 14.2 and 14.4) among the four contrasts. These lines of evidence, as well as Tukey, PCA and PAUP results, suggest that the conception of terrestrial prey capture being unique among salamander feeding behaviors, while aquatic prey capture, aquatic prey transport and terrestrial prey transport are undifferentiated, is misleading. Rather, each of the four behaviors has unique attributes which distinguish it from the others.

Despite the unique qualities associated with each of the four behaviors, an interesting pattern of similarities can be seen among them. Numerous kinematic variables (not associated with tongue protrusion) are statistically indistinguishable between aquatic and terrestrial prey capture, as well as between aquatic and terrestrial prey transport. Furthermore, for all kinematic variables but one, there was always a significant difference between prey capture and prey transport events, regardless of environment. Time to minimum hyoid depression was the only variable showing no significant difference between capture (aquatic) and transport (aquatic and terrestrial) events, although terrestrial prey capture was significantly different from the other three behaviors for this variable. The principal components analysis and PAUP tree construction provided results

similar to those acquired through Tukey tests: prey capture events are more similar to each other than either is to a prey transport event.

The environmental and morphological changes associated with metamorphosis in *A. tigrinum* are extensive. The switch from an aquatic environment, in which drag forces within a relatively dense and viscous fluid predominate, into a terrestrial environment where the fluid is much less dense and viscous, and gravitational forces predominate, has been shown by Frolich and Biewener (1992) greatly to affect axial locomotor kinematics in *A. tigrinum*. This transition could easily be expected to have a strong influence on the feeding kinematics of *A. tigrinum* as well. In addition, the drastic changes in head and hyolingual morphology might also be expected to affect feeding kinematics significantly. However, we would like to emphasize that, in contrast to the drastic morphological and environmental changes associated with metamorphosis, differences in kinematic patterns for prey capture or prey transport across metamorphosis are minimal. In fact, for the majority of statistical variables analyzed (4 out of 7), kinematic patterns for prey capture or prey transport across metamorphosis are statistically indistinguishable. However, within a similar environment (aquatic or terrestrial) and using an identical feeding morphology, prey capture and prey transport, whether suction- or lingual-based, are kinematically very different from each other. Therefore, variation in kinematics of tiger salamander feeding behaviors reflects much more the nature of the feeding event (whether it is a capture or a transport) rather than the environment within which the feeding takes place or the morphology of the feeding mechanism being used.

Prey capture and prey transport

Bramble and Wake (1985) proposed that similar feeding kinematics in turtles could work equally well to transport prey in water or on land. Clearly, this is the case in *A. tigrinum*, where aquatic and terrestrial prey transport are found in similar regions of multivariate space (Fig. 4) and show no significant differences for time to maximum gape, time to minimum hyoid depression, maximum head angle and time to maximum head angle (Table 2). Interestingly, the same pattern holds true for prey capture in *A. tigrinum*, indicating that both suction- and lingual-based prey capture events can also be accomplished using similar kinematic patterns (with the exception of hyolingual movements). No significant differences are found between prey capture behaviors for maximum gape distance, gape cycle time, maximum head angle and time to maximum head angle, and both behaviors occupy similar regions of multivariate space.

An intriguing aspect of the principal components analysis is that aquatic prey transport takes up the smallest portion of multivariate space. It is also noteworthy that the distance spanned by transport space as a whole in the PC1 dimension is only about two-thirds of that spanned by capture space (Fig. 4). These results would seem to indicate that aquatic transport is the most stereotyped of the four behaviors and that prey transport, in general, is more stereotyped than prey capture. Such results may reflect differences in muscle recruitment patterns and/or firing intensity between the transport and capture behaviors. However, more work is needed to generate increased sample sizes for quantifying kinematic variation, and on the motor patterns underlying prey transport, before differences in the extent of variation among behaviors can be quantified or explained.

Regardless of the environment, prey capture and prey transport can be defined as sequential, kinematically distinct feeding behaviors in *A. tigrinum*, and several generalizations can be made concerning the differences found between these behaviors in this study. First, maximum gape distance and head elevation are larger during capture than during transport. Second, timing variables associated with the gape cycle and neurocranial elevation extend for a significantly longer duration during capture than during transport. Whether these two general results are causally related is unknown at present, but the presence of a similar relationship could be looked for in other taxa to determine the phylogenetic extent of this correlation.

One previous conclusion to emerge from studies on feeding in a wide variety of fishes and salamanders is that aquatic prey capture, aquatic transport and terrestrial transport are similar behaviors, whereas terrestrial prey capture is unique because of the addition of novel kinematic and motor patterns. Implicit in this conclusion is the notion that prey capture on land necessitated changes in the kinematic and motor patterns capable of producing prey capture and transport behaviors under water as well as transport on land. We, however, suggest that differentiation in vertebrate feeding kinematics has not exclusively been a result of the aquatic to terrestrial transition and the accompanying change to a lingual-based prey capture feeding mechanism. Instead, we propose that feeding kinematics diverged much earlier in vertebrate evolution with the acquisition of distinct capture and transport behaviors. Quantitative studies of prey transport *and* prey capture in a wide variety of lower vertebrate taxa are needed to examine how phylogenetically widespread this distinction is and how consistent the differences between capture and transport are in order to provide a better understanding of general patterns in the evolution of vertebrate feeding systems.

Analyzing behaviors using parsimony-based phylogenetic methods

The network in Fig. 5B illustrates the same relationship among behaviors described more classically by the statistical analyses discussed earlier. Behaviors that share common states for a particular character tend to be grouped together. Prey capture behaviors exclusively share the same state for four characters (more than either shares with a transport behavior), and hence derive from a common node on the network. While both prey transport behaviors also derive from one node, the same state is shared exclusively for only three characters (more than either shares with a capture behavior). This difference between the number of exclusively shared characters among behaviors is purposefully reflected by our asymmetrical drawing of the network. Although we realize that the network we have drawn in Fig. 5B is identical to one drawn symmetrically, it is meant to illustrate the differential number of kinematic characters that group capture and transport behaviors and the lack of ancestral rooting in this analysis.

To our knowledge, parsimony-based methods of phylogenetic analysis have not been used previously to analyze kinematic variables, and yet such methods are well-suited for these studies. Analyses of variance test for mean differences among behaviors and, in a similar way, statistical contrasts test for differences among means while allowing several groups to be considered together. However, neither of these methods considers all kinematic attributes simultaneously while reconstructing both the unique *and* the shared

kinematic characters among behaviors. When data are available for three or more behaviors (as in Fig. 5A), parsimony-based methods allow the behaviors to be grouped by shared functional attributes and for the individual characters used in such groupings to be reconstructed (in contrast to traditional cluster analyses). Such an analysis need not make any assumptions about the direction of character transformation (characters may be treated as unordered). We thus recommend the use of parsimony-based phylogenetic analysis programs such as PAUP (Swofford, 1993) and MacClade (Maddison and Maddison, 1992) to analyze shared functional and biomechanical features in comparative intraspecific studies of the physiological bases of behavior.

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