

KINEMATICS OF FEEDING IN BLUEGILL SUNFISH: IS THERE A GENERAL DISTINCTION BETWEEN AQUATIC CAPTURE AND TRANSPORT BEHAVIORS?

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Summary

Despite numerous studies of food transport in terrestrial vertebrates, little is known about this aspect of the feeding repertoire in aquatic vertebrates. Previous work had predicted that the kinematics of aquatic prey capture by suction feeding should be similar to those of prey transport. However, recent analyses of aquatic prey capture and transport in the tiger salamander *Ambystoma tigrinum* have contradicted this hypothesis, and document numerous differences between these two behaviors. In this study, using high-speed video and statistical analyses, we compare prey capture and transport kinematics in a ray-finned fish (*Lepomis macrochirus*, the bluegill sunfish) to examine the generality of differences between capture and transport behaviors in aquatic vertebrates. Compared with prey capture, prey transport is significantly more rapid and tends to have reduced lower jaw excursions, while having

similar hyoid movements. A nested analysis of variance was used to analyze six variables common to both this analysis of *Lepomis macrochirus* and a previous study of *Ambystoma tigrinum*; none of these six variables showed significant variation between taxa. These results indicate that aquatic prey transport is kinematically distinct from capture behavior and that the distinctions between these two behaviors are remarkably consistent in two phylogenetically divergent lower vertebrate taxa. Such consistent kinematic differences have not been found in amniote taxa studied to date, but may constitute a plesiomorphic feature of vertebrate feeding systems.

Key words: feeding, kinematics, behavior, fish, *Lepomis macrochirus*, prey capture, prey transport, salamanders, *Ambystoma tigrinum*.

Introduction

The jaws and hyolingual elements of vertebrates are used for many purposes including the capture, processing, transport and swallowing of food. Describing and explaining the diversity of feeding mechanisms within and across taxonomic groups has been a goal for many functional and evolutionary morphologists (e.g. Hanken and Hall, 1993; Bels *et al.* 1994a,b). Research on the functional morphology of feeding in aquatic vertebrate taxa has centered almost exclusively on the mechanics and neuromuscular control of prey capture and on pharyngeal jaw function in fishes (for reviews, see Lauder, 1985; Vandewalle *et al.* 1994). However, the transport of prey to a position where it can be swallowed is as crucial to an organism's energy acquisition as the prey capture and/or swallowing event itself. Yet quantitative work on the mechanics and motor patterns underlying prey transport in aquatic vertebrates is generally lacking, although a few qualitative analyses of hydraulic transport do exist (e.g. Bemis and Lauder, 1986; Bemis, 1987).

The study of feeding in terrestrial taxa, in contrast, has often dealt with aspects other than the prey capture event. Mammalian chewing and transport cycles have been described and compared in a spectrum of taxa (for a review, see Hiiemae and Crompton, 1985). In addition, prey transport has been

studied recently in a variety of lizard species (e.g. Smith, 1984, 1986; Bels and Baltus, 1987; Schwenk and Throckmorton, 1989; Delheusy and Bels, 1992; So *et al.* 1992) and in ambystomatid salamanders (Reilly and Lauder, 1990, 1991).

Examinations of feeding in aquatic vertebrates are therefore often limited to the prey capture event, whereas studies of terrestrial vertebrate feedings have often considered prey transport as well. This bias can be attributed in part to the emphasis on similarities between the kinematic patterns of prey capture and transport in aquatic vertebrates that have been stressed in the literature despite little quantitative data (Reilly and Lauder, 1991; Lauder and Reilly, 1993). Such supposed similarities may have inhibited empirical investigation of aquatic prey transport as a separate behavior. In addition, this bias may be a result of the lingual basis of terrestrial feeding. Significant divergence in vertebrate feeding kinematics has been linked to the incorporation of the tongue into the feeding mechanism (Bramble and Wake, 1985). Furthermore, the tongue is used for multiple functions during feeding in terrestrial vertebrates. For example, Smith (1984) showed that capture, processing, transport, biting, pharyngeal packing and lapping all involve tongue use during feeding in certain lizards. The tongue can also be used for chemosensation and during

social behavior (Schwenk, 1994a, and references therein). It is perhaps not surprising then that many vertebrate functional morphologists are interested in the variation in, and evolution of, tongue function (Smith, 1984, 1986; Bramble and Wake, 1985; Hiiemae and Crompton, 1985; Schwenk and Throckmorton, 1989; Bels *et al.* 1994a; Schwenk, 1994b).

In a previous study of aquatic feeding, we found that aquatic prey transport in larval *Ambystoma tigrinum* was significantly different from aquatic prey capture in the majority of kinematic features investigated, while not being significantly different from adult lingual-based terrestrial transport for most variables (Gillis and Lauder, 1994). Hence, in the tiger salamander, there has been differentiation between capture and transport behaviors under water, and a metamorphic transition into the terrestrial environment and the associated tongue acquisition have not altered the basic kinematic pattern of prey transport. We suggested that a major divergence in vertebrate feeding kinematics occurred prior to the transition to land, with the acquisition of functionally distinct capture and transport behaviors in an aquatic ancestor. If possession of distinct capture and transport phases during feeding is indeed a primitive characteristic for vertebrates, then differences between capture and transport behaviors should be taxonomically widespread and consistent among lower vertebrates.

Thus, the overall goal of this study is to extend the analysis of aquatic prey transport, previously analyzed quantitatively only in salamanders, to ray-finned fishes. The specific goals of this study are fourfold. First, we quantify and describe the kinematics of both prey capture and transport in the centrarchid sunfish *Lepomis macrochirus*. Second, we analyze statistically the two behaviors in order to test the hypothesis that they are kinematically distinct. Third, we compare statistically the relationship between capture and transport kinematics in the sunfish with previous findings for larval tiger salamanders in order to test the hypothesis that there are consistent differences between capture and transport across lower vertebrate taxa. Finally, we compare our data from sunfish and salamanders with values from the literature for a variety of squamate reptile taxa and briefly discuss the nature of the association between capture and transport behaviors in amniotes.

Materials and methods

Prey capture and transport kinematics

The kinematics of prey capture and prey transport events were examined using four bluegill sunfish (*Lepomis macrochirus* Rafinesque) collected from ponds in central and southern California. Individual fish (mean standard length 14.6 cm, range 13.9–15.9 cm) were housed separately in 40 l aquaria (water temperature $19 \pm 1.5^\circ\text{C}$) under a photoperiod regime of 12h:12h: L:D and fed a diet of earthworms (*Lumbricus* sp.).

Fish were trained to feed in a small feeding chamber set up within a 120 l aquarium. The chamber was rectangular (approximately 25 cm \times 18 cm in size) and was filled with water

to a depth of 22 cm. The two walls lateral to the fish were made of clear Plexiglas, while the walls anterior and posterior to the fish were made of opaque plastic. The opaque plastic wall anterior to the fish had a sliding door built into it which could be opened and closed to allow the fish into and out of the chamber. Attached to this wall was a plastic tube (2 cm diameter) through which prey could be dropped into the feeding chamber. A green 4 cm² background grid and clear 4 cm² false bottom grid were used for scaling purposes.

Feeding events were videotaped at 200 fields s⁻¹ with a NAC high-speed video system. To obtain both a lateral and ventral view of each event, two cameras were used simultaneously: one aimed directly at the side of the feeding chamber, and the other recording the ventral view from a front-surface mirror inclined at 45° under the aquarium. Both cameras were positioned so that they recorded the same portion of the feeding chamber at the same magnification. 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.

Once in the feeding chamber, a fish oriented itself with its head facing the plastic tube and a feeding event was initiated by dropping pieces of worm through the tube into the chamber. Worms were cut into relatively long segments (3–4 cm) to encourage transport events by increasing the probability that prey would not be engulfed entirely into the buccal cavity during prey capture. The small size of the feeding chamber helped to minimize the range of movement of the fish after prey capture, increasing the likelihood that prey transport events would take place within the fields of view of the cameras. However, even within the restricted feeding chamber, fish could approach prey from a variety of angles and, after capture, could back away prior to transport. Only rarely did sequential prey capture and prey transport events both take place perpendicular to the longitudinal axes of both cameras. Therefore, the prey capture and prey transport events analyzed did not necessarily occur in sequence. This was not considered problematic as transport events were quite stereotyped and did not appear to be biased by the nature of the capture events preceding them.

A custom video digitizing program was used to analyze the kinematics of prey capture and transport events. Five feeding sequences from each of four different individuals were analyzed. In the capture and transport sequences chosen for analysis, sunfish were always close to perpendicular to the longitudinal axes of the cameras. The analyzed portion of a capture sequence usually consisted of 27 video fields encompassing 290 ms. One video field, designated as time 0, was selected for each sequence as a reference point and represented the field just prior to jaw opening. Video fields -10, -5, 0–80 (in 5 ms increments) and 105–280 (in 25 ms increments) were usually used for digitizing and analysis unless the fish turned out of the proper plane prior to the end of the sequence. Because of the shorter duration of prey transport events, only 19 video fields encompassing 190 ms were analyzed: fields -10, -5, 0–55 (in 5 ms increments) and 80–180 (in 25 ms increments).

For all video fields from each feeding sequence, six kinematic variables were measured and, for each variable, individual mean kinematic profiles were plotted. Gape distance was measured from the lateral view as the linear distance between the most anterior points of the upper and lower jaws; it was not scaled to 0 cm at time 0 in order to account for a prey item located between the jaws. Therefore, gape distance always represents the absolute distance between the upper and lower jaws. Head angle was measured from the lateral view as the angle between two lines: one line defined by a point at the center of the eye and a point at the center of the caudal peduncle; the other defined by two points along the dorsal border of the skull. Lower jaw angle was also measured from the lateral view using two lines, one was the same as that used for head angle (from the center of the eye to the caudal peduncle), while the other connected two points along the ventral border of the lower jaw. Hyoid depression was measured from the lateral view as the linear distance from the center of the eye to the ventral border of the gular region. Opercular expansion was measured from the ventral view as the linear distance between the lateral borders of the operculae just posterior to the eyes. Jaw protrusion was measured from the lateral view as the linear distance from the anterior tip of the premaxilla to the anterior edge of the neurocranium. In addition to these six kinematic variables, initial predator-prey distance was measured from the lateral view for each prey capture event as the linear distance from the anterior-most point on the mandible to the nearest point on the prey item.

The following 14 statistical variables were then derived from the data used to make the kinematic profiles and calculated for each prey capture and transport event (all timing variables were measured relative to time 0 and are accurate to the nearest 5 ms): (1) maximum gape distance, in cm; (2) time to maximum gape, in ms; (3) gape cycle duration (elapsed time from the start of gape opening until gape closure), in ms; (4) maximum hyoid depression, in cm; (5) time to maximum hyoid depression, in ms; (6) maximum head elevation, in degrees; (7) time to maximum head elevation, in ms; (8) maximum lower jaw depression, in degrees; (9) time to maximum lower jaw depression, in ms; (10) maximum opercular expansion, in cm; (11) time to maximum opercular expansion, in ms; (12) maximum jaw protrusion, in cm; (13) time to maximum jaw protrusion, in ms, and (14) jaw protrusion cycle (time from the onset of premaxillary protrusion to the end of premaxillary retraction), in ms.

Comparative data

The kinematics of both aquatic prey capture and transport have also been quantified and compared in *Ambystoma tigrinum* (Gillis and Lauder, 1994), and those data were compared with the data collected in this study to determine whether similar patterns are found between these two feeding behaviors across taxa. Statistical variables used for the comparisons were the six variables common to both studies: (1) maximum gape distance, (2) time to maximum gape, (3) gape cycle duration, (4) time to maximum hyoid depression,

(5) maximum head elevation and (6) time to maximum head elevation.

Statistical analyses

Basic statistics were calculated for the 14 statistical variables for both prey capture and prey transport in *L. macrochirus*. A two-way mixed-model analysis of variance (ANOVA) (Sokal and Rohlf, 1981), with behavior (capture or transport) as the fixed effect and individual as the random effect, was performed on each of the 14 variables. The fixed effect was tested over the interaction (behavior \times individual) mean square while the random effect and interaction term were tested over the error mean square (Zar, 1984). To account for multiple simultaneous ANOVAs, the level of statistical significance was adjusted using the sequential Bonferroni technique described by Rice (1989). To examine differences between prey capture and transport at a multivariate level, we performed a principal components analysis (PCA) using all 14 statistical variables. Fourteen principal components were extracted from the correlation matrix; their component loadings were examined, and factor scores of the four components explaining the most variation were plotted against one another.

Interspecific comparisons of aquatic prey capture and transport between *L. macrochirus* and *A. tigrinum* were performed using both univariate nested ANOVAs and principal components analysis. Data for aquatic capture and transport for *A. tigrinum* were taken from Lauder and Shaffer (1988) and Gillis and Lauder (1994) respectively. Our nested design partitioned variation in kinematic data across taxa into four levels: (1) differences between the two taxa; (2) differences between the two behaviors, nested within taxa; (3) differences among individuals, nested within each behavior; and (4) differences among feeding events within the same individual. This nested design was chosen as the best available method for analyzing these data, given that the analysis included both new and previously collected data. The difficulty with this design is that it assumes that each group of individuals nested within each behavior is different. This is true in the case of the salamanders. However, the same group of sunfish was used to examine both capture and transport, as using the same individuals allowed an appropriate two-way ANOVA to test for behavior and individual effects (e.g. Table 2). Thus, the nested ANOVA presented in Table 4 does not fully meet the assumption of independence of individuals for the second level (individuals nested within behaviors). Although this is problematic, the appropriate analyses of variance have also been performed on each taxon separately. Moreover, we felt it was better to use this nested design than to use an inappropriate three-way ANOVA with taxon, behavior and individual as factors. In this latter case, variation at the behavioral level would be artificially elevated since salamander prey capture and transport were being quantified in different groups of individuals.

In addition, to illustrate the relationships between the two behaviors across taxa in multivariate space, another PCA was performed and analyzed as above, using the six statistical kinematic variables available for both taxa.

Terminology

Since one of the goals of this paper is to compare capture and transport behaviors in fish with those in tetrapods, it is important to understand how different feeding behaviors have been characterized and defined previously in these groups and how we define each of these behaviors in this paper. Lauder (1983a) characterized four separate components of fish feeding behavior based upon distinct kinematic patterns and/or electromyographic data: initial strike, buccal manipulations, pharyngeal manipulations and pharyngeal transport. For generalized tetrapods, three feeding stages have been characterized: ingestion, intra-oral transport (which can include processing) and swallowing (Bramble and Wake, 1985).

Prey capture is defined as the initial acquisition of an item of prey. Prey transport is defined (following Gillis and Lauder, 1994) as the movement of prey, not fully engulfed (still held between the jaws), further into the buccal cavity. While prey movements certainly occur within the oral cavity (and one might wish to define such movements transport events as well), we limit our definition of transport to events in which movement of the prey into the mouth can be directly observed.

Results

Prior to prey capture, initial predator-prey distance at the start of mouth opening is quite variable, ranging from 0.6 to 2.3 cm (mean 1.2 cm). There is a significant positive relationship between gape cycle duration and predator-prey distance during capture, mainly due to changes in the duration of the expansion phase. The first prey transport event usually follows gape closure after prey capture by at least 500 ms, but can sometimes follow as quickly as 60 ms. Depending on the size of the prey item, a variable number of transport events is required to engulf the prey completely; up to about 3 cm of worm can be engulfed during one transport event. Using repeated transport events following a capture, a prey item is moved completely inside the oral cavity, where it may then be subjected to further manipulation, positioning and swallowing motions resulting from the action of the hyoid and branchial arches.

*Capture and transport kinematics in *Lepomis macrochirus**

The kinematics of prey capture and transport are contrasted in Figs 1 and 2, and mean values and results from the associated statistical tests are presented in Tables 1 and 2.

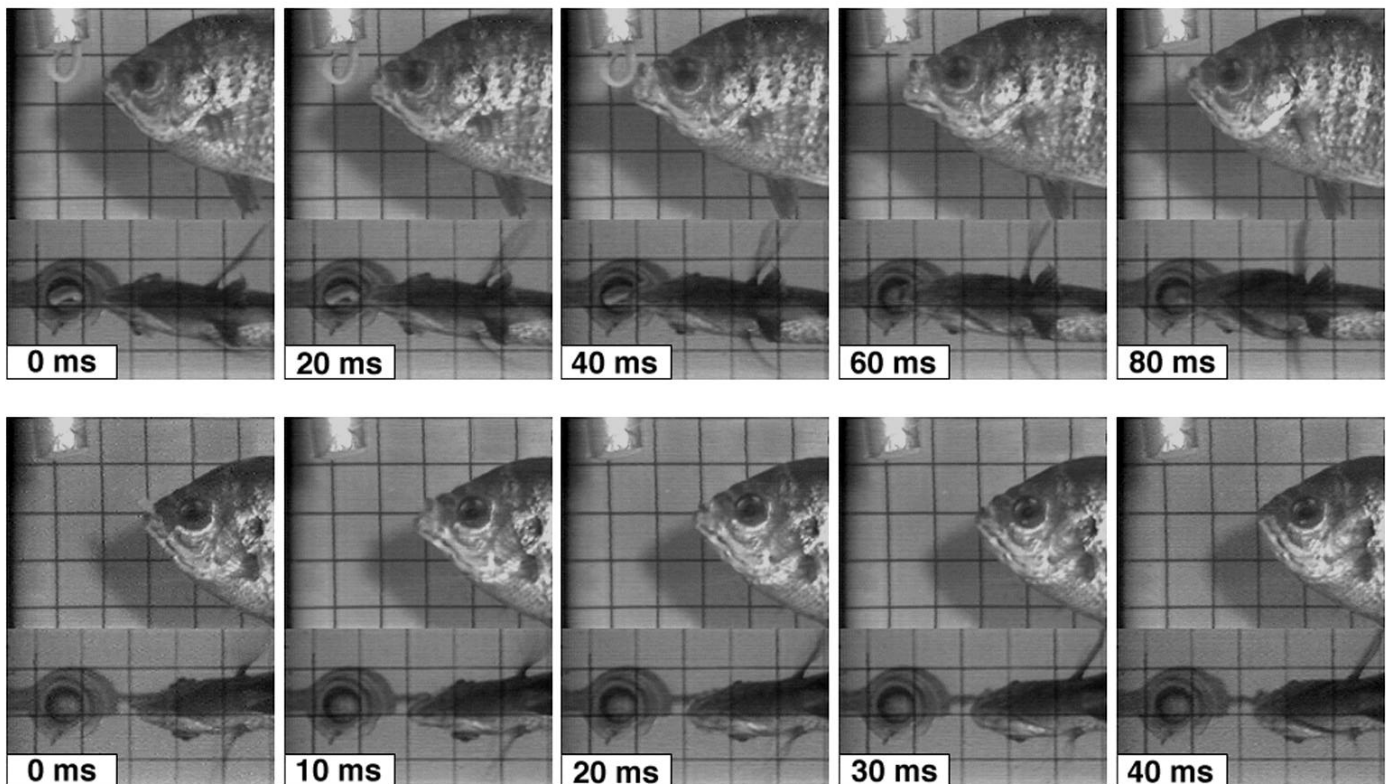


Fig. 1. Two sets of five video fields constituting a representative capture (top row) and transport (bottom row) behavior. Each image represents one field as recorded during an experiment. Note that the lateral and ventral views were obtained using two different cameras recording their respective images simultaneously. The left-hand field of each row represents time zero, and successive times (in ms) after time zero are shown in the bottom left-hand corner of each field. Note that the overall time course of the capture sequence is longer in duration than that of transport (i.e. maximum gape during capture occurs at approximately 60 ms after time zero and the entire gape cycle lasts 80 ms, whereas during transport, maximum gape is reached at 10–20 ms after time zero and the gape cycle lasts 30 ms). Also apparent is the greater maximum gape during capture, relative to transport. Images were cropped and enhanced by modifying brightness and contrast levels from the original high-speed video images using Adobe Photoshop.

Mouth opening in both behaviors occurs by elevation of the neurocranium and depression of the lower jaw (Fig. 2). However, maximal head elevation reaches similar values in both behaviors, while lower jaw depression during the initial strike reaches significantly lower values (Fig. 2; Tables 1, 2), indicating that prey capture involves greater rotation of the lower jaw around the jaw joint. The reduced lower jaw depression during transport events is correlated with significantly reduced gape distances. Maximum opercular expansion tends to be greater during captures than transports, although the difference is not statistically significant with the sample sizes used in this study. Both maximum hyoid depression and upper jaw protrusion reach similar values during both behaviors (Tables 1, 2).

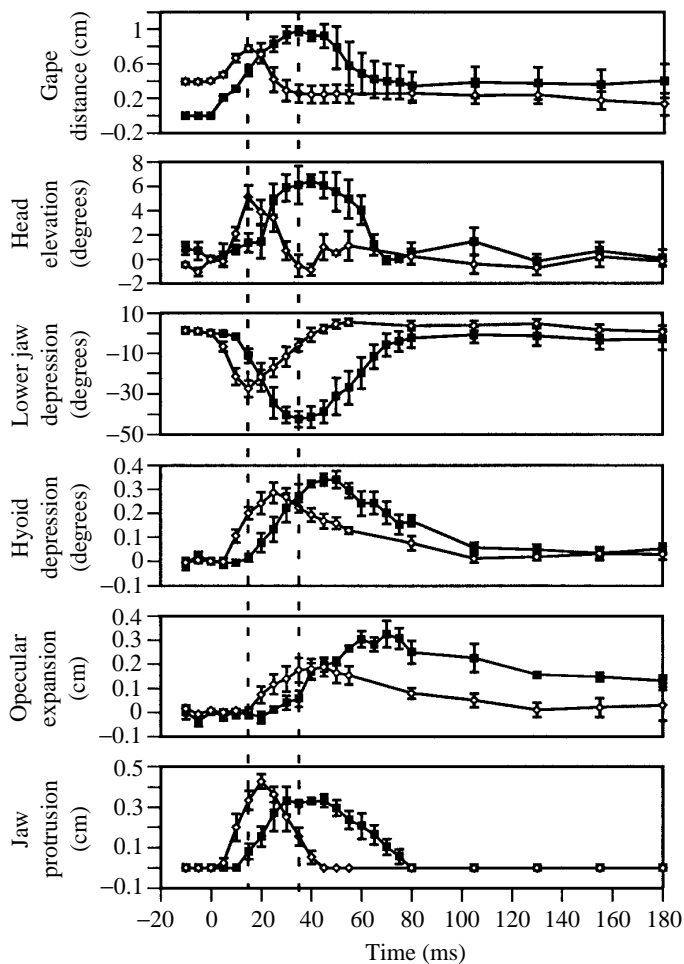


Fig. 2. Mean kinematic profiles, with standard error bars, of six variables during prey capture (filled squares) and prey transport (open diamonds) from one individual sunfish (five capture events and five transport events). Angle variables have been scaled to equal zero at time zero to allow comparisons among capture and transport events in which the initial values for these variables were not identical. The vertical dashed lines represent the time of maximum gape during transport (left-hand line) and the time of maximum gape during capture (right-hand line). Note the greater excursions and durations during capture, relative to transport, for most kinematic variables.

The time course of prey transport kinematics is often much faster than that of prey capture. For example, the times to maximal gape distance, hyoid depression, head elevation, lower jaw depression and jaw protrusion are all significantly shorter during transports than during captures (Table 2). Total gape cycle duration also tends to be substantially shorter during transports than captures, but the difference was not significant in our ANOVA (Table 2). Interestingly, the time to maximal opercular expansion showed no differences between the two behaviors.

Differences in the magnitude of initial gape at the onset of mouth opening (time 0; Figs 1, 2) are due to the presence of prey held between the jaws, and this could explain some differences in the kinematics. For example, if the same motor patterns were driving both transport and capture behaviors and maximal gape distance was not constrained by morphological factors (such the configuration of bony articular surfaces and muscle fiber lengths), then one would predict that transport events would exhibit greater maximal gape values, since they start with a substantial initial gape. However, our data illustrate that bluegill actually show a reduction in gape distance during transport events (Tables 1, 2), indicating that morphological constraints do not limit maximal gape distance during prey transport. This also suggests that different motor patterns are likely to be used during the two behaviors, and that bluegill can actively limit maximum gape distance during transport.

Table 1. Statistical variables measured during prey transport and prey capture behavior in *Lepomis macrochirus*

Variable	Transport	Capture
Maximum gape distance (cm)	0.85±0.04	1.16±0.05
Time to maximum gape (ms)	16.25±1.20	42.50±2.98
Gape cycle duration (ms)	36.50±2.64	65.50±4.23
Maximum hyoid depression (cm)	0.33±0.03†	0.38±0.02
Time to maximum hyoid depression (ms)	27.90±1.88†	51.0±2.89
Maximum head elevation (degrees)	6.5±0.67	9.0±0.50
Time to maximum head elevation (ms)	20.0±1.50	47.75±4.0
Maximum lower jaw depression (degrees)	-22.14±1.63	-39.5±2.13
Time to minimum lower jaw depression (ms)	18.50±1.58	42.25±2.96
Maximum opercular expansion (cm)	0.21±0.02	0.38±0.02
Time to maximum opercular expansion (ms)	46.75±3.96	89.5±12.08
Maximum jaw protrusion (cm)	0.43±0.02	0.46±0.02
Time to maximum jaw protrusion (ms)	21.0±1.65	41.75±2.82
Jaw protrusion cycle (ms)	43.75±4.67	66.5±4.52

Values are means ± S.E.M.

†N=19, in all other cases, N=20.

Table 2. Two-way ANOVA comparing prey capture and prey transport in four bluegill sunfish

Variable	Behavior d.f.=1, 3	Individual d.f.=3, 3	Behavior × Individual d.f.=3, 31–32
Maximum gape distance	89.32*	5.94*	0.40
Time to maximum gape	127.70*	0.95	0.50
Gape cycle duration	25.74	1.81	1.44
Maximum hyoid depression	1.54	1.72	2.30
Time to maximum hyoid depression	86.98*	1.03	0.47
Maximum head elevation	2.51	1.42	4.78
Time to maximum head elevation	97.53*	1.22	0.42
Maximum lower jaw depression	118.23*	8.02*	0.54
Time to maximum lower jaw depression	158.33*	2.70	0.34
Maximum opercular expansion	27.57	1.74	1.54
Time to maximum opercular expansion	4.22	6.84*	4.69
Maximum jaw protrusion	2.62	8.39*	0.41
Time to maximum jaw protrusion	71.02*	1.00	0.55
Jaw protrusion cycle	13.48	1.73	0.96

Table entries are *F*-values.

*Significant at $P < 0.05$, using the sequential Bonferroni method described in Rice (1989).

Furthermore, some variables (such as hyoid depression) show similar maximal excursions even though these excursions are reached in a far shorter time during transport. Hence, for certain kinematic events, the velocity of movement during transport is greater than that during prey capture.

A principal components analysis of capture and transport kinematics reveals that the axis of greatest variation

(accounting for 57% of the variation in the kinematic data set) distinguishes many of the transport from the capture events (Fig. 3). Prey capture behaviors tend to load highly on PC1, a condition attributable primarily to high loadings for variables measuring the time taken to reach peak excursion (Table 3). PC2 explained relatively little of the variation (12%). Capture or transport events loading highly on PC2 were those that had longer times to maximal opercular expansion and lower values of maximal hyoid depression.

Comparisons between *Lepomis macrochirus* and *Ambystoma tigrinum*

Mean values for six variables describing prey transport and capture kinematics in *L. macrochirus* and *A. tigrinum* are

Table 3. Component loadings of statistical variables analyzed during *Lepomis macrochirus* capture and transport behavior

Variable	Component loadings	
	PC1	PC2
Maximum gape distance	0.81	-0.34
Time to maximum gape	0.96	0.13
Gape cycle duration	0.91	0.18
Maximum hyoid depression	0.27	-0.61
Time to maximum hyoid depression	0.86	0.18
Maximum head elevation	0.57	-0.47
Time to maximum head elevation	0.90	0.28
Maximum lower jaw depression	-0.64	0.37
Time to maximum lower jaw depression	0.96	0.13
Maximum opercular expansion	0.79	-0.15
Time to maximum opercular expansion	0.49	0.67
Maximum jaw protrusion	0.39	-0.50
Time to maximum jaw protrusion	0.89	0.09
Jaw protrusion cycle	0.73	0.02

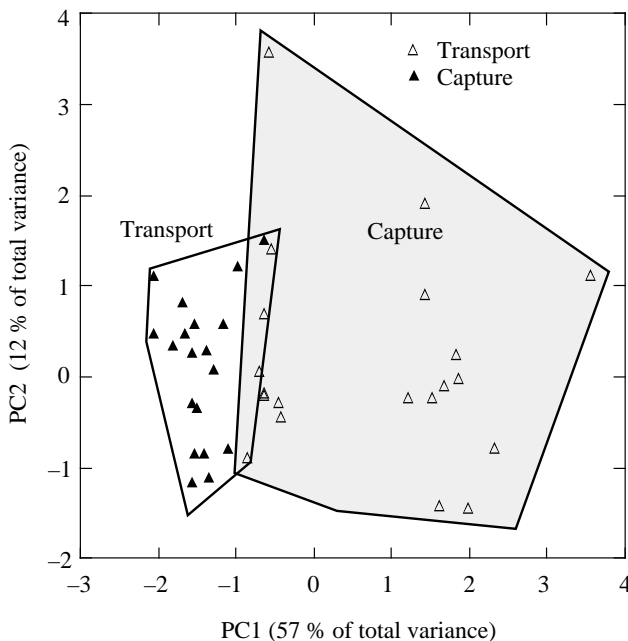


Fig. 3. Principal components analysis of capture and transport behaviors in *Lepomis macrochirus*, based on 14 statistical variables. Each symbol represents one feeding behavior from one individual. Factor loadings for each variable are presented in Table 3. Note that capture and transport behaviors are almost entirely separated along the principal component 1 (PC1) axis and that transport behaviors occupy a much smaller region of principal component space.

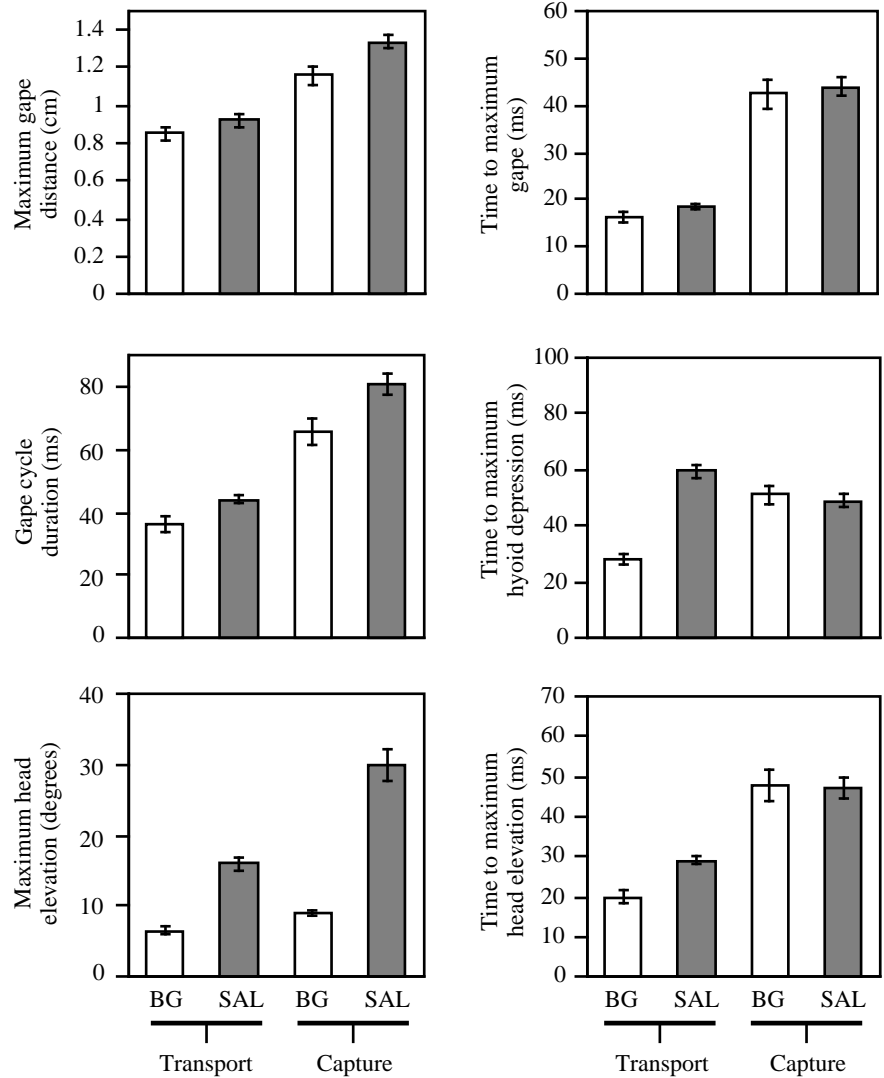


Fig. 4. Bar diagrams (with standard error bars) illustrating the relationships of the kinematic variables between behaviors and across taxa. The top of each vertical bar represents the overall mean for that variable for one type of behavior within a taxon. The two bars on the left of each diagram represent means from aquatic transport behaviors from bluegill sunfish (BG, open bar) and larval tiger salamanders (SAL, shaded bar) respectively, while the two bars on the right of each diagram represent means from aquatic capture behaviors (same conventions as other bars). All timing variables are measured in milliseconds, and angular and linear excursions are measured in degrees and centimeters, respectively. Note that, in all cases except time to maximum hyoid depression in salamanders, prey capture behaviors have longer durations and larger excursions when compared within taxa. Also note that lifting of the neurocranium is more extensive during salamander feeding than during sunfish feeding for both capture events and transport events. See Tables 2 and 4 for results of significance tests between taxa and between behaviors within bluegill sunfish.

presented in Fig. 4, and the results of statistical analyses comparing the behaviors in both taxa are given in Figs 5 and 6 and in Tables 4 and 5. None of the six variables was significantly different between taxa (Table 4). In other words,

when variation among feeding events, individuals and behaviors is accounted for, the two taxa are remarkably similar to each other. Even with the limited degrees of freedom available for testing the taxon effect (d.f.=1, 2; Table 4), only

Table 4. Results from a nested ANOVA for six statistical variables measured during both *Lepomis macrochirus* and *Ambystoma tigrinum*† capture and transport behaviors

Variable	Between taxa d.f.=1, 2	Between behaviors within taxa d.f.=2, 13	Among individuals within behaviors d.f.=13, 79–83
Maximum gape distance	0.20	20.74***	2.90*
Time to maximum gape	0.01	82.82***	1.27
Gape cycle duration	0.21	47.48***	1.26
Time to maximum hyoid depression	1.42	37.58***	0.65
Maximum head elevation	4.00	16.06***	1.76
Time to maximum head elevation	0.05	51.25***	0.82

Significant at * $P < 0.05$, *** $P < 0.001$ using the sequential Bonferroni method described in Rice (1989).

Table entries are F -values.

†Data from Lauder and Shaffer (1988) and Gillis and Lauder (1994).

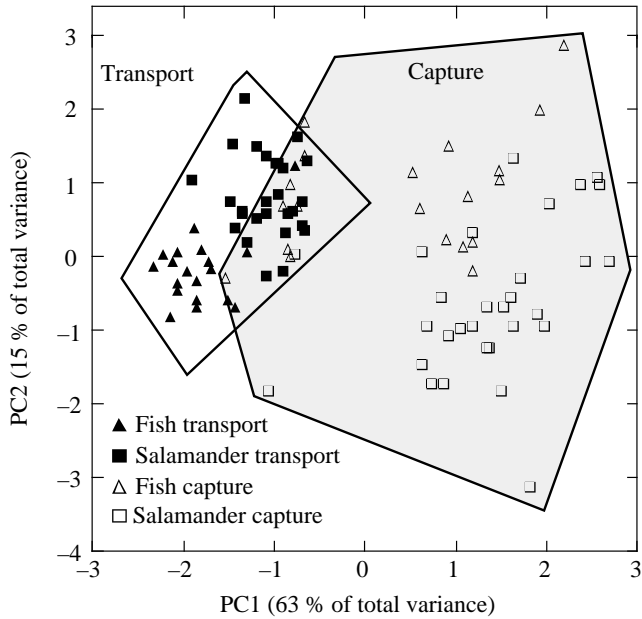


Fig. 5. Principal components analysis (PC1 versus PC2) of aquatic prey capture and transport behaviors in *Lepomis macrochirus* and *Ambystoma tigrinum* based on six statistical variables. Each symbol represents one feeding behavior from one individual. Factor loadings for each variable are presented in Table 5. Again, note that capture and transport behaviors are largely separated along the PC1 axis and that transport behaviors occupy a much smaller region of PC space.

one of the F -values (for maximum head elevation; $F=4.00$) shows any indication of substantial variation between taxa. The other five F -values are all small and reflect the remarkable similarity in feeding kinematics between these two taxa. Within taxa, capture was different from transport, with all variables showing highly significant variation between behaviors. Although gape cycle duration was not significantly different between bluegill capture and transport events alone, the F -value of nearly 26 (Table 2) indicates that there is substantial between-behavior variation present. The data from salamanders (Fig. 4) show that this taxon also exhibits much longer gape cycles during capture than during prey transport and, in the combined statistical analysis, highly significant variation is found between behaviors within taxa for this variable.

The combined principal components analysis (Fig. 5) supports these ANOVA results and indicates that the major axis of variation in the total data set (PC1, 63% of total variance) separates many of the capture events from transport events, regardless of taxon. There is a region of overlap between the capture and transport polygons, and both fish and salamander capture and transport events occur in this region. Major kinematic features separating capture events from transport events (regardless of taxon) are longer duration movements (Table 5). PC3 and PC4, while accounting for a relatively small proportion of total variation (17% together), do show some tendency to separate behaviors by taxon, although there is a large area of overlap (Fig. 6). *L. macrochirus* behaviors load

Table 5. Component loadings of statistical variables analyzed for both *Lepomis macrochirus* and *Ambystoma tigrinum*† capture and transport behavior

Variable	Component loadings			
	PC1	PC2	PC3	PC4
Maximum gape distance	0.81	-0.33	0.07	-0.48
Time to maximum gape	0.93	0.03	0.26	0.03
Gape cycle duration	0.94	0.01	0.16	0.13
Time to maximum hyoid depression	0.53	0.65	-0.52	-0.15
Maximum head elevation	0.58	-0.57	-0.54	0.20
Time to maximum head elevation	0.88	0.24	0.16	0.23

†Data from Lauder and Shaffer (1988) and Gillis and Lauder (1994).

high on PC3, reflecting the shorter time to maximum hyoid depression and lower maximum head elevation.

Discussion

Lepomis macrochirus capture and transport behaviors

Bluegill sunfish use suction to capture and transport prey. Preparatory, expansive, compressive and recovery phases

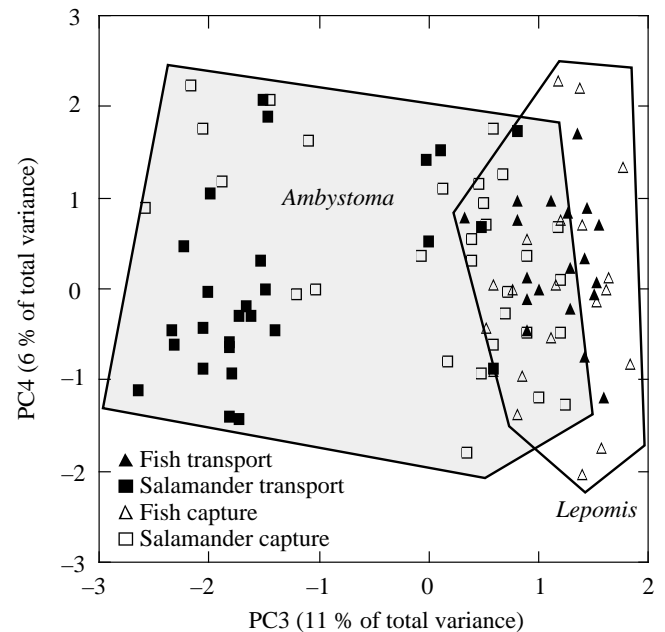


Fig. 6. Principal components analysis (PC3 versus PC4) of aquatic prey capture and transport behaviors in *Lepomis macrochirus* and *Ambystoma tigrinum* based on six statistical variables. The format is the same as in Fig. 5. Note that in this plot, feeding events are separated largely by taxon, rather than behavior (as in Figs 3, 5). This is because the tiger salamanders use neurocranial elevation to a much greater extent than the sunfish during feeding and maximum head angle is the most strongly correlated variable (negative correlation) with PC3.

(Liem, 1978; and reviewed in Lauder, 1985) are typically used to describe and functionally subdivide different aspects of suction feeding events and, therefore, can be examined and compared in both behaviors.

When present, the preparatory phase occurs prior to mouth opening and is chronologically the first subdivision of a suction feeding event. During this phase, the volume of the buccal cavity is reduced *via* protraction of the hyoid and suspensorium. This initial volume reduction allows greater pressure changes within the mouth during the gape increase as the volume of the oral cavity expands during capture or transport. A preparatory phase has been shown to take place occasionally during prey capture in *L. macrochirus* (Lauder, 1980; Lauder and Lanyon, 1980). Although it has not been found during intra-oral buccal manipulations in other fishes (Lauder, 1983b), its presence during prey transport in the sunfish cannot be addressed appropriately without electromyographical or pressure recording techniques.

Expansion is the part of the feeding event during which the mouth is opening. It begins when the mouth first opens and lasts until the time of maximum gape. Expansion is typically the shortest phase during suction-based prey capture behaviors (Lauder, 1985) and this is also the case with prey transport in *L. macrochirus*. Curiously, the expansive phase during prey capture measured in this study does not follow this pattern and is longer in duration than the compressive phase. Although a significant positive relationship was found between the initial predator-prey distance (at the start of mouth opening during a strike) and the duration of the expansive phase, even at the shortest predator-prey distances, expansion tended to outlast compression. In other studies of sunfish feeding, the duration of the expansion phase relative to compression is quite variable [see Figs 6 and 8, respectively, in Lauder (1980) for examples]. The elusivity (or escape speed) of the prey can affect the relative durations of expansion and compression during prey capture, as shown in an ambush hunting cichlid (Liem, 1978), where the relative proportion of the gape cycle taken up by expansion increases with the elusivity of the prey.

Premaxillary protrusion begins during the expansive phase and typically reaches its maximum at the end of this phase in both capture and transport behaviors. The onset of upper jaw protrusion is usually slightly delayed relative to mouth opening during the strike (by approximately 15 ms), although less so during transport (5 ms). This delay in the onset of protrusion relative to mouth opening is also occasionally seen during prey capture in other teleosts [Liem, 1970 (Fig. 49), 1979 (Fig. 7); Lauder, 1980 (Figs 6, 8 and 12)]. Such a delay might be expected if premaxillary protrusion were linked to mandibular depression *via* a mechanical connection with an elastic component [as in nandids, where this connection is ligamentous (Liem, 1970)]. Premaxillary protrusion has often been mechanically linked to mandibular depression [see Motta (1984) for a review of mechanisms], and it has been suggested that a similar mechanical linkage mechanism probably operates in a wide variety of fishes, especially those with 'generalized' perciform cranial anatomy such as *Lepomis*

(Westneat, 1990). Furthermore, Lauder (1980) showed that sternohyoideus stimulation depressed the lower jaw as well as protruded the premaxilla in *L. macrochirus*, so mandibular depression is at least sufficient, and possibly necessary, for upper jaw protrusion in sunfish.

Hyoid depression begins, and increases dramatically, during the expansive phase in both behaviors and has been shown in many aquatic vertebrates to generate the largest changes in buccal volume during this phase (Lauder, 1985). Accordingly, movement of the prey into the mouth *via* suction typically starts to occur near the end of this phase, prior to maximum gape, in both behaviors. There is no significant lateral opercular expansion during either behavior until maximum gape has been reached. Maximum opercular expansion typically does not occur until after the gape cycle has ended, a kinematic attribute found during prey capture in nearly all the ray-finned fishes studied (Lauder, 1985).

The compressive phase encompasses the time from maximum gape until the end of the gape cycle. The compressive phase is slightly longer on average during prey capture than during prey transport, although not significantly so. Closing of the mouth is brought about by simultaneous neurocranial depression and lower jaw elevation (the latter contributing significantly more to mouth closure). Approximately midway through this phase, hyoid retraction reaches its maximum, and it is during this period that significant opercular expansion and premaxillary retraction begin in both behaviors.

During the recovery phase, anatomical elements of the feeding apparatus which move relative to one another during the feeding event return to their original positions prior to mouth opening. The recovery phase can be quite long, lasting for over 250 ms during capture and over 150 ms during transport. It is during this phase that both the position of the hyoid and opercular expansion return to their values prior to mouth opening. Opercular expansion usually takes the longest to return to a resting value. A full recovery phase is not always present because a transport event or other buccal manipulation may begin before the opercular and hyoid apparatus return to their normal positions.

Upper jaw retraction also typically ends near the beginning of the recovery phase. The jaw protrusion cycle itself is similar in duration to the gape cycle during both behaviors. Since protrusion is usually somewhat delayed relative to mouth opening, premaxillary retraction is typically not complete until the recovery phase (after the gape cycle ends). However, Lauder (1980) noted that in *L. macrochirus* full premaxillary retraction either coincides with or follows gape closure, depending upon the speed of the gape cycle, which presumably depends upon several potential factors including prey type. In that study, faster strikes were correlated with coincident premaxillary retraction and mouth closure, whereas during slower feeding events there was a delay, with retraction following the end of the gape cycle. Our use of exclusively non-elusive prey might thus explain the consistent delay in premaxillary retraction relative to gape closure.

Kinematic patterns of prey capture and prey transport across anamniote taxa

A striking finding of this study is the similarity between *A. tigrinum* and *L. macrochirus* in the differences between prey capture and transport (Figs 4, 5). For example, across both taxa, kinematic components of the gape cycle during prey capture consistently have a longer duration, and angular excursions of the neurocranium and lower jaw during capture tend to be greater than during prey transport. Overall, no significant differences between taxa were detected among the six variables tested (Table 4). In addition to the specific kinematic features which differentiate the two behaviors across taxa, another more general difference is also apparent. The distance spanned by transport space (as defined by feedings from both sunfish and salamanders) in the PC1 dimension is only about half that spanned by prey capture space (Fig. 5). A similar result was found in the taxon-specific principal components analyses [Fig. 3 of this paper, and Fig. 4 in Gillis and Lauder (1994)]. Additionally, Reilly and Lauder (1990) showed that prey type had no significant effect on transport kinematics in *A. tigrinum* adults. Such results suggest that prey transport kinematics in anamniotes may be less variable than the kinematics associated with prey capture.

The differences between capture and transport behaviors observed in our earlier study of tiger salamanders thus correspond remarkably well with those found in this study of bluegill sunfish. This correspondence suggests the possibility that the differences observed between capture and transport may be widespread during aquatic feeding by anamniotes. This result contrasts markedly with the hypothesis proposed by Lauder and Reilly (1993). In that paper, qualitative similarities (such as the use of suction to move prey towards the mouth) between aquatic prey capture and transport, and the demonstrated differences between terrestrial prey capture and transport in salamanders (Reilly and Lauder, 1990, 1991), led to the suggestion that both aquatic and terrestrial prey transport are similar to aquatic prey capture and kinematically distinct from terrestrial prey capture. The data presented here, in addition to the previous demonstration of the distinctions between aquatic capture and transport in *A. tigrinum*, show that aquatic prey transport is *not* similar to aquatic prey capture in either *L. macrochirus* or *A. tigrinum*.

We suggest that the consistent differences found between capture and transport in these taxa have important functional consequences. Trying to understand the significance of this kinematic differentiation could lead to a better understanding of the evolution of vertebrate feeding mechanisms in general. One potential functional consequence of the distinct capture and transport profiles relates to the flow of water into the buccal cavity as a result of suction created by posteroventral hyoid movements. Because the jaws are open by a significantly smaller distance during transport, yet the hyoid excursions are statistically similar to those during prey capture, the velocity of the stream of water being sucked into the buccal cavity is likely to be higher during transport. This increased flow

velocity into the mouth may assist in moving an already captured prey item further into the buccal cavity. Concomitantly, the smaller gape distance and decreased duration of the gape cycle during transport may decrease the likelihood of the prey escaping while the mouth is open. The increased gape distance and duration of the expansive phase during prey capture may increase the likelihood that a prey item will cross the plane of the gape while the mouth is open. However, during suction feeding, the greater the gape distance, the slower is the velocity of water flow into the mouth (given that hyoid excursions are similar), although significant forward movements of the fish during capture, which are not present during transport, might make up for this lower flow velocity. Hypotheses relating to the functional bases of capture and transport differentiation could be tested by experimentally manipulating gape distances or gape cycle durations by denervating the muscles involved in mouth opening and determining the effects on capture and/or transport success.

More generally, we suggest that the distinction between capture and transport behaviors may be phylogenetically ancient and probably pre-dates the acquisition of a terrestrial feeding mechanism during the transition to terrestrial vertebrate life. Since differences between capture and transport occur even during terrestrial feeding by ambystomatid salamanders (Reilly and Lauder, 1990), prey transport kinematics used primitively to move aquatic prey into the mouth may have been co-opted without substantial modification to serve terrestrial prey transport. These data also support the ancillary hypothesis that terrestrial lingual-based intra-oral prey transport kinematics in tetrapods is derived phylogenetically from aquatic prey transport kinematics, and that capture–transport differentiation might be retained (as a phylogenetically primitive component of the feeding mechanism) in a variety of amniote taxa. Reptilian clades for which kinematic data are now available might be used to test this hypothesis.

Comparative kinematics of capture and transport in reptiles

Quantitative data on both prey capture and prey transport, defined as being distinct from reduction or chewing, *sensu* So *et al.* (1992), have been collected for several squamate taxa. Schwenk and Throckmorton (1989) quantified kinematic features of both capture and transport in iguanid and agamid lizards. Delheusy and Bels (1992) studied feeding kinematics in a different iguanid, while Wainwright *et al.* (1991) and So *et al.* (1992) did so in chameleons (although the species in which the kinematics of capture was described is different from that in which transport was described).

The two major differences we have found between capture and transport in anamniotes, i.e. longer durations and greater head and lower jaw excursions during capture, do not consistently appear in the lizard species examined to date. Although the durations of kinematic events during capture tend to be longer than those of transport in iguanids and agamids, kinematic excursions of the head and lower jaw are not significantly different between these behaviors (Schwenk and

Throckmorton, 1989; Delheusy and Bels, 1992). In contrast, the extent of neurocranial elevation and mandibular depression tends to be greater during capture than during transport in chameleons, while durations are longer during prey transport than during prey capture (Wainwright *et al.* 1991; So *et al.* 1992).

Several potential problems are inherent in extending our comparison of feeding behaviors to reptilian taxa. First, transport as defined in this study (prey held between anterior jaws is moved posteriorly into the oral cavity) is somewhat different from the intra-oral transport described in the squamate studies referred to above, where prey within the oral cavity is moved to the esophagus. Second, using species from only the iguanian lineage of squamate reptiles, including the highly derived Chamaeleonidae, to represent or typify reptilian feeding systems in general is problematic. Third, in part because of the morphological diversity in cranial design that occurs across vertebrates and differences in feeding environment, it is difficult to define homologous behaviors across distantly related taxa. Such gross behavioral homologies need to be established before it will be possible to conduct broad-based comparative functional analyses. Fourth, we still have only a very limited basis for our data on ray-finned fishes and salamanders: one taxon has been studied in each clade. Further examination of the diversity of capture and transport behaviors in both fishes and salamanders will be essential to establishing the generality of the differences discussed here.

However, we have demonstrated in this paper consistent differences between capture and transport behaviors across two divergent amniote taxa in which homology of the transport behaviors is not in doubt. To determine whether such differences are primitive for amniotes, tetrapods and/or vertebrates in general will require more quantitative studies of both capture and specifically defined transport behaviors across a wide phylogenetic spectrum of vertebrates.

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References

- BELS, V. L. AND BALTUS, I. (1987). First analysis of the feeding sequence of *Chameleo dilepis*. In *Proceeding of the Fourth Ordinary General Meeting of the Societas Europaeae Herpetologica Nijmegen* (ed. J. J. van Gelder, H. Strijbosch and P. J. M. Bergers), pp. 67–70. Nijmegen: University Press.
- BELS, V. L., CHARDON, M. AND KARDONG, K. V. (1994a). Biomechanics of the hyolingual system in Squamata. In *Advances in Comparative and Environmental Physiology: Biomechanics of Feeding in Vertebrates* (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 197–240. Berlin: Springer-Verlag.
- BELS, V. L., CHARDON, M. AND VANDEWALLE, P. (1994b). (Eds) *Advances in Comparative and Environmental Physiology: Biomechanics of Feeding in Vertebrates*. Berlin: Springer-Verlag.
- BEMIS, W. E. (1987). Feeding systems of living Dipnoi: Anatomy and function. In *The Biology and Evolution of Lungfishes* (ed. W. E. Bemis, W. W. Burggren and N. E. Kemp), pp. 249–275. New York: Alan R. Liss, Inc.
- BEMIS, W. E. 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. 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.
- DELHEUSY, V. AND BELS, V. L. (1992). Kinematics of feeding behavior in *Oplurus cuvieri* (Reptilia: Iguanidae). *J. exp. Biol.* **170**, 155–186.
- GILLIS, G. B. AND LAUDER, G. V. (1994). Aquatic prey transport and the comparative kinematics of *Ambystoma tigrinum* feeding behaviors. *J. exp. Biol.* **187**, 159–179.
- HANKEN, J. AND HALL, B. K. (1993). (Eds) *The Skull: Functional and Evolutionary Mechanisms*. Chicago: The University of Chicago Press.
- HIEMAE, K. M. AND CROMPTON, A. W. (1985). Mastication, food transport and swallowing. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 262–290. Cambridge: Harvard University Press.
- LAUDER, G. V. (1980). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. exp. Biol.* **88**, 49–72.
- LAUDER, G. V. (1983a). Functional design and evolution of the pharyngeal jaw apparatus in euteleostean fishes. *Zool. J. Linn. Soc.* **77**, 1–38.
- LAUDER, G. V. (1983b). 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 LANYON, L. E. (1980). Functional anatomy of feeding in the bluegill sunfish, *Lepomis macrochirus*: *in vivo* measurement of bone strain. *J. exp. Biol.* **84**, 33–55.
- LAUDER, G. V. AND REILLY, S. M. (1993). Amphibian feeding behavior: comparative biomechanics and evolution. In *Biomechanics of Feeding in Vertebrates* (ed. V. Bels, M. Chardon and P. Vandewalle), pp. 163–195. Berlin: Springer-Verlag.
- LAUDER, G. V. AND SHAFFER, H. B. (1988). Ontogeny of functional design in tiger salamanders (*Ambystoma tigrinum*): are motor patterns conserved during major morphological transformations? *J. Morph.* **197**, 249–268.
- LIEM, K. F. (1970). Comparative functional anatomy of the Nandidae (Pisces: Teleostei). *Fieldiana: Zool.* **56**, 1–166.
- LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. *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.
- MOTTA, P. J. (1984). Mechanics and functions of jaw protrusion in teleost fishes: a review. *Copeia* **1984**, 1–18.

- REILLY, S. M. AND LAUDER, G. V. (1990). The evolution of tetrapod feeding behavior: kinematic homologies in prey transport. *Evolution* **44**, 1542–1557.
- REILLY, S. M. AND LAUDER, G. V. (1991). Prey transport in the tiger salamander: quantitative electromyography and muscle function in tetrapods. *J. exp. Zool.* **260**, 1–17.
- RICE, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- SCHWENK, K. (1994a). Comparative biology and the importance of cladistic classification: a case study from the sensory biology of squamate reptiles. *Biol. J. Linn. Soc. Lond.* **52**, 69–82.
- SCHWENK, K. (1994b). Why snakes have forked tongues. *Science* **263**, 1573–1577.
- SCHWENK, K. AND THROCKMORTON, G. S. (1989). Functional and evolutionary morphology of lingual feeding in squamate reptiles: phylogenetics and kinematics. *J. Zool., Lond.* **219**, 153–175.
- SMITH, K. K. (1984). The use of the tongue and hyoid apparatus during feeding in lizards (*Ctenosaura similis* and *Tupinambis nigropunctatus*). *J. Zool., Lond.* **202**, 115–143.
- SMITH, K. K. (1986). Morphology and function of the tongue and hyoid apparatus in *Varanus* (Varanidae, Lacertilia). *J. Morph.* **187**, 261–287.
- SO, K. K. J., WAINWRIGHT, P. C. AND BENNETT, A. F. (1992). Kinematics of prey processing in *Chamaeleo jacksonii*: conservation of function with morphological specialization. *J. Zool., Lond.* **226**, 47–64.
- SOKAL, R. R. AND ROHLF, F. J. (1981). *Biometry* (2nd edn). New York: W. H. Freeman and Co.
- VANDEWALLE, P., HUYSSENE, A., AERTS, P. AND VERRAES, W. (1994). The pharyngeal apparatus in teleost feeding. In *Comparative and Environmental Physiology: Biomechanics of Feeding in Vertebrates* (ed. V. L. Bels, M. Chardon and P. Vandewalle), pp. 59–92. Berlin: Springer-Verlag.
- WAINWRIGHT, P. C., KRAKLAU, D. M. AND BENNETT, A. F. (1991). Kinematics of tongue projection in *Chamaeleo oustaleti*. *J. exp. Biol.* **159**, 109–133.
- WESTNEAT, M. W. (1990). Feeding mechanics of teleost fishes (Labridae; Perciformes): a test of four-bar linkages. *J. Morph.* **205**, 269–295.
- ZAR, J. H. (1984). *Biostatistical Analysis* (2nd edn). Englewood Cliffs: Prentice-Hall, Inc.