THE METAMORPHOSIS OF FEEDING KINEMATICS IN *SALAMANDRA SALAMANDRA* AND THE EVOLUTION OF TERRESTRIAL FEEDING BEHAVIOR

STEPHEN M. REILLY

Department of Biological Sciences, Ohio University, Athens, OH 45701, USA

Summary

The striking similarity between aquatic feeding behaviors in fishes and tetrapods and terrestrial prey transports in tetrapods and their contrasts to terrestrial tongue projection kinematics have led to a general hypothesis that terrestrial prey capture evolved from terrestrial prey transport, which, in turn, evolved from aquatic feeding behavior. This hypothesis is examined in *Salamandra salamandra* by comparing the kinematics of prey capture and transport before and after metamorphosis in the same group of eight individuals. Kinematics of aquatic and terrestrial strikes and transports are used to describe the metamorphosis of feeding behavior in *S. salamandra* and provide the first kinematic description of both aquatic and terrestrial feeding behaviors in the family Salamandridae. On the basis of the shared characteristics among the four behaviors, the two aquatic behaviors are most similar, and these are more similar to terrestrial transports than to terrestrial strikes. Given the ontogenetic polarity of these behaviors in salamanders, I suggest, on the basis of the shared similarities and functional shifts, that terrestrial transport is an intermediate behavior between aquatic feeding and terrestrial tongue projection. These results support the hypothesis that a shift from aquatic feeding to terrestrial transport to terrestrial tongue projection represents an evolutionary transformation series in the evolution of terrestrial feeding in early tetrapods.

Key words: feeding, kinematics, ontogeny, behavior, salamander, *Salamandra salamandra*, tetrapods, evolution.

Introduction

The transformation of aquatic vertebrates into terrestrial forms and the transition from living in water to living in air had many consequences for organismal physiology, form and function (Vogel, 1983; Schmidt-Nielsen, 1990). One of the most important, but least studied, aspects of this transition is the evolution of terrestrial feeding behavior from aquatic feeding behavior. Terrestrial vertebrates either retained or modified primitive aquatic feeding behaviors to capture and consume terrestrial prey. When feeding function is compared among extant taxa spanning the aquatic–terrestrial transition, one finds that tetrapods appear both to have retained primitive features from fishes and to have acquired novelties in feeding function (Reilly and Lauder, 1990*a*; Lauder and Reilly, 1994).

Primitively, fishes exhibit two basic aquatic feeding behaviors that involve the jaws and hyobranchial apparatus: prey capture and prey transport (Lauder, 1983, 1985; Liem, 1980). Prey capture involves the initial acquisition of the prey item. In fishes, prey are brought into the mouth by first protracting the hyobranchial apparatus to empty the oral cavity, and then rapidly retracting the hyobranchial apparatus to suck water and prey into the oral cavity (Lauder, 1985). As the hyoid is retracted, the mouth is rapidly opened and then closed, producing a bell-shaped gape profile during aquatic prey capture. Prey transport, in its broadest sense, can involve buccal and pharyngeal prey manipulations in fishes (Bemis and Lauder, 1986; Lauder, 1983; Sibbing *et al.* 1986), hydraulic prey movements in salamanders (Gillis and Lauder, 1994) and a variety of intra-oral prey-processing behaviors in amniotes (Bramble and Wake, 1985; Hiiemae and Crompton, 1985) that reduce and position the prey for swallowing. For the purposes of this paper, however, I will following Gillis and Lauder (1994) in limiting the definition of prey transport to the most general and presumably primitive form that is directly observable: the simple movement of unprocessed prey further into the buccal cavity and esophagus. Kinematic patterns during prey transport movements in fishes are similar to prey capture movements except that prey transport involves less mouth opening; thus, transports are shorter in duration and jaw excursions are smaller (Gillis and Lauder, 1995). Both aquatic prey capture and transport have bell-shaped gape profiles and hyoid retraction beginning with mouth opening and peaking during mouth closing.

Amphibians retain many features of the feeding mechanism and kinematics of fishes (Reilly and Lauder, 1990*a*, 1991, 1992; Lauder and Reilly, 1994). Larval (non-metamorphosed) salamanders and transformed salamanders feeding in water capture and transport prey in essentially the same way that fishes do, with bell-shaped gape profiles and hyoid retraction coinciding with the fast opening phase of the gape cycle (Shaffer and Lauder, 1988; Gillis and Lauder, 1995). Comparisons of data from fishes, amphibians and amniotes show that both amphibians and amniotes retain primitive patterns of feeding and that some functional characteristics are conserved throughout many vertebrate clades (Reilly and Lauder, 1990*a*; Lauder and Reilly, 1994). For example, taxa as divergent as sunfishes, lungfishes, salamanders, turtles, lizards and mammals all exhibit hyoid retraction during the fast opening phase of prey transport (Lauder and Reilly, 1994).

Although tetrapods have retained primitive features from fishes, they have acquired many functional novelties associated with terrestrial feeding. The primary addition is tongue-based prey transport and capture, with varying contributions of the hyoid and tongue observed at different phylogenetic levels (Gans and Gorniak, 1982; Smith, 1984; Crompton, 1989; Schwenk and Throckmorton, 1989; Nishikawa and Roth, 1991; Lauder and Reilly, 1994). In terrestrial prey capture in salamanders, the hyobranchial apparatus supporting the tongue is protracted to project the tongue towards the prey, and then retracted to pull the tongue and prey into the mouth (Lombard and Wake, 1976; Reilly and Lauder, 1989). The mouth opens and closes rapidly but is held open while the tongue is out of the mouth. Thus, a plateau phase is observed in the gape profile during the time the tongue moves out and back. The addition of the plateau in the gape cycle is a prominent feature of tongue-based feeding in basal tetrapods (Reilly and Lauder, 1990*a*; Lauder and Reilly, 1994), but the nature of the plateau has been modified extensively as more complex feeding behaviors have been added to feeding repertoires in various amniotes (Herring, 1985; Heidweiller and Zweers, 1990; Wainwright and Bennett, 1992). Terrestrial captures also appear to be unique in that the hyobranchial apparatus is protracted and elevated from its resting position during the fast opening phase. The retraction of the hyoid and coincident closing of the mouth during prey capture, however, are similar in shape to the same portions of aquatic feeding, indicating aspects of terrestrial prey capture that are conserved from aquatic feeding.

The striking similarity of aquatic feeding behaviors in fishes and tetrapods and their similarity to terrestrial transports in tetrapods (bell-shaped gape profiles, hyoid retracted during mouth closing) and the apparent addition of tongue projection and a plateau phase in terrestrial prey capture, led Reilly and Lauder (1990*a*) and Lauder and Reilly (1994) to propose the following general hypothesis for the evolution of terrestrial feeding in early tetrapods: aquatic prey capture and transport are similar behaviors whose basic patterns are retained in terrestrial prey transport and retained but somewhat modified in terrestrial prey capture. From this general hypothesis for tetrapods, Reilly and Lauder (1994) proposed the more specific hypothesis for salamanders that kinematic patterns of aquatic prey capture, aquatic prey transport and terrestrial transport together would be different from that of terrestrial prey capture. Gillis and Lauder (1994) corroborated this hypothesis in a comparison of capture and transport kinematics in samples of larval and transformed tiger salamanders (*Ambystoma tigrinum*). However, their study revealed complex patterns of differences and similarities among the four types of behavior that suggested that transports and captures were more similar regardless of environment, and they hypothesized that capture and transport behaviors may have diverged early in vertebrate evolution. The authors, however, cautioned that more work was needed to quantify the extent of differences in variation both among and between behaviors and that studies of more than one species were needed to examine the generality of their results.

In this paper, I re-examine the general hypothesis that terrestrial prey capture evolved from terrestrial prey transport, which, in turn, evolved from aquatic feeding behavior, by studying the metamorphosis of feeding kinematics in a second species *Salamandra salamandra*. To control for interindividual and intersample variation, I employed a longitudinal experimental design that compares the kinematics of prey capture and transport before and after metamorphosis in the same group of individuals. This design incorporates the statistical rigor of a repeated-measures analysis of variance to test differences among the four behaviors and to describe metamorphic changes in feeding behavior from which inferences about the evolution of terrestrial feeding can be made. To examine the general hypothesis that aquatic feeding behavior developed into terrestrial transport, which was then modified to enact terrestrial tongue projection, I test the specific hypothesis that terrestrial transports are kinematically intermediate between the aquatic behaviors and tongue projection behaviors. In addition, this study provides the first kinematic description of both aquatic and terrestrial feeding behaviors in the family Salamandridae.

Materials and methods
Experimental animals and kinematic techniques

Feeding behaviors of eight fire salamanders (*Salamandra salamandra* L.) were filmed before and after metamorphosis. The salamanders were fed *Tubifex* worms during aquatic feeding and 6 mm long crickets during terrestrial feeding, both of which were offered directly in front of the animal. All of the animals were from the same litter and were maintained individually. They were fed *ad libitum* on *Tubifex* worms and brine shrimp (as larvae) or small crickets (after metamorphosis). The same individuals were filmed as larvae and 10.5 months later (about 9 months after metamorphosis). Thus, this is a longitudinal experimental design. The eight *Salamandra salamandra* averaged 28.1 mm (as larvae) and 45.8 mm (after metamorphosis) snout–vent length at the times they were filmed.

All feedings were filmed in lateral view at 200 fields s^{-1} using a NAC HSV-400 high-speed video system. Approximately 15 feeding bouts (prey captures followed by a series of prey transport cycles) per individual were filmed before and after metamorphosis and the snout–vent length of each individual was measured after each filming session. Of these, the best 6–10 feedings (based on good lateral views with landmarks clearly visible throughout each sequence) per individual per behavior were digitized and analyzed using principal components analysis. From these, five sequences for each individual, for each behavior, were used for further analysis (because one individual had only five sequences with a full data set, five sequences were randomly selected from each of the other seven individuals to attain equal sample sizes without missing values for statistical analyses). Thus, the repeated-measures analysis is based on five sequences per individual for each of the four types of behavior (aquatic captures, aquatic transports, terrestrial captures and terrestrial transports), giving a total of 160 sequences.

Each sequence was analyzed field by field using Measurement TV software (Updegraff, 1990). Five landmark coordinates were digitized from each image (Fig. 1) and time 0 for each sequence was defined as the frame immediately before the mouth began to open. From the coordinate data, displacement angles were calculated for each frame for the elevation of the head relative to the body, the extent of mouth opening (gape) and the depression of the hyobranchial apparatus. Angles were used to avoid the effects of size on kinematic variables because individuals were larger when the postmetamorphic feedings were recorded. For each feeding sequence, the raw angles for head elevation and hyoid depression were transformed to adjust the angle at time 0 to equal zero. Raw angles for mouth opening during captures were scaled similarly, but transport gape angles were not transformed because the raw angles reflect the slightly open position of the jaws when holding the prey at the beginning of the transport cycle.

Statistical analyses

To illustrate and compare the four behaviors graphically, the five sequences for each behavior were averaged for one individual and plotted as mean ± one standard error of the mean calculated for each frame encompassing each behavioral sequence (plots in Figs 2–4 are from the same individual). For statistical analyses, seven kinematic variables quantifying maximum displacements and durations were calculated for each sequence. These variables were: maximum gape (degrees), maximum head elevation (degrees), maximum hyoid depression (degrees), the time to each of these from time 0 (ms), and the gape cycle time from time 0 to mouth closing (ms). Time to maximum hyoid depression was taken as the point at which ventral movement ceased.

This analysis employs a three-way analysis of variance (ANOVA) with *behavior* (testing differences between strikes *versus* transports) and metamorphic *stage*/environment [testing differences between larval (aquatic) feedings *versus* metamorphosed (terrestrial) feedings] treated as independent
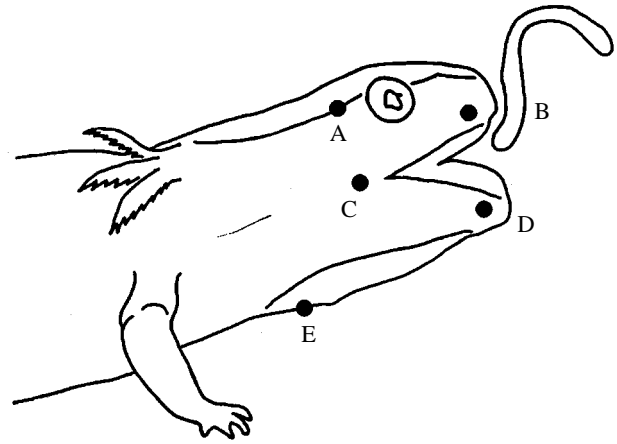

Fig. 1. Landmark coordinates digitized from high-speed video images of aquatic and terrestrial feeding behaviors in *Salamandra salamandra*. The landmarks were (A) the posterior angle of the eyelid, (B) the tip of the upper jaw, (C) the angle of the mouth, (D) the tip of the lower jaw and (E) the point where the tip of the basibranchial element of the hyobranchial apparatus protrudes ventrally. Using these coordinates, angles describing displacements of the head (line AB relative to horizontal), gape (angle BCD) and hyobranchial apparatus (angle BDE) were computed for each feeding event. From these data, the maximum displacements and timing variables were calculated for statistical analyses.

factors crossed with the eight subjects as the *individual* effect. Because all individuals serve in all behavior by stage treatment combinations, this analysis employs a pure within-subjects (repeated-measures) design (Keppel, 1982: p. 368). In addition, because each individual has five trials for each of the four behaviors, within-individual within-behavior variance (termed the *trials* effect) was also accounted for in the analysis. This repeated-measures design has the advantage of testing differences in the main effects after variation within behaviors among individuals, among individuals and residual error have been extracted while accounting for the use of the same individuals in all of the treatment combinations. Because the statistical comparisons I want to make (differences among the four behaviors) are confounded in the behavior and stage factors, I used *post hoc* tests using the least-square means from the ANOVA to identify significant differences among the four behaviors.

In the analysis (performed with SAS version 6.09; SAS Institute, 1988), the main effects (behavior and stage) are treated as fixed effects and individuals are treated as a random effect, thus, the F-ratios for the main effects and their interaction were calculated by dividing the mean square for these effects by the appropriate interaction mean square (behavior/individual×behavior; stage/individual×stage; behavior×stage/individual×behavior×stage), while the feeding effect and remaining interactions were calculated using the error mean square (Keppel, 1982). Because multiple univariate comparisons were being conducted, the sequential Bonferroni method was used to determine statistical significance (Rice, 1989). Principal components analysis (log-

transformed data using correlation matrix) was used to illustrate the multivariate patterns of dispersion of the four behaviors and ANOVA and multivariate analysis of variance (MANOVA) on principal component scores (for components 1–5) were used to test the differences among the behaviors.

Results

Table 1 presents mean values for kinematic variables describing aquatic and terrestrial strike and transport behaviors in *Salamandra salamandra*. Quantitative kinematics for the four behaviors are illustrated in Figs 2–4, which show mean kinematic profiles of three kinematic variables digitized from one individual (*N*=5 per behavior). Results of analyses of variance for trials, stage (larval *versus* metamorphosed feedings), behavior (strikes *versus* transports) and individual effects are presented in Table 2. Trials within individual within behavior did not vary significantly (Table 2, trials effect). Tests of the main effects were confounded by the fact that the aquatic behaviors did not differ and the terrestrial ones did for some variables. Therefore, differences among the four behaviors are illustrated by the results of pairwise *post hoc* tests based on the repeated-measures ANOVA, with underlining indicating those

behaviors that are not significantly different (Table 1). Maximum hyoid depression was not significantly different among the four behaviors. Results of the principal components analysis are presented in Table 3 and Fig. 5.

Aquatic feeding kinematics

The kinematics of aquatic strikes in *Salamandra salamandra* have been described in detail elsewhere (Reilly, 1995). Aquatic transport kinematics were very similar to aquatic strikes. None of the kinematic variables was significantly different (Table 1), and the mean profiles for aquatic strikes and transports lie nearly on top of each other for gape angle, head elevation and hyoid depression (e.g. Fig. 4). The only notable difference between aquatic behaviors is that mouth opening and hyoid retraction occur more slowly during aquatic transports (Fig. 2). Principal components analysis (Fig. 5; Table 3) shows the aquatic strikes and transports occupying the same multivariate space and their patterns of dispersion were not significantly different (ANOVA PC1 scores, *P*=0.241, PC2 scores, *P*=0.352; MANOVA for scores on PCs 1–5, *P*=0.368). On the basis of their tighter grouping (Fig. 5), the aquatic strikes appear to be less variable than terrestrial transports and the other behaviors.

Table 1. *Least-square means from repeated-measures ANOVAs for kinematic variables digitized from aquatic (larval) and terrestrial (metamorphosed) feeding behaviors (captures and transports) for eight* Salamandra salamandra *with five feedings per individual for each feeding type*

Variables	Aquatic strikes	Aquatic transports	Terrestrial transports	Terrestrial strikes
Gape cycle time (ms)	41.0±1.1	39.1±1.3	77.7±3.9	134.6±6.2
Maximum gape angle (degrees)	33.7±2.1	30.7±1.6	47.9±1.9	56.2±2.2
Time to maximum gape angle (ms)	17.4±0.6	17.3±0.8	35.1±1.8	43.1±3.2
Maximum head elevation (degrees)	31.0±2.1	30.7±2.7	22.9±1.7	47.5±2.2
Time to maximum head elevation (ms)	20.9±0.7	23.5±0.6	42.2±1.2	94.5±3.6
Maximum hyoid depression (degrees)	22.2±1.3	22.5±2.3	19.0±1.4	15.1±3.63
Time to maximum hyoid depression (ms)	24.7±0.7	24.3±0.7	42.5±3.0	181.7±10.9

Underlining indicates behaviors that are not significantly different on the basis of Tukey pairwise *post hoc* comparisons with significance determined using a column-wide sequential Bonferroni test (Rice, 1989).

Values are means ± S.E.M.

Table 2. *Results of repeated-measures ANOVAs for the significance of trials (trials within behavior), individual (interindividual), behavior (strikes* versus *transports) and stage (aquatic* versus *terrestrial) effects on kinematic variables measured from eight* Salamandra salamandra

Variable	Trials (4, 96)	Individual (7, 96)	Behavior (1, 7)	Stage (1, 7)	Behavior×stage (1, 7)
Gape cycle time	0.0690	0.7199	0.0001*	0.0001*	0.0001*
Maximum gape angle	0.3090	0.0132	0.0371	0.0001*	0.3007
Time to maximum gape	0.9385	0.5879	0.0623	0.0001*	0.7410
Maximum head elevation	0.0249	0.0024*	0.0002*	0.1350	0.0001*
Time to peak head elevation	0.2106	0.4498	0.0001*	0.0001*	0.0001*
Maximum hyoid depression	0.3933	0.0041*	0.2620	0.0010*	0.2746
Time to peak hyoid depression	0.2601	0.5084	0.0001*	0.0001*	0.0001*

Significance was determined using a column-wide sequential Bonferroni test (Rice, 1989); significant values are indicated by an asterisk.

Values in parentheses are degrees of freedom.

Terrestrial transport kinematics

Terrestrial transports in *Salamandra salamandra* were similar to aquatic feeding in that they had a bell-shaped gape profile and hyoid retraction began during mouth opening and reached its maximum during mouth closing (Figs 2–4). Terrestrial transports have higher initial and final gape angles because the prey is held in the jaws. Maximum hyoid depression and time to maximum hyoid depression in terrestrial transports were not significantly different from those for the aquatic behaviors (Table 1). However, terrestrial transports had significantly smaller maximum head elevation, and significantly greater gape cycle time, maximum gape angle, time to maximum gape angle, and time to maximum head elevation than the aquatic feeding behaviors. In multivariate space (Fig. 5), the terrestrial transports did not

overlap with the aquatic behaviors and were significantly different (*P*<0.0001 for MANOVAs of PCs 1–5). It is evident from the kinematic profiles (Fig. 4) that terrestrial transports involve a delay of about 20 ms in the onset of hyoid retraction that results in a noticeable (but not significant) increase in the time to maximum hyoid depression compared with aquatic behaviors. Hyoid depression in terrestrial transport was very
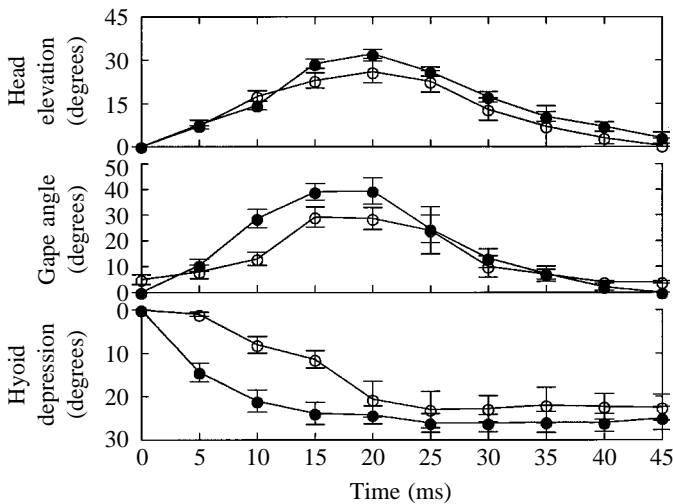

Fig. 2. Mean aquatic feeding kinematics for head, mouth and hyoid movements for one larval *Salamandra salamandra* feeding on *Tubifex* worms. Mean profiles (±1 S.E.M.) for aquatic transports ($\bigcirc$, *N*=5) and strikes ($\bullet$, *N*=5) are plotted against time. Note the slight delay in the mouth opening and hyoid depression in transports.
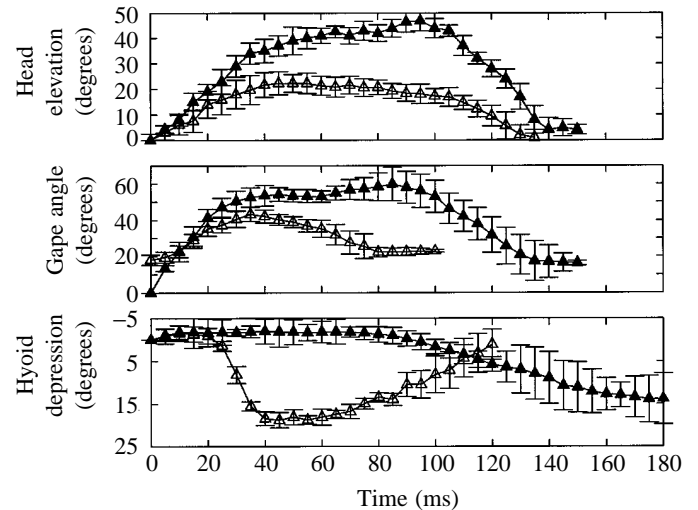

Fig. 3. Terrestrial feeding kinematics for head, mouth and hyoid movements for one adult *Salamandra salamandra* feeding on crickets. Mean profiles (±1 S.E.M.) for aquatic transports ($\triangle$, *N*=5) and strikes ($\blacktriangle$, *N*=5) are plotted against time. Note the 20 ms delay in hyoid retraction, the bell-shaped gape profile, the extended elevation of the head in terrestrial transports, the plateau in the gape profile and the greatly delayed hyoid depression in terrestrial strikes.

Table 3. *Factor loadings (for principal components 1–5) for each kinematic variable measured from the four feeding behaviors of* Salamandra salamandra

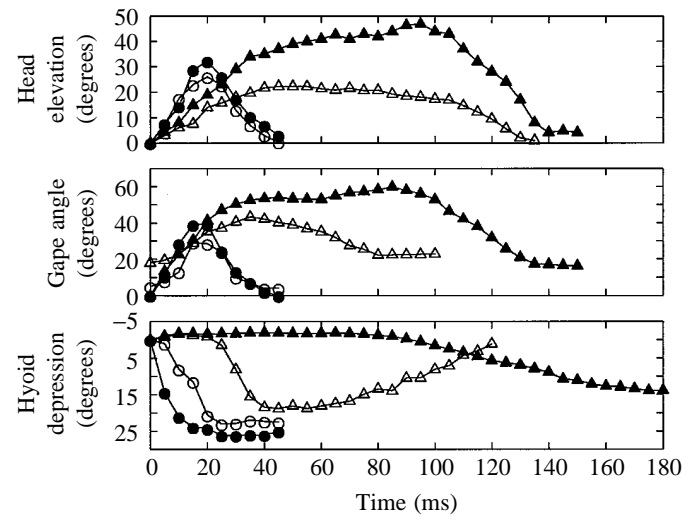| Variable	Factor loadings				
	PC1	PC2	PC3	PC4	PC5
Gape cycle time	0.960	0.162	−0.011	0.132	0.030
Maximum gape angle	0.798	0.150	0.188	−0.550	0.056
Time to maximum gape angle	0.887	0.365	−0.055	0.048	−0.267
Maximum head elevation	0.498	−0.737	0.443	0.024	−0.106
Time to maximum head elevation	0.971	0.063	−0.026	0.152	0.077
Maximum hyoid depression	−0.537	0.473	0.688	0.124	0.016
Time to maximum hyoid depression	0.953	−0.040	0.086	0.184	0.156
Variance explained (%)	67.6	13.6	10.2	5.6	1.7

Fig. 4. Comparison of aquatic and terrestrial feeding kinematics for head, mouth and hyoid movements in one *Salamandra salamandra*. Mean profiles for aquatic transports ($\bigcirc$, *N*=5), aquatic strikes ($\bullet$, *N*=5), terrestrial transports ($\triangle$, *N*=5) and terrestrial strikes ($\blacktriangle$, *N*=5) are plotted against time. Note that profiles for the terrestrial transports lie between those for the aquatic behaviors and terrestrial strikes. Error bars have been omitted for clarity.

similar to aquatic kinematics once retraction began (Fig. 4) and the time to maximum hyoid depression occurred at about the same relative time in the overall gape cycle time (at about 60 % of gape cycle time). In addition, terrestrial transports differ from the other three behaviors in that the head remained elevated for longer, until well after the mouth had closed (Figs 3, 4).

Terrestrial strike kinematics

Terrestrial strikes were significantly different from the aquatic behaviors except for maximum hyoid depression (Table 1). Terrestrial strikes and transports did not differ in maximum gape angle, time to maximum gape and maximum hyoid depression. Strike kinematics differed from terrestrial transports in having greater gape cycle time, maximum head elevation, time to maximum head elevation and time to maximum hyoid depression. From the kinematic profiles (Figs 3, 4), it is evident that terrestrial strikes exhibit a plateau in the gape profile when the tongue moves out of and back into the mouth while transports do not exhibit a plateau. The occurrence of tongue projection during the strike also greatly delayed the retraction of the hyoid (Figs 3, 4). In multivariate space (Fig. 5), the terrestrial strikes were separated from transports (except for one transport). They were significantly different on PC1 ($P<0.0001$), PC2 ($P<0.0001$), and in a MANOVA of PCs 1–5 ($P<0.0001$).

Discussion
Comparisons to feeding kinematics in fishes

The kinematic profiles for gape, head elevation and hyoid depression in *Salamandra salamandra* were very similar to those of aquatic feeding behaviors in fishes (Lauder, 1985; Gillis and Lauder, 1995). Comparisons of quantitative data on aquatic feeding behaviors in the bluegill sunfish *Lepomis macrochirus* (Gillis and Lauder, 1995), *Salamandra salamandra* and the tiger salamander *Ambystoma tigrinum* (Reilly and Lauder, 1992; Gillis and Lauder, 1994) illustrate some of the striking similarities of aquatic feeding behaviors in salamanders and fishes (Table 4). In aquatic feeding behaviors, head elevation and gape angle exhibit bell-shaped curves and peak hyoid depression begins during mouth

opening and peaks during mouth closing; thus, the basic movement profiles are very similar. In addition, during aquatic transports, *S. salamandra*, *A. tigrinum* and the bluegill sunfish had strikingly similar means for timing variables describing kinematic excursions (compare mean values in Tables 1 and 4). Thus, the hypothesis that basic salamander and fish feeding kinematics are similar is strongly supported, particularly for aquatic prey transport behaviors.

Comparisons of aquatic transports and strikes in *Lepomis macrochirus* (Gillis and Lauder, 1995) and *Salamandra salamandra* (Table 1) reveal that gape cycle time, maximum hyoid depression and maximum head elevation were not significantly different among these behaviors within these species, but maximum gape angle, time to maximum gape, time to maximum hyoid depression and maximum head elevation were significantly greater in bluegill sunfish strikes than in bluegill sunfish transports. Thus, although general
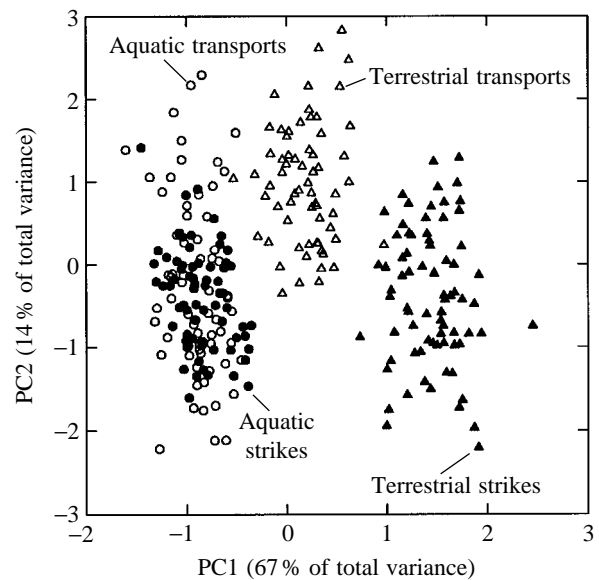

Fig. 5. Principal components analysis of four different feeding behaviors in eight *Salamandra salamandra* based on seven variables (see Table 1). Each symbol represents one aquatic strike (●), aquatic transport (○), terrestrial transport (△) or terrestrial strike (▲) from one individual. Note that the aquatic behaviors overlap and terrestrial transports are intermediate between aquatic and terrestrial strikes.

Table 4. *Kinematic data from studies of feeding in* Lepomis macrochirus *and* Ambystoma tigrinum

| | Ambystoma tigrinum | | | | | Lepomis macrochirus | |
	Aquatic transports	Aquatic strikes		Terrestrial transports	Terrestrial strikes	Strikes	Transports
Reference	1	1	2	1	1	3	3
Time to maximum gape angle (ms)	18.7±3.9	44.0±2.0	26.4±1.2	20.2±1.1	54.6±2.7	42.5±2.3	16.25±1.2
Time to maximum head elevation (ms)	29.0±5.9	47.0±2.5	32.8±0.9	32.0±2.5	55.0±3.8	47.8±4.0	20.0±1.5
Time to maximum hyoid depression (ms)	59.4±10.6	48.7±2.3	36.0±1.5	53.0±6.7	63.0±7.9	51.0±2.89	27.9±1.9
Gape cycle time (ms)	44.0±7.6	80.8±3.7	59.0±0.8	57.4±4.0	89.8±4.6	65.5±4.2	36.5±2.6

1, Gillis and Lauder (1994); 2, Reilly and Lauder (1992); 3, Gillis and Lauder (1995).

kinematic patterns are the same in fishes in salamanders, the timing and excursion details of the two aquatic behaviors are similar in *Salamandra salamandra* and somewhat different in the bluegill, with aquatic strikes involving greater excursions and longer durations of jaw and hyoid movements.

Metamorphosis of feeding behavior in Salamandra salamandra

The transition from aquatic to terrestrial feeding in salamanders involves a change from suction feeding to tongue-based intraoral prey transport and capture (Lauder and Reilly, 1994). Kinematic patterns in *Salamandra salamandra* range from the essentially similar aquatic feeding behaviors to terrestrial transport which resembles an extended version of the aquatic behaviors, to the longer tongue-projection behavior used to capture prey. The basic kinematic patterns of prey transport after metamorphosis are very similar to the aquatic kinematics. The bell-shaped gape profile is retained and hyoid depression begins during mouth opening and peaks during mouth closing (Fig. 4). Although the extent and timing of peak hyoid movements were not significantly different (Table 1), terrestrial transport did exhibit a slightly delayed onset of hyoid depression (Fig. 4) and, thus, a somewhat later timing of peak hyoid depression. A similar delay is seen in *Ambystoma tigrinum* (Reilly and Lauder, 1991; Gillis and Lauder, 1994). This delay in hyoid depression at the beginning of mouth opening in terrestrial transport corresponds to the time when the tongue (genioglossus), interhyoideus and subarcualis rectus I muscles exhibit bursts of activity after being silent prior to mouth opening (Reilly and Lauder, 1991). Thus, a protractive force is exerted on the hyobranchial apparatus and tongue, and therefore on the prey item, early in transport behavior. This is similar to hyoid movements seen in fishes just prior to mouth opening (Lauder, 1985). This may facilitate obtaining a better hold on the prey item just before tongue and hyoid retraction begins. The addition of this prey-crushing movement appears to increase the length of the gape cycle but does not affect its basic bell-shaped profile. In *Salamandra salamandra,* maximum head elevation decreases in terrestrial compared with aquatic transport, as it does in *A. tigrinum* (Gillis and Lauder, 1994). One novel component of terrestrial transport is that the head remains elevated well after the mouth has closed, in contrast to coordinated reduction of the head elevation at the time of mouth closing in the other three behaviors (*A. tigrinum* appears to lower the head at gape closing then immediately elevate it again during swallowing; Gillis and Lauder, 1994). Perhaps the head is elevated after transport to facilitate swallowing behavior as the esophagus moves the prey posteriorly.

Terrestrial strike kinematics were similar to those reported for the salamander *Taricha torosa* by Findeis and Bemis (1990). Terrestrial strike kinematics were more similar to terrestrial transports than to the aquatic behaviors (Table 1). Six of the kinematic variables in terrestrial strikes differed significantly from those for the aquatic behaviors (maximum hyoid depression was similar in all four behaviors). Although terrestrial strikes tended to have greater maximum gape angles and times to maximum gape angle, these were not significantly different from those for terrestrial transports. In addition, both terrestrial behaviors exhibited delays in the onset of hyoid depression at the time when the tongue initially moves anterodorsally early in mouth opening.

Terrestrial strikes differed in having a significantly greater gape cycle time, maximum head elevation, time to maximum head elevation and time to maximum hyoid depression than terrestrial transports. All of these can be attributed to the addition of tongue projection to the feeding behavior. The insertion of a period when the tongue is projected from the mouth and then pulled back into the mouth requires that the mouth remain open while the tongue acquires and pulls the prey back before the mouth can be closed. Thus, the gape cycle is longer and a plateau appears in the terrestrial gape profile. Because the tongue-projection phase is added to the behavior, retraction of the hyoid cannot occur until the tongue returns from being projected, and thus the onset of hyoid retraction and time to maximum hyoid depression are delayed as well. The head angle and gape profiles have delayed times to maximum values and maxima are attained towards the end of the plateau at the time when the tongue and prey are moving back through the jaws. In addition, to accommodate the prey entering the mouth, terrestrial strikes exhibit significantly greater maximum gape angles which appear to be accomplished with a significantly greater maximum head elevation (Fig. 3).

On the basis of the shared characteristics among the four behaviors (statistically similar kinematic variables; Table 1, and shared characteristics of kinematic profiles, Figs 3, 4 discussed above), the two aquatic behaviors are most similar and these are more similar to terrestrial transports than to terrestrial strikes. Dispersion of the four behaviors in principal components space illustrates the same pattern (Fig. 5). If one considers the ontogenetic polarity of these behaviors in salamanders, it is possible to argue, on the basis of shared similarities, that terrestrial transport is an intermediate behavior between aquatic feeding and terrestrial tongue projection. Given this, one can construct a basic description of the metamorphosis of feeding behavior in *Salamandra salamandra.*

(1) Aquatic feeding in *Salamandra salamandra* is basically similar to the ancestral patterns observed in the bluegill sunfish *Lepomis macrochirus* and there are very few differences between strikes and transports. Aquatic transports differ from strikes in having a slightly delayed onset and slower rate of hyoid depression, and gape cycle time and maximum gape angle are somewhat (but not significantly) lower in aquatic transports.

(2) After metamorphosis, terrestrial transports add a new prey-crushing behavior, inserted during early mouth opening, that results in a delay in the onset and completion of hyoid retraction and a longer gape cycle time that retains the ancestral bell-shaped profile. Another novel feature of terrestrial transport in *Salamandra salamandra* is that the head returns to its initial position well after the gape cycle is completed.

(3) The advent of tongue projection adds a period when the tongue moves out of the mouth and returns. It appears that the tongue-projection phase (with its novel motor patterns) is inserted into terrestrial transport behavior during early mouth opening between the prey-crushing movements and the subsequent hyoid retraction. It may, in contrast, be a complex extension of the prey-crushing behavior of transports. Adding the tongue-projection phase lengthens the gape cycle further, causing a plateau to appear in the gape profile, and extends the onset and completion of hyoid retraction well beyond that of terrestrial transport.

In general, the ontogenetic evidence from *Salamandra salamandra* supports the hypothesis of Lauder and Reilly (1994) that terrestrial strikes would be different from the other three behaviors, as was corroborated by Gillis and Lauder (1994) for different samples of *Ambystoma tigrinum.* More specifically, patterns of ontogenetic change from *Salamandra salamandra* support the hypothesis that terrestrial prey capture develops from terrestrial prey transport, which, in turn, develops from aquatic feeding behavior during ontogeny. Although the effects of morphological metamorphosis cannot be separated from purely environmental effects in this study, one can draw some conclusions from functional data available on salamander feeding. For example, biomechanical transformations at metamorphosis (Lauder and Reilly, 1988, 1990; Reilly and Lauder, 1990*b*) are combined with different motor patterns for transports and strikes (Reilly and Lauder, 1990*c*, 1991) to produce the two functionally different terrestrial behaviors. In addition, Lauder and Shaffer (1988) and Shaffer and Lauder (1988) have shown that kinematics and motor patterns during aquatic strikes differ from terrestrial patterns, but that transformed salamanders feeding in the water retain the aquatic kinematics. However, metamorphosed individuals feeding in the water have significantly reduced capture success rates (Reilly and Lauder, 1988). Thus, the primitive behavior is retained through metamorphosis, and morphological changes affecting the addition of terrestrial tongue-based feeding behaviors do not severely compromise the use of aquatic feeding in terrestrial forms but they have critical effects on feeding performance. Morphological changes at metamorphosis appear to have a greater effect on aquatic feeding kinematics than a simple environmental effect, but additional studies of transformed individuals feeding in the water would be needed to better distinguish the effects of environment *versus* morphological stage.

Evolution of terrestrial feeding behavior

Because the Caudata retain many pleisiomorphic features of the feeding mechanism of primitive tetrapods (Schmalhausen, 1968; Carroll and Holmes, 1980; Jarvik, 1980; Duellman and Trueb, 1986) and because *Salamandra salamandra* is a member of a generalized caudate family in which the feeding mechanism has been conserved during evolution (Regal, 1966; Wake, 1982; Özeti and Wake, 1969), the ontogenetic transformation of feeding kinematics in *Salamandra salamandra* represents a reasonable model for transitions that

may have occurred during the evolution of primitive terrestrial tetrapods. Therefore, the metamorphosis of feeding in *Salamandra salamandra* can be used to test the general hypothesis that, in tetrapods, aquatic prey capture and transport are similar behaviors whose basic patterns are retained in terrestrial prey transport and retained but somewhat modified in terrestrial prey capture (Lauder and Reilly, 1994). The ontogenetic changes of feeding kinematics in *Salamandra salamandra* strongly support this hypothesis.

The conclusions based on *Salamandra salamandra* contrast with the conclusions of Gillis and Lauder (1995). In *Ambystoma tigrinum*, they found aquatic and terrestrial strikes to be similar, and aquatic and terrestrial transports to be similar, and hypothesized that capture and transport behaviors may have diverged early in vertebrate evolution. However, their results can be interpreted differently when additional data are compared with theirs. Using other mean kinematic data for aquatic strikes (Reilly and Lauder, 1992) from another sample of *Ambystoma tigrinum* (Table 4), one can argue, on the basis of a simple comparison of the means, that terrestrial transport behaviors are more similar to aquatic strikes and that terrestrial strikes stand alone with obviously longer kinematic excursions than the other three behaviors. This interpretation results in patterns in *Ambystoma tigrinum* similar to those observed in the present study for *Salamandra salamandra* where terrestrial transports were intermediate between the aquatic behaviors and terrestrial tongue projection. Thus, the two salamanders studied to date appear to exhibit similar ontogenetic shifts in feeding behavior that support the hypothesis that aquatic feeding to terrestrial transport to terrestrial tongue projection represents an evolutionary transformation series in the evolution of terrestrial feeding in early tetrapods. Obviously, more comparative data for other extant basal tetrapods are necessary to test further the generality of the ontogenetic transformations observed here and to strengthen inferences about the evolution of terrestrial feeding in tetrapods.

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