

THE ONTOGENY OF AQUATIC FEEDING BEHAVIOR IN SALAMANDRA SALAMANDRA: STEREOTYPY AND ISOMETRY IN FEEDING KINEMATICS

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Summary

To examine the extent to which aquatic prey-capture behavior in salamanders is stereotyped and how feeding kinematics scales with size, the ontogenetic variability of aquatic feeding behavior was examined in eight *Salamandra salamandra*. Feeding kinematics (seven duration and angular displacement variables), kinematic variance and capture performance were quantified and compared in the first several feedings after birth with a series of feedings 8 weeks later, just prior to metamorphosis. Analysis of variance revealed no statistically significant ontogenetic differences in the kinematic variables, and individual differences were found in only two variables (maximum gape angle and gape cycle time). A comparison of the relative kinematic variance within individuals revealed no significant differences in variance during ontogeny. In addition, capture success rate

did not change. The strike is significantly faster than that of other salamanders. These results indicate that the initial prey-capture behavior remains unchanged throughout larval ontogeny. Thus, aquatic strike behavior in *S. salamandra* is developmentally fixed (innate) and does not appear to be influenced by learning or improvement in 'skill', supporting the hypothesis that aquatic salamander feeding is a highly stereotyped, unmodulated behavior. In addition, the lack of kinematic change through ontogeny indicates that feeding kinematics do not scale with body size, contrary to predictions that movements should be slower in larger animals.

Key words: feeding, stereotypy, kinematics, scaling, amphibian, salamander, behavior, *Salamandra salamandra*.

Introduction

The study of vertebrate feeding behavior has been a major focus in functional morphology over the last decade (Hildebrand *et al.* 1985; Lauder, 1985; Lauder and Shaffer, 1993; Schwenk and Throckmorton, 1989; Crompton, 1989). Numerous kinematic studies of fishes (Claes and De Vree, 1991; Sanford and Lauder, 1990; Westneat, 1990), salamanders (Gillis and Lauder, 1994; Reilly and Lauder, 1989a; Schwenk and Wake, 1993), frogs (Deban and Nishikawa, 1992; Gans and Gorniak, 1982; Nishikawa and Roth, 1991), squamate reptiles (Bels, 1989; Smith, 1984; Wainwright and Bennett, 1992), turtles (Lauder and Prendergast, 1992), birds (Van Der Leeuw, 1992; Heidweiller and Zweers, 1990) and mammals (Herring, 1985; Hiiemae and Crompton, 1985) have related feeding behavior to function, ecology and taxonomic variation. More recently, studies comparing feeding kinematics among major vertebrate clades have identified basic patterns of kinematic evolution across the aquatic–terrestrial transition and among tetrapods (Reilly and Lauder, 1990, 1991; Lauder and Reilly, 1994). One striking result of comparisons among vertebrates is that there appears to be a remarkable contrast between the feeding behavior of salamanders and frogs: feeding in salamanders is generally

considered to be highly stereotyped compared with that of frogs (Lauder and Reilly, 1994; Nishikawa and Cannatella, 1991). In other words, when salamanders strike at prey, the strike appears to proceed invariably to completion, whereas frogs can modulate the strike as it happens. This contrast in the apparent degree of control over the strike is supported by several functional studies. Kinematic and neurobiological studies (Anderson, 1993; Anderson and Nishikawa, 1993; Nishikawa and Gans, 1990; Nishikawa *et al.* 1992) have shown that frogs can modulate the timing of movements within the strike depending on both external feedback about the prey position and internal feedback about the position of the tongue and jaws. In contrast, quantitative studies of feeding function in salamanders demonstrate (1) that both aquatic and terrestrial feeding is highly kinematically stereotyped within and among individuals of the same species (Reilly and Lauder, 1989a; Findeis and Bemis, 1990), (2) that suction feeding kinematic variables are not significantly different among four of six aquatic salamander families analyzed using multivariate analysis of variance (Reilly and Lauder, 1992), and (3) that motor patterns are not significantly different during feeding on different prey types (Reilly and Lauder, 1989b), indicating a

lack of modulation for prey of different escape abilities. Thus, salamanders appear to have highly stereotyped or 'hard-wired' feeding behavior compared with that of frogs.

The first goal of this study was to examine the extent of stereotypy of feeding kinematics in salamanders by quantifying individual and ontogenetic variation of aquatic feeding kinematics and capture performance in *Salamandra salamandra*. This is the first study to examine ontogenetic changes in salamander feeding behavior during larval ontogeny. The study of the ontogeny of behavior, or how complex behavioral systems are initially programmed and subsequently modified during life (as reflected in kinematic output), has not been carried out using quantitative analyses of kinematics. Statistical comparisons of the initial performance of a behavior with the same behavior performed later in ontogeny indicate whether kinematics or capture rate change with time and perhaps involve some degree of learning or skill improvement. Ontogenetic variation in feeding kinematics or capture rate would demonstrate that feeding behavior is not as stereotyped or hard-wired as it is hypothesized to be, because it may be modulated over time. In contrast, a lack of kinematic change through ontogeny would indicate that the behavior is fixed or unmodulated.

In comparing behavior during ontogeny, one is also faced with the consequences of changes in body size and scaling that may affect the kinematics of the behavior. Changes in size alone can have significant effects on structural and functional factors that influence behavior (Calder, 1984; Schmidt-Nielsen, 1984), as has been shown extensively for locomotion (e.g. Katz and Gosline, 1993; Bennett *et al.* 1989). In comparing the behavior of different size (or ontogenetic) classes, simple geometric scaling of the components of the feeding mechanism (muscles, bones, ligaments) could directly affect kinematics (Hill, 1950). For example, because muscle contractile studies (Archer *et al.* 1990; Bennett *et al.* 1989; Marsh, 1988) have shown that larger muscles contract more slowly, even if head morphology were to scale isometrically we would expect kinematic excursions of the jaws to occur more slowly in larger animals. Therefore, the second goal of the present study was to examine the effects of increased size on feeding kinematics by considering ontogenetic changes in kinematics in the light of an analysis of head allometry in *Salamandra salamandra*.

Materials and methods

Experimental animals and kinematic techniques

The fire salamander *Salamandra salamandra* (L.) was chosen for this study because fully developed young larvae emerge from the female at a size many times larger than larvae that hatch from eggs, thus avoiding the problems of filming tiny hatchling salamanders. In addition, the 'newborn' larvae can be filmed prior to any aquatic feeding experience in order to record the kinematics of their first open-water feedings (as an indication of the initial feeding pattern). *S. salamandra* are known to be intraoviductal cannibals, so some intraoviductal

feeding experience may have occurred. Young salamanders were born in the laboratory and immediately separated into bowls. Eight of the 30 young born were filmed feeding on *Tubifex* worms on the day they were born. These eight individuals were maintained individually on *ad libitum* *Tubifex* worms and brine shrimp until they were filmed again 2 months later, just prior to metamorphosis at about twice the initial snout-vent length. Thus, this experiment employs a longitudinal design comparing the first feedings of eight individuals (stage 1) with feedings filmed 2 months later (stage 2), representing a doubling of body size.

Salamanders feeding on *Tubifex* worms were filmed in lateral view at 200 fields s⁻¹ using a NAC HSV-400 high-speed video system. Fifteen feedings per individual per stage were filmed, and the snout-vent length of each individual was measured after each filming session. 139 prey-capture sequences (6–10 per individual for stage 1, 7–11 per individual for stage 2, sample sizes in Table 1) with clear lateral views were 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 before the mouth began to open. From the coordinate data, displacement angles were calculated 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. For each feeding, the raw angles were transformed to adjust the angle at time 0 to equal zero. From the kinematic data for each feeding, seven kinematic variables quantifying maximum kinematic displacements and durations during the strike were taken for statistical analysis. These variables were: maximum gape angle (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). The time of maximum hyoid depression was taken as the time at which ventral movement ceased.

Data analysis and experimental design

The experimental design used in this study was a two-way analysis of variance (ANOVA) with individuals and ontogenetic stage as the main effects. In this design, each of the eight individuals was tested at both ontogenetic stages, and stage is treated as a fixed effect and individuals as a random effect. Thus, the *F*-ratios for the stage effect were calculated by dividing the mean square for the stage effect by the interaction mean square, whereas the *F*-ratios for the individuals and the interaction terms were calculated using the error mean square as the denominator (Sokal and Rohlf, 1981). Because multiple univariate comparisons were being conducted, a sequential Bonferroni correction was used to determine statistical significance (Rice, 1989). The two-way ANOVA design has the advantage of quantifying ontogenetic changes in kinematics while controlling for individual differences during ontogeny.

To examine ontogenetic changes in stereotypy further, the

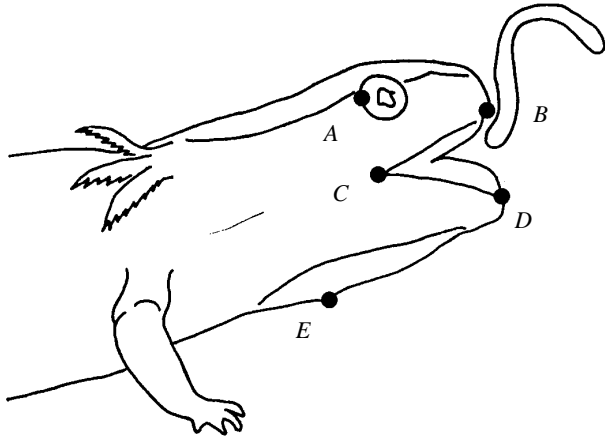


Fig. 1. Landmark coordinates digitized from high-speed video images of aquatic feeding behavior. The landmarks were (A) the posterior angle of the eyelid, (B) the tip of the upper jaw, (C) the angle of the mouth, (D) the tip of the lower jaw, and (E) the point where the tip of the basibranchial element 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 calculated for each feeding. From these data, the maximum displacements and timing variables were taken for statistical analyses.

kinematic variance for each individual for each stage was compared by testing the significance of differences between the variances (s^2) for each kinematic variable (Sokal and Rohlf, 1981). The null hypothesis is that the degree of stereotypy (variance in each kinematic variable) does not change between the initial performance of the behavior (stage 1) and the same behavior performed 2 months later (stage 2). The alternative hypothesis is that the stage variances are unequal, which would indicate a change in the degree of stereotypy.

Prey-capture performance was quantified by calculating the percentage of successful captures in 15 attempts per individual per stage. Ontogenetic differences in capture success rate were calculated using a *t*-test comparing the stage means.

The potential for size-induced changes in kinematics due to changes in the shape of the head was investigated by examining the morphometrics of the head in a parallel group of *S. salamandra*. Eight siblings (raised under identical conditions) of sizes spanning the sizes of the two ontogenetic stages were preserved during the growth of the experimental animals. The following six morphometric variables were selected to account for the overall width and length of the head and skull and the size of the hyobranchial apparatus: (1) head width across the rear of the mandible, (2) snout–mandible length on the midline, (3) snout–axilla length, (4) internarial distance, (5) the length of the first hypobranchial, and (6) the length of the first ceratobranchial. Morphometric variables were \log_{10} -transformed, tested for significance of regressions against \log_{10} (snout–vent length), and then tested for significance from a slope of 1 (isometry) using Bonferroni-corrected probability values (Rice, 1989). The scaling patterns of these representative variables are assumed to provide an initial indication of the scaling of the entire head and feeding apparatus.

Results

The *S. salamandra* larvae were filmed on the day they were born (6 September 1992) and 59 days later (14 November 1992), just prior to metamorphosis. Snout–vent lengths at these two stages averaged 15.8 mm (range 15–17 mm) and 28.1 mm (range 28–29 mm), respectively, representing an approximate doubling in body size between the two filming sessions. Summary statistics for the seven kinematic variables measured for all eight individuals at both stages are given in Table 1. Mean kinematic profiles for a single individual feeding at both

Table 1. Individual means by stage for kinematic variables describing suction feeding behavior in *Salamandra salamandra* larvae feeding on small worms (*Tubifex*)

Variable	Stage	Individual (<i>N</i> stage 1, <i>N</i> stage 2)							
		1 (9, 10)	2 (10, 9)	3 (8, 9)	4 (6, 9)	5 (9, 8)	6 (7, 8)	7 (9, 7)	8 (10, 11)
Gape cycle time (ms)	1	38.9±0.7	37.5±0.8	40.0±1.3	35.0±1.8	43.9±0.7	35.0±1.5	46.7±1.2	41.5±0.8
	2	44.5±0.9	39.4±1.8	42.2±1.5	37.8±1.5	38.8±1.6	41.9±0.9	40.0±1.5	37.7±1.0
Maximum gape angle (degrees)	1	31.0±1.4	39.4±2.7	30.9±1.6	31.7±5.0	33.4±2.3	33.3±2.6	40.3±1.1	40.3±2.5
	2	29.7±3.3	39.6±4.1	33.8±2.7	27.1±2.2	38.3±2.5	27.8±1.3	26.9±1.2	34.9±2.1
Time to maximum gape angle (ms)	1	15.6±0.6	18.0±0.8	16.9±0.9	17.5±1.1	18.3±1.2	18.6±1.3	20.6±0.4	18.5±1.1
	2	18.0±0.8	16.7±0.8	16.7±0.8	16.7±0.8	17.5±0.9	16.9±0.9	17.1±1.0	17.3±0.8
Maximum head elevation (degrees)	1	28.8±1.7	32.2±2.6	30.5±1.9	30.7±1.5	31.3±0.7	37.0±2.6	29.0±2.1	32.6±2.5
	2	29.8±4.3	30.8±1.8	30.4±2.9	25.8±1.4	30.4±2.8	35.3±2.7	30.6±4.4	29.6±2.7
Time to maximum head elevation (ms)	1	21.7±0.8	18.5±0.8	20.0±1.0	17.5±1.1	21.1±0.7	20.0±0.7	22.8±1.2	20.5±0.5
	2	22.5±0.8	20.6±1.0	21.1±0.7	21.1±1.1	20.0±0.9	19.4±0.6	22.9±1.0	20.5±0.8
Maximum hyoid depression (degrees)	1	27.1±2.9	20.7±0.8	21.9±1.5	20.8±1.7	21.0±2.1	25.7±3.7	21.1±1.5	22.7±2.1
	2	22.2±1.9	26.2±1.3	22.7±0.9	18.1±1.8	23.6±2.2	21.0±1.5	23.3±2.2	21.2±1.4
Time to maximum hyoid depression (ms)	1	25.4±0.7	24.0±0.7	23.1±1.4	22.5±1.1	26.1±1.5	23.2±1.1	26.9±0.9	25.5±1.0
	2	26.8±0.8	27.2±1.2	26.1±0.7	23.9±0.7	24.4±1.1	23.5±0.7	23.9±0.7	25.0±0.7

Values are means ± S.E.M.

stages are plotted in Fig. 2. The results of the univariate ANOVAs for the seven kinematic variables describing feeding behavior are presented in Table 2. There is no significant stage effect for any variable and, therefore, no indication that the kinematics changes during ontogeny. The results also show that significant individual variation was found in only two of the seven variables, indicating that individuals were similar except for differences in mean gape cycle time and maximum gape angle. The interaction term was significant in only one of the seven variables (gape cycle time), indicating that individuals responded differently for that variable. Mean

kinematic patterns, pooled for all individuals for both stages, are presented in Table 3.

Comparisons of the relative ontogenetic variance within individuals are summarized in Table 4. Using a table-wide Bonferroni correction, none of the variance comparisons was significantly different at $P < 0.007$, indicating that the kinematic variation of each individual does not change through ontogeny. With a more liberal α level of $P < 0.05$, only five of the 56 comparisons would be significant, with each of these marginally significant comparisons involving ontogenetic increases in kinematic variability.

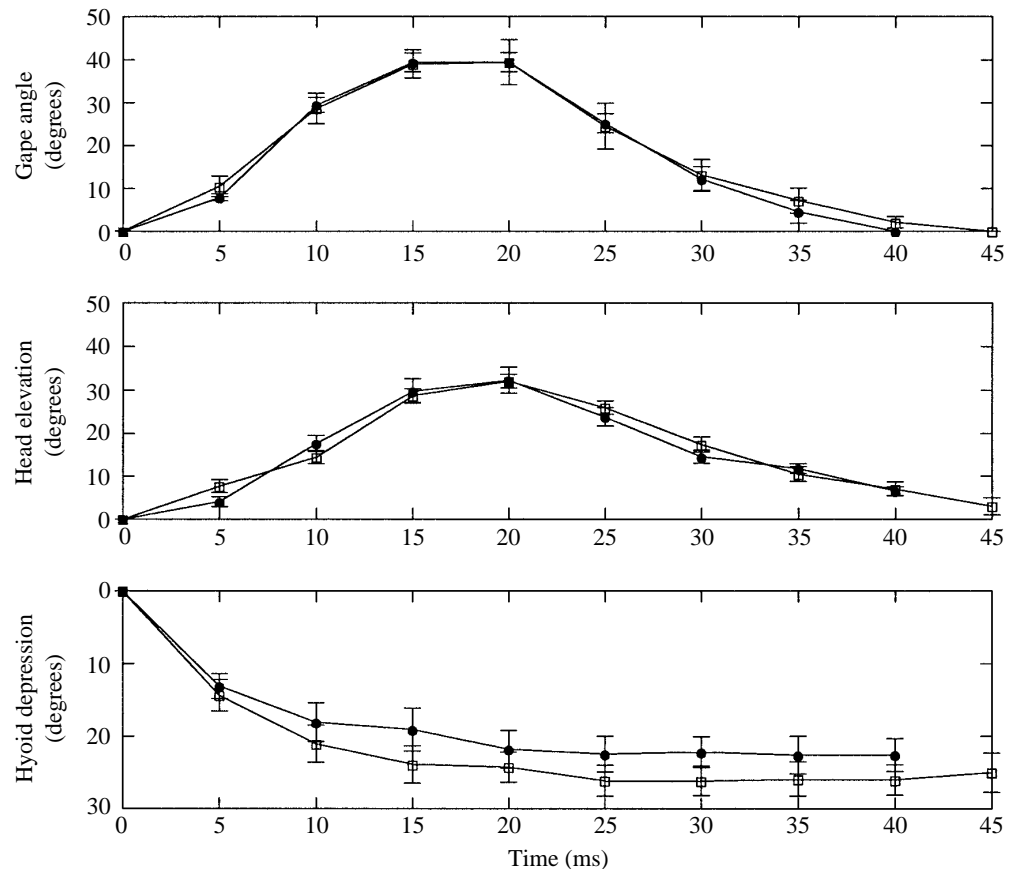


Fig. 2. Feeding kinematics for one *Salamandra salamandra* feeding on *Tubifex* worms at the two ontogenetic stages. The mean profiles (\pm S.E.M.) for the first six feedings after birth (\bullet) are plotted with the mean kinematic profiles ($N=9$) of the same individual feeding 59 days later (\square) at approximately twice the body size.

Table 2. Univariate two-way ANOVA F-statistics (and probabilities) for seven kinematic variables digitized from video recordings of *Salamandra salamandra* feeding just after birth and 59 days later in larval ontogeny (stage effect is fixed, individual effect is random)

Variable	Stage effect (d.f.=1, 7)	Individual effect (d.f.=7, 123)	Interaction (d.f.=7, 123)
Gape cycle time (ms)	0.074 (0.794)	6.037 (0.000)*	8.216 (0.000)*
Maximum gape angle (degrees)	1.946 (0.206)	4.225 (0.000)*	2.396 (0.025)
Time to maximum gape angle (ms)	2.242 (0.178)	1.156 (0.333)	1.687 (0.118)
Maximum head elevation (degrees)	2.629 (0.149)	1.431 (0.199)	0.305 (0.950)
Time to maximum head elevation (ms)	1.998 (0.200)	2.080 (0.050)	1.413 (0.206)
Maximum hyoid depression (ms)	0.066 (0.805)	1.165 (0.328)	1.935 (0.069)
Time to maximum hyoid depression (ms)	0.414 (0.540)	2.187 (0.040)	2.536 (0.018)

*Significant at table-wide level of significance determined by sequential Bonferroni test (Rice, 1989).

Capture success rates for the two stages averaged 90.9±8.6% (S.E.M.) for stage 1 and 86.1±7.1% for stage 2. Although five of the eight individuals showed a decrease in capture success over time (values for the other three remained constant), the mean capture success rate was not significantly different between the stages ($P=0.249$).

The scaling relationships of six variables measured from an ontogenetic group of the same size range as the two stages used for the kinematic study are presented in Table 5. Each variable

scaled isometrically with snout–vent length, indicating that, at least on the basis of these variables, the head and hyobranchial apparatus of *S. salamandra* grow geometrically over the size range encompassing the two ontogenetic stages that were filmed.

Discussion

Ontogenetic stereotypy in aquatic feeding kinematics

The results demonstrate that aquatic feeding behavior in *S. salamandra* is highly stereotyped. First, both the individual plots (Fig. 2) and the ANOVA (Table 2) illustrate the lack of change in the kinematic patterns of feeding during ontogeny. Second, individual variation was low, with significant individual differences in only two of the seven kinematic variables. Maximum gape angle and gape cycle time varied among individuals, yet all of the means fell within a narrow range (13° or 12ms, respectively; Table 1). Third, the uniformity of individual variance (Table 4) shows that the variation in the capture kinematics did not change. Finally, capture success rate did not change, illustrating a lack of ontogenetic improvement in capture ability. Thus, comparisons of the first larval feedings with feedings 2 months later revealed no kinematic or performance change in the feeding behavior of *S. salamandra*.

Table 3. Mean kinematic patterns during suction feeding in larval *Salamandra salamandra*

Kinematic variable	Maximum excursion (degrees)	Time of maximum value (ms)
Maximum gape angle	33.9±8.5	17.5±2.8
Maximum head elevation	30.8±7.6	20.7±2.8
Maximum hyoid depression	22.4±5.7	25.0±3.0
Gape cycle time	–	40.0±4.6

Values are means ± S.D. pooled for all individuals ($N=8$) and all feedings ($N=139$).

Table 4. Ontogenetic kinematic variance in larval *Salamandra salamandra*

Kinematic variable	Individual							
	1	2	3	4	5	6	7	8
Gape cycle time	–	–	–	–	–	–	–	–
Maximum gape angle	*	–	–	–	–	–	–	–
Time to maximum gape angle	–	–	–	–	–	–	*	–
Maximum head elevation	*	–	–	–	**	–	–	–
Time to maximum head elevation	–	–	–	–	–	–	–	–
Maximum hyoid depression	–	–	–	–	–	*	–	–
Time to maximum hyoid depression	–	–	–	–	–	–	–	–

Significance: * $P<0.05$, ** $P<0.02$.

Probabilities of stage differences in kinematic variance are indicated for each individual.

None of the comparisons was significant using Bonferroni-corrected probability values; however, each of the five probabilities less than 0.05 involved increases in variance.

Table 5. Morphometrics of head allometry in larval *Salamandra salamandra* based on eight specimens spanning the size range of the two ontogenetic stages

Variable	Allometric coefficient	Significance of regression (d.f.=1, 6)	Significance from isometry (d.f.=1, 6)
Head width across rear of mandible	1.029	0.000	0.676
Snout–mandible length	1.216	0.000	0.109
Snout–axilla length	1.050	0.000	0.560
Internarial distance	1.310	0.000	0.141
First hypobranchial length	0.972	0.000	0.074
First ceratobranchial length	0.864	0.000	0.182

All statistics were calculated on log₁₀-transformed variables after regression against log(snout–vent length). Each variable shows a significant regression with body size that is not significantly different from isometry.

These results provide evidence that aquatic feeding behavior is not modulated in *S. salamandra*. If the behavior could be modulated, one would expect that 2 months of feeding experience or 'training' would result in some evidence of skill improvement, such as increased capture success rate, reduced kinematic variation or shifts in kinematic patterns, as the behavior is fine-tuned or learned during ontogeny. The lack of ontogenetic variation indicates a high degree of stereotypy in the feeding kinematics in larvae that supports the hypothesis that aquatic feeding is unmodulated or fixed in salamanders (Lauder and Reilly, 1994; Nishikawa and Cannatella, 1991).

Comparisons with other salamanders

Given that aquatic feeding kinematics do not change ontogenetically in *S. salamandra*, the pooled kinematic data provide a description of feeding patterns for this species (Table 3) that can be compared with those of other species for which we have similar data. *S. salamandra* exhibits the same basic kinematic patterns found in suction feeding in aquatic vertebrates (Lauder and Reilly, 1994). There is a bell-shaped gape profile, maximum head elevation occurs at or about the time of maximum gape angle, and hyobranchial retraction begins with mouth opening and peaks during the mouth closing phase (Fig. 2). A maximum gape angle of about 34° occurs in about 17 ms, with the mouth closing in 40 ms. Comparisons with other aquatic-feeding salamanders (*Amphiuma*, *Ambystoma*, *Necturus*, *Siren*, *Cryptobranchus*, *Dicamptodon*; Reilly and Lauder, 1992) reveal that (ignoring size) aquatic feeding in *S. salamandra* is significantly faster than in the other six species for which we have similar data ($P < 0.001$ for *t*-test comparisons among species for each timing variable). Thus, the strike in *S. salamandra* is an extremely rapid behavior, occurring in 40 ms, which is similar to the timing of feeding in fishes, but twice as fast as for other salamanders.

Scaling and kinematics

The second goal of the present study was to investigate the effects of size on feeding kinematics by considering ontogenetic changes in kinematics in the light of an analysis of head allometry. The results of this study indicate that the head of *S. salamandra* scales isometrically (Table 5) (based on a representative subset of measures) and that the kinematic variables do not change (Fig. 2; Tables 2, 4); thus, size had no effect on kinematics. The angular displacements remained constant with a twofold increase in body size, indicating isometry of movements. Constant angular displacements would be expected, given the geometric scaling of the head, and are predicted by several models of kinematic scaling based on geometric scaling (Hill, 1950; O'Reilly *et al.* 1993; Richard and Wainwright, 1995).

The timing of head, hyobranchial and gape movements in *S. salamandra* was also constant over a doubling in body size. This was not expected, given empirical data on the scaling of muscle contractile properties and kinematic scaling models. Studies of time-to-peak twitch and contraction velocities in vertebrate muscles used in locomotion (Archer *et al.* 1990; Bennett *et al.*

1989; Marsh, 1988) demonstrate a slowing of muscle shortening rate with increasing body size, which would predict that kinematic timing variables should increase with body size. Comparisons of the few kinematic scaling studies available for vertebrates show that kinematic scaling relationships in vertebrates range from geometric scaling (slope=1) to size-independence (slope=0). O'Reilly *et al.* (1993) found that the timing of feeding movements in the toad *Bufo alvarius* increased in direct proportion to size over a range of body sizes that scaled isometrically. Their results match the predictions of the kinematic scaling model of Hill (1950) that relates the scaling of muscle force production (cross-sectional area) to mass and which predicts that the timing of kinematic movements would scale with size with a slope of 1. Thus, kinematic durations in the toad seem to increase geometrically with body size (although smaller individuals did not fit the model).

In lizard locomotion, the limb cycle time during running in *Dipsosaurus dorsalis* scales with body length with a slope of 0.714, indicating a slowing of movements with size (Marsh, 1988). Slightly lower scaling coefficients are found in bass. Richard and Wainwright (1995) incorporated predictions from contractile studies (Archer *et al.* 1990; Bennett *et al.* 1989; Marsh, 1988) into a kinematic scaling model to explain the increase in kinematic timing variables in feeding largemouth bass, *Micropterus salmoides*, which grow isometrically. They found that kinematic timing variables in bass scaled with a slope of 0.213–0.584, which matches the mean slope of 0.446 predicted from the scaling of time-to-peak twitch and maximum shortening velocity data in other vertebrates (Archer *et al.* 1990; Bennett *et al.* 1989; Marsh, 1988). Thus, movements in bass seem to increase in duration in relation to the scaling of muscle contractile properties.

In salamanders, the timing of kinematic movements appear to be independent of body size in feeding and locomotion. *S. salamandra* clearly lacks a size effect on the timing of movements during feeding. In a comparative analysis of aquatic feeding in salamanders, Reilly and Lauder (1992) found no significant differences in time-to-peak head elevation and time-to-peak gape among species differing significantly in head size and shape, indicating an interesting conservation of head movement timing during feeding among this diverse group of taxa. In addition, size does not affect the timing of the limb cycle and tail cycle during terrestrial and aquatic locomotion in the salamander *Ambystoma tigrinum*, even though larger muscles have been shown to contract more slowly (Bennett *et al.* 1989). Thus, on the basis of the few comparative data available, the scaling relationships of kinematic movements in vertebrate feeding and locomotion range from slopes of 0 to slopes of 1, and salamanders appear to lack significant size effects on kinematics.

If *S. salamandra* doubles in size, but the timing of feeding kinematics does not change, then something has to change. How can this discrepancy be explained? One explanation could be that a mere doubling in size is not a sufficient change for the expected slowing of kinematic movements to be detected. Another possible solution is that the biomechanical

components of the feeding mechanism do not grow isometrically. Detailed analyses of the levers and muscle morphometrics, such as that of Richard and Wainwright (1995) for largemouth bass, are needed to examine biomechanical ontogeny in *S. salamandra*. Another possible reason why the kinematic variables do not change is that the motor patterns may be changing; however, this is not well supported, given the relative stereotypy of motor patterns among individuals and through ontogeny in other salamanders (Reilly and Lauder, 1992). Alternatively, the lack of size effects on kinematics in salamanders may indicate that the ontogeny of their muscle physiology may be different at some biochemical or design level. Bennett *et al.* (1989) showed that, in contrast to studies of lizards, where variation in morphological, physiological and biochemical factors could be used to explain variation in locomotor performance, a study of the same variables in salamander locomotion was unable to correlate any factor with locomotory performance. The lack of correlations in locomotory traits in salamanders emphasises the complexity of the functional systems used in locomotion and feeding. How can slower muscles move larger salamanders faster using the same limb cycle time? Perhaps the muscles themselves are not scaling isometrically or some other, as yet unknown, physiological or morphological difference unique to salamanders is affecting the kinetics of muscle contraction.

Given the range of scaling patterns in vertebrate behavior patterns, it is obvious that such great variation exists in kinematic scaling among taxa that general conclusions cannot yet be drawn about the effects of size on kinematics. Additional studies of kinematic ontogeny are needed with animal models in which one can explicitly relate the scaling relationships of kinematics with the dimensions of the muscles and bones moving the jaws and hyobranchial apparatus and the moment arms of the insertions of key muscles. In addition, because no single kinematic scaling model fits more than one species, the causal bases for biomechanical relationships between design and behavior will elude us until additional kinematic scaling studies are available.

Kinematic analyses of behavior

Although kinematic analysis has become an important tool in functional morphology, quantitative kinematics have been used very little in studies of animal behavior (Schleidt, 1974). The kinematic analysis of behavior, such as that employed in this study, provides quantitative data and statistical analyses that can be used to quantify variation in movements to address empirically questions about learning and stereotypy in animal behavior. Because 'stereotypy' is so loosely defined and because the few behavior patterns that have been quantitatively studied were variable, Barlow (1977) introduced the modal action pattern that relaxed the level of stereotypy needed for fixed-action patterns. Thus, the idea of truly fixed, fixed-action patterns has fallen into disregard (Gaioni and Evans, 1986), and the idea of the modal action pattern has emerged to describe behavior that is not as constant as Lorenz's definition of a fixed-action pattern suggested (Grier and Burk, 1991).

Because the data for *S. salamandra* show that the kinematics of feeding does not change from the initial capture performance through larval ontogeny, it appears that aquatic feeding is stereotyped, developmentally fixed, unlearned and, thus, innate. The ANOVAs (Table 2) show that feeding behavior is identical among individuals and throughout ontogeny and thus that it is statistically highly stereotyped. The first performance of the behavior is identical to the behavior 2 months later, after considerable experience has occurred. Thus, aquatic strike behavior in salamanders is 'built in' (innate) and does not appear to be influenced by learning or improvement in skill with time. These data can be used to demonstrate that aquatic feeding behavior in *S. salamandra* closely fits the criteria for a fixed-action pattern originally outlined by Tinbergen (1951). Assuming that the complex motor coordination involved in feeding is genetically determined, feeding in *S. salamandra* is (1) common to all members of a species (five of seven variables were statistically invariant in all individuals), (2) unlearned (first feedings were kinematically identical to later feedings), and (3) stereotyped through repeated performances (within-individual within-stage variance was very low, there were no stage effects on kinematic variables, kinematic variance was little changed and there was no stage effect on capture success rate). Thus, this may be the first quantitative demonstration of a fixed-action pattern. This study illustrates how quantitative kinematics can be used as a powerful tool to document behavior patterns empirically and to compare them statistically. Quantifying kinematically the degree of stereotypy over time enables us to identify kinematic scaling relationships and to discriminate between fixed-action patterns and more variant behavior patterns that are subject to learning or other changes during ontogeny.

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