PATTERNS OF VARIATION IN AQUATIC AMBYSTOMATID SALAMANDERS: KINEMATICS OF THE FEEDING MECHANISM

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Summary. — Patterns of variation in the feeding mechanism of three species of ambystomatid salamanders (*Ambystoma dumerilii, A. mexicanum,* and *A. ordinarium*) were studied to provide insight into the nature of variation in kinematic parameters of the jaw mechanism associated with prey capture. A nested analysis of variance design provided an assessment of the amount of variation in six kinematic variables (measured from 200 frames/sec films of feeding behavior) both among species and among individuals within species. For all six variables, a highly significant proportion of the variance was explained at the intraspecific level. Among species, the most robust discriminators were variables associated with movement of the hyoid. The variables reflecting gape and lifting of the head provided no significant discrimination among species and had large error variances. The hyoid apparatus is the most phylogenetically conservative component of the feeding mechanism in lower vertebrates and was the most stereotyped component of feeding behavior within the salamander species studied here.

During the last fifteen years, functional morphologists have increasingly utilized modern analytical tools and experimental approaches to study the relationship between form and function in organisms. The use of new techniques has provided a wealth of information on how organisms work and on the functional significance of different structures. The key goals of research in functional morphology can be summarized as follows: 1) to gain a precise understanding of the interrelations between structure and function (Gans, 1974); 2) to analyze differences in structure and function among species in relation to environmental variables (e.g., Gans, 1974; Stanley, 1970); 3) to document evolutionary transformations of both structure and function within monophyletic clades (Lauder, 1981); and 4) to provide an explanation for the diversity of forms actually observed in relation to the range of theoretically possible morphologies (Raup, 1966, 1972; Thomas, 1976).

In focusing on these goals, functional

morphologists have almost exclusively emphasized patterns of variation in structure and function among species and among higher taxonomic categories. In doing so, functional morphologists have extensively used the comparative approach to infer evolutionary pathways, a different approach from current microevolutionary theory, where the primary emphasis is in describing and modelling heritable variation within populations. If the extensive data generated by research into organismal functional morphology are to be interpreted within this framework of microevolutionary processes, then knowledge of patterns of *intraspecific* variation in functional attributes is critical. While data exist documenting patterns of character correlation and heritability for several structural complexes (for example, the Atchley et al. [1981] study on the rat skull), no study to date has quantitatively addressed patterns of variation and correlation in *functional* attributes per se. Such data are of special interest because, unlike many commonly measured morphological variables which are of uncertain functional significance, analyses of performance data (e.g., prey

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capture, locomotor ability) are likely to be directly relevant to evolutionary fitness.

Our goal in this paper is to provide a quantitative analysis of patterns of intraspecific and interspecific variation in functional attributes of the feeding mechanism in ambystomatid salamanders and to relate observed patterns of variation and character correlation to evolutionary (phylogenetic) patterns in the vertebrate skull. We utilize high-speed cinematography to investigate the process of prey capture, and we partition the phenotypic variance in six functional aspects of the feeding mechanism into interspecific, intraspecific, and within-individual components. This partitioning allows an assessment of patterns of variation and correlation in attributes often used in analyses of the functional morphology of prey capture in aquatic vertebrates (e.g., Lauder, 1980) and in particular allows us to focus on the extent of phenotypic variance among conspecific individuals.

MATERIALS AND METHODS

Functional Morphology

Three species of non-transforming Mexican ambystomatids were chosen to span both the phylogenetic and morphological range of variation found in the group. The Mexican ambystomatids fall into three distinct morphological groups with relatively large, medium, and small heads (Shaffer, 1984*a*); these three groups are easily distinguished morphometrically and are phylogenetically distinct (Shaffer, 1984*b*). We chose one species from each of these three morphometrically defined groups for functional analysis to maximize the potential among-species differences in feeding behavior. *Ambystoma ordinarium* represents the narrow-headed species, *A. mexicanum* the medium-headed group, and *A. dumerilii* the broad-headed form. *Ambystoma ordinarium* and *A. dumerilii* were collected in the field (see Shaffer, 1984*b*; collection localities available upon request from H.B.S.); the *A. mexicanum*

were obtained from the Indiana University axolotl colony. All animals were sexually mature adults at the time of analysis. Individuals were chosen to be as similar as possible in size within a species: *A. mexicanum* mean snout-vent length (*N* = 9) was 9.1 cm, size range was 8.6 cm to 10.5 cm; both *A. dumerilii* were 14.0 cm long; the one individual of *A. ordinarium* was 8.3 cm long.

Animals were maintained individually and filmed in 10 gallon aquaria at approximately 17°C and were fed pieces of earthworm and live fish prior to our experiments. The salamanders were trained for at least two weeks to feed under the bright lights (1,800 Watts) required for cinematography using worm pieces as prey. Filming was carried out with a Photosonics 16-1PL camera using Kodak 4X Reversal film at 200 frames/second.

Feeding trials were conducted as uniformly as possible to minimize amongtrial variance in kinematic variables. Salamanders were always filmed in lateral view, with the prey dropped from above so that it contacted the tip of the snout and induced the feeding response. All experiments described here used 1–2 cm long pieces of live worm as prey. To ensure against satiation effects, a salamander was fed no more than eight prey items per day, and at least three days elapsed between feeding sessions. Filming continued until we recorded ten successful prey captures for each individual, where our only criterion for rejecting a sequence was either that the subject moved substantially (more than 10°) out of the lateral plane of view, or that its head contacted another object in the aquarium, possibly impeding movement.

Twenty additional sequences were filmed of *A. dumerilii* (2 individuals, ten feedings each) using an artificial stimulus to elicit feeding. By lightly touching the tip of the snout with a probe, a complete sequence of prey capture movements is obtained. These experiments were conducted to assess the degree of stereotypy in kinematic parameters by comparing

probe "feedings" to feeding on worm pieces.

Films were projected frame by frame onto a Houston instruments Hipad digitizer (50 μm accuracy), and the distances and angles were digitized. Six kinematic variables were measured from each feeding sequence. Three of these (shown in Fig. 1) are distances and angles achieved by the head during feeding: 1) maximum head angle, the maximum angle achieved during a feeding sequence measured as the angle between the long axis of the body (two distant points were chosen along the back) and the dorsal margin of the skull; 2) maximum hyoid depression, taken from the dorsal surface of the head to the ventral-most extension of the hyoid; and 3) maximum gape, measured as the largest distance achieved between the tips of the upper and lower jaws. The remaining three variables reflected the time taken for the head to achieve various positions during feeding; 4) time to maximum gape, measured as the time from the onset of mouth opening to peak gape; 5) time to maximum hyoid depression, measured as the time from the onset of mouth opening to peak hyoid depression; and 6) total gape cycle, measured as the time taken for the jaws to open and close completely. Times are accurate to within 5 milliseconds (the time between frames at 200 frames/sec). Taken together, this set of variables summarizes the determinants of the size of prey that can be ingested, as well as the essential movements involved in creating mouth cavity volume changes and thus flow into the mouth. Head width (at the angle of the jaw) was measured from the living, anaesthetized specimens several days before the first filming experiment.

Statistical Analysis

To partition the total phenotypic variance in each kinematic variable into "among-species," "among-individuals within-species," and "among-trials within-individuals" components, each variable was subjected to a one-way nested analysis of variance. The statistical model for this analysis may be written as:

$$Y(ijk) = a(i) + b(ij) + c(ijk)$$

where $a(i)$ is the difference among species means ($N = 3$), $b(ij)$ is the variance among individuals nested within species ($N = 12$), and $c(ijk)$ is the variance among trials nested within individuals ($N = 121$). Inter-individual variability in feeding behavior could not be assessed for *A. ordinarium* because only one individual was available. Because species were chosen to span the range of head morphologies in ambystomatids, *a* is a fixed effect, while the other two are random effects in the ANOVA model. Variance components were estimated using the SAS Nested procedure (SAS, 1982). Because of the unbalanced nature of the design (primarily at the individual level), reconstructed denominator mean squares and degrees of freedom were calculated for species/individuals *F*-ratios (Sokal and Rohlf, 1969). While this yields only an approximate *F*-test of significance, the design was sufficiently balanced that the reconstructed mean squares were extremely similar to values for a balanced design, suggesting that the effect of the unbalance is not severe. Differences among species mean values were calculated using Duncan's Multiple Range Test (SAS, 1982) with $P \le 0.05$ significance levels.

To test for differences between food types (worms vs artificial probes) and between individuals of *A. dumerilii*, the data were treated as a two-way factorial analysis of variance. The design was balanced with ten replicates per cell, and the two main effects (prey and individuals) and the prey × individual interaction term were tested using the SAS General Linear Model procedure.

Pearson product-moment correlations among all six kinematic variables were computed (SAS, 1982) for the nine *A. mexicanum* separately. We then averaged the resultant nine matrices to arrive at a mean within-species correlation. No
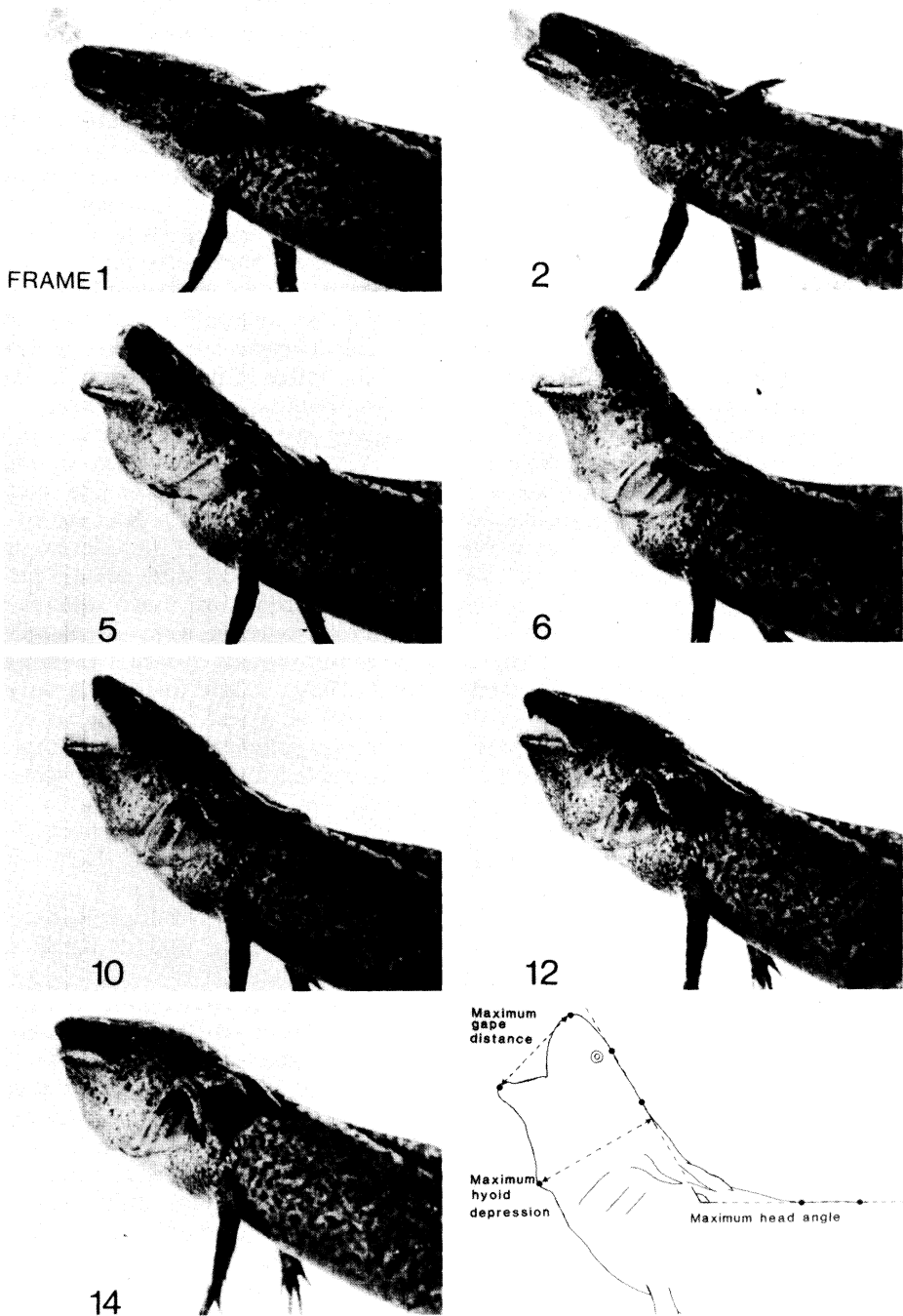
FIG. 1. Seven frames from a high-speed film (200 frames/second) of prey capture in *Ambystoma mexicanum*. The time between successive frames is 5 milliseconds. The prey, a small piece of worm, is only visible in frames 1 and 2, where it is just entering the mouth. Note the elevation of the head as the mouth opens, and depression of the hyoid as the mouth closes. The diagram in the lower right is a key to the three distance and angle variables measured from each feeding sequence. Three variables related to the timing of head movements were also measured.

TABLE 1. Mean correlations of six kinematic variables for nine individual *A. mexicanum*. Head width (column 7) represents the correlations for *A. mexicanum* individuals with the mean of each variable. Ranges of the correlations for the six variables are given in parentheses. Column 8 gives the correlations of individual means for all three species studied (see text).

	1	2	3	4	5	6	7	8
Cranial elevation (1)	1	0.08 (−0.61, 0.52)	0.33 (−0.26, 0.77)	0.23 (−0.40, 0.61)	−0.05 (−0.58, 0.43)	0.28 (−0.21, 0.77)	0.21	0.60
Maximum hyoid depression (2)		1	0.13 (−0.38, 0.69)	−0.01 (−0.59, 0.71)	0.09 (−0.23, 0.47)	0.17 (−0.31, 0.83)	0.60	0.96
Maximum gape distance (3)			1	0.46 (0.01, 0.80)	−0.28 (−0.57, 0.13)	0.60 (0.16, 0.89)	0.42	0.84
Time to maximum gape (4)				1	0.26 (−0.32, 0.75)	0.78 (0.59, 0.94)	0.63	0.69
Time to maximum hyoid depression (5)					1	0.25 (−0.27, 0.57)	0.62	0.73
Time of total gape cycle (6)						1	0.54	0.54
Head width (7)							1	—

weightings of these individual correlations were necessary since sample sizes are equal (one individual had eleven observations, the others had ten). To examine size effects, the means of all kinematic variables were computed for each individual and correlated with head width; this analysis was conducted both within *A. mexicanum* ($N = 9$ individuals) and among all three species ($N = 12$ individuals).

RESULTS

Character Correlations

The six variables we studied are generally not highly correlated with each other or with head width within *A. mexicanum*. In Table 1 we present the mean correlation matrix of all kinematic variables plus head width for *A. mexicanum*. Values range from −0.28 to 0.78, but most are in the −0.2 to 0.3 range. Among kinematic variables, the two large correlations (maximum gape distance, total gape cycle time = 0.60; time to maximum gape, time of total gape cycle = 0.78) suggest that these variables are at least partly functionally coupled. However, even for the largest case, only about half of the phenotypic variance is explained by the pairwise correlation. The correlations are notable for their interindividual variation (Table 1: ranges), and large differences were found between individuals for most variables. Correlations between kinematic variables and head width within *A. mexicanum* are moderate (0.21 to 0.63) and are not statistically significant, although the test is based on only nine observations. When *A. dumerilii* and *A. ordinarium* are added to this analysis, greatly increasing the range of head widths, the correlations of kinematic mean values with head width increased substantially (0.54 to 0.96).

Variance Components of Kinematic Parameters

The six variables span a complete range of response patterns, from the highly stereotyped, interspecifically heterogeneous maximum hyoid depression to cranial

TABLE 2. Patterns of variation in the feeding mechanism of ambystomatid salamanders.

	% of total variance		
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Kinematic parameter	Among species	Among individuals within species	Among trials within individuals
Cranial elevation (angle, in degrees)	22	15**	63
Maximum hyoid depression (distance, in cm)	90**	6**	4
Maximum gape (distance, in cm)	63**	16**	21
Time to maximum gape (in milliseconds)	39*	19**	42
Time to maximum hyoid depression (in milliseconds)	69**	15**	16
Total gape cycle (time, in milliseconds)	38*	18**	44

** Significant at the 0.01 level.
* Significant at the 0.05 level.

elevation, with only slight differences among species (Table 2). With the exception of the distance of maximum hyoid depression, most characters show a high level of variation among trials. Because of the nature of our experimental design, the among-trial component includes both real intra-individual variation in feeding performance and experimental error variance (i.e., measurement error, differences in filming orientation). Such error variance may partly account for the high among-trial components in the angular measurement (63% of the total variance; Table 2), since it involves measurement of less well defined points on the head. However, two of the three temporal measurements, which should involve the least true measurement error, also have relatively large among-trial variance components (Table 2). We analyzed measurement error in three variables (maximum head angle, maximum hyoid depression, and peak gape distance) by remeasuring two sequences at one- and eight-day intervals. The range of variation over three measurements was from 0.4% (head elevation angle) to 4.3% (peak gape distance) of the mean. Thus the measurement error is low. (Of course, other sources of experimental error such as slight differences in filming orientation might account for some of the among-trial variance.)

At the level of differences among individuals within species, only *Ambystoma dumerilii* and *A. mexicanum* enter into the analysis, since only a single spec-imen of *A. ordinarium* was available for study. There is striking uniformity among the variance components of all six variables, ranging from 6–30% of the total variance for each variable; if maximum hyoid depression is not considered, the range is from 15–30% (Table 2). In every case, these differences among individuals represent a highly significant (at the 0.01 level) fraction of the total variance, indicating that large, consistently measurable differences exist among conspecific individuals for all variables.

Variance among species means covers the widest range of variation (22–90% of the total variance), and may be broadly categorized into three response types. Maximum hyoid depression, maximum gape, and time to maximum hyoid depression all have large, highly significant differences among species means (Table 2). These differences are primarily due to the large differences between *A. dumerilii* and the other two species (Table 3) which are indistinguishable. Time to maximum gape and total gape cycle time show an intermediate pattern, with about a third of their total variance attributable to among-species differences (Table 2). Again, these differences are due to the slow feeding responses of the large-headed *A. dumerilii* (Table 3) relative to the fastest species.

The angular measurement shows no detectable difference among species means. The value for cranial elevation approaches significance ($0.05 < P < 0.10$) and accounts for 22% of the total

TABLE 3. Mean (one standard error) for seven kinematic variables* of the feeding mechanism in three species of *Ambystoma*.

Kinematic parameter	A. dumerilii (N = 20)	A. mexicanum (N = 91)	A. ordinarium (N = 10)
Cranial elevation (angle, in degrees)	45.5 (2.2)	32.6 (1.3)	38.1 (3.7)
Maximum hyoid depression (distance, in cm)	2.8 (0.05)	1.9 (0.02)	1.8 (0.02)
Maximum gape (distance, in cm)	2.1 (0.09)	1.5 (0.02)	1.2 (0.04)
Time to maximum gape (in milliseconds)	46.7 (2.6)	33.8 (0.78)	38.0 (1.7)
Time to maximum hyoid depression (in milliseconds)	52.5 (3.7)	28.2 (0.64)	38.0 (2.0)
Total gape cycle (time, in milliseconds)	88.0 (3.5)	69.7 (1.2)	73.0 (2.6)

* Means not significantly different from each other at the $P < 0.05$ level are connected by underlining.

variance. We note that the correlations between the kinematic variables and head width are often large when measured across species (Table 1), and those variables showing the greatest among-species variance components also are most highly correlated with variance in head width.

Variation Among Individuals in Feeding Stimuli

Testing for differences in the effect of prey versus the artificial feeding stimulus in two individuals of *A. dumerilii*, using a two-way ANOVA, again shows a complex pattern of effects. Four of the six variables measured are highly significantly different between the two individuals (Table 4), while the other two were not significantly different. Four of the six variables differed across food types, although in most cases these differences were not as striking as those between individuals. However, the two main effects show very different patterns of variation such that no variable shows non-significant levels of variation for both individual and food effects.

The greatest levels of variation are associated with the food × individual interaction term, where four variables show significant effects (Table 4).

DISCUSSION

Any research program designed to elucidate evolutionary patterns in a complex system should at least include an assessment of phenotypic correlations among

variables of interest and a quantitative assessment of variation within and among species. Without such data, conclusions regarding evolutionary patterns are suspect because of 1) possible (unrecognized) correlations among variables previously thought to be independent, and 2) high levels of intraspecific variation that may render supposed differences between species non-significant. Evolutionary and functional analyses of vertebrate feeding mechanisms have virtually ignored variation among individuals, presumably because it was assumed either 1) that such differences could not be quantified with the techniques currently available, or 2) that the behavioral plasticity in feeding response shown by individuals over repeated feeding trials would swamp out any statistically detectable differences among individuals. Thus, in virtually all published studies of feeding mechanics, either single individuals are considered representative of a species, or the mean response for several individuals is considered the appropriate summary statistic for a species.

However, the major conclusion to emerge from this analysis of patterns of variation in the kinematics of prey capture is that, for all six variables, a large proportion of the total variance is attributable to differences among individuals within species. Variation among individuals within a species was always significant at $P \leq 0.01$, even given the large levels of intra-individual variation. The

two relatively high mean correlations between total gape cycle time and time to maximum gape (0.78) and total gape cycle time with maximum gape distance (0.60) within *A. mexicanum* (Table 1) suggest that these sets of variables may not be independent, and therefore should not be considered as separate. However, the mean correlations of the remaining variables with each other and with head width are surprisingly low within *A. mexicanum* (Table 1), confirming that these kinematic variables are functionally independent. In addition, the large range of variation in correlation coefficients among the individuals studied again suggests that the species mean should not be the only parameter of interest to functional morphologists, and that the variance among individuals in functional character correlations can be extensive (Table 1).

The finding of large differences among conspecifics in kinematic response variables is further strengthened by the results of the second series of experiments designed to explore different responses of individual *A. dumerilii* to different feeding situations (Table 4). Although only two similarly sized individuals were tested, we still detected significant differences between these individuals for four of the six variables. Perhaps more importantly, there were significant food × individual interaction terms for four of the six variables, again emphasizing that different individuals responded differentially to the two prey stimuli. The results thus indicate that even with all the possible sources of error involved in measuring variables of the type used here, significant differences between individuals are easily detected and quantified.

The approach taken here to the analysis of patterns of variation in the feeding mechanism provides new insights into the evolution of stereotyped behaviors. Functional morphologists interested in the control of rapid movement have noted that in many cases feeding behavior appears to be quite stereotyped (Hiiemae, 1978; Liem, 1978) without provid-

TABLE 4.   Two-way ANOVA comparing the effects of worm prey versus an artificial feeding stimulus on two individuals of *Ambystoma dumerilii*.

Source	Sum of squres	Mean square	F-value	PR > F
Cranial elevation (degrees)				
Ind.	26.2	26.2	0.32	0.57
Food	1,040.5	1,040.5	12.9	0.001
Ind. × food	229.0	229.0	2.8	0.10
Error	2,663.1	80.7		
Maximum hyoid depression				
Ind.	0.056	0.056	1.93	0.17
Food	0.150	0.150	5.14	0.03
Ind. × food	0.583	0.583	19.96	0.0001
Error	0.964	0.029		
Maximum gape distance				
Ind.	1.05	1.05	9.64	0.004
Food	0.42	0.42	3.87	0.057
Ind. × food	0.78	0.78	7.18	0.011
Error	3.59	0.11		
Time to maximum gape				
Ind.	749.1	749.1	12.59	0.001
Food	394.3	394.3	6.63	0.01
Ind. × food	493.6	493.6	8.29	0.007
Error	1,963.9	59.5		
Time to maximum hyoid depression				
Ind.	968.9	968.9	8.98	0.005
Food	16.6	16.6	0.15	0.697
Ind. × food	2,501.8	2,501.8	23.18	0.0001
Error	3,561.4	107.9		
Time of total gape cycle				
Ind.	5,079.4	5,079.4	20.5	0.0001
Food	26.5	26.5	0.1	0.75
Ind. × food	26.5	26.5	0.1	0.75
Error	8,175.7	247.7		

ing any yardstick to define stereotypy. Our partitioning of the phenotypic variance allows the plasticity in feeding response to be considered in two parts: the extent to which individuals display stereotyped behaviors across a series of trials, and stereotypy at the "species" level by examining variation in individual means within a species. These two components may give very different insights into the notion of stereotyped responses. For example, cranial elevation shows a great deal of variation among trials within individuals (63%), suggesting that individual salamanders may strike at food in different locations by varying the amount

of head elevation. However, the overall variation among conspecific individual means in cranial elevation is considerably less (although statistically significant), suggesting relatively greater stereotypy at the species level. Other variables reflect different patterns of stereotyped response (e.g., maximum hyoid depression is stereotyped at both levels), emphasizing that individual characters must be evaluated independently. By lumping all observations into an overall species mean, such responses are obscured.

An additional and unexpected finding was the difference between variables in the proportion of the total variance attributable to differences among species. The among-species level accounted for 22% of the variance in cranial elevation, indicating that only very slight differences could be measured between these three anatomically distinct species. On the other hand, 90% of the variance in maximum hyoid depression and 69% of the variance in the time to achieve it are accounted for at the species level. The hyoid variables thus provide the best discrimination between the three species studied and show the least variation within species. Some of the kinematic variables (maximum hyoid depression, maximum gape distance) are relatively highly correlated with head width across all species, suggesting that the differences among species are at least partially a function of differentiation in adult head size.

These results are significant for interpretations of the evolution of the vertebrate skull proposed previously (Lauder, 1980, 1985). It is noteworthy that the variable showing the greatest between-species differences (and the one most stereotyped within species) has been identified by previous research involving functional morphology of aquatic prey capture as the dominant component of the suction feeding mechanism. The hyoid apparatus of lower vertebrates has retained the most conservative functional role in the feeding mechanism of all components of the skull. In all major lower vertebrate clades for which either anatomical or functional data are available (elasmobranchs, ray-finned fishes, coelacanths, lungfishes, and salamanders), the hyoid functions as a crucial link in a mechanism mediating mouth opening. Hyoid depression also produces a larger change in mouth cavity volume than any other head movement and is the major system lowering mouth cavity pressure during feeding. Thus, the phylogenetically most conservative functional component of the lower vertebrate skull is precisely that system identified here as the most different between species, and yet the most stereotyped within species. In addition, the high among-species variance in maximum hyoid depression indicates that there may be significant differences in the performance of these ambystomatid species in suction feeding. The high among-species correlation between maximum hyoid depression and head width (0.96; Table 1) suggests that the differentiation among species is mechanically related to differences in head sizes of mature salamanders.

We emphasize that the correlations and patterns of variation addressed in this study have been phenotypic ones; to fully interpret these patterns, data on both the heritabilities and genetic correlations of the kinematic variables are necessary (Lande, 1979; Atchley et al., 1981; Lande and Arnold, 1983). Unfortunately, such genetic data are currently not available for any species, precluding even a rough estimate of the possible amounts of environmental and genetic variance in these characters. However, the demonstration of individual variation in kinematic parameters at least admits the possibility of genetically-based variation, and our future work with *Ambystoma* using half-sib and full-sib breeding designs will further address this issue.

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