Morphological variation and cannibalism in a larval salamander (Ambystoma macrodactylum columbianum)

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We document morphological variation and its association with larval cannibalism in a population of long-toed salamanders, Ambystoma macrodactylum columbianum. Larvae observed in a natural pond engaged in cannibalism. Additionally, these larvae possessed significantly longer and wider heads, as well as larger vomerine teeth, than did conspecifics of the same size reared in the laboratory for 1 month after capture. This variation in trophic structures is consistent with the characteristics of “cannibal” morphs that have been documented for larvae of another salamander species. We extend current knowledge of the development of this morphology by using multivariate statistical analysis to examine, further, a possible basis for this variation in head shape. Principal component analysis indicated that after the removal of the effects of body size, variation in the distance between the eyes (interocular width) accounted for most of the remaining total overall variation in head shape. Multivariate ontogenetic trajectories of head shape, constructed from linear regressions of principal components (measures of size and shape), were equivalent for the two larval samples. These statistical analyses indicate that this trophic polymorphism is not due to differences in either the rate of change in head shape relative to overall size or the size at which the divergence in head shape begins. Rather, morphological variation in larval A. m. columbianum may be due to fluctuations in the presence of key, influential environmental factors, as has been demonstrated for other larval amphibians that exhibit trophic polymorphism.

Introduction

Phenotypic plasticity is the ability of a genotype to produce variable phenotypes in response to fluctuating environmental conditions (Bradyshaw 1965). Although all such responses are not necessarily adaptive (Smith-Gill 1983), phenotypic plasticity is frequently regarded as an “optimal” response to environmental heterogeneity (e.g., Pfennig 1990 and references therein). Indeed, in a diverse array of organisms, phenotypes appear to vary, in an adaptive fashion, with corresponding fluctuations in the environment (see reviews in Bradyshaw 1965; Schlichting 1986; Stearns 1989). Some of the numerous examples include continuous variation in reproductive investment (and other life-history attributes) in response to environmental uncertainty (e.g., Capinera 1979; Crump 1981, 1984; Kaplan and Cooper 1984; Kaitala 1991; Landa 1992) and plasticity in reproductive behavior (e.g., Austad 1984; Dominey 1984; see Moran 1992 for a review of other examples). Additionally, herbivores and predators may induce morphological, chemical, and (or) life-history changes as a form of defense in plants and algae (e.g., Lubchenco 1980; Schultz 1988; Van Alstyne 1988), protozoans (Wicklow 1988), numerous invertebrates (e.g., Harvell 1984, 1992; Lively 1986; Crowl and Covich 1990; Parijko and Dodson 1991; Riessen 1992; Spitz 1992; see also reviews by Dodson 1989; Harvell 1990), and some fish (Reznick et al. 1990; Brönmark and Miner 1992).

Conversely, predators may express phenotypic variation in response to their food resources. Diet-induced morphological plasticity is exemplified by herbivorous insects (Bernays 1986; Greene 1989; Thompson 1992) and a variety of fishes, such as some cichlids (Meyer 1987, 1989, 1990; Wimberger 1991, 1992) and sunfish (Ehlinger and Wilson 1988; Wainwright et al. 1991; Mittelbach et al. 1992). When alternative morphs of such polymorphic populations occupy different trophic levels at some stage of the life cycle, the population exhibits trophic polymorphism (Pedersen 1991). In some such popula-

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tions, individuals of one alternative morphology are preferentially cannibalistic and (or) consume other macroscopic prey. Such morphological specialization characterizes some ciliated protozoans, slime molds, and rotifers (reviewed in Gilbert 1980; Wadell 1992), as well as the larvae of at least two amphibians (reviewed in Simon 1984; Polis and Myers 1985; Pfennig 1989; Crump 1992).

Knowledge of alternative larval morphologies in amphibians, in which one morph is cannibalistic, has been limited to tadpoles of some species of spadefoot toads (Pelobatidae: Spea = Scaphiopus; Pomeroy 1981; Pfennig 1989, 1990, 1992a, 1992b; Pfennig et al. 1991b) and to the larvae of some populations of tiger salamanders (Ambystomatidae: Ambystoma tigrinum mavoritum; A. t. nebulosum, and A. t. tigrinum; Powers 1903, 1907; Rose and Armentrout 1976; Collins et al. 1980; Collins 1981; Collins and Cheek 1983; Pierce et al. 1983; Lannoo and Bachmann 1984; Holomuzki 1986; Pfennig et al. 1991a; Reilly et al. 1992). In the A. tigrinum complex, cannibals are distinguishable from larvae expressing the more typical morphology (“typical” morphs) because of their larger body size, broader heads, and hypertrophied vomer bones and vomerine teeth, as well as their divergent tooth morphology (Pedersen 1991; see also above references). In this paper, we document previously undescribed alternative larval morphologies, and their association with cannibalism, in another amphibian, the eastern long-toed salamander (Ambystoma macrodactylum columbianum). This polymorphism conforms to the morphological criteria of cannibal and typical morphs in A. tigrinum.

We examine patterns of multivariate variation in larval morphology in A. m. columbianum. We extend current knowledge of the development of alternative larval morphologies in amphibians by using a multivariate statistical technique (Tissot 1988a, 1988b) that facilitates inspection of a possible developmental basis for this morphological divergence. Specifically, we construct “ontogenetic” trajectories (paths depicting the development of a morphological character; Alberch et al. 1979) for both morphs to evaluate whether this variation in morphological development is a consequence of differences in key components of their developmental pathways.

Materials and methods

Natural history of A. m. columbianum and description of the study site

The long-toed salamander, A. macrodactylum, is a polytypic species consisting of five known subspecies (Ferguson 1961). This species is widespread throughout the Pacific Northwest of the United States and Canada, from the Sierra Nevada Range in California, north to southeastern Alaska, and east to southwestern Alberta and western Montana (Ferguson 1961). Additionally, there is a disjunct population (A. m. croceum) located in coastal central California (Russell and Anderson 1956). In Oregon, A. m. columbianum is distributed east of the crest of the Cascade Range (Ferguson 1961).

We studied larvae of A. m. columbianum from a high-altitude (1951 m) ephemeral pond located 24.2 km south of Sisters, Deschutes County, Oregon. This shallow pond (maximum depth 0.60 m during summer) contains a substrate of mud and lava rock and lacks aquatic macrophytes. The pond fills in late autumn with the onset of seasonal rains and, secondly, by runoff from snowmelt in late April, May, or June. At this site, snowmelt triggers the synchronous breeding of the Cascades frog (Rana cascadae), the Pacific treefrog (Hyyla regilla), and A. m. columbianum. Adults of the latter species breed explosively on 1 or 2 nights, adhering their eggs singly, usually in large groups, to the underside of submerged rocks (S. Walls, personal observation). Larvae hatch within 3 weeks and have been observed feeding on hatching tadpoles (H. regilla) prior to the “typical” feeding stage (stage 46; Harrison 1969) described for larval Ambystoma (S. Walls, personal observation). Snowmelt also triggers a bloom of zooplankton (Copepoda) and fairy shrimp (Anostraca), which persists for a maximum of 2 months. The pond typically dries completely by late September.

Behavioral observations in nature

On 22 July and 25 August 1991 we observed and collected larvae of A. m. columbianum. Based on visual counts of larvae taken on 22 July, we estimated that the density of larval Ambystoma averaged 10/m². We visually surveyed the pond and observed the presence of tadpoles (H. regilla and R. cascadae), aquatic insects (adult corixids and larval dytiscids), and fairy shrimp as potential prey; no microcrustaceans were visible. From 17:30 to 19:30 on 22 July we casually observed one successful act of cannibalism in the natural pond, several acts of aggression (i.e., lunges (unsuccessful attempts at biting) and movement toward another larva; Walls and Semlitsch 1991) by larger A. m. columbianum toward smaller conspecifics, as well as several attempts by large individuals to capture tadpoles. From 16:30 to 18:30 on 25 August we observed a second act of cannibalism in the pond.

Collections and maintenance of salamanders

On 22 July we collected 70 larvae with dip nets and transported them to the laboratory in 19-L buckets filled with 9.5 L of pond water. In the laboratory we initially placed larvae of similar size in 38-L aquaria containing 19 L of water (20 larvae per aquarium). After 2–3 days, 6 out of 20 larvae (30%) of the largest size class had disappeared from one aquarium, presumably because of cannibalism by their similar-sized conspecifics. We therefore isolated larvae individually into 9.3 × 9.3 × 6.2 cm opaque plastic containers containing 400 mL of dechlorinated water to minimize the loss of experimental animals. We fed larvae live Tubifex ad libitum and maintained them under a 15 h light : 9 h dark photoperiod at an air temperature of 15°C for 1 month. Each individual was transferred to a clean chamber containing fresh dechlorinated water every 7–10 days. Our maintenance protocol was in accordance with guidelines set by the Canadian Council on Animal Care (1984).

On 25 August we collected 80 additional larvae from the same pond for morphological comparisons with those kept in the laboratory for 1 month. These larvae were collected and maintained in the manner previously described.

Morphometric comparisons

On 27 August we randomly selected 60 larvae, 30 of which had been maintained under laboratory conditions and 30 of which had been recently collected from their natural pond. The larvae were killed by over-anesthesia with Chlorotene, after which the following measurements (Fig. 1) were taken for each individual, using handheld dial calipers (0.05 mm precision): (1) snout—vent length: distance from the anterior tip of the snout to the posterior margin of the vent; (2) head width at gills: distance across the dorsal side of the head at the anterior attachment of the first pair of gills; (3) head width at eyes: dorsal head width as measured through the pupils of the eyes; (4) head width at jaws: width of the head, measured on the ventral surface, at the posterior margins of the mandible; this measurement coincides with the ventral articulations of the quadrate and articular bones (Duellman and Trueb 1986), which were visibly more pronounced in larvae recently taken from the pond than in those reared in the laboratory; (5) head length: distance from the anterior attachment of the first pair of gills to the tip of the snout, measured medially on the dorsal surface; (6) interocular width: distance between the medial margins of the eyes. We based the choice of measurements for analysis on previous reports of characteristics that differentiate cannibalistic and typical morphs in A. tigrinum and Scaphiopus (e.g., Pierce et al. 1983; Pfennig 1989; Lannoo et al. 1989).

After these measurements were taken, specimens were preserved in 10% neutral buffered formalin, then washed and stored in 65% ethanol. All specimens examined were deposited in the Vertebrate Museum, Department of Zoology, Oregon State University, Corvallis.
Statistical analyses

Absolute differences between samples were analyzed using Student's t tests after testing for departures from the parametric assumptions of univariate normality and homoscedasticity (Sokal and Rohlf 1981). Separate t tests were conducted on six different response variables, many of which were highly correlated with each other. To control for an overall experimentwise, Type I error rate of 0.05, we utilized a Bonferroni-adjusted significance level of $\alpha = 0.0083$ (Snedecor and Cochran 1980; Miller 1981).

Additional variation between and within samples was examined in the following manner. First, the raw data were log-transformed to remove potential scale effects, unequal variances, and nonlinearity (Sokal and Rohlf 1981; Tissot 1988). Multigroup discriminant analysis was then performed using the program B-stat (R.A. Pimentel and J.D. Smith 1985, Sigma Soft, Placentia, Calif.) to test for departures from the multivariate assumptions of normality and homoscedasticity. Although our data conformed to the assumption of normality, there were significant differences in the variance-covariance matrices ($F = 1.959$; df = 21, 12,372; $P = 0.00543$). Because symmetry in the variance-covariance matrices is an assumption of multigroup discriminant analysis, we chose to examine patterns of within-sample variation using multigroup principal component analysis (PCA) (Pimentel 1979).

The PCA used was an R-mode analysis (Pimentel 1979) of the log-transformed variance-covariance matrix derived from samples of 30 laboratory-reared and 30 field-caught larvae. To examine variation within samples, principal components were derived from pooled within-group dispersion (i.e., pooled correlation matrix) (Tissot 1984). Examination for deviations from isometry (i.e., allometric growth) was conducted by correlations of PCA eigenvectors with an isometric vector. High correlations with an isometric vector denote proportionally equal increases in the size of all measured variables (Pimentel 1979).

Multivariate measures of size and shape, derived from the within-group PCA, were used to describe ontogenetic trajectories (sensu Alberch et al. 1979) in the development of larval head shape; such trajectories represent a path that depicts the development of a morphological trait (Tissot 1988a). We calculated ontogenetic trajectories using Tissot's (1988a, 1988b) method of regressing first-axis principal-component scores (a measure of size) against second-, third-, and fourth-axis principal-component scores (measures of shape). Analysis of covariance (ANCOVA) was performed to test for differences in the slopes and intercepts of linear regressions. We used trajectories and ANCOVA to test the hypothesis that there is a developmental basis for the observed morphological variation in A. m. columbianum. For example, differences between larval samples in their rates of change in shape relative to size may be indicated by significant differences in the slopes of their regression lines (Tissot 1988a). Likewise, significant differences in the intercepts of regression equations may indicate differences in the size at onset of development of head shape (Tissot 1988a).

Results

After 1 month of isolation and provision of food ad libitum in the laboratory, larvae collected on 22 July exhibited qualitative differences in head shape, body width, limb girth, and gill size, compared with larvae of similar snout—vent length taken from the pond on 25 August (Fig. 2). Subsequent dissection of the buccal regions of the two representative larvae shown
Fig. 2. Comparison of the head shapes and sizes of two larval *A. m. columbianum* from the same pond. The "cannibal" morph (A) was photographed within 48 h of collection from its natural pond. The "typical" morph (B) was photographed at the same time but 1 month after isolation from conspecifics in the laboratory. Note the broader head of the cannibalistic morph, as well as its reduced gills and narrower trunk and limbs (see Powers (1907) for comparison with *A. tigrinum*). Snout-vent lengths of the cannibalistic and typical morphs were 29.6 and 31.3 mm, respectively.

Table 1. Comparisons of six morphological variables for "cannibal" (field-collected) and "typical" (laboratory-reared) larvae of *Ambystoma macrodactylum columbianum*

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cannibal morph</th>
<th>Typical morph</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout-vent length</td>
<td>30  33.92 ± 4.98</td>
<td>34.24 ± 2.24</td>
<td>-0.32</td>
<td>0.37</td>
</tr>
<tr>
<td>Head width at gills</td>
<td>30  9.08 ± 1.16</td>
<td>8.27 ± 0.57</td>
<td>3.42</td>
<td>0.0006*</td>
</tr>
<tr>
<td>Head width at eyes</td>
<td>30  9.22 ± 1.26</td>
<td>7.68 ± 0.67</td>
<td>5.90</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Head width at jaws</td>
<td>30  9.33 ± 1.30</td>
<td>7.84 ± 0.58</td>
<td>5.73</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Head length</td>
<td>30  13.36 ± 1.73</td>
<td>11.82 ± 0.86</td>
<td>4.39</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Interocular width</td>
<td>30  3.75 ± 0.62</td>
<td>3.36 ± 0.26</td>
<td>3.24</td>
<td>&lt;0.0009*</td>
</tr>
</tbody>
</table>

Note: n, sample size of larvae measured; \( \bar{x} \), sample mean (mm); SD, 1 standard deviation of the mean; t, statistic for Student's *t* test (df = 58); P, level of significance (two-tailed). *, significant at \( \alpha = 0.0083 \).

in Fig. 2 revealed that the broad-headed morph (Fig. 2A) possessed enlarged vomerine teeth, a feature that was lacking in narrow-headed conspecifics (Fig. 3). A broad head, hypertrophied vomerine teeth, a more slender trunk and limbs, and reduced gills are distinguishing morphological features of cannibalistic larvae of *A. tigrinum* (Powers 1907). Because we observed broad-headed larvae engaged in cannibalistic behavior, we follow Collins and Cheek's (1983) terminology to designate the larval morphology shown in Figs. 2A and 3A as "cannibal" and that in Figs. 2B and 3B as "typical". Henceforth we use "cannibal" to describe an individual belonging to the class of larvae consisting of structural (morphological) cannibals, of which at least some representatives were known behavioral cannibals as well.

**Variation between samples**

Snout-vent lengths were not significantly different between larvae recently taken from the pond and those reared in the laboratory for 1 month (Table 1). We were therefore able to compare directly absolute values of measurements on these
two groups of larvae (see Pierce et al. (1983) and Pfennig (1989) for problems with differences in body size). In making these comparisons we assume that larval salamanders collected from the pond on both dates were an unbiased representation of the population.

Examination of overall head shape and size revealed that larvae of the two alternative forms differed significantly with respect to five morphological features. Cannibals possessed significantly wider heads than did typical larvae, as indicated by measurements taken at the gills, eyes, and posterior margins of the jaws (Table 1). Additionally, cannibals had significantly longer heads and a greater interocular width than did larvae with the typical morphology (Table 1).

**Variation with samples: multivariate analyses**

The results of PCA on the pooled dispersion of the two samples indicate that four components describe most (97%) of the total variation among variables (Table 2). The first principal component described 85% of the total variation. As illustrated by the highly positive eigenvector loadings for all six traits, the first principal component (PC1) described variation in size. A high correlation between the eigenvector for PC1 and an isometric vector \( r = 0.997 \) indicates that larval size is largely isometric, i.e., all traits increase in similar proportions to one another. In contrast, correlations of an isometric vector with eigenvectors for PC2, PC3, and PC4 were all low \( r < 0.05 \), indicating allometric variation in the remaining axes.

The second principal component (PC2) described 6% of the total variation. Eigenvector loadings indicated that this axis largely accounted for variation in the distance between the eyes (interocular width). The large negative loading for this trait indicates variation in head shape that is due to a decrease in interocular width. Approximately 3.5% of the total variation was attributable to the third principal component (PC3). Eigenvector loadings for PC3 (Table 2) indicated that this axis explained variation in head length. As indicated by the positive loading for this trait, variation in head shape results from an increase in head length. The fourth principal component (PC4) accounted for only 2% of the total variation, and contrasted variation in larval head width at the gills versus snout—vent length and head width at the jaws. The eigenvector loadings for this component revealed that head width at the jaws decreases with decreasing snout—vent length, whereas head width at the gills increases (Table 2).

**Multivariate ontogenetic trajectories**

Ontogenetic trajectories depicting changes in head shape relative to size are shown in Fig. 4. For field-collected and laboratory-reared larvae, interocular width (PC2) and head length (PC3) both decreased significantly with increasing overall larval size (PC1) (Figs. 4A–4D, Table 3). Conversely, changes in snout—vent length and head width at the jaws and gills (PC4) increased proportionately with increasing overall size (PC1) for larval samples from both the field and the laboratory, although not significantly in the latter (Figs. 4E and 4F, Table 3).

Analysis of covariance indicated that there were no significant differences between trajectory slopes for field and labora-
**Table 2. Variation within samples of larval Ambystoma macrourum columbianum: principal components, their correlations, and their percent variation**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Eigenvector Component</th>
<th>Component correlation</th>
<th>Percent variation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2</td>
<td>PC3</td>
</tr>
<tr>
<td>Snout-vent length</td>
<td>0.414</td>
<td>0.116</td>
<td>0.312</td>
</tr>
<tr>
<td>Head width at gills</td>
<td>0.363</td>
<td>0.237</td>
<td>-0.376</td>
</tr>
<tr>
<td>Head width at eyes</td>
<td>0.423</td>
<td>0.372</td>
<td>-0.205</td>
</tr>
<tr>
<td>Head width at jaws</td>
<td>0.417</td>
<td>0.160</td>
<td>-0.331</td>
</tr>
<tr>
<td>Head length</td>
<td>0.370</td>
<td>0.101</td>
<td>0.772</td>
</tr>
<tr>
<td>Intercocular width</td>
<td>0.455</td>
<td>-0.870</td>
<td>-0.119</td>
</tr>
</tbody>
</table>

**Table 3. Results of linear regression analysis used to determine ontogenetic trajectories**

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Slope</th>
<th>Intercept</th>
<th>$R^2$</th>
<th>$F_{(1,28)}$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field-caught larvae (n = 30)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC1 vs. PC2</td>
<td>-0.914</td>
<td>0.0013</td>
<td>0.600</td>
<td>42.06</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>PC1 vs. PC3</td>
<td>-1.367</td>
<td>0.0096</td>
<td>0.765</td>
<td>91.10</td>
<td>&lt;0.00001</td>
</tr>
<tr>
<td>PC1 vs. PC4</td>
<td>0.314</td>
<td>0.0215</td>
<td>0.298</td>
<td>11.86</td>
<td>0.0018</td>
</tr>
<tr>
<td>Laboratory-reared larvae (n = 30)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC1 vs. PC2</td>
<td>-0.606</td>
<td>0.0073</td>
<td>0.137</td>
<td>4.44</td>
<td>0.0444</td>
</tr>
<tr>
<td>PC1 vs. PC3</td>
<td>-1.100</td>
<td>0.0021</td>
<td>0.394</td>
<td>18.22</td>
<td>0.0002</td>
</tr>
<tr>
<td>PC1 vs. PC4</td>
<td>0.324</td>
<td>-0.0212</td>
<td>0.057</td>
<td>1.68</td>
<td>0.2049</td>
</tr>
</tbody>
</table>

**Discussion**

**Trophic polymorphism in larval Ambystoma**

We report acts of larval cannibalism, directly observed in nature and inferred from missing larvae in the laboratory, in association with morphological variation in a population of the salamander *Ambystoma m. colombianum*. Anderson (1967) observed cannibalism in larval *A. m. sigillatum*, as well as competition for food in larval *A. m. croceum*. However, for salamanders, our findings provide the first evidence of alternative trophic morphologies, possibly induced by cannibalism, outside of the *A. tigrinum* complex. Larvae of similar body size varied significantly in the size and shape of their heads; furthermore, we observed qualitative differences in the development of their vomerine teeth, the widths of their trunks and limbs, and the sizes of their gills. These features are key morphological attributes that distinguish cannibalistic and typical morphologies in larval *A. tigrinum* (Powers 1907). It is unlikely that this morphological variation is due to ontogeny; larvae of the cannibalistic morph, from the same pond and of similar body size (and, presumably, age), showed no diminishment in head size at the time that laboratory-reared larvae did (see Anderson (1967) for relative narrowing of the head with increasing snout-vent length in larval *A. m. croceum*). Powers (1907) suggested that the reduced gills and more slender trunk and limbs of cannibalistic *A. tigrinum* was “emaciation,” due to the disproportionate allocation of energy to maintenance of the exaggerated head size and other trophic features of these larvae.

Principal component analysis on the pooled (i.e., combined field-captured and laboratory-reared samples) within-group dispersion indicated that, other than size, morphological variation within samples resulted primarily from a decrease in interocular width and secondly from an increase in head length. Additional variation resulted from a decrease in one dimension of head width (at jaws), with a contrasting increase in another (head width at the gills) as snout-vent length decreased. Although we have yet to determine the relationship of this variation in head shape with environmental factors, we hypothesize that it facilitates intra- and inter-specific predation on larger prey items in a resource-limited environment. Similarly, Pfennig (1989) suggested that the developmental reversal between omnivore and carnivore morphs in tadpoles of *Scaphiopus multiplicatus* permits morphological adjustments in response to changes in environmental conditions that influence morph survivorship.
The possible role of development in morphological variation in larval *A. m. columbianum*

One possible cause of variation in morphometric shape in polymorphic populations is either evolutionary or environmentally induced differences in development. Shape variation may result from heterochronic (evolutionary) alterations in the rate of change in shape relative to size, or in the size (or age) at which development in a morphological character begins (or ends) (Gould 1977; Alberch et al. 1979). Additionally, Blouin and Loeb (1991) postulated that variation in morphological shape may result from ecological (environmentally induced) changes in development rate (e.g., rate of growth or differentiation). For example, environmentally induced differences in the rate at which two individuals reach a given body size may determine their shape at that size (Blouin and Loeb 1991).

Thus, it is conceivable that the shape variation we document for larval *A. m. columbianum* may have resulted from differences in development. However, it is premature to speculate as to whether such possible differences are due to evolutionary or ecological processes.

To examine the possibility that head shape variation in *A. m. columbianum* may be a consequence of such developmental divergence, we used Tissot's (1988a) multivariate statistical technique of regressing first-axis principal-component scores (a measure of size) against the second-, third-, and fourth-axis principal-component scores (measures of shape). The resulting size—shape regression lines thus approximated the pathway of development in larval head shape among constituents of the two samples. Although "ontogenetic" (i.e., age) data per se were not available, this developmental pathway is otherwise analogous to Alberch et al.'s (1979) "ontogenetic trajectory."

Based upon these analyses, the rate of change in components of head shape, relative to overall size, did not differ between the field-captured and laboratory-reared larvae, as indicated by the statistically similar regression slopes of the two samples. Likewise, the size at the onset of head shape development was statistically equivalent for the two groups of larvae, as indicated by the similarities of the intercepts of their regression equations. Thus, the divergence in head shape in larval *A. m. columbianum* does not appear to be due to differences in these two developmental features.
if cannibals experience increased fitness due to faster growth or developmental rates, larger size at metamorphosis and enhanced survivorship and (or) reproduction compared with noncannibalistic individuals (Fox 1975; Polis 1981; Pomeroy 1981; Lanno et al. 1989; Pfennig 1989; Crump 1990, 1992). For some larval amphibians (e.g., Hyla pseudopoma), the attainment of a larger body size, specifically as a result of cannibalism, appears to have favored this behavior over acts of interspecific predation (Crump 1990). Furthermore, cannibalism may be beneficial as an extreme form of interference competition in which potential competitors are eliminated (Fox 1975; Polis 1981). Because competition may slow larval growth and increase the time required to reach a size sufficient for successful metamorphosis from an evaporating habitat, cannibalism and predation may alleviate the adverse effects of competition among survivors (Wilbur 1987). Indeed, even cannibalism of siblings may be favored during life-history stages in which age-specific mortality is high (Eickwort 1973). We hypothesize that the relatively brief time available for larval growth and metamorphosis in high-altitude ephemeral ponds may have served as a selective force in the evolution of the cannibalistic morph of A. m. columbiaanum.

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