

A Comparative Test of the Adaptive Plasticity Hypothesis: Relationships between Habitat and Phenotype in Anuran Larvae

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ABSTRACT: The hypothesis that phenotypic plasticity is maintained by divergent natural selection acting across different environments predicts that populations and species exposed to highly variable environments will express high levels of plasticity. I tested this prediction by measuring the behavioral and morphological responses to aeshnid dragonfly larvae of 16 tadpole species and asking whether predator-induced plasticity is greater in species that experience more variable densities of predators in nature. Tadpole phenotypes were measured in a series of similar experiments in outdoor artificial ponds carried out over a 9-yr period. I quantified tadpole habitats by soliciting evaluations by seven to 36 experienced field observers for each species. There were large differences among species in phenotype, mostly in agreement with earlier descriptions. Nearly all species responded to dragonflies by decreasing activity and body length relative to overall body size and by increasing relative tail fin depth, although the magnitude of the responses differed among species. There was a significant positive phylogenetic correlation between morphological plasticity and variability in exposure to predators, thus upholding the adaptive hypothesis. The correlation between behavioral responses and habitat variability was not significant, and there was little relationship between behavioral and morphological plasticity, raising the possibility that behavioral responses evolve under different scales of environmental variation than morphological responses.

Keywords: behavior, induced defense, morphology, phenotypic plasticity, predation risk, tadpoles.

The idea that the phenotype should be more flexible in variable environments has been discussed for decades (Klopfer and MacArthur 1960; Bradshaw 1965; Cook and

Johnson 1968; Moran 1992). It emerges as a basic prediction of adaptive models for the evolution of phenotypic plasticity, applicable at the level of populations or species. That plasticity is frequently adaptive is supported by many microevolutionary studies illustrating that it is beneficial for individuals and maintained by divergent natural selection across variable environments (Schlichting and Pigliucci 1998). But predictions of the adaptive plasticity hypothesis at higher levels, relating to the differential expression of phenotypic plasticity among populations and species, have been addressed less often and usually involve comparisons of few taxa (Cook and Johnson 1968; Day et al. 1994; Carroll and Corneli 1995; Smith and Van Buskirk 1995; Donohue et al. 2000). Tests for adaptive variation in life histories within heterogeneous environments are more frequently performed (e.g., Rabinowitz et al. 1989; Semlitsch et al. 1990; Leips et al. 2000). If adaptive plasticity evolves under selection imposed by variable environments, then populations or species that experience relatively variable conditions should exhibit greater amounts of plasticity. Here, I report a test of this prediction based on a comparative analysis of predator-induced plasticity in the morphology and behavior of anuran tadpoles.

Larval anurans satisfy the basic assumptions of the adaptive plasticity hypothesis and are therefore well suited for testing it. In many species, a suite of behavioral and morphological traits varies depending on the density of predators (McCollum and Van Buskirk 1996). Comparative analysis is possible because each of these traits can be unambiguously identified and measured across taxa; all tadpoles have the basic components of behavior and morphology that enable them to move about, gather food, and flee from predators.

Functional considerations and microevolutionary studies suggest that plasticity in amphibian behavior and morphology induced by predators is adaptive. Tadpoles decrease activity when they detect predators, and they develop relatively large and muscular tails; individuals responding in this way generally survive better or grow faster

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than would individuals that did not respond (e.g., McCollum and Van Buskirk 1996). The mechanistic bases for the performance consequences of plasticity are in some cases well understood (Azevedo-Ramos et al. 1992; Skelly 1994; Watkins 1996; Van Buskirk and McCollum 2000a). These data suggest that natural selection in the presence and absence of predators favors the evolution of predator-induced plasticity in tadpoles.

There is conspicuous variation among amphibian species in the degree to which their larvae experience variation in predator density at various scales. Some species are characteristic of ponds with stable predator composition, such as those that dry every year (and therefore contain few large predators) or those that are permanent and always have fish. Other species are typical of ponds that dry irregularly and thus are occasionally purged of predators. Tadpoles of some species occur in many kinds of ponds, while others are found within a more narrow range of habitats. It is therefore possible to classify species according to the variability in predator composition that they experience, at least at spatial and temporal scales corresponding to variation among ponds and among seasons or years. If selection for phenotypic plasticity is imposed by variation in the environment at these scales, as suggested by the selection studies, then there should be more extensive plasticity in taxa exposed to highly variable predation environments than in species occurring in constant environments.

Methods

Experiments in Artificial Ponds

The data set consists of 16 anuran species for which I measured phenotypic responses to predators and estimated habitat use to test the prediction that more extensive plasticity is associated with exposure to variable environments. The phenotypic data come from a series of experiments in outdoor artificial ponds carried out between 1992 and 2000. The experimental containers and procedures, summarized in table 1, were broadly similar for all species. In most cases, I reared tadpoles in large tanks (500–1,200 L), except for two species that occur naturally in small pools, for which I used 80-L tanks. The tanks received standard quantities of substrate material (leaf litter, pine straw, or soil), rabbit food to augment the nutrient base for primary production, and multiple aliquots of water and zooplankton from nearby ponds. These ingredients established self-sustaining seminatural pond ecosystems within the tanks (Wilbur 1997), so that tadpoles showed realistic growth, behavior, and morphology and did not have to be fed during experiments.

The experiments included between three and 24 repli-

cates of each of two treatments: dragonfly larvae (Odonata: Aeshnidae) present and absent. The chosen predator was a dragonfly rather than a fish because all of the anuran species encounter aeshnids regularly in nature, whereas several of them almost never co-occur with fish (J. Van Buskirk, unpublished data). The dragonflies were contained within small floating cages (usually 1-L volume) and were fed tadpoles of the experimental species every 2–3 d to ensure that chemical signals were produced to indicate the proximity of predators (Petranka 1989; Lefcort 1998). If tadpoles of the target species were scarce, I fed predators with a more abundant congener or with tadpoles of *Rana esculenta*. Tanks in the treatment without predators contained empty cages.

Species were included within the study on an opportunistic basis, whenever they became available. I collected eggs from crosses performed in the laboratory or from freshly laid clutches in the field. At least four different pairs of adult frogs contributed eggs to every experiment, and in most cases, I was able to include five to 10 families (table 1). The experiments began when tadpoles were 3–10 d old (stage 24–25; Gosner 1960).

The data for *Rana pipiens* came from Relyea and Werner (2000), who reared and measured tadpoles under conditions similar to those in my own experiments. Behavioral data were not available for *R. pipiens*.

Measuring Behavior and Morphology

I observed the behavior of tadpoles when they reached Gosner stages 28–32 and measured morphology when tadpoles were at about stages 32–37 (table 1). Phenotypic differences between treatments reach their maximum extent by this time (Van Buskirk 2002). Behavioral observations were collected one to three times for each species, usually in midafternoon on sunny days. On each day, I recorded the activity of five to six focal tadpoles within each tank for 1 min each; activity was defined as the proportion of time spent feeding and swimming.

Morphological samples came from a single date, when I gathered six to 20 tadpoles from each tank and photographed or preserved them. Using image analysis software, I measured five traits from every tadpole: maximum length and depth of the body, length and maximum depth of the tail fin, and total length. Because of the way these measures were defined, total length was not equal to the sum of the body and tail lengths (Van Buskirk et al. 1997).

I was interested in differences in shape among species and predator treatments; therefore, I focused on the four body and tail traits after correcting for variation in overall body size. One measure of size in situations when individuals are not weighed is the first component from a principal components analysis (PCA) on the covariance

Table 1: Summary of experiments measuring the behavior and morphology of anuran larvae and phenotypic responses to caged aeshnid larvae

Species	Initial date	No. of replicates	Pond vol. (L)	Predator species	Predator density (no./m ²)	Tadpole density (no./m ²)	No. of families	Morphology sample		Behavior sample		Sources
								Age (d)	Stage	No. of days	Age (d)	
<i>Bufo bufo</i>	April 14, 1997	4	560	<i>Aeshna cyanea</i>	2.2	92	20	44	34	2	28–36	J. Van Buskirk, unpublished data
<i>Bufo calamita</i>	May 6, 2000	4	80	<i>A. cyanea</i>	3.5	64	4	20	36	3	12–23	J. Van Buskirk, unpublished data
<i>Bombina variegata</i>	July 4, 1997	5	80	<i>A. cyanea</i>	3.5	64	6	15	32	2	11–19	J. Van Buskirk, unpublished data
<i>Hyla arborea</i>	July 6, 1997	3	500	<i>A. cyanea</i>	2.2	38	6	28	35	3	12–26	J. Van Buskirk, unpublished data
<i>Hyla chrysoscelis</i>	June 1992	8	600	<i>Anax junius</i>	2.6	110	25	33	32	2	16–29	McCollum and Van Buskirk 1996
<i>Hyla versicolor</i>	June 26, 1996	5	1,000	<i>Anax longipes</i>	1.6	96	10	32	35	2	20–36	Van Buskirk and McCollum 2000a
<i>Pseudacris crucifer</i>	April 28, 1995	4	1,050	<i>A. junius</i>	1.6	96	25	32	28	2	24–30	J. Van Buskirk, unpublished data
<i>Pseudacris triseriata</i>	April 28, 1995	8	1,050	<i>A. junius</i>	1.6	96	50	32	29	2	23–30	Van Buskirk et al. 1997
<i>Rana dalmatina</i>	April 28, 1998	4	560	<i>A. cyanea</i>	2.2	36	4	42	33	3	22–36	J. Van Buskirk, unpublished data
<i>Rana esculenta</i>	June 19, 1997	3	560	<i>Anax imperator</i>	2.2	37	5	39	37	3	16–31	J. Van Buskirk, unpublished data
<i>Rana latastei</i>	April 16, 1999	4	560	<i>A. cyanea</i>	2.2	30	5	37	34	1	24	J. Van Buskirk, unpublished data
<i>Rana lessonae</i>	June 19, 1997	3	560	<i>A. imperator</i>	2.2	37	5	39	37	3	16–31	J. Van Buskirk, unpublished data
<i>Rana pipiens</i>	April 1994	6	1,300	<i>A. junius</i>	1.6	71	>10	~38	Relyea and Werner 2000
<i>Rana ridibunda</i>	June 3, 1998	4	630	<i>A. cyanea</i>	2.2	30	5	34	34	2	25–42	Van Buskirk and Saxer 2001
<i>Rana sylvatica</i>	May 6, 1996	24	1,000	<i>A. longipes</i>	1.6	42	24	26	31	2	22–41	Van Buskirk and Relyea 1998
<i>Rana temporaria</i>	April 3, 2000	5	600	<i>A. cyanea</i>	2.2	57	10	32	32	3	21–38	Van Buskirk 2002

or correlation matrix of morphological length measurements (Rohlf 1990). The covariance matrix is usually preferred for this purpose because Euclidean distances among original observations are preserved after rotation (Rohlf and Bookstein 1987; Bookstein 1989). However, the covariance matrix also ensures that traits having more variation are weighted more heavily, and, in the case of tadpoles, the resulting measure of “size” is mostly a measure of tail length. To illustrate this, I carried out a PCA on the covariance matrix of the four body and tail traits and found that the coefficient of the dominant eigenvector corresponding to tail length (0.82) was much greater than that for the next most important trait (body length, 0.46). The first component from this PCA is a poor reflection of tadpole size because about 83% of the mass of a tadpole is in the body rather than the tail ($SD = 4.4\%$, $N = 16$ *Rana temporaria* tadpoles). I therefore performed PCA on the correlation matrix of all five traits for the entire sample of 2,598 tadpoles. Although the first component from this analysis cannot be entirely independent of shape (Mosi-mann 1970; Bookstein 1989), it is probably closer to true size than any available alternative, and it weights all traits equally (coefficients ranged from 0.44 to 0.46; 93.3% of the variance explained). Moreover, interpretation of this measure of body size is straightforward, since changes in the size axis can be understood as changes in standard deviation units of the original variables.

Hereafter, analyses focus on size-corrected measures that are interpreted as predominantly representing the shape of the body and tail. These are the residuals of the four body and tail measurements after regression against body size (PC-1). The values of R^2 for these regressions were between 0.91 and 0.95.

I measured plasticity in both behavior and morphology as the change in the trait value (for activity) or the size-corrected trait value (morphology) divided by the value of the trait in the no-predator environment. Positive values of plasticity reflect an increase in the value of the trait in the treatment with caged dragonflies. The magnitude of plasticity in different kinds of traits can be compared directly because they are all represented in unitless measures of proportional change.

An obvious objection to my comparative approach is that variation among species is confounded with other unknown differences among the separate experiments. Phenotypes of the 16 species were measured in 14 independent experiments (the *Rana lessonae* and *Rana esculenta* experiments and the *Pseudacris crucifer* and *Pseudacris triseriata* experiments were carried out simultaneously, with species fully randomized). To what extent are “species effects” caused by uncontrolled variation among the experiments? I assessed this problem by assembling data from six different experiments on *R. temporaria*

conducted in outdoor tanks (Arioli 1999; Van Buskirk 2001, 2002; J. Van Buskirk, unpublished data). These experiments included tadpoles drawn from 10 different populations reared at four different densities (21–86/m²), reared in four different years (1997–2000), exposed to two kinds of caged aeshnids (*Aeshna* and *Anax*), and whose morphology was sampled between ages 22 and 37 d. In spite of these many differences, the among-experiment variance component averaged only 12% for the four measures of body and tail shape (range 5.6%–24%, $N = 1,212$ *R. temporaria* tadpoles). Within the sample of 16 species, the among-species variance component was between 62% and 73% (mean = 66%, $N = 2,598$ tadpoles). The among-species component averaged 7.1 times greater than the among-experiment component (range 2.6–11.8 times greater). For both analyses, variation not explained by the species or experiment effects was due to differences among predator treatments, replicate tanks within treatments, and individual tadpoles within tanks. These results suggest that species differences are generally much larger than uncontrolled differences among separate experiments.

Tadpole Habitat Distributions

The adaptive plasticity hypothesis predicts that predator-induced plasticity will be especially strong in species that are exposed to extensive variability in predator numbers. I estimated the habitat distributions of all species by surveying herpetologists in Europe and North America and asking them to rate the frequency of occurrence of each species in different habitat types according to their own field observations. This approach was necessary because there are no comparable and quantitative habitat data available for most species included within this study. Advantages of the approach are that it quantified habitats in a standardized way that allowed comparisons among species occurring on different continents, it was based on actual field experience rather than on conventional wisdom, and it integrated the assessments of many different people rather than just one or a few.

For each species, the participants scored the frequency with which tadpoles reach metamorphosis on a four-point scale (0 = never, 3 = most commonly) within five habitat types. The habitats corresponded to five positions along a gradient extending from ephemeral to permanent freshwater ponds (Wellborn et al. 1996). My descriptions of the habitats were designed to be recognizable to people who are familiar with either pond hydroperiod or predator distributions: (1) dries within weeks, few or no predators; (2) dries every year, small invertebrate predators; (3) dries every few years, irregularly contains many invertebrate predators; (4) permanent, no fish, many invertebrate pred-

ators; and (5) permanent, dangerous fish. Key features of the habitat gradient include an increase in the size and density of predators in more permanent habitats and reduced temporal variability in predators at the ends of the gradient, since very permanent ponds always have predators and very ephemeral ponds rarely do.

I calculated the mean and variability in habitat use of each species after assigning numerical values to each habitat, as listed above. Habitat variation relevant for the evolution of plasticity could arise from either spatial (among ponds) or temporal (within ponds but among years or seasons) sources; therefore, I constructed a composite index of habitat variability that incorporates approximately equal contributions from both sources. The extent to which tadpoles occurred in different kinds of ponds was reflected by the breadth of habitats within which the species at least rarely reached metamorphosis (mean occurrence score >1). The extent to which tadpoles were exposed to temporal variation in predator numbers was calculated as $(p_2 + 2p_3 + p_4)$, where p_i is the occurrence score in the i th habitat. Intermittent temporary ponds (habitat 3) have the highest temporal variation in predator composition (Schneider 1997), and the weightings in this equation ensured that use of intermittent ponds contributed most strongly. Ponds at either end of the gradient have the lowest levels of temporal variability in predator composition because at the ephemeral end they dry frequently, and thus support no large predators, and at the permanent end they predictably support fish. The first component of a PCA conducted on the two measures served as an index of habitat variability.

The survey produced realistic assessments of habitat use. There were between seven and 35 people delivering judgments for each species. For six of the species, I have quantitative field samples collected in Switzerland over 4 yr, and there was close agreement between the survey results and the field sampling results (J. Van Buskirk, unpublished data).

Phylogenetic Analyses

Tests for correlations among traits and habitats were performed within a phylogenetic context to control for differing degrees of statistical independence of species that have differing degrees of evolutionary relatedness (Felsenstein 1985; Martins and Hansen 1996). I used the program COMPARE 4.4 (Martins 2001) to ask whether evolutionary changes in species' attributes, such as phenotypes, plasticities, and habitats, have taken place in a correlated fashion. For every trait of interest, the method first uses information on extant species to reconstruct expected trait values for the ancestors in the phylogeny. A contrast score is then calculated for each speciation event in the phy-

logeny, reflecting the direction and magnitude of the change in the trait within one daughter taxon relative to the other. The final step is to ask whether those contrast scores are correlated, which occurs when evolutionary shifts in one trait tend to be associated with changes in another trait.

The phylogenetic relationships among species were distilled from published studies, as described in figure 1. Because estimates of branch lengths are not available, I calculated contrast scores for 200 phylogenies having the topology shown in figure 1 but with branch lengths drawn from a uniform random distribution between 0 and 1. The distribution of correlation coefficients between contrast scores derived from two traits across all 200 phylogenies was used to infer the strength and significance (two tailed) of correlated evolution between the traits.

I performed two kinds of phylogenetic comparisons. The first asked whether there has been correlated evolution in average trait values and plasticities. Mean trait values may be correlated if there are strong functional correlations among traits (Larson and Losos 1996); plasticities

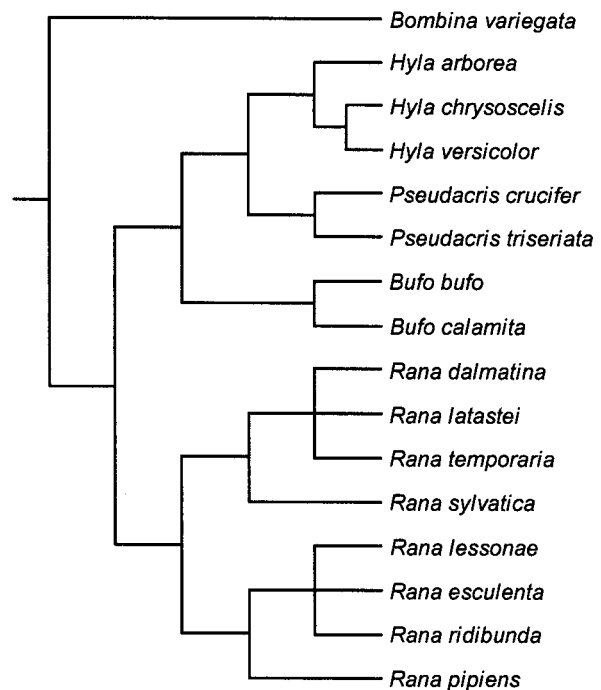


Figure 1: Phylogenetic hypothesis depicting relationships among the 16 anuran species included in this study, compiled from molecular, protein, and morphological data in Hillis and Davis (1986), Mensi et al. (1992), Ford and Cannatella (1993), Coccoft (1994), Duellman and Trueb (1994), Hay et al. (1995), and Ruvinsky and Maxson (1996). Comparative analyses were based on phylogenies having this topology but with randomly generated branch lengths.

might be correlated if different kinds of responses to predators compensate for one another or act in a synergistic fashion (DeWitt et al. 1999). The second kind of comparison tested for associations between evolutionary shifts in phenotypes and habitat use. Here, I asked whether mean phenotypes (averaged across both treatments) were correlated with mean habitats, as expected if temporary and permanent pond environments select for different morphologies and behaviors. I also asked whether predator-induced plasticities in phenotypes were correlated with habitat variability, as expected under the hypothesis that plasticity evolves in heterogeneous environments.

Results

Phenotypic Variation among Tadpole Species and Predator Treatments

The experiments illustrated numerous phenotypic differences among tadpoles and strong effects of the caged-predator treatment (figs. 2–4). Hylids (*Hyla* and *Pseudacris*) had relatively short bodies and deep tails. *Hyla* were consistently more active than *Pseudacris*. *Bufo* tadpoles had relatively long and shallow bodies, shallow tails, and high activity levels. *Bombina* had a very short but deep tail and an intermediate level of activity. *Rana* tadpoles had rela-

tively long bodies, a wide range of tail shapes, and intermediate activity levels.

Species were highly variable in the extent of predator-induced phenotypic plasticity. The proportion of time active was lower in the presence of aeshnids for all species, although the response was strongest in *Rana* (especially the closely related brown frogs *Rana dalmatina* and *Rana latastei*) and almost negligible in the two *Bufo* (fig. 4). Many taxa tended to develop short bodies when in the presence of dragonflies, while the depth of the body was substantially reduced in two brown frogs (*R. latastei* and *Rana sylvatica*; fig. 3A). Aeshnids caused an increase in tail fin depth in all species, with the magnitude of the response varying from 2%–14% (fig. 3B). Changes in tail length, up to about 5%, were positive in some species and negative in others. For measures of both body and tail shape, plasticity was generally stronger in *Hyla* and *Bombina* than in *Pseudacris* and *Bufo*.

The differences among species and predator treatments were highly significant, as was variation among species in plasticity (table 2). For the morphological traits, I referred to the dominant eigenvectors from MANOVA to ascertain which traits were responsible for the significant effects (Morrison 1976). Variation among species arose from all four measures of shape, although relative body depth and tail fin depth were especially important. The predator

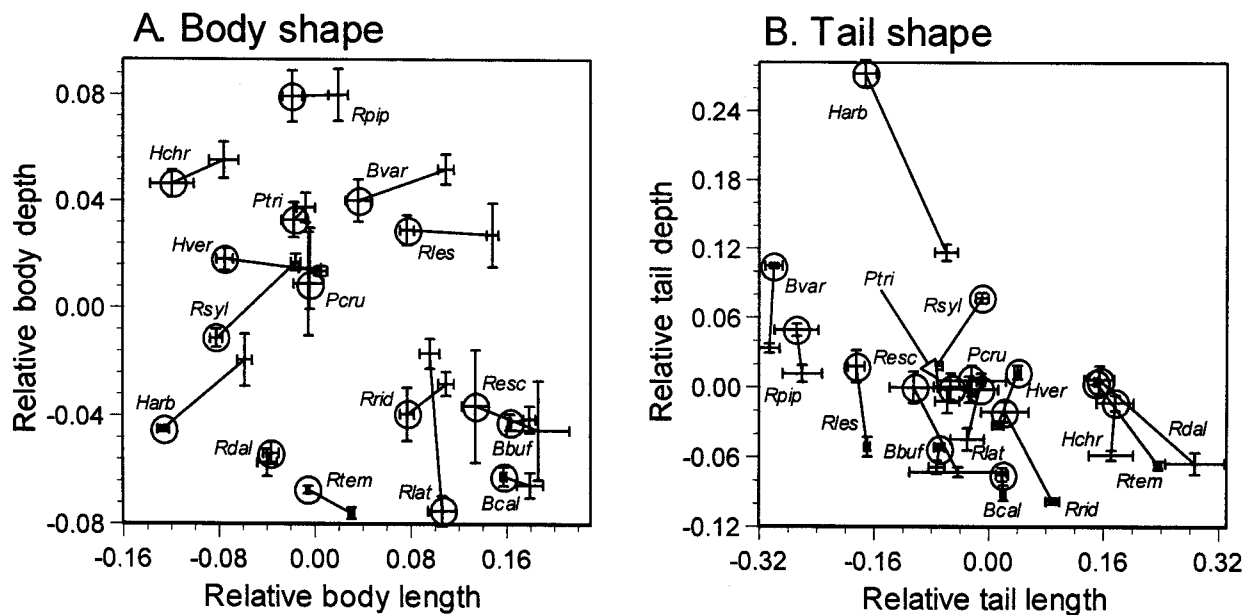


Figure 2: Body and tail shape of 16 species of anuran larvae reared outdoors in experimental ponds. All traits are residuals after regression against size, which was the first component from a principal components analysis on five measures of the body and tail. Lines connect phenotypes in the presence and absence of nonlethal aeshnid dragonflies; open circles indicate the treatment with dragonflies. Bars indicate ± 1 SE. Species symbols are the first letter of the genus (capitalized) and the first three letters of the specific epithet (see table 1).

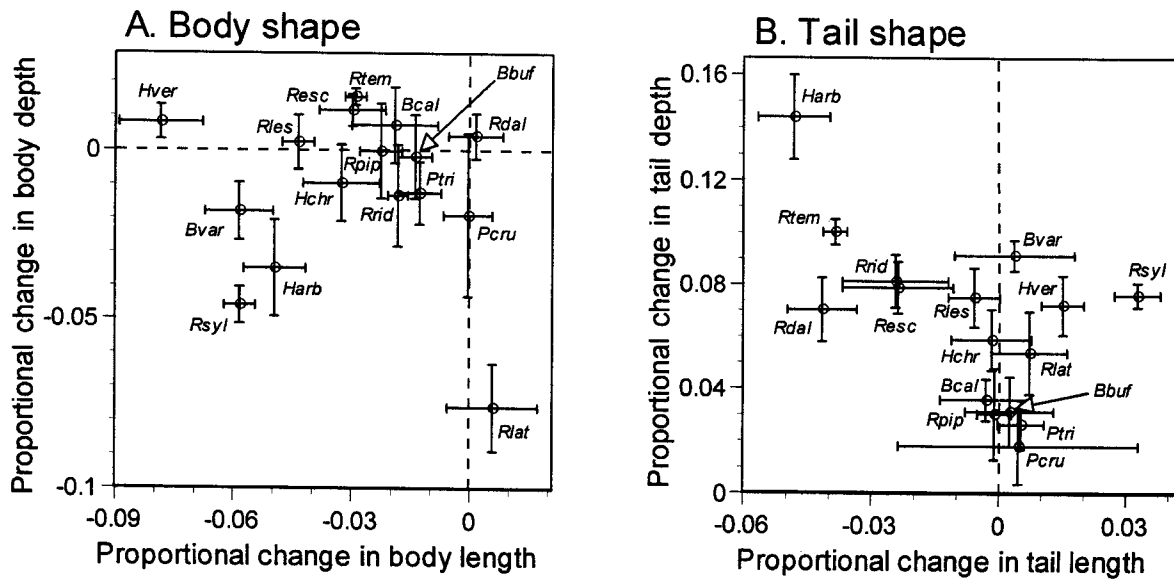


Figure 3: Predator-induced plasticity in the body and tail shape of 16 species of anuran larvae reared in outdoor experimental ponds. The figure shows proportional changes in shape due to the presence of nonlethal aeshnid dragonflies (± 1 SE). Dashed lines indicate the case in which there was no plasticity. Many species developed relatively short bodies in the presence of dragonflies; all species developed deeper tail fins. Species symbols are the first letter of the genus and the first three letters of the specific epithet.

treatment effect was caused mostly by changes in tail fin depth and, to a lesser extent, body length. The significant species-by-predator interaction arose from variation among species in plasticity of the tail fin and body length. A univariate analysis of activity revealed highly significant differences among species ($F = 67.0$, $df = 14, 101$, $P = .0001$, Type III SS) and predator treatments ($F = 227.8$, $df = 1, 101$, $P = .0001$) and a strong species-by-predator interaction ($F = 6.3$, $df = 14, 101$, $P = .0001$). All of these effects are clearly visible in figures 2–4.

The foregoing multivariate analysis accounts for correlations among the morphological traits, but it may be disproportionately influenced by species that have large sample sizes. This turned out to be unimportant here because the outcome was similar when I performed meta-analysis on the separate traits, treating each experiment as an independent estimate of predator effects on morphology and behavior. I employed random effects models within MetaWin (Rosenberg et al. 1997). Across the 16 species, relative body length, relative tail fin depth, and activity differed between predator treatments (effect sizes in SD units $\pm 95\%$ CI: body length, -2.0 ± 0.87 ; tail fin depth, 2.7 ± 0.86 ; activity, -2.4 ± 0.75), and predator-induced changes in all five variables differed significantly among species (homogeneity statistics, Q_{WR} , all >39 , all $P < .0009$). These tests confirm that aeshnids triggered changes in behavior and some components of morphology

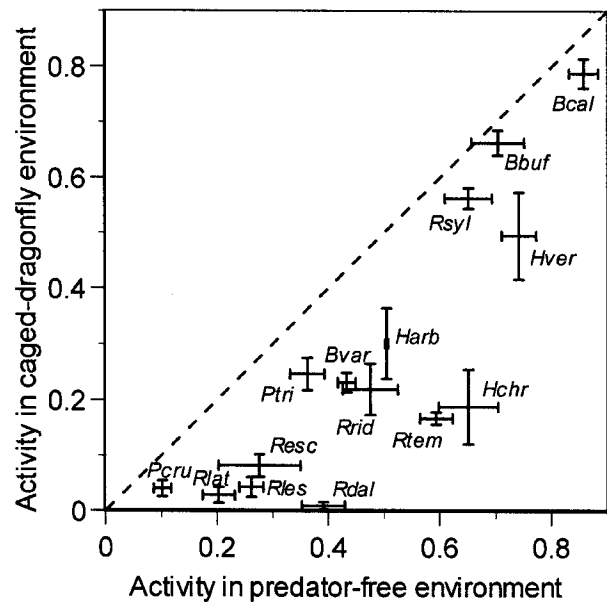


Figure 4: Proportion of time spent actively swimming and feeding by 15 species of anuran larvae in the presence and absence of caged dragonfly larvae. Species near the dashed line showed little behavioral response to predators; species falling far below the line decreased their activity strongly when dragonflies were present. Bars show ± 1 SE. Species symbols are the first letter of the genus and the first three letters of the specific epithet.

Table 2: MANOVA on four size-corrected measures of morphological shape for 16 species of larval anuran reared in the presence and absence of caged dragonfly larvae

Source	df	Wilks's <i>F</i>	<i>P</i>	Coefficients of the dominant eigenvector			
				Body length	Body depth	Tail length	Tail fin depth
Species	60,599	109.0	.0001	12.53	20.16	9.05	14.15
Predator treatment	8,306	31.0	.0001	-2.36	-1.90	-1.46	-6.95
Species by predator	56,597	3.8	.0001	-3.77	-1.62	-1.54	-7.58

Note: The dominant eigenvector represents the linear combination of traits that differed most strongly between species or treatments. Replicates are tanks means.

when viewed across all species and that plasticity in all traits differed among species.

Allometric patterns suggest that differences in shape between predator environments and among species did not simply arise from variation in size or growth rate. Figure 5 illustrates results for two traits and three representative species, showing clear differences in size and shape between species and treatments. *Rana dalmatina* tadpoles had a longer body than did those of *Hyla chrysoscelis*, even within the region where the two species overlapped in size. Both *R. dalmatina* and *H. chrysoscelis* showed predator-induced changes in body shape that were consistent across all sizes. *Bufo bufo* had a very long body and showed little plastic response to predators. The three species had similar average tail fin depths, but *R. dalmatina* and *H. chrysoscelis* had deeper tails in the presence of dragonflies. In some cases, the phenotypic difference between treatments increased as tadpoles grew larger. Analysis of the entire data set confirmed that the species effect was always significant ($N = 2,598$, all $P < .0001$), and the predator effect was significant for all traits except relative tail length ($P < .0001$) when body size was also included in the model.

Interspecific Correlations among Phenotypes and Plasticities

There was evidence for correlated evolution in morphological traits (table 3, above the diagonal). Evolutionary changes toward increasing depth of the tail fin relative to overall size have been accompanied by strong reductions in the length of the tail (fig. 2B) and body. A slight decrease in relative body depth has accompanied increases in body length (fig. 2A) and tail length. Evolutionary changes in activity have not been associated with changes in the shape of the body and tail.

There were negative correlations among predator-induced plasticities for several morphological traits (table 3, below the diagonal). For example, evolutionary increases in plasticity of the depth of the tail fin have been associated

with decreasing or negative plasticity in tail length (fig. 3B) and body length. Within some species, tadpoles have become relatively longer in the presence of dragonflies, while in other species the tadpoles have become deeper overall. Plasticity in tail length was negatively correlated with plasticity in body depth, although the relationship was not especially strong and would not withstand Bonferroni correction (adjusted $\alpha = 0.005$).

I checked for a negative association between behavioral and morphological plasticity, as expected if the two kinds of response represent alternate and compensatory mechanisms of avoiding predation. Morphological responses to predation act to reduce vulnerability to a predator's strike, whereas behavioral responses presumably decrease the likelihood of detection in the first place (Van Buskirk et al. 1997). Morphological plasticity was estimated by the average of the absolute values of proportional responses to predation in the four measures of body and tail shape. There was no relationship between plasticity in behavior and morphology, partly because the two *Bufo* species exhibited little response of either sort (fig. 6; mean $r = -0.20$, $P = .15$; two-tailed test based on 200 phylogenies with randomly generated branch lengths). However, if *Bufo* are disqualified from the analysis on the grounds that they escape predation at least in part from chemical defenses (Heusser 1971; Denton and Beebe 1991), the remaining taxa support the prediction ($r = -0.42$, $P = .02$).

Comparison of Habitat, Phenotype, and Plasticity

The occurrence of species along the habitat gradient exhibited several patterns of potential biological interest (fig. 7), although phylogenetic correlations between tadpole phenotypes and habitat use were mostly weak (table 4). In comparison with those occurring in permanent ponds, for example, anurans in irregularly drying ponds toward the middle of the gradient had somewhat shallow bodies, with long and deep tails. Moreover, there were indications

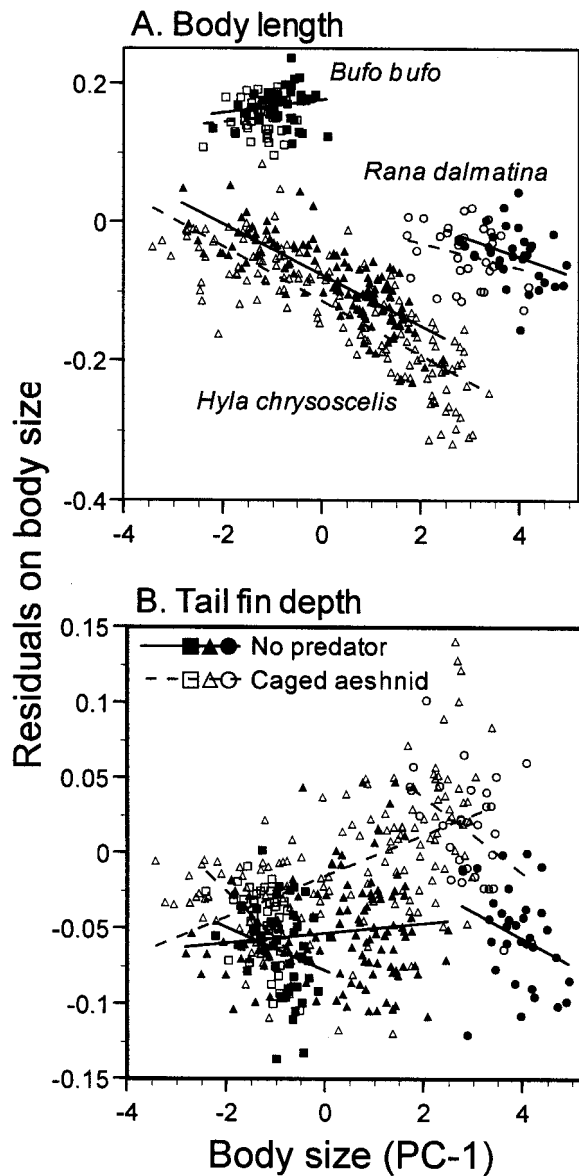


Figure 5: Patterns of shape and body size for individual tadpoles from three representative species: *Bufo bufo* (squares), *Hyla chrysoscelis* (triangles), and *Rana dalmatina* (circles). Filled symbols represent the no-predator treatment, and open symbols are the caged-aeshnid treatment. Body size is the first component from a principal components analysis on the correlation matrix of five measures of the body and tail. The species and treatments show different allometric relationships, demonstrating that species differences and predator-induced plasticity were independent of size.

that species occupying permanent habitats were inactive, with relatively long bodies and shallow tail fins. Tadpoles of the two *Bufo* species were similar to one another in phenotype, in spite of occurring at opposite ends of the

habitat gradient. *Bufo bufo* was in most ways typical for a permanent pond species, except for its high activity. *Bufo calamita*, in contrast, possessed traits that seemed atypical for its temporary habitats, such as a disproportionately shallow tail fin and an unusually long and shallow body. Any conclusions about phenotypes of tadpoles in highly ephemeral ponds cannot be supported strongly by these data, however, since only a small number of such species are included in the sample.

Predator-induced plasticity in both behavior and morphology was more extensive in species occurring in relatively variable predation environments, although this relationship was significant only for morphology (fig. 8). The phylogenetic correlation between total morphological plasticity (average of the four traits) and variation in habitat use was significant ($r = 0.45$, $P = .01$), while the corresponding relationship for behavioral plasticity was not significant ($P = .96$). This suggests that evolutionary shifts into more variable predation environments have been accompanied by evolutionary increases in predator-induced plasticity of body and tail shape, but not by changes in behavioral plasticity.

Discussion

Species Differences in Plasticity

This comparative study supports the hypothesis that interspecific differences in phenotypic plasticity are adaptive. A positive relationship between plasticity and environmental heterogeneity is expected if divergent selection, imposed in this case by exposure to variable numbers of predators, acts to promote the evolution of plasticity within species and if species differ in the extent to which they experience divergent selection. This relationship was significant for the morphological responses of 16 tadpole species to odonate predators, while the corresponding relationship for behavioral responses was not significant.

An obvious but noteworthy result of this project is that species showed extensive variation in plasticity that was not associated with environmental heterogeneity. This was true not only for behavioral responses, which showed no pattern across habitats, but for morphological responses as well, which were related to habitat variability but nevertheless showed considerable interspecific variability (fig. 8). Here, I begin with a discussion of the different outcomes for behavior and morphology and then explore general explanations for among-species variation in plasticity.

Heterogeneous predation risk seems likely to impose selection for behavioral plasticity because behavioral responses are costly and yet effective for defense against predators (Sih 1987; Lima and Dill 1990; Kotler et al.

Table 3: Correlations among morphological and behavioral traits (above the diagonal) and among proportional changes in the same traits when exposed to dragonflies (below the diagonal)

	Body length	Body depth	Tail length	Tail fin depth	Activity
Body length	1.0	-.38 (.03)	-.13 (.40)	-.41 (.00)	-.24 (.18)
Body depth	-.21 (.19)	1.0	-.52 (.02)	.18 (.27)	-.21 (.18)
Tail length	-.16 (.39)	-.47 (.03)	1.0	-.63 (.00)	.28 (.15)
Tail fin depth	-.56 (.00)	.06 (.80)	-.56 (.00)	1.0	-.08 (.61)
Activity	-.40 (.05)	-.09 (.52)	.28 (.13)	.08 (.45)	1.0

Note: The table shows mean correlation coefficients, calculated from 200 phylogenies with randomly generated branch lengths, for relationships among phylogenetic contrast scores for traits and plasticities. In parentheses are two-tailed *P* values derived from the distribution of coefficients from all 200 phylogenies. Trait values are averaged across both treatments, and plasticities are measured relative to the no-predator environment. Morphological traits are corrected for differences in body size. $N = 14$ branching events for comparisons involving activity, and $N = 15$ for all other comparisons.

1994). But the scale of variability that favors behavioral plasticity may differ from that which favors morphological plasticity, and this difference may explain the weak correlation between behavioral plasticity and my index of habitat variation. In general, phenotypic modes that show different rates of development in response to environmental cues should be associated with different scales of environmental heterogeneity. Behavioral responses require less time to develop than morphological responses (West-Eberhard 1989) and therefore may be promoted by variation in predation risk occurring on very short time scales. My measure of habitat heterogeneity was intended to reflect large-scale variability between years and ponds, so it may show no relationship to the kind of fine-scale variation that selects for behavioral responses to predators. My preferred explanation for the behavioral results is therefore not that responses are nonadaptive but that behavioral plasticity was not compared with the correct scale of habitat heterogeneity. The appropriate comparison would be difficult at present, since it is not known which habitats contain the most short-term variability in risk. Small-scale variation in predation risk could exist in any habitat that contains predators (Sih 1992).

The negative correlation between behavioral and morphological plasticity among 14 non-*Bufo* species further suggests that the two modes of response evolve under different environmental conditions. There are several possible explanations; both kinds of plasticity may be costly, they may interfere with each other, or either one may render the other unnecessary. Regardless of the cause, a consequence is that both modes of response cannot possibly be positively related to the same feature of the environment. Additional evidence that behavioral and morphological defenses evolve independently comes from a study showing that the two responses are triggered by different cues (Van Buskirk and Arioli 2002).

A further observation that may have general implica-

tions is that species' traits and plasticities, for both behavior and morphology, exhibit much variation not related to known features of the environment (figs. 7, 8). Theory suggests several kinds of explanation for species differences (e.g., Niklas 1994; Whitlock et al. 1995; van Tienderen 1997). For example, a particular predator can impose se-

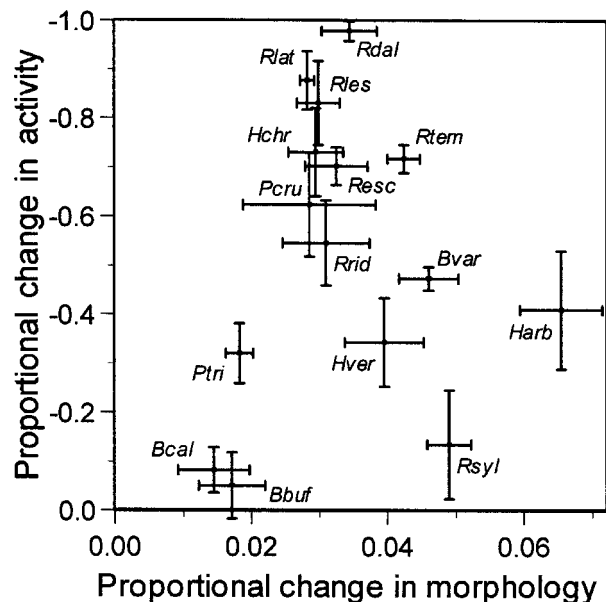


Figure 6: Relationship between behavioral plasticity and morphological plasticity for 15 species of anuran larvae reared in outdoor artificial ponds. Plasticity in behavior is represented by the proportional difference between treatments in the time spent actively feeding or swimming. Plasticity in morphology is the mean of the absolute values of proportional differences between treatments in four size-corrected traits. All proportions are calculated relative to the predator-free environment, and bars indicate ± 1 SE. Species symbols are the first letter of the genus and the first three letters of the specific epithet.

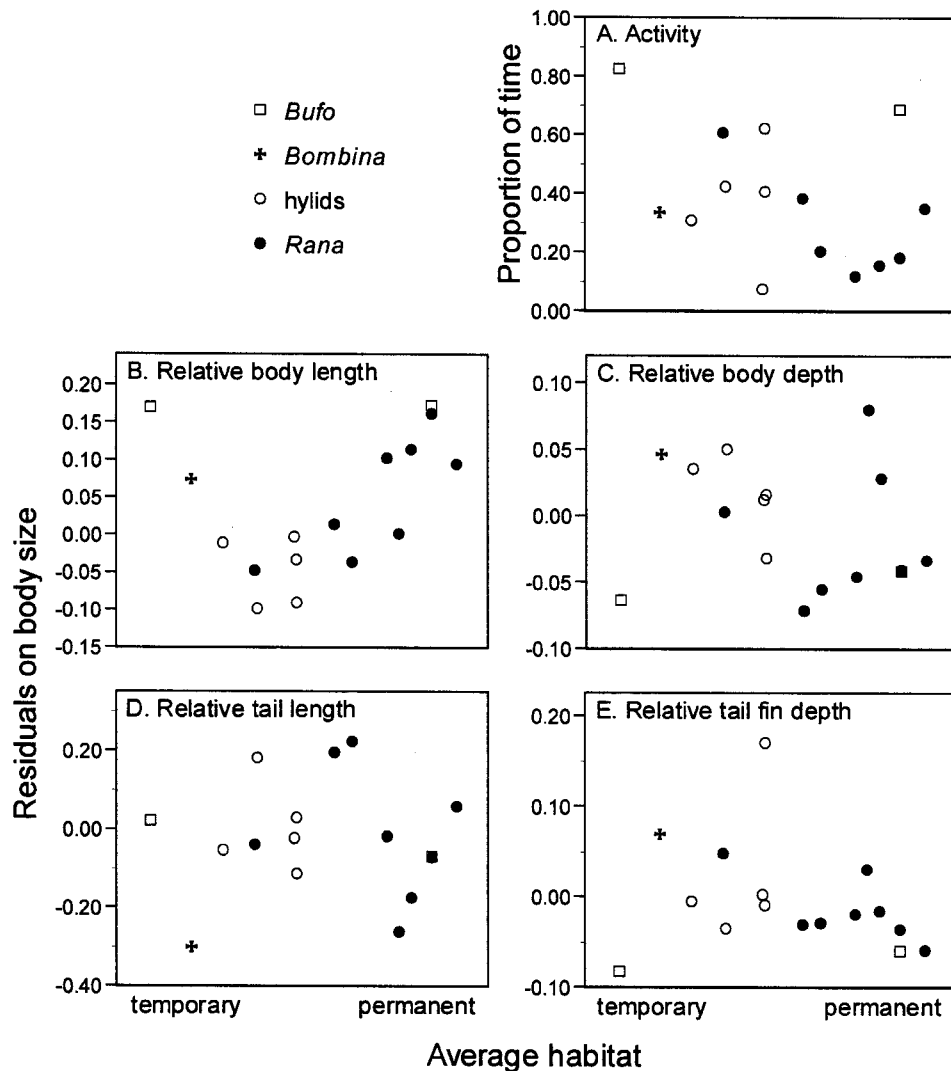


Figure 7: Relationships between phenotypes (averaged across both treatments) and habitat distributions for tadpoles of 15–16 anuran species. Average habitat is the mean position along a gradient from ephemeral to permanent ponds.

lection for different trait values in each species that experiences it, in part because the functional consequences of any specific trait depend on many other components of the phenotype. Some of these other components are surely not among the five traits that I measured. *Bufo* offers an obvious example in which chemical deterrents have probably evolved under selection imposed by predators (Woodward 1983; Kats et al. 1988). As a consequence, the behavioral and morphological phenotypes conferring highest fitness for *Bufo* tadpoles may be quite different from those for more palatable species. All taxa presumably possess similar, although less dramatic, attributes that combine to modify the exact combination of traits favored in any given environment. The strong negative correlations

between plasticity in tail depth and other traits support the idea that responses in different traits can be dependent (see also Richardson 2001) due to relationships among their functions or developmental origins.

Another reason to expect an imprecise relationship between plasticity and environmental heterogeneity is that the costs of plasticity may differ among species. Even if predator escape was most effectively accomplished with the same combination of traits in every kind of tadpole, it is unlikely that all species could exhibit those traits due to species-specific differences in the difficulties of detecting environmental conditions and responding appropriately (DeWitt et al. 1998). Although little is known about the cost of plasticity in any organism, it is clear that costs can

Table 4: Correlations between phylogenetic contrast scores for average phenotypes and habitat use (upper two rows in the table) and between contrast scores for predator-induced phenotypic plasticity and variation in habitat use (lower rows)

	Trait				
	Activity	Body length	Body depth	Tail length	Tail fin depth
Mean habitat versus mean phenotype:					
<i>r</i>	-.29	.29	-.15	-.08	-.07
<i>P</i>	.07	.02	.30	.51	.54
Habitat variation versus phenotypic plasticity:					
<i>r</i>	-.01	-.39	.20	-.05	.20
<i>P</i>	.96	.01	.11	.79	.23

Note: The table shows mean correlation coefficients, averaged across 200 phylogenies with randomly generated branch lengths, and two-tailed *P* values judged from the distribution of correlation coefficients. Morphological traits are corrected for body size. Mean phenotypes are averaged across both experimental treatments. Mean habitat is the position along a gradient extending from ephemeral to permanent ponds; habitat variation is a composite measure of exposure to multiple predation environments. *N* = 14 nodes for activity, and *N* = 15 for morphological responses.

act as a constraint on the extent of plasticity that evolves (van Tienderen 1991). Differences in the expression of costs among species in my sample might act to modify the precise positions of the phenotypes that confer optimal fitness. Furthermore, differences between behavior and morphology in the costs of plasticity could help explain

why the two kinds of response showed different relationships with habitat.

If costs of plasticity do exist, then trait expression is expected to more closely approach the optimum within habitats that are experienced frequently or within which selection is especially strong (van Tienderen 1991). This

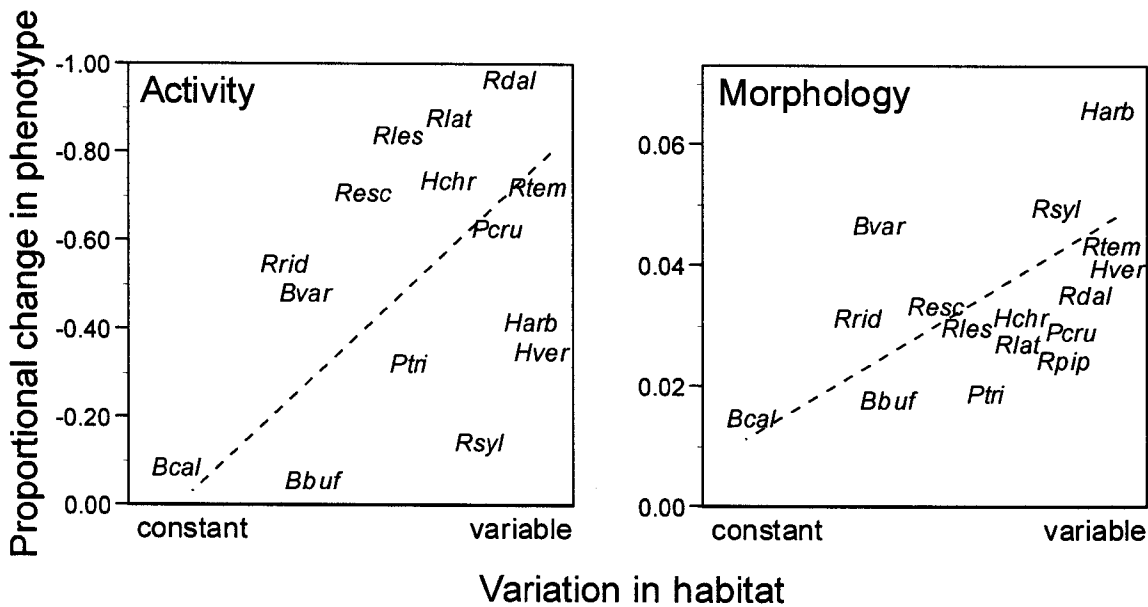


Figure 8: Relationships between predator-induced plasticity and variation in habitat use for 15–16 species of anuran tadpoles. Plasticity is the proportional phenotypic difference between treatments in time spent swimming and feeding (activity) and four measures of body and tail shape (morphology). Habitat variation is a composite index that incorporates the use of multiple habitat types and habitats with temporally varying predator composition. Dashed lines depict major axis regressions. Species symbols are the first letter of the genus and the first three letters of the specific epithet.

suggests yet another explanation for interspecific variation in the extent of plasticity. Although I chose to screen tadpoles within two environments that are experienced by all species, there remain differences among species in the frequency with which they are exposed to odonates and predator-free situations in nature. Phenotypes exhibited by tadpoles within rarely encountered environments may be far from optimal, and this may help explain why environmental heterogeneity does not strictly predict plastic responses induced by two specific habitats.

The general message emerging from these explanations is that species-specific attributes may often obscure the relationship between plasticity and environmental heterogeneity. On the one hand, this makes the positive relationship between morphological plasticity and habitat variability all the more impressive. But at the same time, it supports Roff's (1992) argument that within-species comparisons among populations exposed to different environments can provide a more powerful approach to testing the prediction that plasticity and environmental heterogeneity are correlated.

Ecological and Evolutionary Implications

This study encourages caution when interpreting the ecological consequences of species differences in phenotype. Optimistic inferences are often made about the functional implications of phenotypic differences and their consequences for species distributions along habitat gradients (e.g., Werner and McPeck 1994; Smith and Van Buskirk 1995; Wissinger et al. 1999). But these conclusions can be based on species differences in just a single trait (usually a component of behavior), and the functional data may be sketchy or absent. Tadpole studies suggest that idiosyncratic differences among species, and compensatory relationships among multiple traits, can obscure the trade-offs assumed to govern habitat distributions (Richardson 2001). Phenotypic manipulations sometimes fail to confirm connections that are assumed to exist between phenotype and performance (Van Buskirk and McCollum 2000a, 2000b), and my comparison of 16 species illustrates that associations between phenotypes and habitat distributions can be weak.

Results of this project also illustrate how functional or genetic constraints can modify the response to natural selection. Experiments find that predators usually impose selection for increasing tail depth and length and never impose selection for decreasing tail length (Van Buskirk et al. 1997; Van Buskirk and Relyea 1998). Yet I found here that species exhibiting the greatest predator-induced increase in tail depth also showed a shorter tail with predators. This may reflect a constraint arising from functional

relationships (i.e., deep tails work best if they are short) or design limitations (i.e., construction or maintenance of tails that are both long and deep is difficult). If so, plasticity in tail length of such species as *Hyla arborea*, *Rana temporaria*, and *Rana dalmatina* (fig. 3B) may represent an example of nonadaptive phenotypic plasticity arising from adaptive shifts in correlated characters. Such nonadaptive explanations for plasticity are often discussed in theory (Via and Lande 1985; van Tienderen 1990) but are rarely found in nature (Huey and Hertz 1984).

The predictions underlying this study were derived from short-term experiments demonstrating divergent selection on traits at different points along a predation gradient (Anholt and Werner 1995; Van Buskirk et al. 1997). Straightforward extrapolation of those results over long periods of time to higher taxonomic levels predicts that both behavior and morphology should be more flexible in species occurring in habitats with variable predator composition. My results support this expectation for morphology, but perhaps not for behavior, and they also suggest that it may be difficult to predict accurately the attributes of higher taxa from microevolutionary studies of selection and response. It remains to be seen whether this difficulty can be overcome by fine-tuning predictions emerging from microevolutionary studies, perhaps by incorporating additional components of the phenotype and estimating costs of plasticity.

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