

PREDATOR- AND COMPETITOR-INDUCED PLASTICITY: HOW CHANGES IN FORAGING MORPHOLOGY AFFECT PHENOTYPIC TRADE-OFFS

RICK A. RELYE¹ AND JOSH R. AULD

Department of Biological Sciences, University of Pittsburgh, Pittsburgh, Pennsylvania 15260 USA

Abstract. Studies of phenotypic plasticity frequently demonstrate functional trade-offs between alternative phenotypes by documenting environment-specific costs and benefits. However, the functional mechanisms underlying these trade-offs are often unknown. For example, predator-induced traits typically provide superior predator resistance but slower growth, while competitor-induced traits provide better growth but inferior predator resistance. While the mechanisms underlying predator resistance have been identified, the mechanisms underlying differential growth have remained elusive. To determine whether competitor and predator environments affect individual growth by induced changes in foraging morphology, we raised wood frog tadpoles (*Rana sylvatica*) under a factorial combination of competitors and predators and assessed changes in mouthparts that might affect growth. In general, competitors induced relatively larger oral discs, wider beaks, and longer tooth rows, while predators induced relatively smaller oral discs, narrower beaks, and shorter tooth rows. These effects were interactive; the largest competitor-induced responses occurred under high predator density and the largest predator-induced responses occurred under low competition. Further, one of the tooth rows that commonly appeared under low predation risk was frequently absent under high predation risk. These discoveries suggest that predator and competitor environments can have profound effects on prey foraging structures and that these effects set up growth trade-offs between phenotypes that favor the evolution of phenotypically plastic responses.

Key words: competition; foraging morphology and individual growth; inducible defense; phenotypic plasticity; polyphenism; predation; *Rana sylvatica*; trophic polymorphism.

INTRODUCTION

Phenotypic plasticity is pervasive in nature and the ability to develop environmentally induced traits plays an important role in the normal development and evolution of nearly all organisms (Stearns 1989, Agrawal 2001, West-Eberhard 2003). Theory predicts that adaptive plasticity will evolve when a population is exposed to variable environments (with reliable cues) and when selection favors different phenotypes in different environments (Via and Lande 1985, Moran 1992). Such adaptive plastic responses should improve an individual's fitness relative to those exhibiting nonplastic traits (Schlichting and Pigliucci 1998).

In examining the plasticity of organisms' traits, researchers have frequently documented phenotypic trade-offs, but the mechanisms underlying these trade-offs are often elusive. Inducible defenses offer a prime example. Many plants and animals respond to herbivory and predation by inducing defensive structures and chemicals that deter predation, but at the cost of slower growth and reproduction (Tollrian and Harvell 1999, Cipollini et al. 2003). In most cases, the mechanisms responsible for the predation deterrent are understood

(e.g., chemicals that are distasteful or morphological changes that make prey harder to capture), but the mechanisms responsible for the reduced growth and development are not. By identifying underlying mechanisms, we will likely find that a diversity of taxa operate in similar ways and that parallel mechanisms produce the ubiquity of evolved plastic responses that we observe in nature.

Larval anurans have proven to be a useful system for exploring plasticity and phenotypic trade-offs because they show consistent responses to variation in predation and competition. In predator environments, tadpoles typically forage less and develop relatively large tails and small bodies (although the suite of traits can be species specific; Relyea 2001, 2003, Van Buskirk 2002). These responses make animals more resistant to predation (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998), but come at the cost of slower growth and development (Van Buskirk 2000, Relyea 2002b). In competitor environments, herbivorous tadpoles forage more and develop relatively small tails and large bodies (Relyea 2002a, 2004, Relyea and Hoverman 2003; for alternative responses by cannibalistic tadpole species, see Pfennig 1992a, b). Competitor-induced tadpoles grow faster than uninduced tadpoles, but at an increased risk of predation. In short, both types of environments cause important phenotypic trade-offs.

Manuscript received 20 December 2004; revised 8 February 2005; accepted 9 February 2005. Corresponding Editor: E. Brodie III.

¹ E-mail address: relyea@pitt.edu

Given these performance trade-offs, we need to understand the underlying mechanisms. We have a good understanding of what causes differences in predation risk; individuals with lower activity and relatively larger tails are harder for predators to detect and capture (Skelly 1994, Van Buskirk and Relyea 1998). However, differences in growth are likely driven by several mechanisms. First, both predator and competitor environments affect foraging activity (in opposing directions), and foraging activity is positively correlated with growth (Relyea and Werner 1999). Second, predator and competitor environments affect relative intestine length, retention time, and the concentration of digestive enzymes; all three factors affect assimilation efficiency and, therefore, growth (Sibly 1981, Skelly and Golon 2003, Relyea and Auld 2004). While our focus has thus far been on behavior during foraging and digestive efficiency after foraging, little attention has been paid to the suite of morphological traits that actually do the foraging. If predator and competitor environments can affect foraging morphology, then we will have discovered an important mechanism by which competitor and predators environments can affect prey growth and set up performance trade-offs that favor the evolution of phenotypic plasticity.

In this study, our goal was to determine whether predator and competitor environments affect the mouthparts of tadpoles in ways that might affect growth. In nature, tadpoles exhibit considerable variation in their tooth rows (Bresler 1954, Hampton and Volpe 1963, Pedersen 1991, Walls et al. 1993, Gollmann and Gollmann 1995, Chou and Lin 1997), but we know little about the impacts of predator and competitor environments (but see Bragg 1956, Pfennig 1992a, Reilly et al. 1992, Pfennig and Murphy 2000). Using wood frog tadpoles, we tested the following hypotheses: (1) competitors induce relatively larger mouthparts to provide a larger scraping surface, (2) predators induce relatively smaller mouthparts, and (3) because predators and competitors typically induce traits in opposite directions, combinations of predators and competitors have interactive effects on tadpole mouthparts.

METHODS

The experiment was conducted at the University of Pittsburgh's Pymatuning Laboratory of Ecology in northwest Pennsylvania (USA) with the original goal of understanding how wood frog tadpoles alter their behavior and external morphology in response to different competitor and predator environments (for additional details see Relyea [2004]). The experiment employed a randomized block design with a factorial combination of four densities of intraspecific competitors (20, 40, 80, and 160 individuals) and four densities of caged predators (0, 1, 2, and 4 individuals). The four competition treatments corresponded to 11 tadpoles/m², 22 tadpoles/m², 44 tadpoles/m², and 89 tadpoles/

m², respectively, well within relevant natural densities (up to 400 tadpoles/m²; E. E. Werner, R. A. Relyea, D. K. Skelly, and K. L. Yurewicz, *unpublished data*). The predator was a late-instar Aeshnid dragonfly naiad (*Anax junius*), a natural predator of wood frog tadpoles. The 16 treatment combinations were replicated four times (four spatial blocks) for a total of 64 experimental units.

The experimental units were 1200-L cattle-tank mesocosms filled with 1000 L of well water on 24–26 April 2001. We added 300 g of deciduous leaves (primarily *Quercus* spp.) and 25 g of rabbit chow to each tank to provide an initial nutrient source for periphyton growth. The tanks were inoculated with an aliquot of pond water containing phytoplankton and zooplankton from 10 nearby ponds to simulate natural pond conditions. On 5 May 2001, we added wood frog tadpoles (initial mass = 108 ± 8 mg [mean ± SE]) from a mixture of 10 egg masses that we collected from a single population. Prior to the experiment, wood frog hatchlings were reared in wading pools filled with well water to keep the tadpoles predator naïve. Each tank was covered with a lid constructed of 60% shade cloth to prevent colonization by insects and other amphibians.

All tanks in the experiment were equipped with four predator cages constructed of 10 × 10 cm well pipe covered with window screen at each end. These cages allow the chemical cues emitted during predation to diffuse through the water while preventing the predators from killing the target animals (Petraska et al. 1987, Kats et al. 1988). Depending on treatment, each cage was either empty or housed a single dragonfly nymph. Each dragonfly was fed ~300 mg of wood frog tadpole biomass three times per week.

The experiment ended on 31 May–1 June 2001. Upon removing all animals from the tanks, 10 tadpoles were euthanized and preserved in 10% formalin. External morphological traits were measured in 2001 and then the preserved tadpoles were returned to the preservative (data reported in Relyea [2004]). In 2003 we extracted these tadpoles again, weighed them, and took a picture of their oral disc. The oral disc is composed of a centrally located keratinized beak, an upper labium with three or four labial tooth rows, and a lower labium with four labial tooth rows (Fig. 1). Collectively, these mouthparts are used for scraping periphyton from pond surfaces (Wassersug 1976, 1980, Wassersug and Yamashita 2001). From the photo of the oral disc, we used an image-analysis system (Optimas BioScan, Bothell, Washington, USA) to measure the maximum width of the oral disc, the maximum width of the beak, and the length of each tooth row segment. The density of labial teeth did not vary across or within individual rows of labial teeth, so any change in tooth-row length reflects a change in tooth number. Of the eight tooth rows, one of them (the fourth tooth row) was often missing; thus, for the fourth top row, we also quantified

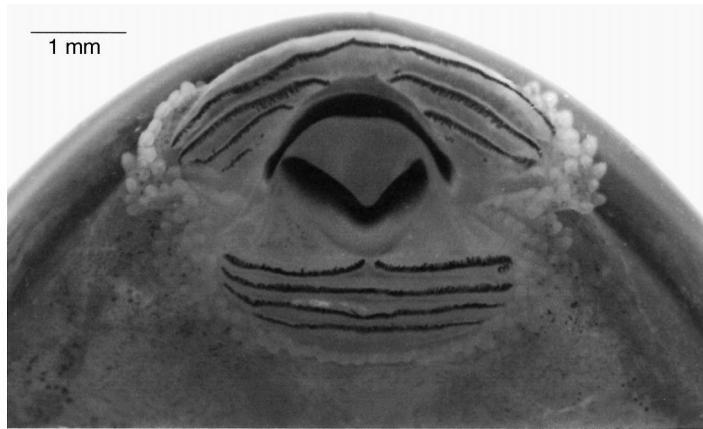


FIG. 1. The oral disc of a wood frog tadpole. The anterior end is oriented toward the top of the figure and the keratinized beak is centrally located. Four rows of labial teeth are present on the upper labium and four rows of labial teeth are present on the lower labium. For further details, see *Methods*.

the frequency of its occurrence (counted as present if a fourth tooth occurred on either side of the oral disc). Throughout this article, we use Bresler's (1954) tooth-row numbering system. Tooth row 1 is the most rostral row on the upper labium, followed posteriorly by rows 2 through 4. Tooth row 5 is the most rostral row on the lower labium, followed posteriorly by rows 6 through 8 (Fig. 1).

When we consider the impact of environments on traits, we must always consider the possibility that the traits are not adaptive responses, but simply the outcome of allometric relationships of how traits change with growth and development. For example, while there appear to be no studies on the changes in relative oral morphology over ontogeny, we do know that the number of tooth rows increases over ontogeny (Bresler and Bragg 1954, Hampton and Volpe 1963), suggesting that we need to consider allometric explanations. In wood frogs, growth and development are highly correlated (Relyea 2005), allowing us to use growth data to evaluate whether predator- and competitor-induced changes in mouthparts are simply due to predators and competitors causing retarded growth.

Statistical analyses

Differences in morphological dimensions can be due to differences in overall size (i.e., mass) as well as differences in shape. To determine whether the relative size of tadpole mouthparts was affected by competition and predation, we had to simultaneously control for tadpole mass. We conducted a principal-components analysis (PCA) on mass and 9 of the 10 mouth dimensions (the fourth tooth row was often missing and, therefore, we omitted it from the PCA). The PCA resulted in two principal components (PC-1 and PC-2), which corresponded to shape and size, respectively. Using the mean PC-1 and PC-2 scores from each tank, we then conducted a multivariate analysis of variance on the two principal components to test for effects of block, competitors, caged predators, and all two-way interactions. When treatments were significant at the multivariate level, we examined the univariate effects.

For significant univariate effects, we conducted mean comparisons using Fisher's LSD test. We also tried an alternative method of making the mouthparts size independent by regressing the dimensions against mass, saving the residual values for each tadpole, and analyzing the mean residuals for each pool (as in Relyea 2004). This alternative analysis provided results very similar to the PCA (results not shown), but we used the PCA approach because it condensed the 10 response variables down to two easily interpretable variables.

RESULTS

In the first analysis, we subjected tadpole mass and nine mouth dimensions to a PCA. We found that the first principal component (PC-1) explained 63% of the multivariate variation (eigenvalue = 6.3) while the second principal component (PC-2) explained 10% of the variation (eigenvalue = 1.0). PC-1 loaded strongly for all nine mouth dimensions (0.6 to 0.9) and weakly for mass (0.2) whereas PC-2 loaded strongly for mass (0.9) and weakly for the nine morphological dimensions (−0.1 to 0.2; Table 1). Thus, the two PC axes are best interpreted as measures of relative mouth shape and overall tadpole size, respectively.

TABLE 1. Loadings of tadpole mass and nine mouthpart dimensions as determined from a PCA.

Dimension	PC-1	PC-2
Mass	0.218	0.938
Mouth width	0.902	0.166
Beak width	0.782	0.212
Tooth-row length		
1st upper row	0.878	0.009
2nd upper row	0.890	−0.025
3rd upper row	0.846	−0.088
1st lower row	0.867	−0.141
2nd lower row	0.849	−0.143
3rd lower row	0.804	−0.160
4th lower row	0.639	−0.092

Notes: The first principal component (PC-1) explained 63% of the variance while PC-2 explained 10% of the variance. The eigenvalues for PC-1 and PC-2 were 6.3 and 1.0, respectively.

TABLE 2. Results of a MANOVA that examined the effects of competition and caged predators on wood frog mass (PC-2) and relative mouth morphology (PC-1).

Factor(s)	df	Multivariate tests		Univariate tests <i>P</i> [†]	
		Wilks' <i>F</i>	<i>P</i>	PC-1	PC-2
Block	6	1.4	0.245
Competition	6	27.4	<0.001	<0.001	<0.001
Predation	6	9.5	<0.001	<0.001	0.054
Block × Competition	18	1.9	0.037	0.014	0.314
Block × Predation	18	0.9	0.583
Competition × Predation	18	4.0	<0.001	0.001	0.004

[†] Results are given for all significant multivariate tests.

REPORTS

We then analyzed the mean PC-1 and PC-2 scores from each experimental unit in a MANOVA. We found no block effects, but there were significant effects of competitors, predators, and a competitor-by-predator interaction (Table 2, Fig. 2). There also was a significant competitor-by-block interaction, but the impact of the interaction had no effect on the overall interpretation of the competitor effects. Univariate analyses of PC-1 indicated competitors, predators, and a competitor-by-predator interaction affected relative mouth shape. In general, tadpole mouthparts were relatively large when predators were absent but relatively small when predators were present (Fig. 2A). The magnitude of the predator effect depended upon competitor density. The predator-induced reduction in mouth size was large when competition was low ($P < 0.001$) but marginal when competition was high ($P = 0.069$). Similarly, the impact of competitors on mouth shape depended upon predator density. Increased competition had little effect on mouth shape when predators were absent ($P = 0.077$), but increased competition induced larger mouthparts when four predators were present ($P < 0.001$).

While the PCA made it clear that competitors and predators can induce changes in the mouthparts, it was not clear how large a change occurred. Thus, for three of the mouthparts (oral disc width, beak width, and first tooth row), we regressed the log-transformed dimension against log-transformed mass and saved the residuals. Using the mean residual values for each treatment, one can estimate the absolute size of the mouthparts for the average tadpole and then calculate the percentage difference among treatments. When we did this, we found that the three mouthparts exhibited a 20–27% decrease in size when predators were added at low competition but a 6–9% decrease in size when predators were added at high competition. We also found that the three mouthparts exhibited a 0–17% increase in size when competition was increased under no predation risk but a 12–28% increase when competition was increased under high predation risk. In short, the magnitude of change in the mouthparts was substantial.

Consistent with the earlier reporting of the mass data (Relye 2004), PC-2 (a measure of overall tadpole size)

was affected by competitors, predators, and a competitor-by-predator interaction (Table 2, Fig. 2B). Competitors had a large negative impact on overall size when there were no predators ($P < 0.001$) and a moderate negative impact when four predators were present ($P = 0.001$). Predators caused a significant reduction in overall size under low competition ($P = 0.019$) but had no effects under high competition ($P > 0.18$) except for a small increase in size under the highest predator density ($P = 0.027$).

The frequency of occurrence of the fourth tooth row was variable, but this variation was related to the predator and competitor environments in which the tadpoles

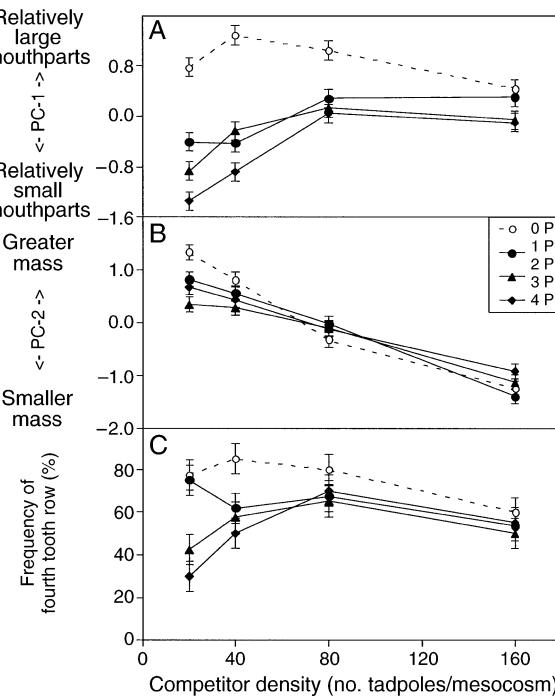


FIG. 2. Phenotypic changes in wood frog tadpoles when reared under a factorial combination of four intraspecific competitor densities (20, 40, 80, and 160 individuals) crossed with four predator densities (0P = no predators, 1P = one predator, etc.). The response variables are as follows: (A) the change in relative mouth shape (PC-1); (B) the change in mass (PC-2); and (C) the frequency of occurrence of the fourth tooth row. Data are means \pm SE.

lived (Fig. 2C). The ANOVA on the fourth tooth row indicated that occurrence was not affected by block ($F_{3,8} = 0.2, P = 0.888$) or the block-by-predator interaction ($F_{9,27} = 1.1, P = 0.367$). However, it was affected by the block-by-competitor interaction ($F_{9,27} = 2.5, P = 0.029$). Among the effects of primary interest, we found no effect of competitors ($F_{3,9} = 1.7, P = 0.234$) but there was an effect of predators ($FF_{3,9} = 8.8, P = 0.005$) and a competitor-by-predator interaction ($F_{3,9} = 2.4, P = 0.041$). When caged predators were added, there was a large decrease in the frequency of the fourth tooth row under low competition ($P = 0.006$), but not under high competition ($P = 0.457$). When competitors were added, the frequency of the fourth row tended to decrease when no predators were present and increase when four caged predators were present, but neither trend was significant ($P = 0.175$ and $P = 0.122$, respectively). In short, the occurrence of the fourth tooth row was high with low competition and no predators (78% of all tadpoles), low with low competition and many predators (30% of all tadpoles), and intermediate with high competition and many predators (55% of all tadpoles).

DISCUSSION

The results of this study demonstrate that competitors and predators have dramatic impacts on the mouth morphology of tadpoles and that these changes likely affect the growth performance of predator- and competitor-induced individuals. In general, competitors induced mouths that had wider oral discs, wider beaks, and longer tooth rows, whereas predators induced mouths that had narrower oral discs, narrower beaks, and shorter tooth rows. Moreover, the fourth tooth row was present in 80% of tadpoles raised with low competition and no predation risk, but was absent in 80% of tadpoles raised with low competition and high predation risk.

When exploring the potentially adaptive nature of environmentally induced traits, it is important that we consider whether the observed phenotypic responses are simply the outcome of allometric relationships caused by the environment's impact on the organism's growth and development (Schlichting and Pigliucci 1998). Assuming that the relative size of mouthparts increases over ontogeny and given that tadpole mass and development are correlated in wood frogs (Relyea 2005), a strictly allometric mechanism would cause both predator- and competitor-induced tadpoles, which grow more slowly, to have relatively smaller mouthparts and fewer tooth rows. However, we found that the two environments had opposing effects on tadpole mouthparts, arguing against a simple allometric explanation for the observed changes.

Several studies have documented that tadpole mouthparts can exhibit variation in nature (Bresler and Bragg 1954, Bragg and Hayes 1963, Bragg et al. 1963, Hampton and Volpe 1963, Pfennig 1992b). As with most

traits, mouth variation can have a genetic basis when examined under common-garden conditions (Hampton and Volpe 1963, Gollmann and Gollmann 1995). However, natural variation in mouthparts has been frequently assumed (either implicitly or explicitly) to be primarily genetic, allowing analyses of biogeography among populations (Chou and Lin 1997) and discrimination among species (Dubois 1995, Altig and McDiarmid 1999). While it is known that intraspecific variation exists, the underlying cause of this variation has been uncertain (e.g., Hampton and Volpe 1963). The important discovery in our study is that much of the variation in mouthparts is actually inducible by predators and competitors.

Few data exist on the environmental induction of mouthparts. In larval amphibians, higher rearing temperatures can disrupt proper mouth development (Bresler 1954) and competition can induce carnivorous mouthparts in a few species of tadpoles and larval salamanders (Bragg 1956, Pedersen 1991, Pfennig 1992a, b, Reilly et al. 1992, Walls et al. 1993). The competitor-induced mouth changes documented in our study were not associated with carnivorous morphology; the tadpoles remained herbivorous. In an earlier study, Relyea (2000) examined the length of just the longest tooth row in wood frogs and leopard frogs (*Rana pipiens*) reared in field pens alone and together. He found that adding the heterospecific competitor caused a relative increase in the longest tooth row of both species. Little research has examined the impact of predators on prey mouthparts although Relyea (2000) found that adding caged predators reversed the effect of competitor induction on the longest tooth row. The current study took a much more extensive approach by discovering that a whole suite of oral dimensions change across a wide array of predator and competitor combinations. If this result is common to other amphibian species (as is true for other predator- and competitor-induced traits), then environmentally induced variation in mouthparts is likely a general phenomenon.

The induction of mouthpart changes also occurs in non-amphibian taxa. For example, a number of organisms alter their foraging morphology when consuming different diets (Bernays 1986, Meyer 1987, Wainwright et al. 1991, Reilly et al. 1992). In most cases, the diet-induced changes in mouth morphology improve the foraging ability on the inducing diet, suggesting an adaptive response. If it is competition that forces organisms to forage on different diets, then competitor-induced changes in mouthparts may be more common than we currently appreciate. We are unaware of any studies that have documented predator-induction of mouthparts in other taxa; however, this probably reflects a lack of investigation. It may be that many species of inducible prey build their morphological defenses at the cost of smaller mouthparts and that this morphological trade-off sets up the performance trade-off (predator deterrence vs. growth) that is commonly

observed across a diversity of prey species (Tollrian and Harvell 1999).

The changes in mouth morphology documented herein are part of a suite of traits induced by predators and competitors. Over the past decade, researchers have discovered that predators can induce larval anurans (via chemical cues) to hide more, feed less, and develop relatively large tails and small bodies, and these responses allow tadpoles to avoid predators and escape predatory strikes (Van Buskirk 2000, Relyea 2001, 2003). However, the smaller body contains shorter intestines, thereby reducing foraging efficiency and growth (Van Buskirk 2002, Relyea 2003, Relyea and Auld 2004). The current study suggests that predator-induced reductions in the scraping mouthparts should further reduce the ability of the tadpole to consume periphyton and contribute substantially to the reduction in growth. Competitors induce tadpoles (via per capita food availability) to forage more and develop relatively smaller tails, larger bodies, and relatively longer intestines that should allow more efficient digestion (Sibly 1981, Relyea 2002a, 2004, Relyea and Hoverman 2003, Relyea and Auld 2004). The current study suggests that competitors also induce larger scraping mouthparts, which should substantially increase the amount of periphyton that the tadpoles can acquire. All of this leads to greater growth by competitor-induced tadpoles compared to uninduced tadpoles (Relyea 2002a).

Predator and competitor environments had interactive effects on mouthparts. Similar interactive effects have been observed in examinations of the tail and body morphology of tadpoles (Relyea and Hoverman 2003, Relyea 2004) and also common across a variety of prey species and in different types of prey traits (Gilliam and Fraser 1987, Werner and Anholt 1996, Van Buskirk and Yurewicz 1998, Weetman and Atkinson 2002). When competitors and predators induce opposite phenotypic effects, competitor-induced effects are generally larger under high predation risk than low predation risk, and predator-induced effects are generally larger under low competition than under high competition. In the current study, this suggests that the tadpole mouth responses are not threshold responses that respond to environmental variation in a step-wise fashion, but fine-tuned responses to the two opposing forces of predation and competition (Relyea 2004). Hence, individuals can balance these opposing forces and arrive at an effective compromise between the risk of predation and the risk of starvation.

Conclusions

The evolution of plasticity relies upon functional trade-offs that occur across different ecological contexts. In the case of predator- and competitor-induced plasticity, the mechanisms underlying predator resistance have been identified, but the mechanisms underlying differential growth ability have not. Our study

appears to be the first to discover that predator and competitor environments can induce changes in the foraging morphology of animals and that these induced changes help explain the growth costs associated with predator-induced defenses and the growth benefits associated with competitor-induced offenses. If these insights prove to be generalizable across other taxa, then we may have discovered an important functional mechanism that helps explain the repeated evolution of predator- and competitor-induced traits.

ACKNOWLEDGMENTS

We thank Jason Hoverman, Nancy Schoeppner, and Matt Schult for helping to execute the experiments. We also thank Jason Hoverman and Nancy Schoeppner for providing helpful criticisms of the manuscript. This work was funded by the National Science Foundation grant DEB-0234327 to R. A. Relyea (including an REU supplement) and a McKinley grant to J. R. Auld.

LITERATURE CITED

- Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* **294**:321–326.
- Altig, R., and R. W. McDiarmid. 1999. Diversity: familial and generic characterizations. Pages 24–51 in R. W. McDiarmid and R. Altig, editors. *Tadpoles: the biology of amphibian larvae*. University of Chicago Press, Chicago, Illinois, USA.
- Bernays, E. A. 1986. Diet-induced head allometry among foliage-chewing insects and its importance for graminivores. *Science* **231**:495–497.
- Bragg, A. N. 1956. Dimorphism and cannibalism in tadpoles of *Scaphiopus bombifrons* (Amphibia, Salientia). *Southwestern Naturalist* **1**:105–108.
- Bragg, A. N., and S. Hayes. 1963. A study of labial teeth rows in tadpoles of Couch's spadefoot. *Wasmann Journal of Biology* **21**:149–154.
- Bragg, A. N., R. Mathews, and R. Kingsinger, Jr. 1963. The mouthparts of tadpoles of Hunter's spadefoot. *Herpetologica* **19**:284–285.
- Bresler, J. 1954. The development of labial teeth of Salientian larvae in relation to temperature. *Copeia* 1954:207–211.
- Bresler, J., and A. N. Bragg. 1954. Variations in the rows of labial teeth in tadpoles. *Copeia* 1954:255–257.
- Chou, W.-H., and J.-Y. Lin. 1997. Geographical variations of *Rana sauteri* (Anura: Ranidae) in Taiwan. *Zoological Studies* **36**:201–221.
- Cipollini, D., C. B. Purrington, and J. Bergelson. 2003. Costs of induced responses in plants. *Basic and Applied Ecology* **4**:79–89.
- Dubois, A. 1995. Keratodont formulae in anuran tadpoles: proposals for a standardization. *Journal of Zoological Systematics and Evolutionary Research* **33**:I–XV.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**:1856–1862.
- Gollmann, B., and G. Gollmann. 1995. Morphological variation in tadpoles of the *Geocrinia laevis* complex: regional divergence and hybridization (Amphibia, Anura, Myobatrachinae). *Journal of Zoological Systematics and Evolutionary Research* **33**:32–41.
- Hampton, S. H., and E. P. Volpe. 1963. Development and interpopulation variability of the mouthparts of *Scaphiopus holbrookii*. *American Midland Naturalist* **70**:319–328.
- Kats, L. B., J. W. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology* **69**:1865–1870.
- Meyer, A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their im-

- plications for specialization in cichlid fishes. *Evolution* **41**: 1357–1369.
- Moran, N. A. 1992. The evolutionary maintenance of alternative phenotypes. *American Naturalist* **139**:971–989.
- Pedersen, S. C. 1991. Dental morphology of the cannibal morph in the tiger salamander, *Ambystoma tigrinum*. *Ampibia-Reptilia* **12**:1–14.
- Petrranka, J. W., L. B. Kats, and A. Sih. 1987. Predator–prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. *Animal Behaviour* **35**:420–425.
- Pfennig, D. W. 1992a. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionary stable strategy. *Evolution* **46**:1408–1420.
- Pfennig, D. W. 1992b. Proximate and functional causes of polyphenism in an anuran tadpole. *Functional Ecology* **6**: 167–174.
- Pfennig, D. W., and P. J. Murphy. 2000. Character displacement in polyphenic tadpoles. *Evolution* **54**:1738–1749.
- Reilly, S. M., G. V. Lauder, and J. P. Collins. 1992. Performance consequences of a trophic polymorphism: feeding behavior in typical and cannibal phenotypes of *Ambystoma tigrinum*. *Copeia* 1992:672–679.
- Relyea, R. A. 2000. Trait-mediated effects in larval anurans: reversing competition with the threat of predation. *Ecology* **81**:2278–2289.
- Relyea, R. A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. *Ecology* **82**:523–540.
- Relyea, R. A. 2002a. Competitor-induced plasticity in tadpoles: consequences, cues, and connections to predator-induced plasticity. *Ecological Monographs* **72**:523–540.
- Relyea, R. A. 2002b. The many faces of predation: how selection, induction, and thinning combine to alter prey phenotypes. *Ecology* **83**:1953–1964.
- Relyea, R. A. 2003. How prey respond to combined predators: a review and an empirical test. *Ecology* **84**:1827–1839.
- Relyea, R. A. 2004. Fine-tuned phenotypes: tadpole plasticity under 16 combinations of predators and competitors. *Ecology* **85**:172–179.
- Relyea, R. A. 2005. The heritability of inducible defenses in tadpoles. *Journal of Evolutionary Biology*, *in press*.
- Relyea, R. A., and J. R. Auld. 2004. Having the guts to compete: how intestinal plasticity explains costs of inducible defenses. *Ecology Letters* **7**:869–875.
- Relyea, R. A., and J. T. Hoverman. 2003. The impact of larval predators and competitors on the morphology and fitness of juvenile tree frogs. *Oecologia* **134**:596–604.
- Relyea, R. A., and E. E. Werner. 1999. Quantifying the relation between predator-induced behavior and growth performance in larval anurans. *Ecology* **80**:2117–2124.
- Schlücht, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland, Massachusetts, USA.
- Sibly, R. M. 1981. Strategies of digestion and defecation. Pages 109–139 in C. R. Townsend and P. Calow, editors. Physiological ecology. Blackwell Scientific Publications, Oxford, UK.
- Skelly, D. K. 1994. Activity level and susceptibility of anuran larvae to predation. *Animal Behaviour* **47**:465–468.
- Skelly, D. K., and J. Golon. 2003. Assimilation of natural benthic substrates by two species of tadpoles. *Herpetologica* **59**:37–42.
- Stearns, S. C. 1989. The evolutionary significance of phenotypic plasticity. *BioScience* **39**:436–445.
- Tollrian, R., and D. Harvell, editors. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.
- Van Buskirk, J. 2000. The costs of an inducible defense in anuran larvae. *Ecology* **81**:2813–2821.
- Van Buskirk, J. 2002. A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. *American Naturalist* **160**:87–102.
- Van Buskirk, J., S. A. McCollum, and E. E. Werner. 1997. Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* **51**:1983–1992.
- Van Buskirk, J., and R. A. Relyea. 1998. Selection for phenotypic plasticity in *Rana sylvatica* tadpoles. *Biological Journal of the Linnean Society* **65**:301–328.
- Van Buskirk, J., and K. L. Yurewicz. 1998. Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos* **82**:20–28.
- Via, S., and R. Lande. 1985. Genotype–environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**:505–522.
- Wainwright, P. C., C. W. Osenberg, and G. C. Mittelbach. 1991. Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus*): environmental effects on ontogeny. *Functional Ecology* **5**:40–55.
- Walls, S. C., S. S. Belanger, and A. R. Blaustein. 1993. Morphological variation in a larval salamander: dietary induction of plasticity in head shape. *Oecologia* **96**:162–168.
- Wassersug, R. J. 1976. Oral morphology of anuran larvae: terminology and general description. *Occasional Papers of the Museum of Natural History* **48**:1–23.
- Wassersug, R. J. 1980. Internal oral features of larvae from eight anuran families: functional, systematic, evolutionary and ecological considerations. *Miscellaneous Publications of the Museum of Natural History*, University of Kansas **68**:1–146.
- Wassersug, R. J., and M. Yamashita. 2001. Plasticity and constraints on feeding kinematics in anuran larvae. Comparative biochemistry and physiology A: Molecular and Integrative Physiology **131**:183–195.
- Weetman, D., and D. Atkinson. 2002. Antipredator reaction norms for life history traits in *Daphnia pulex*: dependence on temperature and food. *Oikos* **98**:299–307.
- Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects in anuran larvae. *Ecology* **77**:157–169.
- West-Eberhard, M. J. 2003. Developmental plasticity and evolution. Oxford University Press, Oxford UK.