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Predator-induced morphological changes in an amphibian: predation by dragonflies affects tadpole shape and color

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Abstract Predator-induced defenses are well studied in plants and invertebrate animals, but have only recently been recognized in vertebrates. Gray treefrog (*Hyla chrysoscelis*) tadpoles reared with predatory dragonfly (*Aeshna umbrosa*) larvae differ in shape and color from tadpoles reared in the absence of dragonflies. By exposing tadpoles to tail damage and the non-lethal presence of starved and fed dragonflies, we determined that these phenotypic differences are induced by non-contact cues present when dragonflies prey on *Hyla*. The induced changes in shape are in the direction that tends to increase swimming speed; thus, the induced morphology may help tadpoles evade predators. Altering morphology in response to predators is likely to influence interactions with other species in the community as well.

Key words *Aeshna* · *Hyla* · Inducible defense · Phenotypic plasticity · Predation

Introduction

Inducible defensive structures are those expressed only in individuals exposed to some predator-related stimulus during development (Havel 1987; Dodson 1989; Karban and Myers 1989; Harvell 1990). While constitutive (i.e., fixed and genetically predetermined) defenses typically provide broad-spectrum protection, inducible defenses may vary depending on the specific predator involved

(Stemberger and Gilbert 1987; Zagarese and Marinone 1992), essentially permitting an individual to fine-tune its phenotype to its environment. Defensive morphologies are thought to be costly to produce and maintain and are therefore detrimental to fitness in the absence of predators (Lively 1986; Clark and Harvell 1992; Moran 1992). Inducible defenses thus appear to be an optimal solution in situations where predators are variable in their presence or abundance, and prey can reliably detect predators via nonlethal encounters or other cues (Dodson 1989). This view is supported by the observation that all known predator-induced defenses in animals are found in aquatic habitats, where waterborne chemicals provide accurate information about local predation regimes (Havel 1987).

Vertebrates are conspicuous by their absence in Havel's (1987) review of organisms having inducible defenses. Recently, a few studies have suggested that induced morphological defenses occur in aquatic vertebrates. Brönmark and Miner (1992) found that carp develop deeper bodies in response to piscivorous pike. Smith and Van Buskirk (1995) found that tail shape in chorus frog tadpoles varies among ponds with and without odonate predators. Caldwell (1982) found that tail color in cricket frog tadpoles varied among ponds with and without odonate predators, but interpreted this as evidence for genetic differences among populations. In this paper, we demonstrate that tadpoles of the gray treefrog, *Hyla chrysoscelis*, respond to predation on conspecifics by altering body shape and color.

H. chrysoscelis breeds primarily in temporary ponds that dry at intervals of a few weeks to a few years, but may also breed in more permanent waters (Martof et al. 1980; Semlitsch and Gibbons 1988; S.A. McCollum, personal observation). The abundance of predatory dragonflies in temporary ponds varies over space and time, depending on its history of extinctions (caused by e.g., drying or scouring) and subsequent colonizations (Smith 1983; Van Buskirk 1990). When large dragonflies are present, they can constitute a substantial source of mortality (Caldwell et al. 1980; Smith 1983; Van Buskirk

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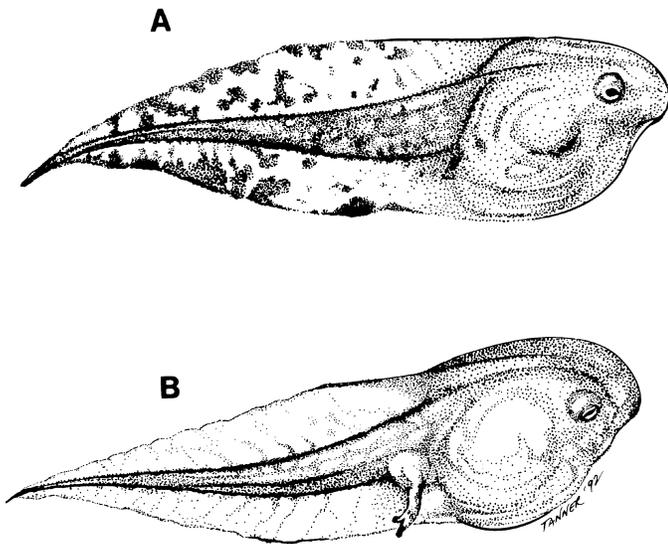


Fig. 1 Representative tadpoles of the dragonfly morph (A) and the typical morph (B) (redrawn from photographs). Differences in body shape cause the two morphs to lie in slightly different orientations

1988; McCollum 1993). In a previous experiment (McCollum 1993), we observed that *H. chrysoscelis* tadpoles in ponds containing dragonfly larvae (*Aeshna umbrosa*) have a relatively deep tail fin, which is yellow to red with distinct black spots (dragonfly morph, Fig. 1A). Tadpoles in ponds without predators lack these features (typical morph, Fig. 1B). A companion study (McCollum and Van Buskirk 1996) indicates that the dragonfly morph is less susceptible to predators than is the typical morph, but survives less well when not at risk of predation.

This study addresses three questions. (1) Are dragonfly morph tadpoles induced by cues from dragonflies? (2) If so, what cues are sufficient to trigger this induction? Induction could require contact cues such as a non-lethal injury, non-contact cues, such as exposure to chemicals produced by dragonflies, or a combination of contact and non-contact cues. (3) Do the morphological differences between the two morphs affect swimming performance, which could improve escape ability? These questions are important in determining if the observed phenotypic variation represents an inducible defense.

Materials and methods

The tadpoles used in this experiment were full sibs collected as eggs from a single pair of *H. chrysoscelis* on 6 August 1990, and were reared in a covered, outdoor wading pool at the Duke University Zoology Field Station in Durham County N.C. We took these tadpoles into the laboratory on 20 September, and maintained them at room temperature on a 14-h light:10-h dark cycle.

We exposed groups of ten tadpoles to two levels of tail damage and three levels of predator stimuli in a 2×3 full factorial experiment. These treatment combinations provided most of the range of possible inducing cues. For the damage treatments, we either cut off the distal half of the tadpole's tail ("clipped") or left the tadpole

intact ("intact"). To ensure that the tadpoles in the two damage treatments were similar, we took pairs of tadpoles matched for size, anesthetized both in 0.2% chloretone, then cut off the distal half of the tail of one of the tadpoles. All tadpoles recovered from the anesthesia and the surgery. On 21 September, we randomly assigned groups of ten clipped or intact tadpoles to 40-l aquaria containing 8 l of carbon-filtered water and a cylindrical cage (10 cm diameter \times 20 cm long) constructed of fiberglass window screen. Within the cage was one of three nonlethal predator treatments: (1) "none" – nothing, i.e., an empty cage; (2) "starved" – a dragonfly larva (*A. umbrosa*) which had not been fed for at least 2 days, and (3) "fed" – a dragonfly larva which was fed one tadpole daily. Each of the six treatment combinations was replicated four times in a randomized complete-block design, with laboratory shelves serving as replicate blocks. To alleviate the need for water changes which would dilute chemical cues, we fed the tadpoles a ration of finely ground fish food sufficient for rapid growth without fouling the water and we periodically removed solid wastes with a fine mesh net.

On 4 October, the first *Hyla* metamorphosed and we terminated the experiment. On 5 October, each tadpole was weighed and scored as either having distinct black tail spots or not. Four tadpoles from each tank were selected at random for detailed study of swimming speed and morphology. We measured swimming speed for each of these four tadpoles in a recirculating flow tank (Vogel and La-Barbera 1978): we placed the tadpole in the tank in still water, then increased the flow at a constant rate until the tadpole was immobilized against a screen at the downstream end of the tank. The resulting measure, while presented in units of speed (cm/s) is a composite of speed and stamina; to attain a higher speed, a tadpole also swam longer, since it had to first swim at all the lower speeds. We selected this measure of swimming performance because we found it more repeatable than measuring initial burst speed or acceleration in still water from video recordings.

Tadpoles were then preserved in 10% formalin. We collected the following morphological data from the preserved tadpoles: body length (tip of snout to most posterior point on body excluding cloacal tailpiece), tail length (anterior dorsal insertion of tail on body to tip of tail), maximum tail depth, maximum body depth and maximum body width. In order to reduce the number of dimensions needed to describe the variation in shape, these morphometric data were log transformed and subject to principal-component analysis (PCA) using the covariance matrix (Marcus 1990).

We used multivariate analysis of variance (MANOVA) to determine if there were significant overall differences among treatments in the response vector including tank means of tadpole growth rate, shape (PC2, see Results), and color. We used univariate analysis of variance (ANOVA) to elucidate which responses contributed to a significant multivariate response.

We tested for differences among treatments in size-adjusted swimming speed by analyzing the residuals of the regression of log swimming speed on size (PC1, see Results) with ANOVA. These residuals are the deviations from the expected speed for an animal of a given size.

To determine if variation in tadpole shape influenced swimming speed, we regressed adjusted swimming speed on the shape (PC2) scores obtained from the PCA. We also conducted these analyses on a sample of tadpoles collected by dipnetting from two local ponds and one naturally colonized 2.13-m-diameter stock tank. Dipnetting revealed dragonflies in only one of these sources. The wild-collected sample provided an independent measure of the relationships between various aspects of shape and swimming speed.

In the MANOVA and all ANOVAs, tank means were analyzed. Proportions were arcsine-square root transformed prior to analyses. Block was treated as a random effect; we used the predator \times block mean square as the denominator for *F*-tests of predator main effects and the damage \times block mean square as the denominator for tests of damage main effects. In the event of a significant ANOVA, we used Student-Newman-Keuls tests to determine which means differed from one another. PC-SAS was used for all analyses (SAS 1988).

Results

The first two axes (PC1 and PC2) of the PCA of *H. chrysoscelis* morphology summarize approximately 80–85% of the variation in tadpole size and shape (Table 1). Since all of the morphological variables correlate positively with PC1, we interpret PC1 as a size axis. Since PC2 contrasts depth and length measures, primarily those of the tail, we interpret PC2 as a shape axis that describes variation from long, shallow-tailed tadpoles to short, deep-tailed ones. Since there is close concordance between the field and laboratory results for PC2, this axis describes similar variation in shape in both samples.

MANOVA indicated that only the predator treatment had a significant effect on the response vector of tadpole shape (PC2), tail color (arcsin $\sqrt{\text{proportion black-spotted}}$), and log growth rate (Table 2). Damage had no significant effect in the overall MANOVA, even though the morphological responses of clipped tadpoles were always slightly greater than the responses of otherwise similar intact tadpoles (Fig. 2).

Table 1 Principal component analysis of *Hyla chrysoscelis* tadpoles generated in the experiment described in the text (*Lab*) and wild-caught tadpoles (*Field*). The elements of these eigenvectors are the correlation coefficients of each of the morphometric variables with size (*PC1*) and shape (*PC2*) scores

Morphometric variable	PC1		PC2	
	Lab	Field	Lab	Field
Tail length	0.51	0.63	-0.53	-0.67
Body length	0.37	0.37	-0.27	-0.15
Body width	0.40	0.36	-0.06	0.21
Body depth	0.46	0.39	0.01	0.45
Tail depth	0.49	0.43	0.80	0.53
Percent variance	79.2	68.4	10.2	16.4

Tadpoles reared with fed *Aeshna* were significantly more likely to have black spots on their tails than were tadpoles in either of the other predator treatments (Fig. 2A, Table 2). Tail damage had no significant effect on tail color (Fig. 2A, Table 2).

Tadpole shape (PC2) differed among predator treatments, with tadpoles exposed to fed dragonflies having deeper tails (higher PC2 scores) than tadpoles from the

Table 2 MANOVA and ANOVAs of *H. chrysoscelis* tadpole growth, shape, and tail color responses to tail damage and non-contact cues that indicate predator presence

MANOVA				
Source	<i>df</i>	Wilks' lambda	<i>F</i>	<i>P</i>
Damage	3,1	0.1161	2.5388	0.4252
Predator	6,8	0.0073	14.2426	0.0007
Block	9, 9.9 ^a	0.2437	0.8635	0.5827
Damage × predator	6,8	0.5078	0.6346	0.7673
Damage × block	9, 9.9 ^a	0.1223	1.5062	0.2668
Predator × block	18, 11.8 ^a	0.0547	1.1762	0.3966
ANOVAs				
Source	<i>df</i>	Mean square	<i>F</i>	<i>P</i>
Tail color				
Damage	1,3	0.0698	0.8566	0.4229
Predator	2,6	1.9621	44.5683	0.0003
Block	3,6	0.0451	0.5248	0.6811
Damage × predator	2,6	0.0224	0.2607	0.7788
Damage × block	3,6	0.0815	0.9487	0.4744
Predator × block	6,6	0.0440	0.5125	0.7819
Error	6	0.0859		
Shape (PC 2)				
Damage	1,3	0.0114	8.9159	0.0583
Predator	2,6	0.0067	10.5959	0.0107
Block	3,6	0.0014	1.800	0.2473
Damage × predator	2,6	0.0004	0.5467	0.6052
Damage × block	3,6	0.0013	1.5995	0.2854
Predator × block	6,6	0.0006	0.7931	0.6072
Error	6	0.0009		
Growth rate				
Damage	1,3	0.0109	5.8433	0.0944
Predator	2,6	0.0465	14.8210	0.0048
Block	3,6	0.0016	0.47	0.7161
Damage × predator	2,6	0.0005	0.1395	0.8725
Damage × block	3,6	0.0019	0.5434	0.6703
Predator × block	6,6	0.0031	0.9152	0.5415
Error	6	0.0034		

^a Satterthwaite's approximated degrees of freedom (Satterthwaite 1946; SAS 1988)

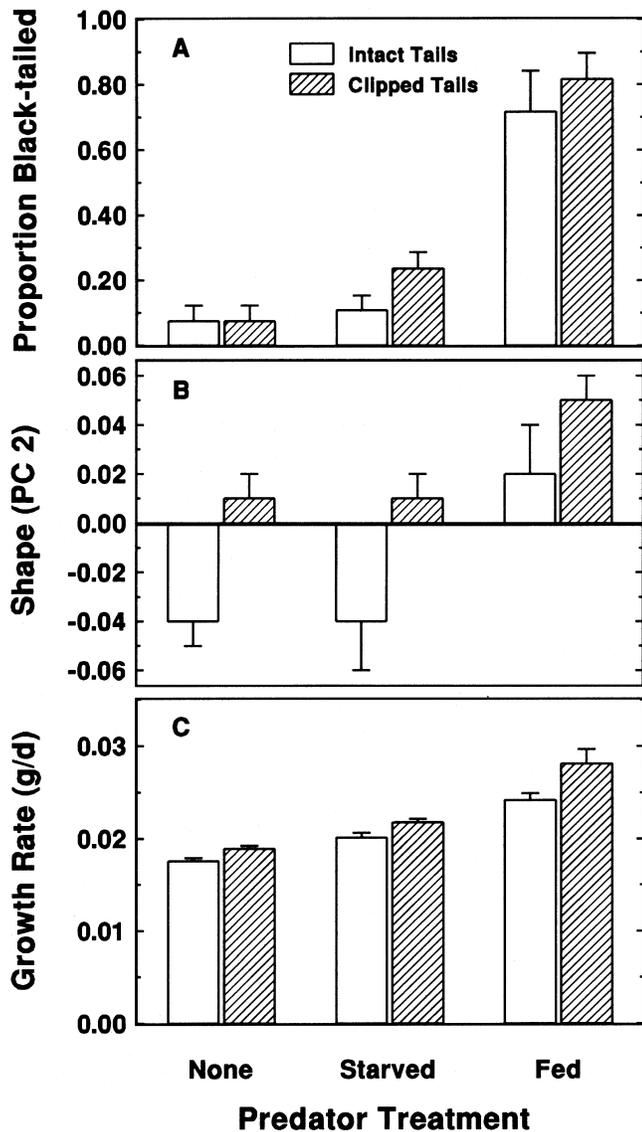


Fig. 2 Responses (mean \pm SE) of *Hyla chrysoscelis* tadpoles to tail damage and the non-lethal presence of starved or fed *Aeshna umbrosa*. Fed predators significantly increased the proportion of black-tailed tadpoles (A) the tail shape score (from the second axis of a principal component analysis of tadpole morphology; see text) (B), and growth rate (C). Tail damage did not significantly influence any response. Positive values for tail shape (PC2) indicate relatively deep tails, while negative values indicate shallow, long tails (Table 1)

other two predator treatments (Fig. 2B, Table 2). Tail damage had only a marginally significant effect on shape (Fig. 2B, Table 2). While this univariate effect of damage was nearly significant, recall that the MANOVA indicated no overall effect of damage (Table 2).

Predator treatment had a significant effect on growth rate (Table 2). Tadpoles grew faster when reared with fed *Aeshna* (Fig. 2C). Damaged tadpoles tended to grow faster than intact tadpoles. While the effect of damage was not significant, it was in the direction that indicates that tail loss did not reduce growth rate as one might expect.

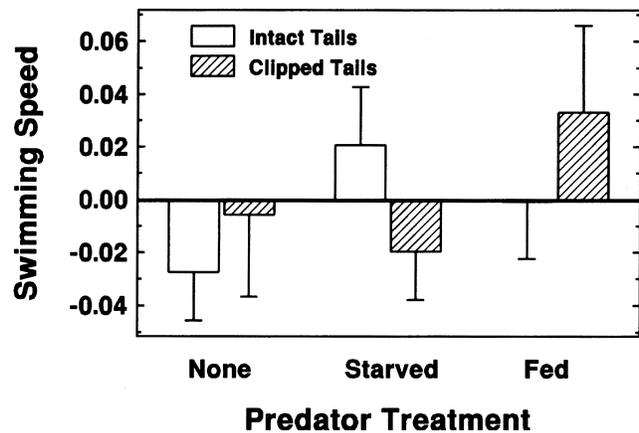


Fig. 3 Size-adjusted swimming speeds (mean \pm SE) of *H. chrysoscelis* tadpoles exposed to tail damage and the non-lethal presence of starved or fed *A. umbrosa*. Adjusted swimming speed is the residual of log swimming speed (cm/s) regressed on tadpole size, the first axis of a principal component analysis of tadpole morphology

Swimming speed did not differ significantly among treatments (Fig. 3, Table 3). However, swimming speed was positively related to a tadpole's shape score (Fig. 4) in both the laboratory and the field-collected samples, with the relationships being stronger in the field-collected tadpoles.

Discussion

From these results it is clear that the dragonfly morph is induced and that non-contact cues associated with predation by dragonflies on tadpoles are sufficient to induce both the shape and color changes characteristic of dragonfly morph tadpoles. Starved dragonflies do not provide a sufficient stimulus to induce any significant changes. The fact that tail damage has a marginal effect on tadpole shape, but does not influence either growth rate or tail color, suggests that regenerated tails do not return to their normal shape in 2 weeks. Damage alone is not sufficient to induce all aspects of the dragonfly morph, but may enhance certain of its features. The critical inducing cue appears to be either some metabolite of digestion of tadpoles by dragonflies (e.g., Parejko and Dodson 1990), or perhaps an alarm pheromone released by tadpoles when attacked (e.g., Hews 1988).

Whatever the exact cue, the dragonfly-induced phenotype appears to be an adaptive response. McCollum and Van Buskirk (1996) demonstrated that dragonfly morph tadpoles are less susceptible to predation by dragonflies than typical tadpoles. In these tadpoles, color, shape, and growth rate change together. Exactly how much each feature of the dragonfly-induced phenotype contributes to a tadpole's defense is unknown, but each has at least one potential benefit.

The predator-induced color pattern may direct strikes by predators toward the tail rather than the vulnerable

Table 3 ANOVA of size-adjusted swimming speeds of *H. chrysoscelis* tadpoles exposed to tail damage and non-contact cues that indicate predator presence

Source	df	Mean square	F	P
Damage	1,3	0.0002	0.0678	0.8113
Predator	2,6	0.0021	1.1705	0.3722
Block	3,6	0.0037	1.4919	0.3090
Damage × predator	2,6	0.0032	1.2719	0.3463
Damage × block	3,6	0.0023	0.9089	0.4904
Predator × block	6,6	0.0018	0.7341	0.6415
Error	6	0.0018		

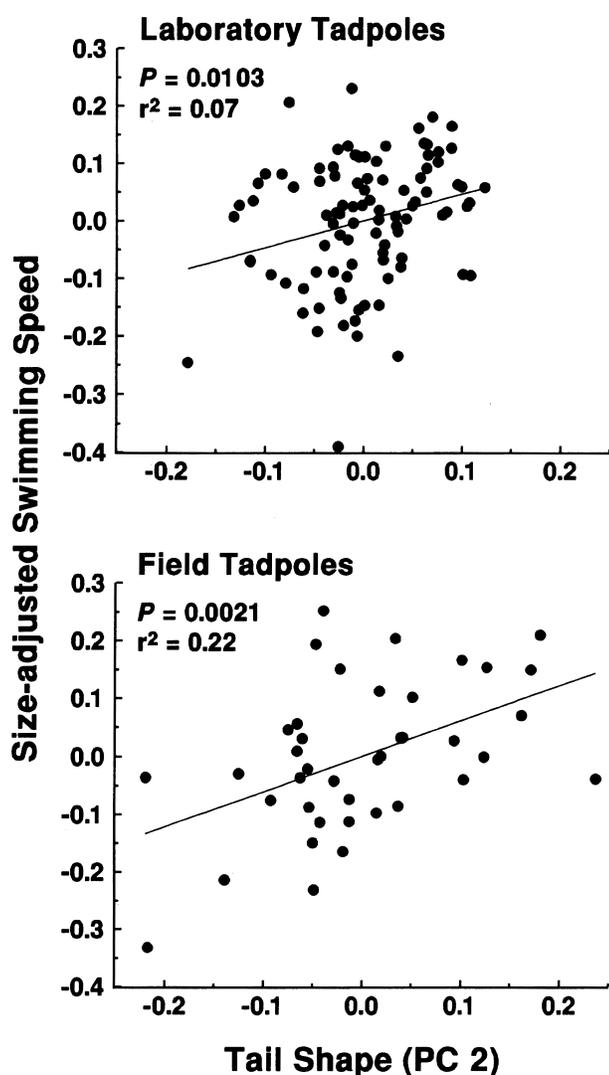


Fig. 4 The relationship between swimming speed and tail shape (PC2 – the second axis of a principal component analysis of tadpole morphology) of laboratory-reared and field-collected *H. chrysoscelis* tadpoles

head and body region (Caldwell 1982; Meadows 1993). Strikes on the body are usually fatal; strikes to the tail are of little consequence if the tadpole escapes (Semlitsch 1990; Wilbur and Semlitsch 1990; Figiel and Semlitsch 1991). Alternatively, the color pattern could act as camouflage, breaking up the tadpole's outline and making it more cryptic. If either of these is the case,

dragonfly morph tadpoles are defended by induced coloration.

Increased tail depth should improve caudal fin transient propulsion (Webb 1975, 1984), resulting in faster starts and powered turns, both of which may help to evade predators. While inactivity in tadpoles may reduce detection, improved swimming ability can help tadpoles escape from predators once they are detected (Caldwell et al. 1980; Lawler 1989; Azevedo-Ramos et al. 1992). Though tadpole swimming speed did not vary significantly among treatments (Fig. 3, Table 3), swimming speed was significantly related to tadpole shape (Fig. 4), and the morphological shifts induced by predators were in the direction that tended to increase swimming speed.

By growing faster, tadpoles may also reduce their cumulative predation risk by quickly reaching an invulnerable size (Caldwell et al. 1980; Smith 1983; Travis et al. 1985) or by metamorphosing earlier (Skelly and Werner 1990; Wilbur and Fauth 1990), leaving the pond and the aquatic predators behind. Rapid growth leads to early metamorphosis and/or large size at metamorphosis (Wilbur and Collins 1973; Werner 1986; Alford and Harris 1988). This translates into increased fitness via early onset of reproduction or increased adult size and thus increased fecundity (Smith 1987; Semlitsch et al. 1988). Whether rapid growth is an induced response to dragonflies is still an open question. Dragonflies could trigger changes in the tadpoles' feeding rate, efficiency, or allocation. Enhanced growth of tadpoles in the presence of caged dragonflies has been observed several times in experiments in laboratory aquaria and outdoor stock tanks (McCollum 1993; McCollum and Van Buskirk 1996; E.E. Werner, personal communication). However, the increased growth in the presence of fed predators in container experiments may be an artifact resulting from nutrients added to the system when the predators are fed. Skelly (1992) observed reduced growth in *H. versicolor* tadpoles exposed to caged salamanders in field enclosures. A definitive answer on this issue must await further experimentation.

Induced morphological defenses in animals tend to occur in aquatic habitats in which the risk of predation is spatially or temporally variable (Dodson 1989). We presume this is because water is a good vehicle for chemical signals, which can convey information about predators without physical contact between predators and prey. By-products of predation are unequivocal indicators of dangerous predators, and make reliable cues for inducing defenses. Because predators are highly

variable within and among temporary pond habitats (Smith 1983; Van Buskirk 1990) and prey can reliably assay predation risk in aquatic habitats (Petranka et al. 1987; Hews 1988; Kats et al. 1988; R. Relyea, personal communication), we might expect inducible defenses to be common among both invertebrates and vertebrates in temporary pond communities. If this type of plasticity is widespread, we should consider the strengths of ecological interactions not as constant, but as dependent on the community in which the interacting species are found. Clearly, predators can affect prey populations other than by simply consuming individuals. Induced changes in the traits of a species may alter its interactions with other species in the community. To date, research on such trait-transmitted effects has mostly focused on the consequences of behavioral responses to predators and competitors (Soluk and Collins 1988; Werner 1992; Abrams 1995; Werner and Anholt 1996). Although behavior clearly plays an important role in multispecies interactions, plasticity in morphology may be equally important. For example, the susceptibility of *H. chrysoscelis* tadpoles to *Anax* larvae appears to be more strongly associated with tadpole tail color and shape than with behavior (McCullum and Van Buskirk 1996). We believe that separating trait-transmitted effects into components attributable to behavior and morphology will enhance our understanding of species interactions and aid in the development of mechanistic models of multispecies interactions.

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