

PREDATORS COME AND PREDATORS GO: THE REVERSIBILITY OF PREDATOR-INDUCED TRAITS

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Abstract. While numerous studies have been conducted on the ecology and evolution of phenotypic plasticity, to really understand plasticity we need to expose organisms to different environments over several ontogenetic stages. In this way, we can examine whether organisms change their phenotypic strategy over ontogeny, whether there are developmental windows that constrain the development of plastic traits, and whether behavior is more reversible than morphology if the environment reverts back to its original state. I addressed these questions by examining predator-induced plasticity in gray treefrog tadpoles (*Hyla versicolor*). Using aquatic mesocosms, I reared tadpoles with a constant absence of predators, a constant presence of predators, and the addition or removal of predators at three different times during their larval period. Tadpoles changed their phenotypic strategy over ontogeny; early in ontogeny they responded to predators by hiding, reducing their activity, and developing relatively deep tail fins. Later in ontogeny the tadpoles no longer employed behavioral defenses but relied on a combination of greater mass, deeper tails, and shorter bodies. The phenotypic changes were inducible throughout most of ontogeny, suggesting that there were few developmental windows. Activity, tail depth, and body depth were highly reversible early in ontogeny but less reversible later in ontogeny; because hiding was only used early in ontogeny, I could not assess its reversibility. This reversibility should affect not only the induced species, but will likely transmit the effects throughout the larger ecological community.

Key words: *anuran*; *Hyla versicolor*; phenotypic plasticity; predator-induced plasticity; tadpole.

INTRODUCTION

The ability of individuals to alter their phenotype in response to environmental changes is a pervasive phenomenon. Over the past century, and especially during the past two decades, we have accumulated a vast amount of data on phenotypic plasticity. We have determined which organisms are plastic (nearly all are, Travis 1994), which traits have greater ranges of plasticity (e.g., behavioral vs. morphological traits [Relyea 2001a]), whether there are costs and benefits of alternative phenotypes (Wimberger 1991, Kingsolver 1995, Dudley and Schmitt 1996, Van Buskirk and Relyea 1998, Relyea 2002a), and whether environmental induction can have larger, community level effects (Werner and Anholt 1996, Beckerman et al. 1997, Relyea 2000).

A substantial portion of what we know about phenotypic plasticity comes from studies of predator- and herbivore-induced defenses (Lima and Dill 1990, Weis 1992, Karban and Baldwin 1997, Kats and Dill 1998, Tollrian and Harvell 1999). However, in much of this work our focus has largely been on the induction of organisms at a single ontogenetic stage. In a recent review, Schlichting and Pigliucci (1998) argued that to really understand the ecology and evolution of phe-

notypic plasticity we need to examine phenotypes over multiple ontogenetic stages. This more extensive approach has two primary benefits. First, by examining phenotypes over ontogeny, we can observe how an organism's phenotypic strategy changes over time (Pigliucci 1997, Baldwin 1999, Huber et al. 1999, Koumoundouros et al. 1999, Thompson 1999, Relyea and Werner 2000). Some phenotypic changes (e.g., behavior) might only be effective early in ontogeny or serve as a short-term solution to predation or herbivory, whereas other phenotypic changes (e.g., morphology) might be more effective later in ontogeny or serve as a long-term solution. While numerous studies have examined predator-induced behavior or morphology at a particular ontogenetic stage (Lima and Dill 1990, Tollrian and Harvell 1999), few have examined how prey change these traits at multiple ontogenetic stages.

Second, by examining multiple ontogenetic stages, we can determine whether there are periods during ontogeny that restrict plastic responses to particular developmental stages (i.e. "developmental windows" [Krueger and Dodson 1981, Hensley 1993, Leips and Travis 1994]) and determine whether induced phenotypes can be subsequently reversed. Because predators are often heterogeneous in distribution and predator-induced phenotypes typically have lower fitness when predators are absent (Lima and Dill 1990, Tollrian and Harvell 1999), natural selection should favor inducible phenotypes at all points in ontogeny (providing that

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the prey remain vulnerable). However, developmental constraints could prevent prey from being induced later in ontogeny. In most studies of predator-induced plasticity (particularly those examining morphological plasticity), prey are exposed to predators early in ontogeny to ensure that the prey will respond (Brönmark and Miner 1992, Arnqvist and Johansson 1998, Mateo and Holmes 1999, Relyea and Werner 2000). Therefore, we frequently do not know whether prey can be induced by predators later in life (but see Krueger and Dodson 1981).

If the costs of antipredator phenotypes are substantial, selection also should favor the reversal of antipredator phenotypes if the predators leave (Gabriel 1999). However, predator environments may place organisms on developmental trajectories that cannot be reversed even though there is selective pressure to do so (Schlichting and Pigliucci 1998). Whereas some types of environmentally induced traits can be reversed, suggesting an absence of constraints (Pfennig 1992, Piersma and Lindström 1997, Denver et al. 1998), few studies of predator-induced traits have assessed the reversibility of behavior (Forward and Hettler 1992, DeMeester et al. 1994, Loose and Dawidowicz 1994, Yamada et al. 1998) and morphology (Kuhlmann and Heckmann 1994, Pettersson and Brönmark 1994, Tollrian and Dodson 1999).

Empirically testing predator-induced traits over ontogeny requires a well-studied system, and larval anurans are an excellent choice. When predators are present, tadpoles typically exhibit spatial avoidance, reduced activity, relatively large tails, and relatively small bodies (Lawler 1989, Laurila et al. 1997, Van Buskirk and Relyea 1998, Relyea 2001a, 2002b, d). In this study, I exposed gray treefrog tadpoles to the constant presence and absence of predators, as well as the colonization and metamorphosis of predators at different points in time. I tested the following hypotheses: (1) phenotypic strategies change over ontogeny, from a dependence on behavioral defenses early in ontogeny to a dependence on morphological defenses later in ontogeny, (2) there are developmental windows that restrict predator-induced responses to the early stages of ontogeny, and (3) behavioral traits are reversible while morphological traits are irreversible.

METHODS

I conducted the experiment using a completely randomized design that simulated ponds with the following conditions: (1) predators always absent, (2) predators always present, (3) predators initially absent but subsequently colonizing at one of three times, or (4) predators initially present but leaving the pond at one of three times (i.e., metamorphosing). Thus, there were eight treatments (each replicated four times) for a total of 32 experimental units. Predator colonization or metamorphosis was simulated on days 6, 10, and 14,

and the experiment was terminated after 18 d (the tadpoles were approaching metamorphosis).

The experimental units were 100-L wading pools that served as pond mesocosms. On 22 June, I filled the pools with well water and added 100 g of leaves (primarily *Quercus* spp.), an aliquot of pond water from a nearby pond (a source of periphyton, phytoplankton, and zooplankton), and 5 g of rabbit chow (to serve as an initial nutrient source). On 26 June, I added 60 tadpoles to each pool (60 tadpoles/m², mean mass = 14 mg) from a mixture of four egg masses. This is on the high end of natural densities (range = 1–90 tadpoles/m²; R. A. Relyea, E. E. Werner, D. K. Skelly, and K. L. Yurewicz, unpublished data), but newly hatched tadpoles can be found at extremely high densities that rapidly thin over time. Because I removed tadpoles over time to quantify their morphology, my removal of tadpoles simulated the natural condition.

Each pool was equipped with a single predator cage (Relyea 2000), which permitted prey to detect the chemical cues of the predators without being subjected to actual predation (Petranka et al. 1987, Kats et al. 1988). Each cage contained either no predators or a single dragonfly larva (*Anax longipes*) (see Plate 1). Predators were fed ~1 g of treefrog tadpoles every two days; in pools assigned the no-predator treatments, I lifted the cages to equalize disturbance among all treatments. To simulate predator metamorphosis and colonization, I switched the predator and no-predator cages between appropriate pools at the end of each time period. This provided an efficient way of switching environments and reflected the natural situation of predators emerging from a pond and leaving their waste products behind. Predators were fed after the cages were switched.

I observed tadpole behavior (hiding behavior and activity level) at the end of each time period by counting the number of tadpoles that I could see in the pools and the proportion of observed tadpoles that were active (moving). I observed each pool 10 times and then calculated the mean number of observed tadpoles and the mean activity percentage for each pool. This has proven to be a very effective protocol (Peacor and Werner 1997, Relyea 2002a, b).

I also collected 10 tadpoles from each pool at the end of each time period and preserved them in 10% formalin for subsequent morphological measurements. The preserved tadpoles were placed under a video camera to project their image onto a computer monitor using Optimas image analysis software (Bioscan, Bothell, Washington). Unlike past experiments in which I have examined up to eight dimensions (Relyea 2000, 2001b, 2002c), in this experiment the results were relatively complex (eight treatments sampled over four time periods). Therefore, I restricted my analysis to the two morphological traits that most consistently respond to predators (tail depth and body length [Relyea 2000: Fig. 1; also see Smith and Van Buskirk 1995, Mc-



PLATE 1. An aeshnid dragonfly larva capturing an undefended tadpole (photo by Rick Relyea).

Collum and Van Buskirk 1996, Relyea 2000, 2001b, Relyea and Werner 2000)).

The data were analyzed using a nested multivariate analysis of variance (MANOVA). For most of the responses (i.e., mass, tail depth, and body length), a nested analysis was more appropriate than a repeated-measures analysis because sampled animals were not replaced. There was a significant multivariate interaction of treatment and time, so I examined the univariate responses within each time period. The most powerful way to compare the predator and no-predator phenotypes at each time period (for questions related to ontogeny) was to use planned comparisons of all treatments that possessed a constant presence or absence of predators from the start of the experiment (e.g., during the first time period four treatments had predators constantly present and four treatments had predators constantly absent). To compare the final phenotypes of the treatments (for questions related to developmental windows and phenotypic reversibility) I used Fisher's exact

test. Because survival was only quantified at the end, I conducted a separate ANOVA on survival.

RESULTS

Tadpole survival was relatively high (mean \pm 1 SE = $82 \pm 1\%$) and did not differ among treatments ($F_{7,24} = 0.7$, $P = 0.656$). There were significant multivariate effects of both treatment and time as well as their interaction (Table 1, Figs. 1 and 2). Univariate tests indicated that tadpole mass increased over time but was unaffected by the predator treatments, whereas the four behavioral and morphological traits were affected by treatment, time, and the interaction. (Unless stated otherwise, P values listed below are from planned comparisons or final mean comparisons.)

During the first time period, I observed fewer tadpoles with predators constantly present than with predators constantly absent ($P < 0.00001$; Table 1, Fig. 1). However, in the subsequent three time periods, the tadpoles were equally observable among all eight predator treatments (three univariate tests, $P > 0.25$). Thus, hiding behavior was used only early in ontogeny, preventing any assessment of its reversibility.

Tadpoles constantly reared with predators were less active than tadpoles constantly reared without predators during the first three time periods ($P < 0.04$), but not by the end of the experiment (univariate test, $P = 0.578$; Table 1, Fig. 1). When predators colonized on day 6, the tadpoles continued to maintain higher activity than tadpoles raised with constant predators (day 10, $P = 0.032$) but converged by day 14 ($P = 0.307$). When predators colonized on day 10, tadpole activity converged with tadpoles raised with constant predators by day 14 ($P = 0.134$). When predators metamorphosed on day 6, the tadpoles rapidly increased their activity to be similar to predator-free tadpoles by day 10 ($P = 0.726$) and day 14 ($P = 0.798$). When predators metamorphosed on day 10, tadpole activity was not different

TABLE 1. Results of a nested multivariate analyses of variance that examined the impact of switching predator and no-predator treatments on the mass, behavior, and morphology of gray treefrog tadpoles over time.

A) Multivariate tests			
Source	df	<i>F</i>	<i>P</i>
Treatment	35, 86	2.8	0.0001
Time	15, 188	48.3	<0.0001
Treatment \times Time	105, 337	4.1	<0.0001
B) Univariate tests			
Trait	Treatment	Time	Treatment \times Time
Mass	0.113	<0.0001	0.303
Activity	0.011	<0.0001	<0.0001
Number observed	0.039	<0.0001	<0.0001
Tail depth	<0.0001	<0.0001	<0.0001
Body length	0.001	<0.0001	0.023

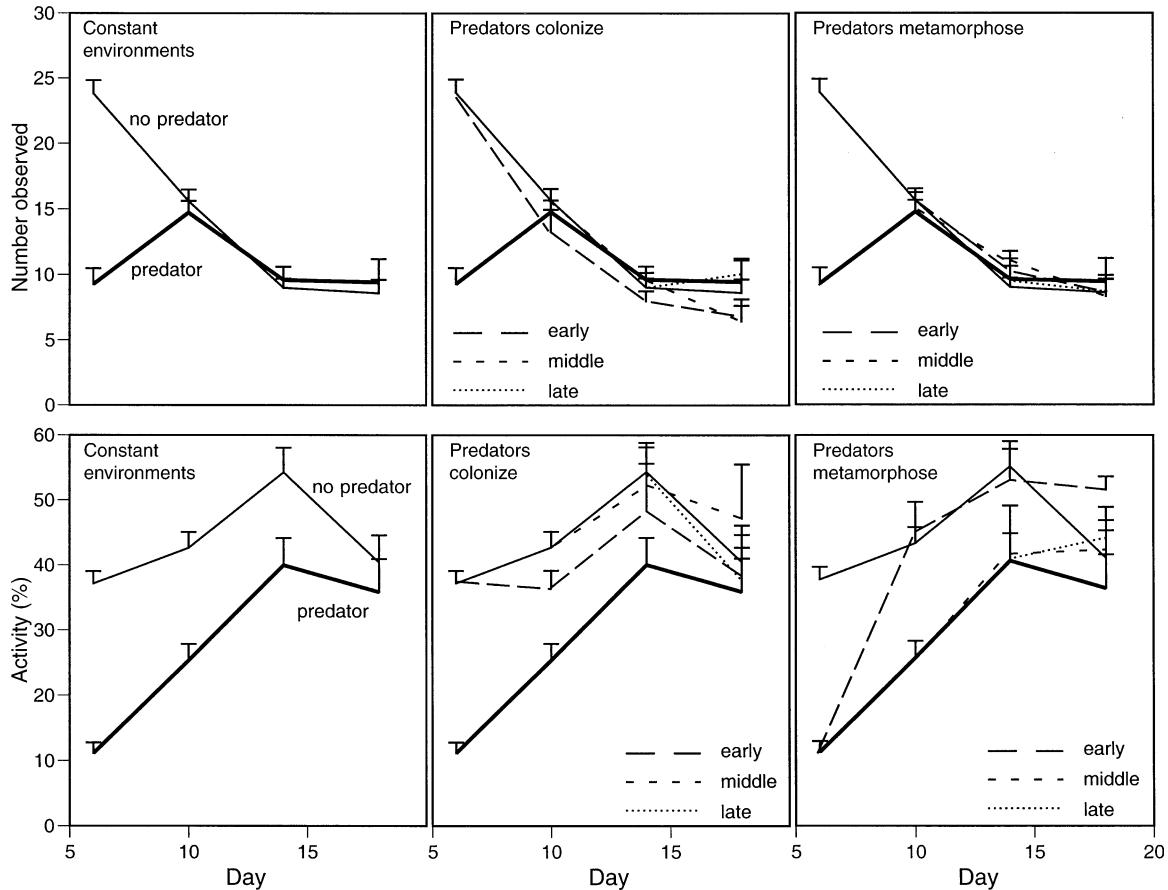


FIG. 1. The number of gray treefrog tadpoles observed (top panels) and the percentage of tadpoles observed that were active (bottom panels) when tadpoles were reared in one of eight treatments. The treatments simulated either the constant presence or absence of a predator (all panels), colonization by a predator into a pond (center panels), or metamorphosis of a predator out of a pond (right panels). The number of tadpoles observed over time generally declines because 10 tadpoles are removed at the end of each time period. Data are means + 1 SE.

from predator-free tadpoles on day 14 ($P = 0.134$). At the end of the experiment, there were no differences in activity among the eight treatments (univariate test, $P = 0.578$). Thus, activity reduction was used only early and midway through the larval period; during these times, activity was completely reversible by the end of the third time period (day 14).

During all time periods, predator tadpoles had deeper tails than predator-free tadpoles ($P \leq 0.00001$; Table 1, Fig. 2). When I simulated predator colonization, tadpole tails converged to be similar to predator tadpoles by the end of the experiment (for the three colonizations, $P = 0.21$, $P = 0.07$, and $P = 0.27$, respectively). In some cases, this reversal occurred within four days. When I simulated predator metamorphosis, tadpole tails converged to be similar to predator-free tadpoles, providing that metamorphosis occurred by the end of the first or second time period ($P = 0.79$ and $P = 0.34$, respectively). Again, this reversal was possible within four days. If metamorphosis occurred by the end of the third time period, tadpole tails did not converge ($P <$

0.00001). In summary, increased tail depth was used as an antipredator strategy throughout the larval period. When I colonized the mesocosms with predators, tail depth was reversible. When predators metamorphosed, tail depth also was reversible, but only if predator metamorphosis occurred early to midway through the larval period.

Tadpoles reared with and without predators had similar body lengths at the end of the first time period (univariate test, $P = 0.299$; Table 1), but predators induced shorter bodies in subsequent time periods ($P < 0.03$; Fig. 2). When I simulated predator colonization, tadpole bodies converged to be similar to predator tadpoles ($P > 0.2$), providing that the colonization occurred by the end of the first or second time periods. These reversals occurred within eight days. When colonization occurred at the end of the third period, tadpole bodies did not converge ($P = 0.042$). When I simulated predator metamorphosis at any time period, tadpole bodies converged to be similar to predator-free tadpoles ($P > 0.3$). In summary, body length changes

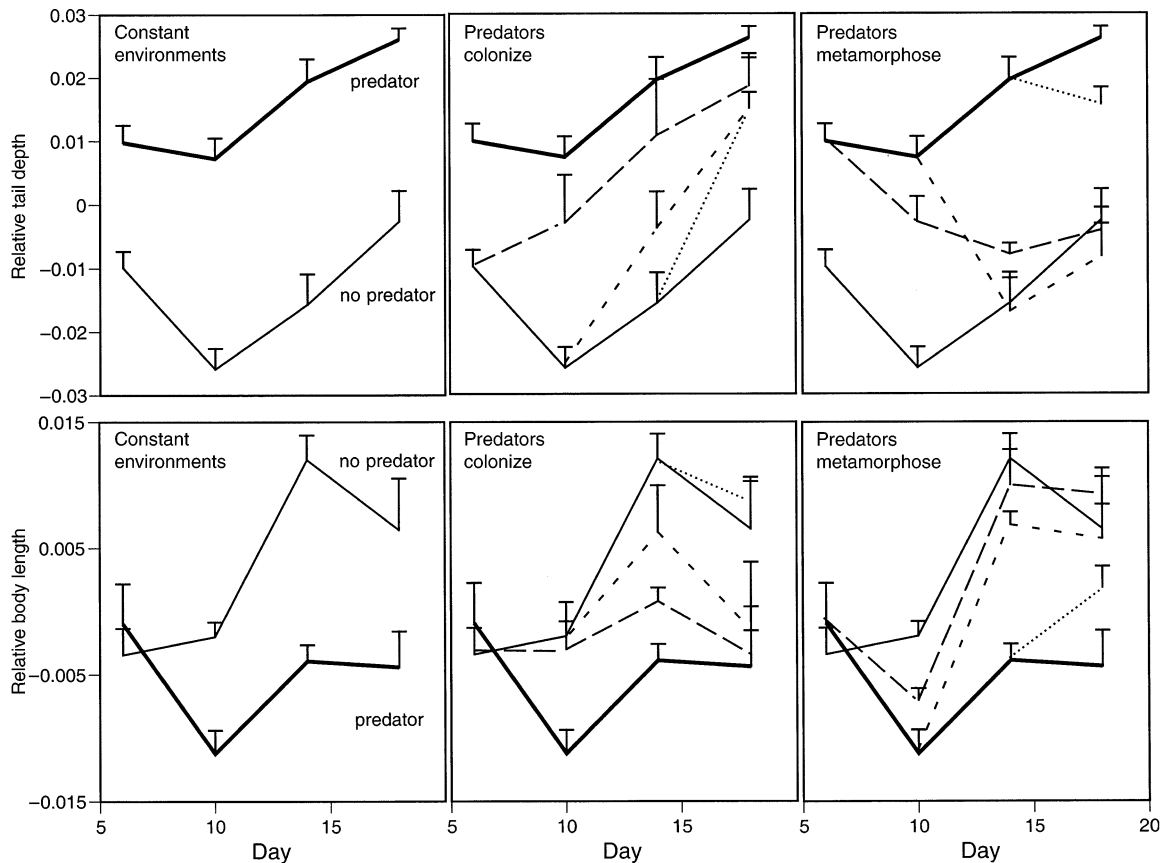


FIG. 2. The change in relative tail depth (top panels) and body length (bottom panels) when tadpoles were reared in one of eight treatments. The treatments simulated either the constant presence or absence of a predator (all panels), colonization by a predator into a pond (center panels), or metamorphosis of a predator out of a pond (right panels). Measurements were made size independent by regressing the tail depth and body length of all individuals against mass and then saving the residuals. Data are means + 1 SE (see Fig. 1 for explanation of the dashed lines).

occurred midway to late in the larval period. The body length changes were reversible when predators colonized, but only if colonization occurred early or midway through the larval period. Body length changes also were reversible when predators metamorphosed throughout the entire larval period.

DISCUSSION

The experiment demonstrated that the tadpoles responded to predator cues over ontogeny by changing their phenotypic strategies, and that the phenotypic responses were frequently reversible. Tadpoles initially responded to predators by hiding, reducing their activity, and increasing their relative tail depth. Midway through ontogeny, tadpoles no longer hid but continued to reduce their activity, exhibited deeper tails, and began to exhibit shorter bodies. Later in ontogeny, tadpoles responded to predators by altering only their morphology. Increased hiding and reduced activity allow prey to reduce their probability of encountering predators; however, this benefit comes at the cost of slower growth and development when predators are absent

(Gerritsen and Strickler 1977, Juliano and Reminger 1992, Short and Holomuzki 1992, Semlitsch 1993, Werner and Anholt 1993, Grill and Juliano 1996, Relyea and Werner 1999, Relyea 2001c). Similarly, tadpoles with relatively deep tail fins and short bodies are better able to avoid predatory strikes, but this morphological phenotype is slower growing when predators are absent (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Relyea 2001c, 2002a). In this study, the predator treatments never affected tadpole growth, which is a common result when there are no other competitors in the system to consume the food left behind (Relyea and Werner 2000, Relyea 2001a). In studies of nonpredatory environments, phenotypically plastic strategies commonly change over ontogeny (Werner and Hall 1974, Arnquist and Johansson 1998, Baldwin 1999, Persson and Christenson 2000).

Previous studies of predator-induced tadpoles over ontogeny have been limited to morphological traits. Like the gray treefrog larvae in this study, larval wood frogs (*Rana sylvatica*) and leopard frogs (*R. pipiens*) exhibit changes in tail depth and body length relatively

early in ontogeny, and these changes are maintained throughout the larval period (Relyea and Werner 2000). However, the inclusion of behavioral traits in the current study demonstrates that gray treefrog tadpoles use several defenses (both behavioral and morphological) against predators early in ontogeny. As they increase in mass, which further reduces prey vulnerability, (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998), the morphological defenses and large size apparently defend the tadpoles sufficiently to make the behavioral responses no longer necessary. This same pattern also has been observed in predator-induced fish (*Carassius carassius*; Pettersson et al. 2000). Given that predator-induced behavior and morphology both have growth costs, this pattern suggests that the more rapid behavioral responses may be more costly than the slower morphological responses. This supports arguments that tadpole species from temporary ponds use greater morphological defenses and weaker behavioral defenses, because large behavioral defenses may reduce growth to a point that would prevent timely metamorphosis (Relyea 2001a, c).

There were few developmental windows in the predator-induced traits of the tadpoles. Activity and morphology were inducible at the beginning of the experiment, when predators colonized on day 6, and when predators colonized on day 10. After day 14, there were no behavioral responses to predators, so the presence of developmental windows for behavioral defenses could not be assessed. However, morphological defenses continued after day 14; when predators colonized late on day 14, the tadpoles were not able to induce the full suite of morphological changes. Tadpoles are vulnerable to predation from aeshnid dragonflies throughout a wide range of body sizes (Travis et al. 1985, Richards and Bull 1990, Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Van Buskirk and McCollum 1999), suggesting that there may be selective pressures to remove developmental constraints and allow predator-induced responses throughout much of ontogeny. The lack of developmental windows throughout much of the larval period is in contrast to the predator-induced morphology of cladocerans and bryozoans, which produce defensive spines only when they are exposed to predatory cues in the earliest ontogenetic stages (Krueger and Dodson 1981, Harvell 1991). Similar developmental windows exist for diet-induced tiger salamander larvae (*Ambystoma tigrinum*); younger larvae are more likely to be induced than older larvae (Hoffman and Pfennig 1999).

Past authors have hypothesized that behavioral plasticity is a distinct type of plasticity because it is highly reversible, in contrast to morphological plasticity, which is generally irreversible (West-Eberhard 1989). In my study, the behavioral responses were completely reversible. The morphological traits also were completely reversible as long as the environments changed before the final time period. Thus, in gray treefrog tad-

poles, there were only small differences in the reversibility of behavioral and morphological traits. The reversibility of predator-induced behavior has been observed frequently (Forward and Hettler 1992, DeMeester et al. 1994, Loose and Dawidowicz 1994, Wibe et al. 2001). In contrast, the reversibility of predator-induced morphology has rarely been studied; it is completely reversible in three species of protists and one species of cladoceran, and partially reversible in one species of fish (Kuhlmann and Heckmann 1994, Pettersson and Brönmark 1994, Tollrian and Dodson 1999). Studies of nonpredatory trait induction have found that behavioral traits are generally easy to reverse, particularly those behaviors that simply involve doing a repetitive behavior more or less frequently (e.g., feeding, mating, scanning for predators; Krebs and Davies 1997). While many nonpredatory morphological traits are irreversible (e.g., Day and McPhail 1996), a substantial number are rapidly reversible, including changes in snail foot size (*Littorina obtusata*) and shell shape (*Nodilittorina australis*) in habitats of different tidal flow, seasonal fat loads in birds and mammals, and changes in internal organ size in a variety of vertebrate animals during migration, reproduction, or changes in diet (Powers 1907, Piersma and Lindström 1997, Trussell 1997, Yeap et al. 2001).

When there are substantial costs of possessing a particular phenotype in the "wrong" environment, selection should favor the evolution of reversibility (Gabriel 1999). However, at least three factors could determine whether environmentally induced traits will be reversible. First, reversibility should be favored when there is a high probability that current environmental conditions will revert back to previous environmental conditions. For example, some prey experience relatively constant predators (e.g., fish in a lake) such that if the predators are present early in ontogeny, then they are likely to be present throughout ontogeny. In contrast, other prey experience changing predator communities over ontogeny (e.g., aquatic insect predators that metamorphose and leave ponds). When prey experience predators that colonize the environment and then leave, natural selection should favor phenotypic reversibility.

Second, morphological changes that involve simple changes in relative shape as the organism grows may be easier to reverse than changes that involve the removal of complex structures. For example, tadpoles develop relatively larger tails with predators present. When predators leave the environment, the tadpoles continue to grow over time and can revert to the nonpredator phenotype by preferentially shunting energy for growth to the body, which makes the tail relatively smaller. These options are likely not available to prey species such as *Daphnia*, which develop predator-induced spines; reversibility would require including resorption of the spiny exoskeleton or an abscission of the spines. While it is not clear whether these processes require a more complex physiology, it is clear that we

need more experiments in other taxa to begin to draw generalities.

Third, organisms that are built modularly should have less reversible morphology than organisms that are not built modularly. For example, plants typically grow modularly by committing tissues to specific functions in response to environmental cues (e.g., stem elongation) and then continue to build upon those tissues with further stem, leaf, and flower growth. In this case, the plant cannot go back and alter tissues that are already committed to another functional role. Thus, a plant that has grown tall cannot become short, and a stem that terminates in a flower (due to day length cues) cannot revert back to a terminal bud for future vegetative growth (Raven et al. 1986). In summary, while there may be selective pressures to reverse environmentally induced traits, frequencies of environmental switching and underlying physiological mechanisms may prevent the reversal from occurring.

While variable environments should favor phenotypic reversibility in a species, the effects of reversible phenotypes may not be restricted to that species. Environments that alter the phenotype of a species frequently alter the competitive ability and predator resistance of that species (Van Buskirk and Relyea 1998, Relyea 2002a). As a result, per capita interactions between the induced species and the predators and competitors in the community can change (i.e., trait-mediated indirect effects; Werner 1992, Wootton 1993, Beckerman et al. 1997, Peacor and Werner 1997, Relyea 2000, Relyea and Yurewicz 2002). When the environment changes but the induced phenotype is irreversible, the trait-mediated indirect effects should continue to operate. In contrast, when the environment changes but the induced phenotype is reversible, the trait-mediated effect should also reverse, causing the community structure to move back toward its original state. Whether the community moves completely back to its original state will depend on the details of the study system. This hypothesized community effect of reversibility has yet to be tested.

CONCLUSIONS

This study demonstrated that the phenotypic strategies can change over ontogeny and that these changes are highly reversible in tadpoles. While we need many more studies before we can draw any strong generalizations about developmental windows and the reversibility of predator-induced traits, the current work casts doubt upon the commonly held assumption that plastic behavioral traits are much more reversible than plastic morphological traits. Future studies should investigate the developmental biology underlying these phenotypic reversals as well as the predicted impacts that reversible traits have on the larger ecological community.

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