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Source: *Ecology*, Feb., 2006, Vol. 87, No. 2 (Feb., 2006), pp. 340-346

Published by: Wiley on behalf of the Ecological Society of America

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SURVIVAL TRADE-OFFS BETWEEN TWO PREDATOR-INDUCED PHENOTYPES IN PACIFIC TREEFROGS (*PSEUDACRIS REGILLA*)

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Abstract. In many organisms, specific predator species induce defensive phenotypes that are qualitatively different from the phenotypes induced by other predator species. This differential induction implies that there is no optimal phenotype that works best against all predators. However, few studies have actually tested the hypothesis that each predator-induced phenotype provides the highest survival rate in encounters with the predator that induced that phenotype. In this experiment, I reared Pacific treefrog (*Pseudacris regilla*) larvae with chemical cues from two different predators (bluegill sunfish and predaceous diving-beetle larvae), and without predator cues. The Pacific treefrog larvae in the three treatments differed in their morphology and foraging behavior. I then exposed tadpoles from each treatment to free-foraging predaceous diving beetles and bluegill sunfish. Tadpoles survived best when exposed to the predator whose cues they were reared with, and worst when exposed to the other predator. In both predator environments, the tadpoles reared in the nonpredator control treatment had intermediate survival between the two predator-induced groups. Thus, there is no generalized “antipredator” response to these predators; rather, there was a clear trade-off in survival abilities between the predators.

Key words: amphibian; bluegill sunfish; inducible defense; phenotypic plasticity; predaceous diving beetle; predator; *Pseudacris regilla*.

INTRODUCTION

Predator-induced phenotypic plasticity is widespread in nature. Many studies have demonstrated changes in behavior and morphology in response to the risk of predation (Lima 1998, Tollrian and Harvell 1999, Benard 2004). These studies have generally found that individuals with the predator-induced behavioral or morphological phenotype are more likely to survive attacks by the predator than are individuals without the induced phenotype (e.g., Lively 1986, McCollum and Van Buskirk 1996). However, in nature, prey face different predators in different environments. These different predators may induce phenotypic changes in prey that differ quantitatively, but not qualitatively (e.g., Barry 2000, Relyea 2000), presumably because similar defense strategies work against both predators. Alternatively, different predators may capture prey in very different ways, and as a consequence induce qualitatively different phenotypes in the prey (e.g., Krupa and Sih 1998, Peckarsky and McIntosh 1998, DeWitt et al. 2000). Thus prey may utilize either nonspecific defenses in response to a variety of predators, or predator-specific defenses (Sih et al. 1998). In a recent review, Relyea (2003) found that in approximately half of the studies he examined, prey responded to different pred-

ators in a qualitatively similar way (nonspecific predator response), while in the other half, prey responded to different predators in a qualitatively different way (predator-specific defenses). The observation that some species exhibit predator-specific defenses suggests that there may be adaptive trade-offs between these different phenotypes when faced with different predators (Sih et al. 1998). However, little work has examined differences in susceptibility of a phenotype induced by one predator to predation by another predator.

Experimental tests for survival trade-offs between different induced defenses are critical for understanding why different phenotypes are induced in response to different predators. For instance, Do all predator-induced phenotypes confer higher survival than non-induced prey phenotypes? *Physa* snails are a system in which this problem has been investigated. These snails develop rounder shells in response to the presence of fish and more elongate shells in response to the presence of crayfish (Dewitt 1998). Snails with rounder shells have higher survival in the presence of fish, while snails with elongate shells have higher survival in the presence of crayfish (Dewitt et al. 2000). Thus, a survival trade-off explains the different shell shapes induced in response to each predator.

Substantial research on predator-induced responses has been conducted using larval amphibians (e.g., Petranka et al. 1987, McCollum and Van Buskirk 1996, Van Buskirk et al. 1997, Relyea 2001). Many studies have examined selection on tadpole phenotypes in the presence of one predator (e.g., McCollum and Van Bus-

Manuscript received 7 March 2005; revised 3 August 2005; accepted 25 August 2005. Corresponding Editor: J. Loman.

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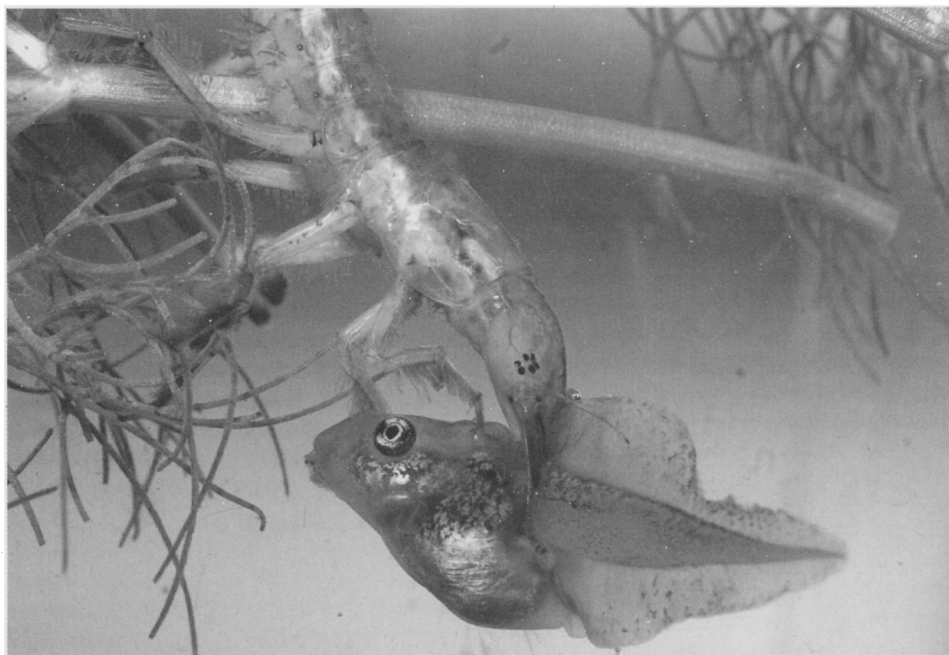


PLATE 1. Predaceous diving beetle larvae consuming Pacific treefrog tadpole. Photo credit: M. Bernard.

kirk 1996, Van Buskirk et al. 1997). Several studies that tested for induction of different larval phenotypes by different predators found that induced phenotypes are similar or differ only quantitatively between predators (Relyea 2001, Van Buskirk 2001). However, a few other studies have found qualitative differences in the morphology induced by different predators (Relyea 2001, Teplitsky et al. 2005). Additionally, several amphibians exhibited different behavioral responses to different types of predators, in some cases when there is no difference in induced morphology (Eklöv and Werner 2000, Van Buskirk 2001, Teplitsky et al. 2005). Only one study on amphibians has tested whether different phenotypes induced by different predators are correlated with differential survival in the presence of those predators. Kishida and Nishimura (2005) found that *Rana pirica* tadpoles develop different phenotypes in response to predation risk from salamanders and dragonfly nymphs, and that a survival trade-off exists across these two phenotypes. How general are such trade-offs between phenotypes induced by different predators? This critical question must be answered to determine the factors responsible for the evolution and maintenance of alternative predator-induced phenotypes.

I conducted experiments to examine two aspects of phenotypic plasticity in response to different predators. First, I tested for differences in behavior and morphology between Pacific treefrog tadpoles (*Pseudacris regilla*) raised without cues from a predator, tadpoles raised with chemical cues from bluegill (*Lepomis macrochirus*), and tadpoles raised with chemical cues from predaceous diving beetles (*Dytiscus* sp.; see Plate

1). Second, I tested if treefrog tadpoles reared in the three treatments differed in their susceptibility to predation by bluegill sunfish and predaceous diving beetles. I was specifically interested in whether there were generalized or specialized responses to predators. If the tadpoles exhibited predator-specific responses, was there a survival trade-off between predators so that tadpole survival was higher when encountering the “inducing” predator, and lower when encountering the other predator?

METHODS

Pacific treefrogs (*Pseudacris regilla*) are a geographically widespread anuran ranging from Baja California to British Columbia. In Napa County, California, USA, they breed from January through late April. Historically, fish were absent from many of the habitats of pond-dwelling amphibians in western North America. The introduction of many different fish species, including bluegill sunfish (*Lepomis macrochirus*), over the last hundred years has had a negative effect on many native amphibians, including Pacific treefrogs (Fisher and Shaffer 1996, Adams 2000). While the Pacific treefrogs used in this study came from ponds where fish were not present, ponds containing bluegill are within several kilometers of these ponds. Surveys of ponds in Napa County have found that Pacific treefrogs occur with both bluegill and predaceous diving beetles (*Dytiscus* spp.), although only rarely have ponds been identified in which both predaceous diving beetles and bluegill occur, or in which there are no predators (*unpublished data*).

I obtained fertilized eggs from five amplexed pairs of Pacific treefrogs collected on 20 April 2004 from ponds on the University of California Natural Reserve System's Quail Ridge Reserve (Napa County). After the eggs hatched, the tadpoles were taken to an animal care facility at the University of California-Davis, and maintained at $\sim 19^{\circ}\text{C}$. On 10 May 2004 the larvae were split into 30 groups. Each group contained two larvae from each of the five sibships. Each group was placed in a $40 \times 26 \times 14$ cm plastic box containing 7 L of artificial pond water (25% Holtfreter's solution, Armstrong et al. 1989). The tadpoles were fed ground fish food (Wardley Spirulina Discs [Hartz Mountain Corporation, Secaucus, New Jersey, USA]) every other day, and the water was regularly changed.

Each group of 10 tadpoles was randomly assigned to one of three induction treatments: fish cue, beetle cue, or control cue (hereafter, "control"). Ten bluegill sunfish (total length [mean \pm SE] = 11.7 ± 0.3 cm), and 20 predaceous diving beetles (total length = 4.9 ± 0.31 cm) were used as predators. The predator cues were applied to the induction treatments approximately two out of every three days, beginning on 10 May 2004 and ending on 26 May 2004. For each fish cue, ~ 2 g (4–10 individuals) of live Pacific treefrog larvae were added to a randomly chosen tank containing two bluegill sunfish and 30 L of water. After the sunfish had eaten the larvae, 200 mL of water from this tank were added to each fish-cue treatment. To generate the beetle cue, ~ 0.5 g (1–4 individuals) of Pacific treefrog tadpoles were fed to individually housed predaceous diving beetle larvae. The water from the beetle treatments was diluted so that the concentration of consumed tadpole mass was equal between beetle-cue and fish-cue treatments. Each beetle-cue treatment received 200 mL of beetle-cue water. Each control treatment received 200 mL of plain water. The tadpoles fed to predators to generate cues were derived from the same clutches as the experimental animals, and reared in the laboratory.

Behavioral assays

Behavioral assays were conducted on 26 May 2004. To test for induction treatment effects on the amount of time that larvae spent foraging, I observed the tadpoles in each tank for 5 s, recording the number of tadpoles (out of 10) moving during those five seconds. I recorded activity in each tank 5 times, and took the average number of tadpoles moving across all five observation periods as my measure of tadpole foraging activity. I then added the cues, waited for 15 min, and repeated the observation of the tanks. The first measurement is a "baseline" estimate of activity for tadpoles that have been exposed to predator cues for the last 16 days. The second measurement indicates an immediate response to chemical cues. I tested for differences between the treatments using repeated-measures ANOVA on the average number of tadpoles moving

before cues were applied, and the average number moving after cues were applied.

Morphological measurements

On 27 May 2004 I anesthetized each tadpole in 0.02% buffered MS-222 (Tricaine; Argent Chemical Laboratories, Redmond, Washington, USA), digitally photographed it in profile out of water on a tray, weighed it, and returned it to its tank. Each tadpole was removed from the water for a brief period, and all tadpoles recovered within 10 minutes. Five morphological characters were measured on each tadpole using SCION Image (Scion Corporation, Frederick, Maryland, USA): body length, body depth, tail length, tail depth, tail muscle depth (see Appendix). Mass and all morphological characters were log-transformed to fit statistical assumptions. I performed a MANOVA to test for overall differences in morphology between induction treatments. Univariate ANOVAs were used to test for differences between specific traits. While I report the log-transformed sizes in this paper, the results are not qualitatively different if I correct for a tadpole's size through other methods (e.g., Relyea 2001). Assumptions of normality and homogeneity of variances were met for all response variables except mass, which exhibited different variances among the treatments. To correct for this, I used a Welch ANOVA to test for differences between treatments in log-transformed mass.

Predator assays

Twenty-four hours after the tadpoles were photographed, they were exposed to free-foraging predators. These predators were the same individuals as those used to generate chemical cues. In each predation trial, a subset of tadpoles from a single rearing box was exposed to either a beetle or a bluegill. Since bluegills and predaceous diving beetles are substantially different in size, handling time, satiation, and strike distance, the predation trials were conducted differently for each predator. However the predation trial venues were similar in that the tanks contained no refuges for the tadpoles or any type of substrate.

Twenty-four (24) groups of three tadpoles (7 groups from the fish-cue treatment, 9 groups from the control treatment, and 8 groups from the beetle-cue treatment) were placed in separate plastic boxes ($31.5 \times 17 \times 9.6$ cm). Each box contained one beetle larva and 2.8 L of water. Each tank was observed every 6 min. The trial was ended when the last beetle captured a tadpole. Due to the long handling times the beetles had while consuming a tadpole (often >60 min), I ended the trials after each beetle had captured a single tadpole. I tested for differences in the capture rate between the three induction treatments using a log-rank survivorship test.

Twenty (20) groups of four tadpoles (7 groups from the fish-cue treatment, 5 groups from the control treatment, and 8 groups from the beetle-cue treatment) were

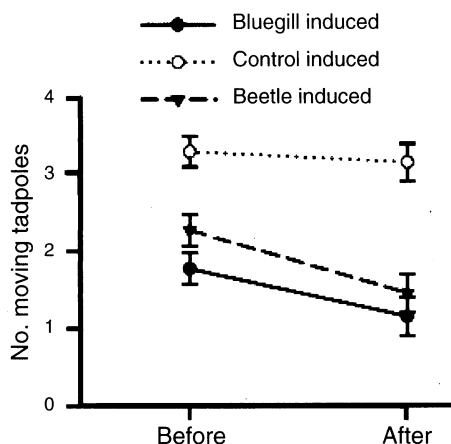


FIG. 1. Number of tadpoles moving during 5-s observation periods before and after the treatment cues were applied. Data are means \pm SE. Larvae from both predator-cue treatments had significantly lower average activity levels than tadpoles from the control treatment (Control vs. Bluegill contrast, $F = 61.29$, $df = 1, 27$, $P < 0.0001$; Control vs. Beetle contrast, $F = 36.60$, $df = 1, 27$, $P < 0.0001$). However, there was no significant difference in activity between tadpoles in the two predator treatments ($F = 3.17$, $df = 1, 27$, $P = 0.09$).

fed to randomly assigned pairs of bluegill sunfish. The bluegill trials were conducted in glass aquaria (50.8 \times 26 \times 30.5 cm). Because the bluegill captured tadpoles much more quickly than the beetles, I observed them for the entire 10-min duration of each trial. In each fish trial, the tadpoles were placed on one side of an opaque plastic partition. Once the partition was removed, I recorded the time (in seconds) at which each tadpole was eaten. In many trials, the bluegill ceased feeding after three tadpoles had been captured. Therefore, I used a log-rank survivorship test to test for differences between induction treatments in the rate at which bluegill captured tadpoles up to the third tadpole captured. Each pair of bluegills was used multiple times, and tadpoles were randomly assigned to each pair. To avoid satiation, the trials were conducted over two days, with one trial in the morning and one in the afternoon each day.

All statistical analyses were conducted using JMP-IN 5.1 (SAS Institute 1989–2002).

RESULTS

Tadpole activity was significantly affected by induction treatment (Fig. 1, repeated-measures ANOVA, treatment effect exact $F = 33.68$, $df = 2, 27$, $P < 0.0001$) so that tadpoles reared with fish cues or beetle cues had significantly lower activity than tadpoles from the control treatment. Activity levels were significantly lower in all induction treatments fifteen minutes after the application of the predator cue ($F = 8.21$, $df = 1, 27$, $P < 0.01$) than before the application of the predator cue. However, there was no interaction between predator cue and time ($F = 1.21$, $df = 2, 27$, $P = 0.31$).

All three treatments were significantly different from one another (MANOVA Wilks' lambda $F_{12,44} = 5.71$, $P = 0.0001$; bluegill vs. control contrast $F_{6,22} = 6.21$, $P < 0.0006$; beetle vs. control contrast $F_{6,22} = 3.02$, $P < 0.026$; bluegill vs. beetle contrast $F_{6,22} = 12.46$, $P = 0.0001$). Tadpoles reared with beetle cues had a significantly greater mass than tadpoles in the other two treatments (Fig. 2A, Welch ANOVA $F_{2,15.8} = 0.04$). There was no treatment effect on body length (Fig. 2B, ANOVA $F_{2,27} = 0.026$, $P < 0.97$), tail length (Fig. 2D, ANOVA $F_{2,27} = 0.56$, $P < 0.57$), or tail muscle depth (Fig. 2F, ANOVA $F_{2,27} = 1.16$, $P < 0.327$). The body depth of tadpoles in the bluegill-cue treatment was significantly lower than that of tadpoles in the beetle-cue treatment, but neither predator-cue treatment was significantly different from the control treatment (Fig. 2B, ANOVA $F_{2,27} = 6.52$, $P < 0.005$). All three treatments differed significantly from one another in tail depth; tadpoles reared in the presence of bluegill cues had the shallowest tails, and tadpoles reared in the presence of beetle cues had the deepest tails (Fig. 2E, ANOVA $F_{2,27} = 24.80$, $P < 0.0001$).

The type of predator cue the tadpoles were raised with had a significant effect on their survival when exposed to predaceous diving beetle larvae (survival analysis, log-rank test, $\chi^2 = 7.69$, $df = 2$, $P < 0.02$, Fig. 3A). In the presence of predatory beetles, tadpoles from the bluegill-cue treatment had significantly lower survival rates than tadpoles from the beetle-cue treatments (survival analysis, log-rank test, $\chi^2 = 8.31$, $df = 1$, $P < 0.004$). There was no significant difference between tadpoles from either predator treatment and tadpoles from the control treatment (Beetle vs. Control: survival analysis, log-rank test, $\chi^2 = 0.91$, $df = 2$, $P < 0.34$; Fish vs. Control: survival analysis, log-rank test, $\chi^2 = 2.32$, $df = 2$, $P < 0.13$). Predator-cue treatments had a marginally significant effect on survivorship in the presence of bluegill (survival analysis, log-rank test, $\chi^2 = 4.99$, $df = 2$, $P < 0.08$, Fig. 3B). Tadpoles reared in the presence of bluegill cues tended to be more likely to survive in the presence of lethal bluegill than tadpoles reared in the presence of beetle cues, which is the expected direction if there is a trade-off between predator morphologies.

DISCUSSION

Most studies of predator-induced plasticity in response to multiple predators in amphibians have found that a broad range of predators may induce very different responses (Petranka et al. 1987, Eklöv and Werner 2000, Van Buskirk 2001, Relyea 2001). While several studies have demonstrated that predator-induced traits confer a survival advantage against one predator type (e.g., McCollum and Van Buskirk 1996, Van Buskirk et al. 1997, Teplitsky et al. 2005), few studies have tested for adaptive trade-offs in survival between different predators in the same study. Benard and Fordyce (2003) found that an induced defense in western toads

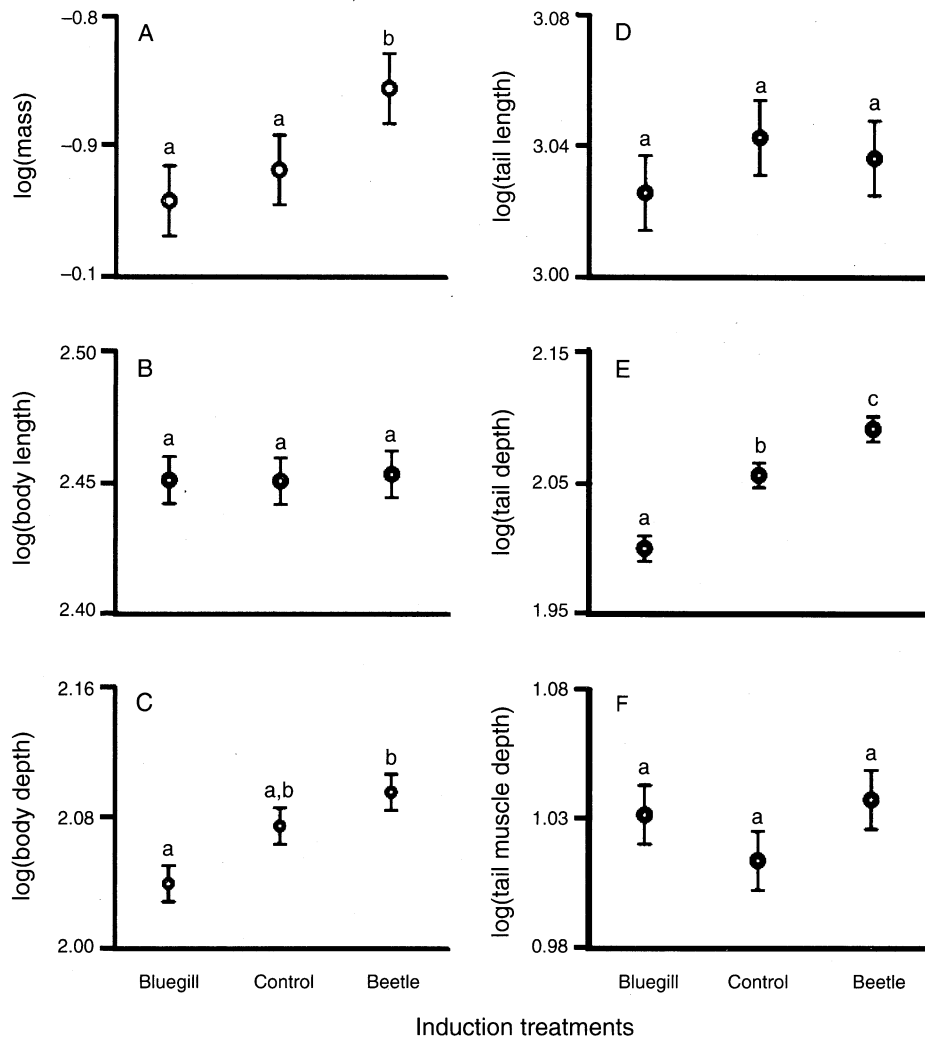


FIG. 2. Effects of induction treatment on Pacific treefrog larval mass and morphology. Mass was measured in grams; length and depth were measured in millimeters. The data presented are least-squares means \pm SE. Treatment data with the same lowercase letter are not significantly different at $\alpha < 0.05$ (Tukey's test).

(*Bufo boreas*) in response to a single, generalized predation cue conferred increased survival in the presence of two different predators, but at different stages in larval development. Kishida and Nishimura (2005) found evidence for a trade-off in survival between a "deep tail" morphology induced by a dragonfly nymph, and a "bulgy" morphology induced by a predatory salamander in *Rana pirica*. In the present study I demonstrated that Pacific treefrog larvae developed qualitatively different responses to the different predators. Relative to the control, the tadpoles reared with bluegill cues had relatively shallower tails and bodies. Other studies using smaller species of fish have found that many amphibians do not respond to fish or develop deeper tails in response to cues from fish (Relyea 2001, Teplitsky et al. 2005). In contrast to tadpoles reared with bluegill, tadpoles reared with beetle cues had deeper tails. This result is consistent with many other studies that have investigated phenotypes induced in

amphibians by predatory invertebrates (McCollum and Van Buskirk 1996, Relyea 2001). Tadpoles from both predator treatments had reduced their activity to a similar degree in response to predator cues.

The phenotypes induced by one predator incurred a survival cost when a tadpole faced the other predator. Tadpoles from the beetle-induction treatment had significantly higher survival rates than tadpoles from the bluegill-induction treatment when exposed to foraging predaceous diving beetles. In contrast, tadpoles from the bluegill-induction treatment tended to have higher survival rates than tadpoles from the beetle-induction cues when exposed to bluegill. In both predator environments, tadpoles in the control treatment, which had intermediate morphological phenotypes, had intermediate survival. Thus, there was a trade-off in survival between the two different predator environments. Additionally, since the intermediate phenotype always had intermediate survival, there was no generalized in-

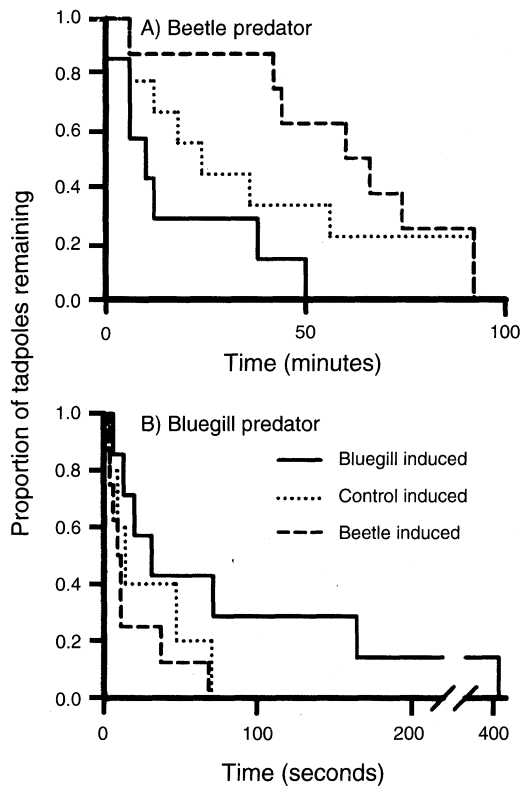


FIG. 3. Survival plot for Pacific treefrog larvae in each tank in the bioassays. (A) Predaceous diving beetle as a predator; the response variable is the time taken for each predaceous diving beetle to have captured the first tadpole. (B) Bluegill as a predator; the response variable is the time taken for each bluegill to have consumed the first three tadpoles. In the bluegill plot, the x-axis was truncated to save space.

duced morphological defense that provided a survival advantage against both predators.

Why is it important to establish whether or not survival advantages exist? While many predator-induced defenses have been shown to provide a clear survival advantage in escaping predation (e.g., Lively 1986, Stemberger and Gilbert 1987, McCollum and Van Buskirk 1996, Dewitt et al. 2000), there are other ways in which predator-specific morphology may be adaptive. For instance, prey may avoid predation through life-history transitions that allow them to escape predation (Crowl and Covitch 1990). Reduced tail depth in tadpoles, like that induced by bluegill in this experiment, has been correlated with higher growth rates (Benard 2004). Without a bioassay in this experiment, it may have appeared that the bluegill-induced morphology was a strategy to increase growth rate, and thus metamorphose earlier and escape bluegill predation. However, the bioassay demonstrated that the bluegill-induced phenotype conferred increased survival in the presence of predatory bluegill.

Since the goal of this study was to investigate trade-offs between fish-induced phenotypes and beetle-induced phenotypes in Pacific treefrogs, I did not include

a combined-predator cue treatment. The effects of combined-predator effects on prey are increasingly recognized as important (Sih et al. 1998, Relyea 2003). In this system, however, combined-predator environments may not be common in nature. Surveys of ponds in Napa County, California, USA, found that bluegill and predaceous diving beetle larvae only rarely occur together (*unpublished data*).

Currently, there are only a few studies that have investigated the functional mechanisms that explain why certain phenotypes provide a survival advantage. The relatively deep tails induced by many predatory invertebrates may serve to distract a predator's strike away from the tadpole's body and towards that tail (Van Buskirk and McCollum 2000, Van Buskirk et al. 2003). A strike on a tadpole's tail is much less likely to be lethal than a strike on a tadpole's body (Van Buskirk et al. 2003). Interestingly, in grey tree frog tadpoles (*Hyla versicolor*), relatively larger tail shapes are negatively correlated with tadpole escape velocity (Van Buskirk and McCollum 2000). If Pacific treefrog tadpoles exhibit a similar relationship between morphology and escape velocity, it would indicate that the fish-induced tadpoles have greater escape speed than the beetle-induced tadpoles. During the bluegill trials, I observed that tadpoles were often able to swim rapidly away from the bluegill as they approached, although I did not record the number of attempted escapes in each trial. This observation suggests that directly escaping bluegill is important for *Pseudacris regilla* tadpoles. Clearly, functional studies will be critical for understanding the diversity of morphological forms induced by predators.

From the rapidly growing literature on predator-induced defenses in amphibians, it is clear that a wide range of traits respond to predators, and thus future studies should incorporate a wide range of traits (Relyea 2004). Prey exhibit variable responses to predators, some of which are nonspecific defenses, and some of which are predator-specific defenses. Van Buskirk (2001) found that tadpoles of *Rana temporaria* had nonspecific morphological responses, but predator-specific behavioral responses. In contrast, the reduced foraging activity that the *P. regilla* tadpoles exhibited in response to both predators can be considered a nonspecific defense, and the induced morphological phenotypes can be considered predator-specific defenses. It also appears that the reduced activity induced by beetle cues and fish cues did not have an effect in the predation trials, since in each case the tadpoles from the control had intermediate survival in the bioassays although they had high activity in the behavioral assays. One possible explanation of this is that when the tadpoles from different treatments were placed in the experimental arenas, they all reduced activity to a similar degree when they detected chemical cues from the predators in the arena. The wide variety of differences between prey taxa in how they respond to a variety of

predators indicates that additional work is needed to test for the survival advantages of different defenses, as well as the role of these induced defenses in overall population dynamics.

ACKNOWLEDGMENTS

I thank the University of California Natural Reserve System for support and access to the Quail Ridge Reserve. Logistical support was provided by B. Ajie, V. Boucher, A. Carroll, D. Hulsey, D. Tolson, and S. Waddell. The illustration was provided by J. Grant. This manuscript was improved by comments from B. Ajie, A. McCollum, B. Shaffer, A. Sih, M. Turelli, members of the Shaffer Laboratory, and an anonymous reviewer. I was supported by the UC Davis Center for Population Biology, a Sherley Ashton Fellowship, and an Achievement Rewards for College Scholars (ARCS) fellowship.

LITERATURE CITED

- Adams, M. J. 2000. Pond permanence and the effects of exotic vertebrates on anurans. *Ecological Applications* **10**: 559–568.
- Armstrong, J. B., S. T. Duhon, and G. M. Malacinski. 1989. Raising the axolotl in captivity. Pages 220–227 in J. B. Armstrong and G. M. Malacinski, editors. *Developmental biology of the Axolotl*. Oxford University Press, New York, New York, USA.
- Barry, M. J. 2000. Inducible defences in *Daphnia*: responses to two closely related predator species. *Oecologia* **124**:396–401.
- Benard, M. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. *Annual Review of Ecology, Evolution and Systematics* **35**:651–673.
- Benard, M. F., and J. A. Fordyce. 2003. Are induced defenses costly? Consequences of predator-induced defenses in western toads, *Bufo boreas*. *Ecology* **84**:68–78.
- Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* **247**:949–951.
- DeWitt, T. J. 1998. Costs and limits of phenotypic plasticity: tests with predator-induced morphology and life history in a freshwater snail. *Journal of Evolutionary Biology* **11**: 465–480.
- DeWitt, T. J., B. W. Robinson, and D. S. Wilson. 2000. Functional diversity among predators of a freshwater snail imposes an adaptive trade-off for shell morphology. *Evolutionary Ecology Research* **2**:129–148.
- Eklöv, P., and E. E. Werner. 2000. Multiple predator effects on size-dependent behavior and mortality of two species of anuran larvae. *Oikos* **88**:250–258.
- Fisher, R. N., and H. B. Shaffer. 1996. The decline of amphibians in California's great central valley. *Conservation Biology* **10**:1387–1397.
- Kishida, O., and K. Nishimura. 2005. Multiple inducible defences against multiple predators in the anuran tadpole, *Rana pirica*. *Evolutionary Ecology Research* **7**:619–631.
- Krupa, J. J., and A. Sih. 1998. Fishing spiders, green sunfish, and a stream-dwelling water strider: male–female conflict and prey responses to single vs. multiple predator environments. *Oecologia* **117**:258–265.
- Lima, Steven L. 1998. Nonlethal effects in the ecology of predator–prey interactions. *BioScience* **48**:25–34.
- Lively, C. M. 1986. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* **40**: 232–242.
- McCollum, S. A., and J. Van Buskirk. 1996. Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla chrysoscelis*. *Evolution* **50**:583–593.
- Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. *Oecologia* **113**:565–576.
- Petranka, 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 Behavior* **35**:420–425.
- Relyea, R. A. 2000. Trait-mediated indirect 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. 2003. How prey respond to combined predators: a review and an empirical test. *Ecology* **84**:1827–1839.
- Relyea, R. A. 2004. Integrating phenotypic plasticity when death is on the line: insights from predator-prey systems. Pages 176–194 in M. Pigliucci and K. Preson, editors. *Phenotypic integration: studying the ecology and evolution of complex phenotypes*. Oxford University Press, Oxford, UK.
- SAS Institute. 1989–2002. JMP-IN, version 5.1. SAS Institute, Cary, North Carolina, USA.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13**:350–355.
- Stemberger, R. S., and J. J. Gilbert. 1987. Multiple-species induction of morphological defenses in the rotifer *Keratella testudo*. *Ecology* **68**:370–378.
- Teplitsky, C., S. Plenet, J. P. Lena, N. Mermet, E. Malet, and P. Joly. 2005. Escape behaviour and ultimate causes of specific induced defences in an anuran tadpole. *Journal of Evolutionary Biology* **18**:180–190.
- Tollrian, R., and C. D. Harvell. 1999. The ecology and evolution of inducible defenses. Princeton University Press, Princeton, New Jersey, USA.
- Van Buskirk, J. 2001. Specific induced responses to different predator species in anuran larvae. *Journal of Evolutionary Biology* **14**:482–489.
- Van Buskirk, J., P. Anderwald, S. Lupold, L. Reinhardt, and H. Schuler. 2003. The lure effect, tadpole tail shape, and the target of dragonfly strikes. *Journal of Herpetology* **37**: 420–424.
- Van Buskirk, J., and S. A. McCollum. 2000. Influence of tail shape on tadpole swimming performance. *Journal of Experimental Biology* **203**:2149–2158.
- Van Buskirk, J., S. A. McCollum, and E. E. Werner. 1997. Natural selection for environmentally induced phenotypes in tadpoles. *Evolution* **51**:1983–1992.

APPENDIX

Figure showing the five measurements made on the Pacific treefrog tadpoles (*Ecological Archives* E087-020-A1).