

HOW PREY RESPOND TO COMBINED PREDATORS: A REVIEW AND AN EMPIRICAL TEST

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Abstract. Studies of phenotypic plasticity frequently ask how organisms respond to a change in their environment, but most organisms do not experience single environmental changes. Therefore, we need to move to the next step and understand how organisms respond to combinations of environmental changes. Recent studies of predator-induced plasticity have addressed how prey respond to different combinations of predators. I briefly review 22 studies of combined predator effects on prey phenotypes and identify four factors that make it difficult to interpret the results of these studies: (1) uncontrolled prey consumption, (2) a low number of prey traits, (3) a low number of predator combinations, and (4) confounded predator composition and total predator density.

I address these challenges in an experiment that examined how wood frog tadpoles (*Rana sylvatica*) altered 12 behavioral, morphological, and life historical traits in response to four different caged predators (*Erythemis*, *Belostoma*, *Dytiscus*, and *Anax*). The predators were present alone at low density, alone at high density (2×), or combined into six pairwise combinations. When each predator was alone (at either low or high density), tadpoles discriminated among different predators and produced predator-specific phenotypes. The doubling of predator density rarely induced more extreme prey phenotypes. When predators were combined, the tadpoles generally developed phenotypes that were similar to those induced by the more risky predator alone (90% of all traits examined, at either low or high density). These results suggest that tadpoles perceive the risk of combined predators as being similar to the risk of the most dangerous predator in the pair, and not as a summed or averaged predation risk. The actual risk from these predator combinations remains to be tested. This appears to be the first study to take a comprehensive approach that controls prey consumption, examines a large number of prey traits, uses a large number of predator combinations, and separates the effects of predator composition and predator density. There is a clear need for more such studies to determine whether these results can be generalized to other taxa.

Key words: anti-predator responses; anuran; behavior; morphology; phenotypic plasticity; *Rana sylvatica*; wood frog.

INTRODUCTION

Environmental heterogeneity presents a substantial challenge for organisms because an individual's performance and subsequent fitness vary under different environmental conditions. Because performance is a function of an individual's traits, many species have evolved phenotypically plastic traits as a way to adaptively deal with environmental heterogeneity. Ecologists have documented an amazing amount of phenotypic plasticity in a wide variety of species including protists, plants, and animals in response to a wide variety of biotic and abiotic changes (Bradshaw 1965, Schlichting 1986, Sultan 1987, West-Eberhard 1989, Via et al. 1995, Schlichting and Pigliucci 1998). Predator-induced plasticity has received a great deal of attention, in both plants and animals, because of the dramatic range of behavioral, morphological, and physiological responses that predators and herbivores induce

in their prey (Havel 1987, Sih 1987, Lima and Dill 1990, Karban and Baldwin 1997, Kats and Dill 1998, Tollrian and Harvell 1999). While most studies of predator-induced plasticity have focused on how prey respond to a single predator species, there is a growing number of studies that demonstrate that prey can discriminate among different predators and exhibit predator-specific phenotypes (Havel 1985, Kuhlmann and Heckmann 1985, Lawler 1989, Black 1993, Kusch 1995, Pettersson et al. 2000, Turner et al. 2000, Relyea 2000, 2001*b*).

We now have over 100 studies documenting how prey respond to separate predators (Lima and Dill 1990, Kats and Dill 1998, Tollrian and Harvell 1999). However, we still lack a good understanding of how prey respond to combined predators, even though experiencing combined predators is the more natural condition (Schoener 1989, Polis 1991, Polis and Strong 1996). In this paper, I review past studies that have examined the effect of combined predators on prey phenotypes and identify shortcomings in these experiments that complicate our interpretations. I then con-

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duct an empirical test of combined predator effects that addresses these experimental shortcomings.

A review of the literature

Prey responses to combinations of predators have not been studied extensively, but I found 22 studies that address the phenomenon (Table 1). These studies have been conducted almost entirely in aquatic systems and generally fall into one of two scenarios: (1) prey responding to two species of free-ranging predators, or (2) prey responding to two species of caged predators. The first scenario is certainly the more natural one. The primary focus of these studies is to document how predators can alter each other's predation rates, with a secondary focus on how prey respond to combined predators (Sih et al. 1998). The second scenario places the primary focus on prey responses to combined predators by preventing the predators from interacting. In both scenarios, one predator is typically more risky than the other (poses a higher risk of mortality to the prey).

The collection of studies demonstrates that two different predators can induce prey traits in either the same direction (e.g., Relyea 2000) or in opposite directions (e.g., Turner et al. 1999). When predators induced prey traits in the same direction (11 studies), prey phenotypes either exceeded those induced by the more risky predator alone (12% of all traits examined), were similar to the more risky predator alone (63%), were intermediate to those induced by the more and less risky predators alone (4%), or were similar to the less risky predator alone (21%). When predators induced prey traits in opposite directions (11 studies), prey phenotypes never exceeded those induced by the more risky predator alone (0%), were similar to the more risky predator alone (61%), were intermediate to those induced by the more and less risky predators alone (26%), or were similar to the less risky predator alone (13%). Thus, by a slim majority, most prey respond to combined predators the same way that they respond to the more risky predator in the pair. However, there is still a large number of contradictory results. These contradictions are likely due, in part, to a number of experimental shortcomings: (1) uncontrolled prey consumption, (2) a low number of prey traits, (3) a low number of predator combinations, and (4) the confounding of predator composition with predator density.

Controlling prey consumption.—When free-ranging predators are combined, prey consumption by each predator can be different than when each predator is alone (Soluk and Collins 1988, Soluk 1993, Wissinger and McGrady 1993). Of the 22 studies reviewed, 17 of them (77%) did not control prey consumption. If a predator consumes a different number of prey when alone than when combined, there can be differences in the amount of cue produced by each predator. This is especially a problem for chemical cues, which can be affected by the amount of prey that are consumed (i.e., the amount of cue produced) and composition of the

consumed prey (Anholt et al. 1996, Laurila 2000). That is not to say that every predator must eat the same amount of prey. For researchers to interpret how prey respond to predators when predators are either separate or together, a given predator must consume the same amount of prey in each treatment regardless of other predators. Once this is established, one can allow the predation rates to vary to more natural rates and see how prey respond to the changing foraging patterns of their predators due to predator–predator interactions. Variable predation rates also affect the number of prey that remain alive in each treatment, and these density differences can alter many of the same traits that predators alter (Werner and Anholt 1993, Relyea 2002a). Predation can be controlled either by placing predators in cages and feeding them a constant amount of prey (Relyea and Werner 1999, Turner et al. 2000) or by disabling the predators' mouthparts (Wissinger and McGrady 1993, McIntosh and Peckarsky 1999). While these manipulations assume that caged or disabled predators induce the same phenotypic changes that lethal predators induce, few studies have tested this assumption (Peacor and Werner 2001, Relyea 2002c).

Choosing prey traits.—Most prey can alter suites of traits in response to predators, yet 8 of the 22 studies (36%) examined only one trait (Table 1). If we only focus on one trait, we may not observe a combined-predator effect because prey are simultaneously changing other traits. For example, prey fish (*Leiostomus xanthurus*) move to shallow water in the presence of predatory flounder (*Paralichthys lethostigma*), and move to deep water in the presence of a predatory bird assemblage. When both predators are present, the predicted intermediate use of deep and shallow water is not observed because the prey simultaneously increased their use of a second trait, schooling behavior (Crowder et al. 1997). Similarly, fishing spiders (*Dolomedes vittatus*) scare water striders into open water, while sunfish scare water striders to the pool edge. When the two predators are combined, the predicted intermediate habitat use is not observed, because the prey simultaneously change a second trait, activity (Krupa and Sih 1998). These studies inform us that when we ignore the diversity of antipredator traits that prey possess, our predicted responses to combined predators often will not be observed. In some cases, observing how a single trait changes may be sufficient for understanding the prey response (providing that the observed trait turns out to be the most important trait). However, we would often benefit from examining larger suites of antipredator traits so that we have a higher probability of observing all of the important traits.

Choosing predator combinations.—If we want to ask how prey generally alter their phenotype in response to combinations of predators, we should examine multiple combinations of predators. Of the 22 studies, 21 (95%) used only one predator combination (Table 1). Further, several of the studies combined a predator that

TABLE 1. Studies documenting the effect of separate and combined predators on a prey's phenotype.

Effect of separate predators and taxon†	Controlled predation?	Experimental design	Number of traits‡	Number of predator combinations	Response to predator combination§	References
Same direction						
Tadpole (1)	yes	additive	1 (G)	2	same as more risky predator	Relyea and Werner (1999)
Tadpole (2)	yes	additive	8 (MG)	1	same as more risky predator	Relyea (2000)
Mayfly (1)	no	additive	1 (B)	1	same as more risky predator	Scrimgeour and Culp (1994)
Water strider (1)	no	additive	3 (B)	1	same as less risky predator	Sih and Krupa (1996)
Isopod (1)	no	additive	1 (B)	1	same as more risky predator	Huang and Sih (1991)
Tadpole (1)	no	additive	2 (BG)	1	same as less risky predator	Eklöv (2000)
Tadpole (2)	no	additive	1 (B)	1	intermediate	Eklöv and Werner (2000)
Tadpole (1)	no	additive	1 (G)	1	same as more risky predator	Fauth (1990)
Salamander (1)	no	additive	2 (BG)	1	same as more risky predator	Resetarits (1991)
Water strider (1)	no	additive	2 (B)	1	exceeds more risky predator	Krupa and Sih (1998)
Crayfish (1)	no	additive	2 (BG)	1	same as more risky predator (B) exceeds more risky predator (G)	Resetarits (1991)
Opposite direction						
Mayfly (1)	yes	additive	2 (B)	1	intermediate (B) same as more risky predator (B)	McIntosh and Peckarsky (1999)
Mayfly (1)	yes	additive	3 (BGD)	1	intermediate (B) same as more risky predator (GD)	Peckarsky and McIntosh (1998)
Snail (1)	yes	additive	2 (B)	1	intermediate (B) same as less risky predator (B)	Turner et al. (2000)
Fish (1)	no	additive	2 (B)	1	intermediate	Rahel and Stein (1988)
Isopod (1)	no	additive	2 (B)	1	same as more risky predator (B) same as less risky predator (B)	Huang and Sih (1990)
Water strider (1)	no	additive	2 (B)	1	same as more risky predator	Krupa and Sih (1998)
Daphnia (3)	no	additive	1 (B)	1	same as more risky predator	Gonzalez and Tessier (1997)
Snail (1)	no	additive	1 (B)	1	intermediate	Martin et al. (1989)
Tadpole (2)	no	additive	2 (BG)	1	same as more risky predator	Nyström and Åbjörnsson (2000)
Fish (1)	no	additive	2 (BG)	1	same as more risky predator	Crowder et al. (1997)
Fish (1)	no	additive	1 (G)	1	less than less risky predator	Eklöv and Van-Kooten (2001)
Gerbils (2)	no	additive	3 (B)	1	same as more risky predator	Kotler et al. (1992)

† Numbers in parentheses indicate the number of prey species examined.

‡ Abbreviations are: B = behavioral traits, M = morphological traits, G = growth, and D = development.

§ When more than one result is listed, it indicates that different traits led to different conclusions.

posed a high risk of predation with another predator that posed a very low risk of predation. The first predator typically induces a strong response in the prey, the second predator induces a small or nonsignificant response, and the combined predators induce a response

that is similar to the first predator. Such experiments are weak tests of how prey should respond to combined predators. Using only two predators may be sufficient for systems containing only two major predators. However, in systems containing a greater diversity of pred-

ators, we should be using numerous predator combinations that span a wide range of riskiness to provide a more rigorous test of combined predator hypotheses, from low-risk/low-risk combinations to high-risk/high-risk combinations.

Confounding predator composition with predator density.—Studies of combined predator effects have confounded a change in predator composition with a change in total predator density. Of the 22 studies, 100% (including the author's own studies) have tested for a combined predator effect using an additive design (no predators, predator A, predator B, predator A+B), and then compared the effect of each predator when alone to the effect of the predators when combined. However, in the combined treatment there are twice as many total predators. To separate the effects of predator composition and total predator density, we must include additional treatments that double the density of each predator when alone (a substitutive design). By comparing the phenotypes exhibited with combined predators to the phenotypes exhibited with low and high densities of conspecific predators, we can determine whether phenotypic changes are due to changes in predator composition or changes in total predator density. This more comprehensive approach of including both additive and substitutive treatments has yet to be attempted.

In summary, interpreting prey responses to combined predators has proven difficult because past studies have used either uncontrolled prey consumption, a single prey trait, a single predator combination, or an additive design. My goal was to address these challenges empirically by controlling the number of prey consumed by each predator, examining multiple prey traits, using multiple predator combinations, and separating the effects of predator composition and total predator density.

Study system

Because larval anurans have been well studied for their predator-induced responses, they make an excellent choice of study system. Aquatic predators induce tadpoles to change their behavior, morphology, and life history (Lawler 1989, Feminella and Hawkins 1994, Smith and Van Buskirk 1995, McCollum and Van Buskirk 1996, Relyea 2000, 2001b, Relyea and Werner 2000). These phenotypic changes reduce the tadpole's probability of being killed by predators, but come at the cost of reduced growth and competitive ability in the absence of predators (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Relyea 2002a). Furthermore, most tadpoles can discriminate among different species of predators and exhibit predator-specific phenotypes (Relyea and Werner 1999, Eklöv and Werner 2000, Relyea 2000, 2001b). In wood frog tadpoles (*Rana sylvatica*), more risky predators induce more extreme phenotypes (Relyea 2001a, c). This positive correlation between predation risk and phenotype change is not uni-

versal (Relyea 2001c), but it does allow us to develop straightforward hypotheses about the effects of combined predators (see *Hypotheses* below).

I chose four species of predators that coexist with wood frog tadpoles (R. A. Relyea, D. K. Skelly, E. E. Werner, and K. L. Yurewicz, *unpublished data*). Larval aeshnid dragonflies (*Anax junius*) are relatively large (up to 50 mm) and voracious predators of tadpoles (Werner 1991, Werner and Anholt 1996, Van Buskirk and Yurewicz 1998, Relyea 2000). Larval predaceous diving beetles (*Dytiscus* sp.) also are large predators (up to 40 mm) that readily kill a variety of tadpoles, but they pose less of a predation risk than *Anax* due to their lower capture efficiencies and longer handling times (Relyea 2001c). Adult water bugs (*Belostoma* sp.) are medium-sized predators (up to 25 mm) that pose an even lower predation risk due to a low capture efficiency, a long handling time, and a likely smaller gut capacity (Relyea 2001c). Larval libellulid dragonflies (*Erythemis* sp.) are the smallest of the four predators (up to 16 mm). While I had no data on the predation risk of *Erythemis*, its small size suggested that it would pose the lowest predation risk to wood frogs.

Hypotheses

Using both an additive and substitutive design, we can make a number of predictions about how prey should respond to low densities of conspecific predators (A or B), high densities of conspecific predators (A+A or B+B), and high densities of combined (A+B) predators. We start by making three assumptions: (1) prey perceive risk accurately, (2) different predators induce prey phenotypes in the same direction (but different magnitudes) (Lima and Dill 1990, Kats and Dill 1998), and (3) prey perception of risk combines in an additive fashion. If two predators pose different predation risks (predator A is less risky than predator B), prey should exhibit less extreme phenotypes with predator A than predator B. Further, high densities of a predator (A+A) should induce more extreme phenotypes than low densities of the same predator (A). Combined predators (A+B) should induce more extreme phenotypes than either predator alone at low density (A or B). However, combined predators should induce phenotypes that are intermediate to high densities of the less risky predator (A+A) and high densities of the more risky predator (B+B). If predation risk is more than additive, the relative ranking of the prey phenotypes would not change. However, if predation risk is less than additive, prey could respond to combined predators in a number of ways: (1) prey could respond to the predation risk posed by only the more risky of the two predators; (2) prey could respond to the mean predation risk of the two predators; or (3) prey could respond to the predation risk posed by the less risky of the two predators. Naturally, when predators induce prey traits in opposite directions (e.g., Turner et al. 1999), these predictions would change. By examining

numerous predator combinations and numerous traits, we can determine which of these predictions is best supported and perhaps gain insights into how prey perceive combined risk.

I tested the following four hypotheses based on the additive predation risk assumption: (1) prey can discriminate among predators, at either low or high predator densities, and produce predator-specific phenotypes (a well-documented, but necessary, first step); (2) high densities of conspecific predators induce more extreme phenotypes than low densities of conspecific predators; (3) combined predators induce more extreme phenotypes than either predator alone at low density; and (4) combined predators induce phenotypes that are intermediate to either predator alone at high density.

METHODS

I conducted the experiment in 1000-L pond mesocosms (protocols are detailed in Van Buskirk and Relyea 1998). After waiting 11 days to establish periphyton (a source of tadpole food), I added 30 newly hatched wood frogs to each tank (mean mass = 42 mg), drawn from a mixture of 30 egg masses from Janette Tryon Reserve in northwestern Pennsylvania. This density of wood frogs (17 frogs/m²) is well within natural densities (R. A. Relyea, E. E. Werner, D. K. Skelly, and K. L. Yurewicz, *unpublished data*). I set aside 20 wood frog tadpoles to assess 24-h mortality due to handling; survival of this group was 100%. I equipped each tank with four predator cages that were constructed of 10 × 10 cm plastic drain pipe with window screen on each end. In these cages, wood frog tadpoles have little opportunity to escape predation from hungry predators (Relyea 2002c). I covered all tanks with 60% shade cloth to prevent colonization by aquatic predators and other amphibians.

I used a randomized block design with 15 treatments and four replicates. The first treatment contained no predators (empty cages). In the next four treatments, I assigned a low density (two caged individuals) of either aeshnid dragonflies (mean size ± 1 SE = 41 ± 1 mm), predaceous diving beetles (40 ± 1 mm), water bugs (23 ± 0 mm), or libellulid dragonflies (16 ± 0 mm). In the next four treatments, I assigned a high density (four caged individuals) of each predator. In the final six treatments, I assigned a high density of combined predators (two caged individuals of one predator plus two caged individuals of another predator) using all six pairwise combinations. Each predator was fed ≈300 mg of wood frog tadpoles (3–10 tadpoles) three times per week. The predators' rations stayed constant throughout the experiment because the predators did not show substantial growth. Empty cages were lifted and placed back into their tanks to equalize disturbance among treatments.

During the experiment, I quantified tadpole behavior. I counted the number of tadpoles that I could see on the sides and bottom of each tank and the number of

observed tadpoles that were active (moving). The proportion of observed tadpoles (i.e., the proportion not hiding) was the number of observed tadpoles divided by the initial density (30 tadpoles). The proportion of active tadpoles was the number of active tadpoles divided by the number observed (see protocols in Peacor and Werner 1997, Relyea 2002a, b). I conducted 20 observations on each tank during 3 and 11 May and used the mean activity of each tank as the response variable.

I terminated the experiment when the tadpoles were approaching metamorphosis. First, I counted all tadpoles left in each predator cage. Second, I counted and weighed all tadpoles in the tank to determine the survival and growth rate ((final mass – initial mass) / 24 or 25 days). I preserved a sample of 10 tadpoles in 10% formalin for subsequent measurements of tadpole morphology. To measure the tadpoles, I placed preserved tadpoles under a video camera that was connected to a computer with Optimas image analysis software (Bioscan, Bothell, Washington). From the lateral view, I measured the body length, body depth, tail length, tail depth, and muscle depth. From the ventral view, I measured the tail muscle width, body width, and mouth width (see Relyea 2000 for a photo of all dimensions).

Because I was interested in quantifying both changes in tadpole size (i.e., growth rate) and shape (i.e., relative morphology) in response to the treatments, I had to derive size-independent measures of shape. For each linear dimension, I regressed log-transformed mass against the log-transformed dimension for all 640 tadpoles (64 experimental units × 10 tadpoles per experimental unit). The data were log transformed to improve the linearity of the response. I saved the residuals (size-independent morphology) from this single regression and calculated the mean residuals for each tank. These mean residuals served as the morphological response variables (see Relyea 2000, 2002a, c).

Statistical analyses

I analyzed the data using a multivariate analysis of variance (MANOVA). There were 12 response variables: survival, growth rate, proportion observed, proportion active, and eight morphological dimensions. Blocks and treatments were the main effects. The interaction of the two main effects was not significant, so I pooled the interaction degrees of freedom with the error term. When a significant multivariate effect was detected, I examined the univariate effects. For significant univariate effects, I conducted mean comparisons using Fisher's test. The data quantifying the number of tadpoles remaining in the predator cages (mean number per tank) were heteroscedastic, so I used nonparametric Kruskal-Wallis tests to analyze differences among predator species and differences among treatments within each predator species.

TABLE 2. Results of a MANOVA examining the impact of different combinations of nonlethal (caged) predators on the survival, growth rate, activity, and relative morphology of wood frog tadpoles.

A) Multivariate tests			
Source of variation	df	F	P
Block	36, 99	2.0	0.004
Treatment	168, 307	1.7	0.00008

B) Univariate tests		
Trait	P values	
	Block	Treatment
Survival	0.466	0.426
Growth rate	0.159	0.0008
Number observed	0.268	<0.00001
Activity	0.685	<0.00001
Tail length	0.289	0.691
Tail depth	0.214	<0.00001
Muscle depth	0.874	0.024
Muscle width	0.001	0.00002
Body length	0.001	<0.00001
Body depth	0.124	0.224
Body width	0.011	0.757
Mouth width	0.003	0.0001

RESULTS

Prey responses to predators

There was a significant multivariate effect of both block and treatment on the prey phenotypes. Blocks

did not affect survival, growth, or activity, but they did affect four of the morphological responses (Table 2, Figs. 1 and 2). The predator treatments did not affect tadpole survival, relative tail length, relative body depth, or relative body width, but they did affect the other eight traits. To simplify the description of the large number of results, I first report how each predator affected the eight traits relative to the no-predator treatment. I then examine the eight traits in light of the four hypotheses.

At low conspecific densities, all four predators reduced tadpole growth ($P \leq 0.02$), *Belostoma*, *Dytiscus*, and *Anax* reduced tadpole activity ($P \leq 0.01$), and *Belostoma* and *Anax* reduced the proportion of tadpoles observed ($P \leq 0.02$). Relative tail depth was increased by *Belostoma*, *Dytiscus*, and *Anax* ($P \leq 0.02$), while tail muscles became deeper only with *Erythemis* ($P = 0.037$). Some dimensions were only affected by *Anax* ($P \leq 0.01$); muscles and mouths became narrower and bodies became shorter.

At high conspecific densities, all four predators reduced tadpole growth ($P \leq 0.005$) and activity ($P \leq 0.05$), but only *Dytiscus* and *Anax* reduced the proportion of tadpoles observed ($P \leq 0.002$). Relative tail depth was increased by *Belostoma*, *Dytiscus*, and *Anax* ($P \leq 0.01$), whereas tail muscles became deeper only with *Erythemis* ($P = 0.056$). Relative muscle width was increased with *Dytiscus* and *Anax* ($P \leq 0.04$), body length was decreased with *Anax* ($P < 0.001$), and

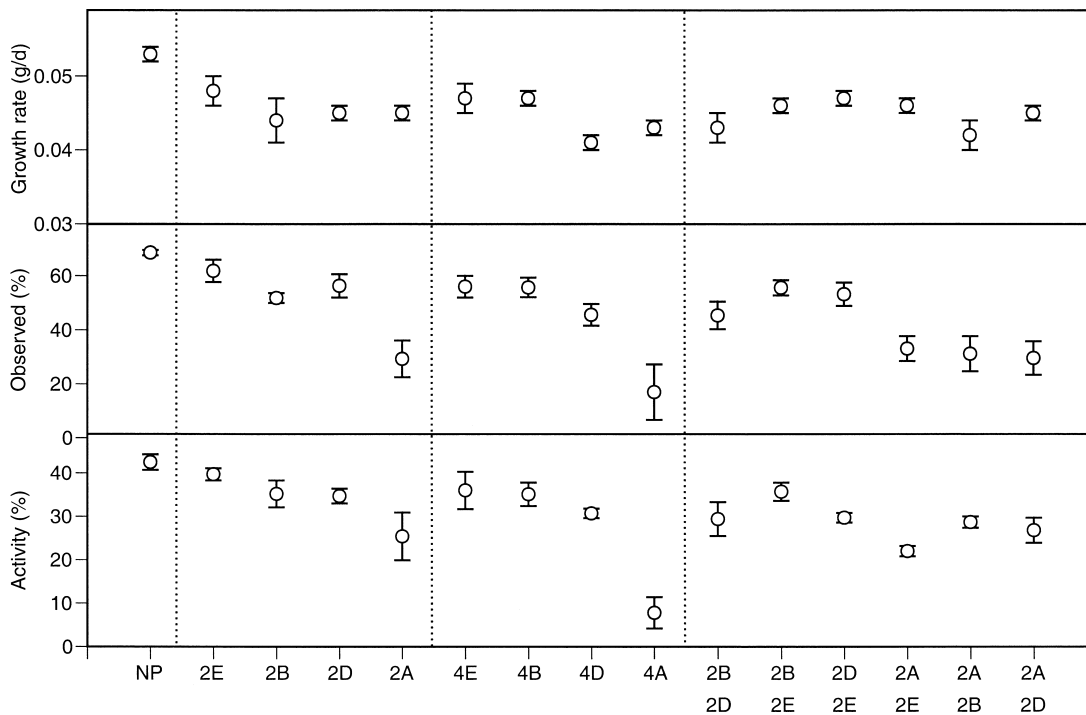


FIG. 1. The growth rate, percentage of tadpoles observed, and percentage of tadpoles active when wood frogs were reared with different combinations of predators (NP = no predator, E = *Erythemis*, B = *Belostoma*, D = *Dytiscus*, A = *Anax*). Data are means \pm 1 SE.

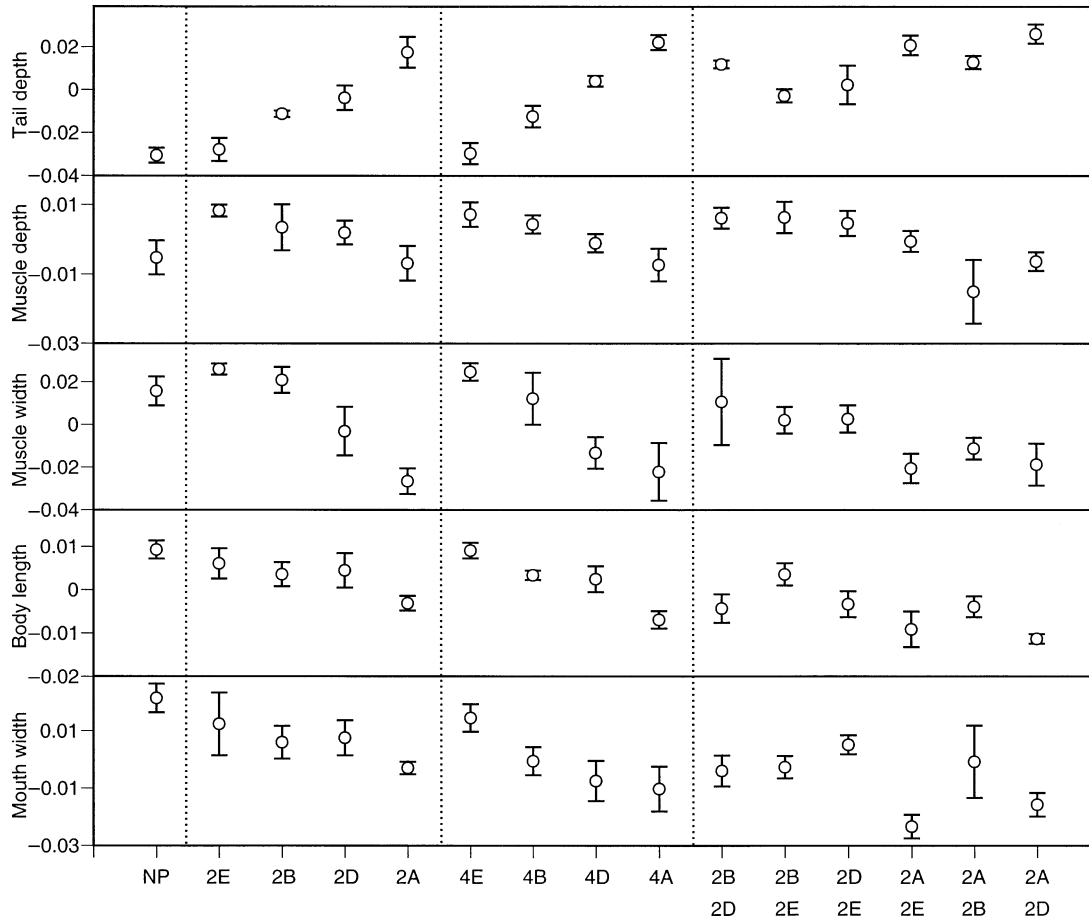


FIG. 2. The relative morphology of wood frog tadpoles when reared with different combinations of predators (NP = no predator, E = *Erythemis*, B = *Belostoma*, D = *Dytiscus*, A = *Anax*). Only significant dimensions are shown. Differences in overall size were removed prior to analysis. For each dimension, log-transformed mass was regressed against the log-transformed dimension; data are the mean residuals (± 1 SE) for each tank.

mouth width was decreased by *Belostoma*, *Dytiscus*, and *Anax* ($P \leq 0.02$).

The first hypothesis was that tadpoles could discriminate among predators (at both low and high predator densities). I defined discrimination as the ability of the tadpoles to produce significantly different phenotypes between at least two of the predators. At low predator densities, tadpoles discriminated among predators for six of the eight traits: tail depth, muscle depth, muscle width, body length, and activity ($P < 0.05$). At high predator densities, tadpoles discriminated among predators for all eight traits ($P < 0.05$). Thus, wood frog larvae exhibited predator discrimination with 75% of their traits at low predator densities and 100% of their traits at high predator densities.

The second hypothesis was that high densities of conspecific predators would induce more extreme phenotypes than low densities of the same conspecific predators. Doubling the density of each predator had no effect on tadpole growth ($P > 0.06$), the proportion of tadpoles observed ($P \geq 0.1$), or any of the morpho-

logical traits ($P > 0.1$). Doubling the density of *Anax* further reduced activity ($P = 0.013$), but doubling the density of *Erythemis*, *Belostoma*, and *Dytiscus* had no effect on activity. Thus, doubling the density of the four predators had an effect in only one (3%) of the 32 possible comparisons.

The third hypothesis was that combined predators would induce phenotypes that were more extreme than phenotypes induced by low densities of either predator alone. Given the eight traits that changed significantly and the six predator combinations, there were 48 possible comparisons. Compared to the more risky of the two predators, combined predators induced more extreme phenotypes in four comparisons (8%), less extreme phenotypes in one comparison (2%), and similar phenotypes in 43 comparisons (90%). Compared to the less risky of the two predators, combined predators induced more extreme phenotypes in 20 comparisons (42%), less extreme phenotypes in one comparison (2%), and similar phenotypes in 27 comparisons (56%). Thus, many of the responses to combined predators

overlapped with the responses to each predator alone (27 comparisons). This happened when the predators induced similar phenotypes when alone (e.g., *Erythemis* plus *Belostoma* vs. *Erythemis* alone or *Belostoma* alone). When the response to combined responses overlaps the responses to both predators alone, it is difficult to determine whether the prey reared with combined predators are attempting to exhibit phenotypes that are similar to the more risky predator or less risky predator. However, one can restrict the set of responses to include comparisons in which the response to combined predators only overlaps one of the two responses to separate predators (16 comparisons). Using this restricted set of comparisons, the response to combined predators was always similar to the more risky predator and never similar to the less risky predator. Therefore, prey generally responded to combined predators the same way they responded to the more risky predator alone at low density.

The fourth hypothesis was that combined predators would induce phenotypes that were intermediate to those phenotypes induced by high densities of low risk and high risk predators alone. Again, there were 48 possible comparisons. Compared to the more risky of the two predators, combined predators induced more extreme phenotypes in zero comparisons (0%), less extreme phenotypes in five comparisons (10%), and similar phenotypes in 43 comparisons (90%). Compared to the less risky of the two predators, combined predators induced more extreme phenotypes in 20 comparisons (42%), less extreme phenotypes in one comparison (2%), and similar phenotypes in 27 comparisons (56%). Again, many of the responses to combined predators overlapped the responses to both predators alone (26 comparisons), making it difficult to interpret the results. When I restricted the set of responses to include comparisons in which the response to combined predators only overlapped one of the two responses to separate predators (19 comparisons), the response to combined predators was similar to the more risky predator in 17 comparisons (89%), and similar to the less risky predator in two comparisons (11%). Therefore, prey generally responded to combined predators the same way they responded to the more risky predator alone at high density.

Predator consumption of prey

The number of tadpoles remaining in the predator cages allowed me to assess whether the predators differed in their consumption rates both across species and across predator combinations. Averaged across treatments (mean \pm SE), *Anax* ate $100 \pm 0\%$ of the tadpoles, *Dytiscus* ate $99 \pm 1\%$ of the tadpoles, *Belostoma* ate $69 \pm 3\%$, and *Erythemis* ate $34 \pm 2\%$. These differences among predator species were significant (Kruskal-Wallis test statistic = 72.9, $P < 0.00001$). Within each of the predator species, however, there were no differences in predation rate when the

predators were alone at low densities, alone at high densities, or combined with other predators ($P > 0.6$).

DISCUSSION

This appears to be the first study to test extensively how prey respond to combined predators. The wood frog tadpoles were able to discriminate among different predators by producing different behavioral, morphological, and life history phenotypes. The ability to discriminate among predators is quite common among diverse prey taxa including mammals, amphibians, fish, aquatic insects, zooplankton, and protists (see reviews by Sih 1987, Lima and Dill 1990, Kats and Dill 1998). Natural selection likely favors the evolution of predator-specific responses, the most obvious condition being when different predators favor opposite phenotypes. For example, snails survive predatory crayfish (*Orconectes rusticus*) by avoiding cover habitats and using open-water habitats, but they survive predatory sunfish (*Lepomis gibbosus*) by avoiding open-water habitats and using cover habitats (Turner et al. 2000). Snails that discriminate between these two predators should be favored by selection. However, natural selection should also favor predator-specific responses even when different predators select for phenotypes in the same direction. For example, tadpoles can reduce their predation risk to many predators by reducing their activity level; lower activity makes tadpoles less apparent to predators (Gerritsen and Strickler 1977, Azevedo-Ramos et al. 1992, Anholt and Werner 1995, Relyea 2001c), but it also reduces foraging opportunities, leading to slower growth (Skelly 1992, Relyea and Werner 1999). Thus, selection should favor the ability to optimize the trade-off between the different risks of predation (from different predators) and the fitness costs associated with slower growth. Selection to optimize this trade-off should translate into selection to discriminate between high- and low-risk predators (Abrams 1983, Houston and McNamara 1993, Werner and Anholt 1993). This is likely the mechanism that explains why so many different prey have evolved the ability to produce predator-specific phenotypes (Lima and Dill 1990, Kats and Dill 1998, Tollrian and Harvell 1999).

The ability to discriminate among predators requires the presence of different predator cues. In this study, the primary cues were likely chemicals coming from the caged predators (Petranka et al. 1987, Kats et al. 1988, McCollum and Leimberger 1997). While it is possible that the prey were responding to different amounts of a single chemical, previous work has ruled out this possibility in tadpoles, suggesting that the predators are producing either unique chemicals or unique combinations of chemicals (Relyea 2001a). Indeed, there is growing evidence that both predator identity (Martin et al. 1989, Peckarsk and McIntosh 1998, Turner et al. 1999, Nyström and Åbjörnsson 2000) and predator diet (Keefe 1992, Mathis and Smith 1993, Wilson

and Lefcort 1993, Laurila et al. 1998) affect prey phenotypes.

Because predator cues are integral to inducing antipredator responses, it is critical that a given predator produce the same predator cues in all treatments. However, the amount of prey consumed has not been controlled in most previous studies (77% of studies, see *A review of the literature*). I used caged predators to control predation rates and found that a given predator consumed the same number of prey when alone at low density, when alone at high density, and when in any of its three combinations. Previous experiments with gray treefrog tadpoles have shown that caged predators induce behavioral and morphological traits in the same direction and to the same magnitude as uncaged predators (Relyea 2002d).

The antipredator responses to each predator were related to the risk that each of the predators posed to the wood frogs. There appear to be no previous studies of wood frog tadpoles and *Erythemis*, but the cage survival data demonstrated that *Erythemis* only killed one-third of the tadpoles placed in their cages, while *Belostoma* ate two-thirds of their tadpoles and *Dytiscus* and *Anax* ate all of their tadpoles. Previous predation experiments have shown that there is an increasing risk of death when wood frogs are reared with *Belostoma*, *Dytiscus*, or *Anax*, respectively (Relyea 2001c). Therefore, *Erythemis*, *Belostoma*, *Dytiscus*, and *Anax* are increasingly dangerous to wood frog tadpoles, in that order. As expected for wood frog tadpoles (Relyea 2001c), *Erythemis* typically induced the smallest changes, *Belostoma* and *Dytiscus* induced moderate changes, and *Anax* induced the most extreme phenotypic changes. While a pattern of more risky predators inducing more extreme antipredator phenotypes has been described (Sih 1987), this pattern has been based primarily on studies using only two predator species and one antipredator trait. When we include many more predator species and a more diverse array of traits, the pattern is not generally supported in other tadpole species (Relyea 2001c). Tadpoles (and many other prey taxa) have suites of traits that can be used against different predators, and these traits do not necessarily adjust in an integrated way when more risky predators are experienced. Thus, while the direct relationship between risk and phenotypic change in wood frogs provides an excellent first step in extensively testing the effects of combined predators on prey phenotypes, it is clear that future investigations in other taxa may yield results that are more complex.

Increasingly risky predators induced increasingly lower activity, relatively deeper tails, and relatively smaller bodies, and these responses are likely adaptive. Less active prey are more likely to survive but at the cost of slower growth (Woodward 1983, Azevedo-Ramos et al. 1992, Juliano and Reminger 1992, Short and Holomuzki 1992, Skelly 1992, Anholt and Werner 1995, Relyea and Werner 1999, Relyea 2001c). Ad-

ditionally, tadpole prey with deeper tails and shorter bodies are better at escaping strikes by predators (Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Van Buskirk and McCollum 2000; R. A. Relyea, *unpublished data*). However, tadpoles with this phenotype experience slower growth and development (Van Buskirk and Relyea 1998, Van Buskirk 2000, Relyea 2002a). Thus, tadpoles in predator-free environments exhibit high activity, shallow tails, and large bodies. These opposing selective force in the presence and absence of predators should help maintain phenotypic plasticity in prey (Van Buskirk and Relyea 1998, Relyea 2002a).

Although the prey could discriminate among low-, moderate-, and high-risk predators, doubling the conspecific density of each predator had little effect on the phenotypes expressed by the prey. Past studies have found that prey exhibit stronger anti-predator responses as predator density increases (Loose and Dawidowicz 1994, Kusch 1995, McKelvey and Forward 1995, Anholt et al. 1996). In the current study, it is possible the two conspecific predators caused the tank water to be saturated with chemical cues, or that the sensory mechanisms of the prey were saturated with cues. If this was the case, then adding two more predators could not induce more extreme phenotypes. However, it seems unlikely that two relatively small predators could saturate 1000 L of water with a chemical that they emit. The tadpoles further reduced their activity when *Anax* density was doubled. This rejects the idea that the cues were already saturated at low density of *Anax*, and may suggest that the cues were probably not saturated for low densities of the other predators as well. A more likely explanation is that doubling the density of the conspecific predators did increase the amount of cue in the water. However, doubling the densities of the less dangerous predators (*Erythemis*, *Belostoma*, or *Dytiscus*) did not cause an increase in perceived risk, and the prey responded accordingly by not further altering any of their traits. In contrast, doubling the density of the most dangerous prey (*Anax*) did cause an increase in the prey's perceived risk, and the prey responded accordingly by further reducing their activity. We currently do not have the data to test whether these patterns of prey perception match the actual risk posed by doubling each predator's density.

Using the assumption of additive predation risk (or more than additive predation risk), I predicted that combined predators should induce more extreme phenotypes than either of the predators alone at low density. There was little support for this prediction. The alternative hypothesis was that prey respond to combined predators using less than additive predation risk, posing the possibilities that prey could induce phenotypes that are the same as the more risky predator, intermediate to the more and less risky predators, or the same as the less risky predator. Relative to low densities of each predator alone, combined predators

induced the same phenotype as the more risky predator in 90% of the total comparisons and in 100% of the restricted comparisons. Relative to high densities of each predator alone, combined predators induced the same phenotype as the more risky predator in 90% of all comparisons and in 89% of the restricted comparisons. This suggests that even when we account for the increase in total predator density, prey responded to combined predators the same way as they responded to the more risky predator. Prey did not respond to combined predators by exhibiting intermediate phenotypes nor by exhibiting phenotypes that were similar to the less risky predator. This suggests that the prey did not perceive an increase in predation when a less risky predator was added to an already risky environment. An alternative explanation is that the first predator had already induced the maximum prey response and the prey could not respond further when the second predator was added. However, this scenario could only have occurred for the predator combinations that contained *Anax* (which induced the largest prey responses). Because the other predator combinations also induced phenotypic changes similar to the more risky predator in the pair, it appears that phenotypic constraints are not the driving force underlying this combined predator phenomenon.

Taken together, the data from doubling conspecific predators and combining heterospecific predators suggest that tadpoles possess fairly straightforward decision rules when it comes to altering their phenotypes. In the vast majority of cases, the decision rule is to respond to the riskiest predator in the environment. Alternative strategies, in which prey respond to the less risky of the two predators in a combination, or in which prey respond with intermediate phenotypes, should not be favored by natural selection because prey making these decisions would incur a higher probability of death from the more risky predator (unless predators interact).

In the literature review noted earlier, 63% of the comparisons supported the hypothesis that prey respond to the more risky of two predators when predators are combined. For example, predatory salamanders (*Ambystoma barbouri*) induce a small increase in sand burrowing by isopods (*Lirceus fontinalis*), while sunfish (*Lepomis cyanellus*) induce a large increase in sand burrowing by isopods. When the two predators were combined, the isopods exhibited the same amount of burrowing behavior as they exhibited with sunfish alone (i.e., there was no additive effect; [Huang and Sih 1991]). However, in that study (and all others), the change in predator composition was confounded with a change in total predator density, so we must be careful in how strongly we draw conclusions. A number of other studies have concluded that prey do not respond to combined predators the same way that they respond to separate predators. For example, Eklöv (2000) examined how bullfrog tadpoles (*R. catesbeiana*) re-

sponded to predatory fish (*Lepomis macrochirus*), larval dragonflies (*Anax* sp.), or fish and dragonflies combined. The tadpoles exhibited small activity reductions with fish, large activity reductions with dragonflies, and small activity reductions with both predators combined, suggesting that tadpoles respond to combined predators by responding to the less risky predator. However, this study lacked substitutive treatments and, more importantly, each predator ate different amounts of prey when it was alone compared with when the predators were combined. Tadpole consumption was low with fish alone, high with dragonflies alone, and intermediate with both predators combined. Thus, one cannot rule out that the weaker response to combined predators was simply due to a decrease in predation and a concomitant decrease in predatory cues. This underscores the importance of carefully designing combined predator experiments.

A decision rule to respond to the more risky of the two predators should work well when predators select for similar phenotypes (e.g., decreased activity). However, this decision rule would not work well when predators favor opposite phenotypes. When predators favor opposite phenotypes (e.g., each predator hunts in a different habitat; Martin et al. 1989), responding to only one of the two predators necessarily puts the prey at a higher risk of being killed by the other predator. In this case, the optimal decision rule might be an intermediate strategy that balances the relative risk of the two predators. For example, snails (*Physella gyrina*) use covered habitat 72% of the time in the presence of fish (*L. macrochirus*), 22% of the time in the presence of crayfish (*Orconectes rusticus*), and 46% of the time in the presence of both predators (Turner et al. 2000). Further, when predators favor opposite phenotypes, doubling the density of conspecific predators should induce phenotypes that are more extreme than the phenotypes induced at low densities of conspecific predators and different from those induced by combined predators.

Conclusions

This study represents the first comprehensive attempt to determine how prey respond to combined predators. It builds upon the best aspects of past studies by including multiple traits, multiple predator combinations, controlled prey consumption, and the separation of the effects of predator composition and predator density. The results suggest that prey respond to combined predators by simply responding to the most dangerous predator of the pair rather than responding to combined predators in an additive fashion. Clearly, we need to apply this more comprehensive approach to many more empirical systems to determine whether these conclusions are generalizable. The majority of studies have been conducted on freshwater aquatic organisms (and only a few aquatic groups, predominantly snails, tadpoles, and mayflies). Thus, we need to diversify our taxonomic focus to include other systems including

marine and terrestrial systems. We also need to combine our knowledge of how prey respond to combinations of predators with studies of how predators interact in their consumption of prey (see review by Sih et al. 1998), for this determines actual predation risk. When we are able to understand predator-prey interactions from both perspectives, we will have a much better understanding of species interactions in general; combined density-mediated and trait-mediated interactions both determine the structure of natural communities (Abrams 1995, Beckerman et al. 1997, Peacor and Werner 1997, Relyea 2000, Relyea and Yurewicz 2002).

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