QUANTIFYING THE RELATION BETWEEN PREDATOR-INDUCED BEHAVIOR AND GROWTH PERFORMANCE IN LARVAL ANURANS

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Abstract. Because the nature and magnitude of species interactions are functions of the traits that species possess, understanding how individual traits affect performance is important to our understanding of community structure. To examine the relation between species traits and performance, we first assessed behavioral responses of two larval anurans to three predator species in the laboratory. We then correlated these responses with growth performance of the two anurans when they competed in the field. In the laboratory experiment, larval bullfrogs (*Rana catesbeiana*) and green frogs (*R. clamitans*) exhibited no reduction in activity or spatial avoidance to bluegill sunfish (*Lepomis macrochirus*), moderate reductions in activity and spatial avoidance of mudminnows (*Umbra limi*), and large reductions in activity and spatial avoidance of larval dragonflies (*Anax* spp.). In the field experiment, these behavioral responses were directly related to corresponding reductions in growth of the anuran larvae. Thus, for both species, changes in growth in the field could be correlated to the behavioral responses observed in the laboratory. Further, proportional changes in behavior in the presence of the different predators appeared to be related to changes in competitive relations in the field.

Key words: Anax *spp.; anuran behavior and growth;* Lepomis macrochirus; *predator induction;* Rana catesbeiana; Rana clamitans; Umbra limi.

INTRODUCTION

A central goal of community ecology is to predict the consequences of species interactions for community structure. In order to predict the consequences of such interactions, we must understand the underlying mechanisms of the interactions (Schoener 1986, Tilman 1987, Werner 1998). These mechanisms, in turn, are largely functions of individual traits such as behavior, morphology, and life history. Thus, it is crucial to develop the quantitative relations between species' traits and performance in the field if we are going to be able to predict the consequences of species interactions. If particular traits critical to interactions are common to many taxa, then results from such studies may be generalizable to other communities (Werner 1998).

A useful experimental approach to quantifying the relation between species' traits and performance is to take advantage of species whose traits are phenotypically plastic. Traits of individuals can be altered by exposure to different environments and these individuals then subjected to interactions with other species. This approach allows us quantitatively to relate trait changes to consequences for species interactions. One problem with this approach is that important traits such as behavior are often very dynamic and difficult to

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assess under field conditions. It would be useful, then, to assess if short-term measurements of behavioral responses or other trait changes conducted under controlled laboratory conditions offer any insight into species performance in the field when interacting with other species.

In this study, we examined the relation between short-term behavioral observations in the laboratory and performance under more natural conditions in the field. To accomplish this, we first conducted laboratory experiments examining the responses of two anuran larvae, bullfrogs (*Rana catesbeiana*) and green frogs (*R. clamitans*), to three potential predators. These predators, bluegill sunfish (*Lepomis macrochirus*), mudminnows (*Umbra limi*), and odonate larvae (*Anax junius* and *A. longipes*), are common predators found on the gradient of pond hydroperiod along which the two anuran larvae are distributed (Collins and Wilbur 1979, Werner and McPeek 1994, Wellborn et al. 1996). Because the three predators represent different risks to the anuran larvae (Werner and McPeek 1994; Relyea, *unpublished manuscript*), we expected that they would generate variation in the magnitude of the behavioral responses of the anuran larvae. We examined activity and spatial responses of the anurans, both of which are ubiquitous responses to predators (Sih 1987, Lima and Dill 1990, Werner 1992). Both of these behaviors also are related to a species' competitive ability and vulnerability to predators (Werner 1991; Werner and Anholt 1993; Relyea, *unpublished manuscript*).

We then assessed the relation between behavioral responses measured in the laboratory and performance of the anuran larvae when competing under more natural conditions in the field. We hypothesized that the behavioral responses to predators would result in different growth responses and competitive performances. Competition studies conducted in the nonlethal presence of these predators in the field indicated that the behavioral responses in the laboratory were highly correlated with growth responses and relative competitive performance.

METHODS

For both the laboratory and field experiments, we examined larval bullfrog and green frog responses to the absence and presence of different species of caged predators: *Anax, Umbra,* or *Lepomis.* Caged predators simulate predation risk without mortality to the experimental populations, since a major part of the predator cue is a water-soluble chemical (Kats et al. 1988, Werner 1991, McCollum and Van Buskirk 1996, Werner and Anholt 1996). Thus, this system provides the opportunity to examine competitive relations between the two anuran prey under a variety of predator combinations that should alter prey behavior in different ways.

Laboratory experiments

We collected multiple clutches of green frog eggs from the University of Michigan's E. S. George Reserve and bullfrog eggs from the Michigan Department of Natural Resources' Saline Fish Hatchery. We hatched the eggs and reared the tadpoles in small, predator-free wading pools for ~3 wk before the experiments were initiated. The experiments were conducted in plastic containers filled with 7 L of aged well water. Each container was equipped with a single predator cage, constructed of two wooden slats suspending a mesh bag in the container (mesh size = 1×2 mm). Ten tadpoles (initial mass of bullfrogs, 18.6 ± 1.0 mg; of green frogs, 21.0 ± 1.3 mg) were fed a 3:1 ration of rabbit chow : Tetramin fish flakes three times/wk at a rate of 6% of body mass/d. The laboratory light : dark schedule was 14:10 h.

The first experiment, conducted in 1994, quantified activity and spatial avoidance responses of green frogs and bullfrogs separately in the absence or presence of a single caged *Umbra* or *Anax.* We fed the predators 1–2 small tadpoles (~50 mg) of the appropriate species three times/wk to maintain the predator cue in the water. We quantified the proportion of tadpoles active (moving) and occupying the predator half of the container by approaching a container and scan sampling (Altmann 1974). These observations were repeated 35–40 times over a 5-wk period and included 0–2 observations/d. Examination of the data by weekly intervals provided no evidence of habituation to the predators over time.

A second laboratory experiment was conducted in 1995 to determine the behavioral responses of bullfrogs and green frogs to *Lepomis.* The experimental protocol was similar to the first experiment with the exceptions that we fed *Lepomis* 2 bullfrog larvae and 2 green frog larvae (~100 mg) three times per week, which better matched the experimental conditions of the field experiment that was run concurrently. The data consisted of 25 scan samples taken over a 9-d period to determine the proportion of tadpoles moving in each container and their spatial distribution.

For both experiments, we averaged the proportions of tadpoles active or on the predator side of the container over all observations for each tank. Means were arcsine-square-root transformed and analyzed with a MANOVA.

Field experiment

We conducted the field experiment in 1995 to determine whether the behavioral responses to the predators in the laboratory could be used to predict growth differences in a more natural setting and when the anuran larvae were competing. The field experiment was conducted in screened pens placed in the littoral zones of a 10-yr-old experimental pond that was raked clear of vegetation to provide a bare surface for the pens. Pens were $1.5 \times 1.0 \times 0.8$ m and constructed of a 5×5-cm lumber frame covered with 0.25-mm nylon mesh to exclude predators present in the ponds. We laid out three spatial blocks of eight pens each. Once the pens were in place, 300 g of leaves (primarily *Quercus* spp.) were added to each pen to provide a substrate for periphyton growth.

Each pen was equipped with four predator cages. Three small cages constructed of 10×11-cm drain pipe and capped with 1.7-mm fiberglass mesh were placed in the shallow end of each pen. A small cube of polystyrene was added so that the cages floated. The fourth cage was a large mesh bag ($1.0 \times 0.8 \times 0.3$ m) attached to the deep end of the pen. The small cages were designed to hold a single *Anax* and the large cage to hold either three *Umbra* or *Lepomis.* The density of predators ($1.5/m^2$) was within natural predator densities of the two predators for which we have data (larval Aeshnid dragonfly density = $0.2–4.1/m^2$, *Umbra* density = $0.5–10.5/m^2$, Werner et al., *unpublished data*). The placement of *Anax* in the shallower water and the fish in the deeper water represents the depth distribution of these predators in natural ponds.

The experimental design consisted of three treatments lacking predators and five treatments containing different combinations of predators. The first three treatments were an additive competition design, with 50 bullfrog larvae alone ($33/m^2$), 50 green frog larvae alone ($33/m^2$), or 50 bullfrog and 50 green frog larvae together; these treatments tested whether competition occurred between the two anuran species at these densities. We only have estimates of natural densities for green frogs; on the scale of an entire pond, green frog

TABLE 1. MANOVA results (*P* values) from the two laboratory experiments investigating the effect of the absence or caged presence of *Anax* and *Umbra* (first experiment) or the effect of the absence or caged presence of *Lepomis* (second experiment) on the activity and spatial distribution of larval bullfrogs and green frogs reared separately.

Experiment	Multivariate test	Univariate tests	
		Activity	Spatial distribution
First lab experiment			
Anuran species	0.006	0.004	0.230
Predator	<0.001	<0.001	<0.001
Anuran × Predator	0.566	0.913	0.290
Second lab experiment			
Anuran species	0.011	0.035	0.094
Predator	0.129	0.047	0.856
Anuran × Predator	0.881	0.661	0.683

densities range from 0.3 to 29.3/m², whereas on a more localized scale within a pond, green frog densities can be as high as 350/m². These data indicate that the densities we employed were within natural ranges (Werner et al., *unpublished data*). The five predator treatments each contained 50 bullfrog larvae and 50 green frog larvae. The treatments consisted of either three caged *Lepomis* (mean standard length = 75 mm), three caged *Umbra* (mean standard length = 66 mm), three caged *Anax* (penultimate instar), three caged *Anax* plus three caged *Lepomis,* or three caged *Anax* plus three caged *Umbra.* These predator treatments tested whether caged predators reduced growth of the anuran larvae and affected their competitive interactions.

Tadpoles and predators were added to the pens on 29 June 1995. Initial individual wet mass of bullfrogs was 20.5 ± 1.5 mg and of green frogs was 16.6 ± 1.3 mg. Predators were fed three times per week to maintain the predator cue; each *Anax* was fed ~100 mg each of bullfrog and green frog larvae, while each fish was fed ~50 mg each of bullfrog and green frog larvae and ~100 mg of small earthworms. The earthworms were provided to supplement food and increase survivorship of the fish, since they do not consume these species of tadpoles as readily as other foods (Werner and McPeek 1994). The experiment was terminated on 27 July 1995. Upon termination, all tadpoles were sorted from the leaf litter, counted, and weighed. All unconsumed tadpoles that remained in the predator cages were also removed and counted.

ANOVAs were used to test for significant differences in survivorship and growth among treatments and between prey species. The survivorship and growth responses both met the assumptions of normal and homoscedastic residuals. One pen was a significant outlier (*P* = 0.05) using Dixon's (1950) test statistic, and this pen (*Anax* plus *Umbra*) was removed from the analysis. For significant treatment effects, means were compared using Fisher's test. The data for the mortality of tadpoles in the predator cages were heteroscedastic and could not be corrected by any transformation; these data were analyzed using the nonparametric Kruskal-Wallis test.

To test whether predator-induced behavioral changes in the laboratory experiment were associated with tadpole performance in the field experiment, we regressed growth in the field on the behavioral responses (activity and spatial avoidance) to the four predator treatments (no-predator, *Anax, Lepomis,* and *Umbra*) using growth data for the four treatments experiencing interspecific competition and the same four predators. Because behavioral responses were derived from two separate laboratory experiments conducted in two different years, the baseline activity of the two anurans in the absence of predators was different (possibly due to differences in experiment duration or differences in genetic composition in the two groups of hatchlings). To standardize *Lepomis* responses in the second experiment to the baseline behavior of the first experiment, we divided the *Lepomis* responses by the no-predator, baseline response in the second experiment and then multiplied this quotient by the no-predator, baseline response in the first laboratory experiment.

RESULTS

Laboratory experiments

The two laboratory experiments demonstrated that bullfrog and green frog larvae responded to the presence of predators both through activity reduction and spatial avoidance (Table 1). The presence of caged *Umbra* caused a 4–6% reduction in absolute activity in both anuran species (Fig. 1, *P* = 0.040), while the presence of *Anax* caused an 8–13% reduction in activity (*P* = 0.00001). *Lepomis* had no effect on activity of either species. Bullfrogs were consistently more active than green frogs in all treatments; there were no interactions.

In contrast, the anuran species did not differ in spatial distribution. Both exhibited a moderate spatial response (5–12% avoidance) to the presence of caged *Umbra* (Fig. 2, *P* = 0.014), and a strong response (15–30% avoidance) to the presence of *Anax* (*P* < 0.00001). *Lepomis* had no effect on the spatial distribution of either anuran species.
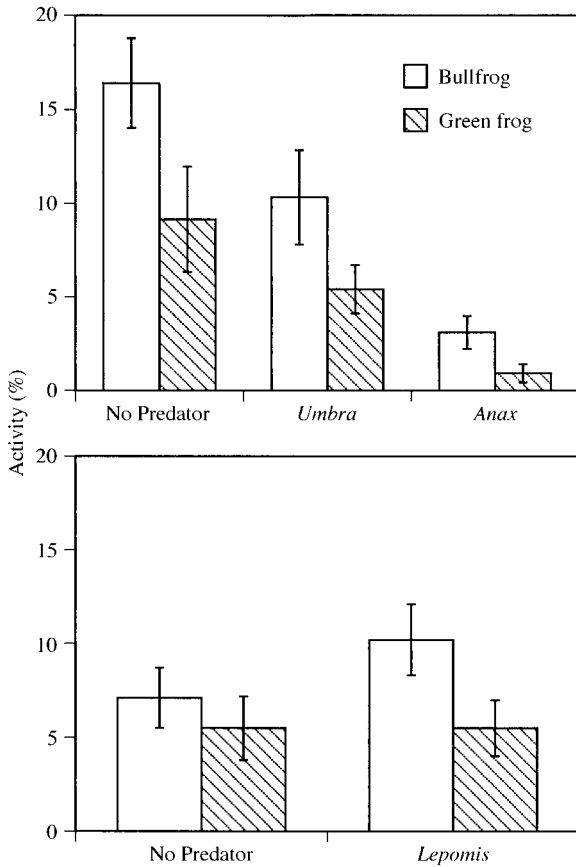
FIG. 1.   Percent activity (mean ± 1 SE) of bullfrogs and green frogs that were reared separately in a series of laboratory experiments in the presence of no predators, caged *Umbra,* and caged *Anax* (upper panel), and in the presence of no predator and caged *Lepomis* (lower panel). Responses are based on the means of 25–40 observations of 10 tadpoles per replication.

FIG. 2.   Spatial avoidance (mean ± 1 SE) of bullfrogs and green frogs reared separately in a series of laboratory experiments in the presence of no predators, caged *Umbra,* and caged *Anax* (upper panel), and in the presence of no predator and caged *Lepomis* (lower panel). Responses are based on the means of 25–40 observations of 10 tadpoles per replication.

Field experiment

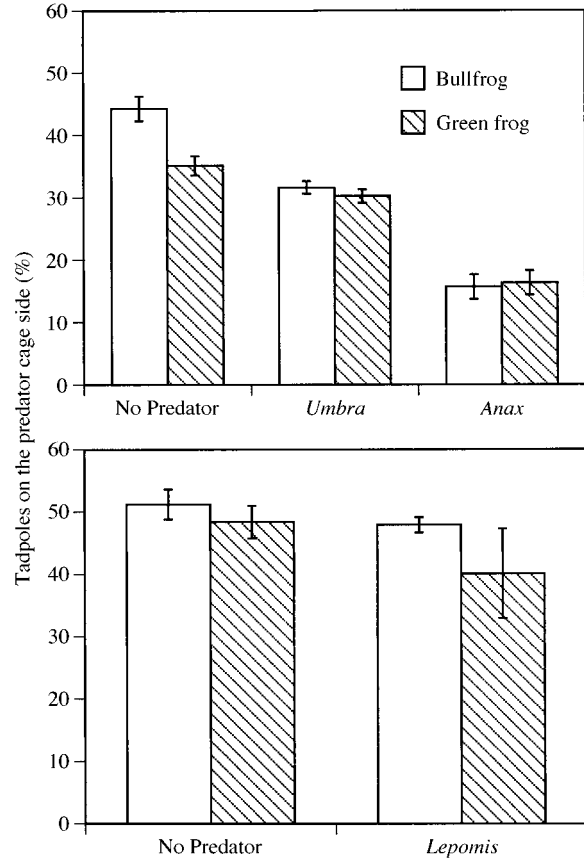Survivorship did not differ among treatments in the field experiment, but growth did (Table 2, Fig. 3). The changes in growth among treatments were relatively symmetrical for the two prey species (no significant interaction). For both anurans, the greatest growth occurred when alone. The addition of interspecific competitors reduced bullfrog growth by 37% and green frog

TABLE 2.   MANOVA results (*P* values) from the field experiment investigating the effect of blocks and treatments (see *Materials: Field experiment* for the list of eight treatments) on the survival and growth of larval bullfrogs and green frogs reared separately, together, and together under five different caged predator treatments.

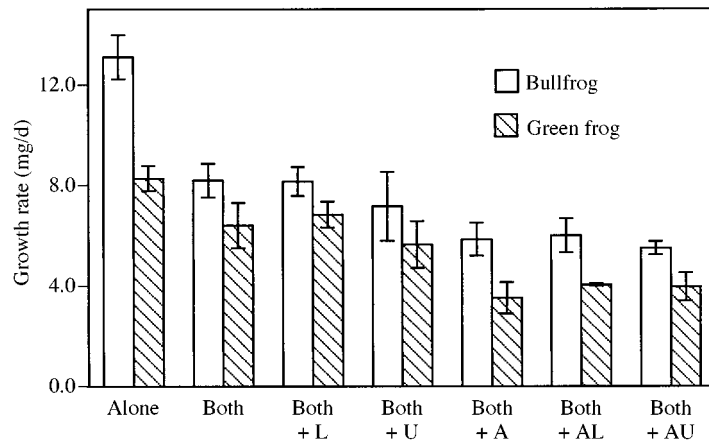| Treatment effects	df	Mean square	F	P
Survival				
Block	2	0.017	1.19	0.321
Treatment	6	0.010	0.72	0.634
Prey species	1	0.001	0.08	0.786
Treatment × Prey species	6	0.006	0.44	0.847
Error	24			
Growth				
Block	2	2.7	1.8	0.190
Treatment	6	26.0	16.9	<0.001
Prey species	1	46.6	30.3	<0.001
Treatment × Prey species	6	2.18	1.4	0.248
Error	24			

FIG. 3. Growth rates (mean ± 1 SE) of bullfrog and green frog larvae in field pens when reared alone, when reared together ("both"), and when reared together in the presence of caged *Lepomis* (L), *Umbra* (U), and *Anax* (A).

growth by 23% ($P < 0.001$). The addition of caged *Lepomis* or *Umbra* to the bullfrog–green frog competition treatment did not affect growth of either species ($P = 0.791$ and $P = 0.223$, respectively). However, predator treatments containing *Anax* exhibited reduced growth rates compared to the no-predator, competition treatment ($P < 0.007$); bullfrog growth was reduced 30%, and green frog growth was reduced 40%. Growth in the presence of *Lepomis* and *Umbra* did not differ ($P = 0.142$), growth in the presence of *Lepomis* was greater than all three treatments containing *Anax* ($P < 0.005$), and growth in the presence of *Umbra* was nearly greater than the three treatments containing *Anax* ($P \leq 0.07$). The three treatments containing *Anax* did not differ from each other ($P > 0.6$).

Activity and spatial responses to the different predators in the laboratory were highly correlated with growth rates in the field (Table 3, Fig. 4). The predator treatments that caused the greatest reduction in activity and greatest spatial avoidance in the laboratory also caused the greatest reduction in growth in the field (Table 3).

The unconsumed tadpoles that remained in the predator cages provided additional evidence concerning the relative risk posed by each of the predators (Fig. 5). All of the tadpoles died in the *Anax* cages. In contrast,

TABLE 3. Linear regression results comparing laboratory-derived behavioral responses under four different predator treatments to field-derived growth rates under the same treatments.

Response	R^2	P
Bullfrog activity	0.966	0.017
Green frog activity	0.992	0.004
Bullfrog spatial distribution	0.989	0.006
Green frog spatial distribution	0.876	0.064

Notes: Decreased activity induced by the different predators in the laboratory was related to decreased growth in the field experiment. Likewise, increased spatial avoidance of the predator in the laboratory experiment was related to decreased growth in the field experiment.

66% of bullfrogs and green frogs died in the *Umbra* cages, while 30% of bullfrogs and green frogs died in the *Lepomis* cages. These three mortality rates differed significantly (bullfrogs, $H_2 = 17.9$, $P = 0.0001$; green frogs $H_2 = 18.2$, $P = 0.001$).

DISCUSSION

The laboratory experiment demonstrated that the two anuran species exhibited prey- and predator-specific behavioral phenotypes. Activity and spatial responses in the bullfrog and green frog larvae were minor when with *Lepomis,* increased in strength with *Umbra,* and were quite strong with *Anax.* Thus, it appears that larval anurans can discriminate among species of predators. In this experiment, we cannot rule out the possibility that predators produced different amounts of a single chemical cue, as opposed to unique cues that differentiate each predator. However, other experiments on larval anurans suggest that the latter is indeed the case (Relyea, *unpublished manuscript*).

The behavioral responses were related to the risk posed by the different predators. *Anax* induced the strongest behavioral responses, and larval odonates are voracious predators of anuran larvae (Chovanec 1992, Azevedo-Ramos et al. 1992, Werner and McPeek 1994; Relyea, *unpublished manuscript*). In comparison, *Umbra* and *Lepomis* caused successively weaker behavioral responses, and both fish pose a lower risk to bullfrogs and green frogs because these anurans are somewhat unpalatable to fish (Kruse and Francis 1977, Petranka et al. 1987, Kats et al. 1988, Werner and McPeek 1994; Relyea, *unpublished manuscript*). The mortality of bullfrogs and green frogs in the predator cages provides further evidence of this relationship (Fig. 5); the highest mortality occurred in the *Anax* cages, with successively lower mortality in *Umbra* and *Lepomis* cages, respectively. This direct relationship between magnitude of antipredator response and predation risk has been observed frequently in a wide range of taxa (Sih 1987).
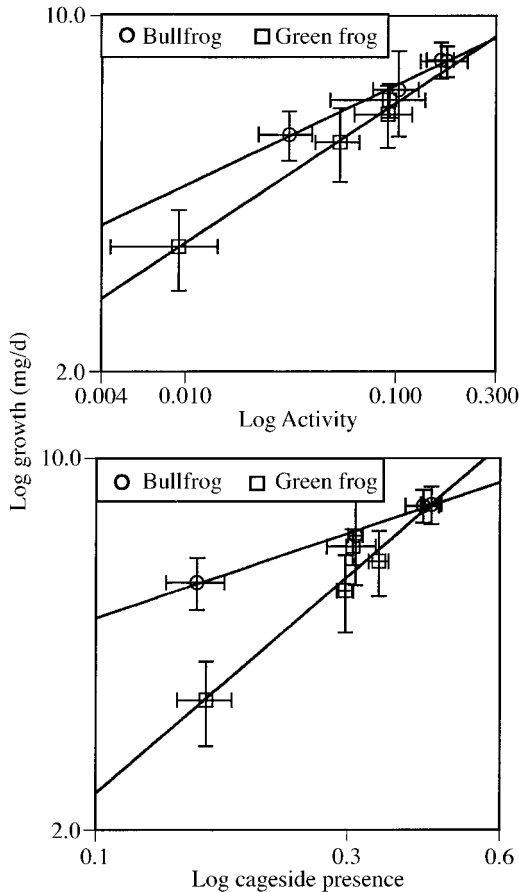
FIG. 4. The positive linear regressions of relative growth rates on activity (upper panel) and spatial avoidance (lower panel) in the field experiment in the presence of four different predator environments. Means ± 1 SE are plotted. The behavioral responses were based on observations from laboratory experiments in which prey species were reared separately, whereas the growth responses were based on observations in a field experiment in which the prey species were reared together.

Predator-induced changes in prey behavior should affect prey growth. Higher activity often results in greater resource acquisition and competitive ability at the cost of increased risk of predation; thus, many taxa reduce activity when predators are present (Sih 1987, Lima and Dill 1990, Werner 1992, Werner and Anholt 1993). In the laboratory experiment, bullfrogs were always more active than green frogs. Thus, one would predict that bullfrogs would grow faster than green frogs under all field treatments, but that both species would exhibit successively lower growth in the *Lepomis, Umbra,* and *Anax* treatments, respectively.

Similarly, increased spatial avoidance of predators also should cause reduced growth in the field, because resources near the predator become unavailable. Spatial avoidance of predators is common and often leads to reduced growth in prey (Sih 1980, 1982, Werner et al. 1983, Fraser and Huntingford 1986, Holomuzki 1986,

Sih 1987, Lima and Dill 1990, Skelly and Werner 1990, Turner and Mittlebach 1990, Persson and Eklöv 1995). We observed increasing spatial avoidance of both anurans in the laboratory in the *Lepomis, Umbra,* and *Anax* treatments, respectively, but found no differences in how the two anuran species responded to the treatments, which supports the earlier results of Werner (1991). Thus, based upon the spatial avoidance results, one would expect successively lower growth in the *Lepomis, Umbra,* and *Anax* treatments, respectively, but no growth differences between the two anurans within any of these treatments.

The behavioral responses of the anuran larvae in the laboratory were highly correlated with growth in the field. *Lepomis* induced no change in activity or spatial distribution in the laboratory, and growth was unaffected in the field. *Umbra* induced moderate reductions in activity in both prey species in the laboratory and moderate, although nonsignificant, reductions in growth in the field. *Anax* induced the strongest activity and spatial responses and the strongest growth reductions in the field. Other studies have demonstrated that the presence of a predator can alter growth in the field (Skelly 1992, Schmitz et al. 1997); the current study suggests that this effect varies among predator species and, in our case, may be described as a log-linear function of activity and spatial responses (Fig. 4).
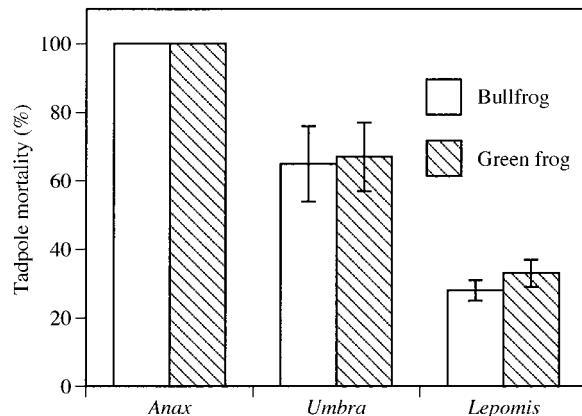
The differences in growth between the two anurans

FIG. 5. The mortality percentages (mean ± 1 SE) of bullfrog and green frog tadpoles from the predator cages containing either *Anax* alone, *Umbra* alone, or *Lepomis* alone. Mortality was based on the number of animals recovered at the end of the field experiment divided by the number of animals fed to the predators in the cages. We do not have the data to ascertain how much of the anuran mortality in the predator cages can be attributed to starvation, but our observations of this and other experiments (Werner 1991, Werner and Anholt 1996, Peacor and Werner 1997) indicate that *Anax* almost always consume all tadpoles placed into their cages within 2 d of feeding, whereas tadpoles in the fish cages were not readily consumed, and some of the observed mortality could be attributed to starvation.

in the field were likely due to differences in activity rather than spatial distribution. Bullfrogs exhibited higher activity than green frogs, and this may account for their higher growth (Morin 1983, Werner 1991, Werner and Anholt 1993). In contrast, bullfrog spatial distribution did not differ from that of green frogs; thus, spatial distribution cannot account for the differences in growth between the two anurans. We cannot attribute the reduced growth within species across treatments, however, to just one of the behaviors; both activity and spatial responses correlated well with growth. In fact, the two responses may reinforce each other in reducing growth in the presence of predators.

The field experiment also demonstrated that the growth of bullfrogs and green frogs in the presence of *Anax* plus *Lepomis* or *Anax* plus *Umbra* was not different from their growth in the presence of *Anax* alone. This suggests that the behavioral responses of the prey in these treatments also did not differ—that is, the anurans were simply responding to the riskiest predator, *Anax*. There are few comparative data on the responses of prey to the simultaneous presence of multiple predators. Eklöv and Werner (*unpublished manuscript*) found that uncaged dragonfly larvae (offering both chemical and visual cues) caused a large reduction in bullfrog activity; however, in treatments where *Lepomis* also were added, the dragonfly larvae moved less and caused less mortality, and the bullfrogs reduced activity less than when *Anax* was the sole predator. Thus, in cases where the addition of a second predator can alter the cues produced by the first predator, predation risk on the prey may increase or decrease (Soluk and Collins 1988, Huang and Sih 1990, 1991, Matsuda et al. 1993, Soluk 1993, Wissinger and McGrady 1993; Eklöv and Werner, *unpublished manuscript*). Because our predators were caged, it is unlikely that the addition of a second predator had an impact on cues presented to the prey by the first predator. In this case, prey may simply adjust their response to the riskiest predator.

In the field experiment, the two anurans had strong competitive effects on each other; the growth rate of bullfrogs declined 37%, while that of the green frogs declined 23% compared to the single-species controls. It has been repeatedly shown that bullfrog and green frog larvae compete under a range of conditions, though the symmetry of the interaction appears to depend on experimental conditions (e.g., see Werner 1991 [8-L laboratory containers], Werner 1994 [pens in experimental ponds], and Werner and Anholt 1996 [1300-L pond mesocosms]).

Behavioral changes due to the presence of the predators may influence these competitive relations. In the presence of two of the predators, *Lepomis* and *Umbra,* the competitive relations remained similar to those in the absence of predators. *Lepomis* had no effect on behavior and thus would not be expected to alter competitive relations. The presence of *Umbra* decreased activity, and therefore growth rates, moderately in both

anurans; the proportionate decline in activity was similar in the two anurans, and therefore the relative growth responses were similar to the no-predator treatment. In contrast, there is a suggestion of an alteration in relative competitive relations in the presence of *Anax* that is correlated with a disproportionate change in activity of the two species in the presence of *Anax*. The bullfrog : green frog activity ratio was 3.3 in the presence of *Anax,* compared to 1.8–1.9 in the absence of *Anax*. Correspondingly, the ratio of growth rates of the two species averaged across treatments lacking *Anax* (1.28 ± 0.11) was nearly different from the ratio of all treatments containing *Anax* (1.54 ± 0.09, $P = 0.08$). This result is in accord with a previous laboratory study where Werner (1991) found that the ratio of bullfrog : green frog activity was 1.4 in the absence of *Anax* and 2.4 in the presence of *Anax* and that the bullfrog obtained proportionately more of the resources in the presence of *Anax* (see also Peacor and Werner 1997). There are several processes possibly contributing to the effect of *Anax* on competitive relations in this experiment. First, the direct effect of the presence of *Anax* on activity levels of the anurans will alter the proportion of shared resources obtained by the two species. Second, there may be trait-mediated indirect effects though resources that contribute to the greater resource acquisition of the bullfrog with *Anax*. We have evidence from other experiments that trait-mediated indirect effects can be important (Werner 1991, Peacor and Werner 1997). This analysis again points to the critical importance of activity level in influencing the growth performance in the field. None of the alterations in competitive relations is associated with spatial responses, since the latter were similar across all predator treatments.

This study illustrates how individual traits (behavior, in this case) measured under controlled laboratory conditions can be quantitatively related to species performance (growth rate) in the field. Phenotypically plastic responses allow us to examine the consequences of possessing different trait values to performance in species interactions. Developing the relationships between trait values and performance will permit a more mechanistic understanding of species interactions and enable a priori predictions of the consequences of these interactions. When the traits involved are common to many species (e.g., activity), we may be able to generalize these predictions to other taxa.

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