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Michelle D. Boone · Raymond D. Semlitsch

Interactions of bullfrog tadpole predators and an insecticide: predation release and facilitation

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Abstract The effect of a contaminant on a community may not be easily predicted, given that complex changes in food resources and predator-prey dynamics may result. The objectives of our study were to determine the interactive effects of the insecticide carbaryl and predators on body size, development, survival, and activity of tadpoles of the bullfrog (*Rana catesbeiana*). We conducted the study in cattle tank mesocosm ponds exposed to 0, 3.5, or 7.0 mg/l carbaryl, and no predators or two red-spotted newts (*Notophthalmus viridescens*), bluegill sunfish (*Lepomis macrochirus*), or crayfish (*Orconectes* sp.). Carbaryl negatively affected predator survival by eliminating crayfish from all ponds, and by eliminating bluegill sunfish from ponds exposed to the highest concentration of carbaryl; carbaryl exposure did not effect survival of red-spotted newts. Because crayfish were eliminated by carbaryl, bullfrogs were released from predation and survival was near that of predator controls at low concentrations of carbaryl exposure. High concentrations of carbaryl reduced tadpole survival regardless of whether predators survived carbaryl exposure or not. Presence of crayfish and newts reduced tadpole survival, while bluegill sunfish appeared to facilitate bullfrog tadpole survival. Presence of carbaryl stimulated bullfrog tadpole mass and development. Our study demonstrates that the presence of a contaminant stress can alter community regulation by releasing prey from predators that are vulnerable to contaminants in some exposure scenarios.

M. D. Boone · R. D. Semlitsch
Division of Biological Sciences, University of Missouri,
105 Tucker Hall,
Columbia, MO 65211, USA

M. D. Boone (✉)
USGS Columbia Environmental Research Center,
4200 New Haven Road,
65201 Columbia, MO, USA
e-mail: michelle_boone@usgs.gov
Tel.: +1-573-4412943
Fax: +1-573-8761896

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Introduction

Predation, competition, and pond hydroperiod are known to regulate aquatic amphibian communities and the presence of these natural stresses in the environment typically results in fewer than 5% of amphibians surviving through metamorphosis (Herreid and Kinney 1966; Calef 1973; Semlitsch 1987; Berven 1990; Semlitsch et al. 1996). Although successful juvenile recruitment into the terrestrial population may be sporadic under natural environmental pressures, it is normally sufficient to sustain amphibian populations. The addition of anthropogenic stressors, however, may diminish a populations ability to persist. The presence of a chemical contaminant in a system represents an additional stress to a community that is already balancing natural pressures; therefore, contamination may disrupt normal community function. It has been suggested that chemical contamination could be one cause of worldwide amphibian declines, along with habitat destruction or alteration, invasive or exotic species, and pathogens or disease (Barinaga 1990; Blaustein 1994; Corn 1994). Recently, Davidson et al. (2001, 2002) found significant correlations between amphibian population declines and upwind agriculture for several amphibian species in California, which suggests that sublethal pesticide exposure may, in some way, contribute to amphibian declines. We should understand how contaminants may affect and alter communities, even if they do not contribute to declines, because contaminants are environmentally widespread.

To understand the effect of a contaminant in nature, researchers often examine the impact of a given substance on one particular species, while excluding other organisms within the food web. Although the species of interest may be affected by a contaminant directly through effects on individual physiology, the contaminant may indirectly affect a species by influencing survival of its predators or competitors, or the abundance of its food resources. While some species may be unfavorably affected by a contaminant, others may benefit from chemical exposure, directly or indirectly and, when detrimental species (e.g., exotic or invasive species) benefit from chemical exposure, the ramifications of contamination may be great. It is conceivable that any direct chemical effects may be negligible, but effects on the food base or predators in the pond may result in large differences in amphibian fitness and population dynamics. Previous studies have demonstrated that insecticides can reduce zooplankton (Hanazato and Yasuno 1987, 1989; Havens 1995), which can negatively affect salamander larvae through elimination of their food resources (Boone and James 2003), and positively affect anuran growth and survival by increasing algal food resources (Boone and Semlitsch 2002). Additionally, larval amphibian predators (including fish, crayfish, and larval insects) can be more sensitive to some contaminants than amphibians (Phipps and Holcombe 1985; Mayer and Ellersieck 1986; Bridges et al. 2002). Therefore, amphibian predators may be eliminated from ponds exposed to contaminants, allowing amphibians to prosper when direct chemical effects are sublethal and minimal. Consequently, the addition of a chemical may alter the intensity of natural stresses (by either reducing or increasing them) by altering the food resource base and/or the predator abundance or presence in the food web.

The most extensive examination of the effects of a single pesticide on amphibians has been with the insecticide carbaryl, a carbamate neurotoxin that appears to have low toxicity for amphibians (Bridges 1997; Boone and Semlitsch 2001, 2002) at realistic environmental concentrations (≤4.8 mg/l; Norris et al. 1983; Peterson et al. 1994). This short-lived chemical can alter survival, body mass, and time to metamorphosis for some amphibian species at realistic, post-application levels in the laboratory and field (reviewed in Boone and Bridges 2003a). Field studies indicate that carbaryl affects amphibian communities through changes in the food resource base (i.e., indirect effects), rather than direct effects on individual physiology (Mills 2002). The indirect effect occurs largely by reducing or eliminating zooplankton populations, which are sensitive to insecticides (Mayer and Ellersieck 1986; Hanazato and Yasuno 1989; Havens 1995). A reduction in zooplankton causes an algal bloom that can increase survival and mass at metamorphosis for herbivorous anurans (Mills 2002; Boone and Semlitsch 2002) when detrimental direct chemical effects are small compared to indirect benefits.

Our objectives were to examine the effects that realistic environmental levels of the insecticide carbaryl have on: (1) body size, development, survival, and activity of tadpoles of the bullfrog, *Rana catesbeiana*; (2) survival and mass of three important amphibian predators, crayfish (*Orconectes* sp.), bluegill sunfish (*Lepomis macrochirus*), and red-spotted newts (*Notophthalmus viridescens*); (3) presence or absence of zooplankton in pond mesocosms; and (4) the relationship between predators and their prey. Some amphibian predators are known to be sensitive to expected environmental levels of carbaryl; 96-h LC50s for bluegill sunfish range from 1.8 to 16.0 mg/l (Phipps and Holcombe 1985; Mayer and Ellersieck 1986) and for crayfish (*Orconectes immunis*) equal approximately 2.87 mg/l (Phipps and Holcombe 1985). The 48-h LC50 of bullfrog tadpoles is approximately 15.24 mg/l (C.M. Bridges, personal communication) and, although the LC50 of adult red-spotted newts is unknown, they have been found to survive in environments with exposure up to 7.0 mg/l (Boone and Semlitsch 2001, 2002). Because the sensitivity of larval amphibian predators varies, their influence on a population of bullfrogs may also vary under different exposure scenarios.

Materials and methods

Experimental design

Three egg masses of the bullfrog (*R. catesbeiana*) were collected at Little Dixie Recreational Area near Millersburg (Callaway County), Missouri, United States on 22 July 1997. Eggs hatched in the laboratory at 23–25°C and were held until tadpoles were free-swimming (Gosner stage 25; Gosner 1960). We mixed tadpoles from all clutches before use in the experiment to homogenize genetic variation. Bullfrogs, incidentally, are considered invasive species and have been implicated in amphibian declines in the western United States (Hayes and Jennings 1986).

We created replicate aquatic communities in 36 polyethylene ponds (1.85 m in diameter; 1,480 l volume) by adding 1,000 l water, 1 kg leaf litter, and plankton from natural ponds (500 ml plankton/pond at four different times) in late July. Zooplankton populations were well established in the ponds before any animals were introduced. The ponds were located in a fenced field at the University of Missouri Research Park in Columbia, Boone County, Missouri. Screen-mesh lids covered each pond to exclude incidental predators and anuran colonists. Use of outdoor, artificial ponds increases the environmental relevance and maximizes the benefits of laboratory and field experiments by maintaining relatively controlled environments while incorporating natural elements such as sunlight and shifts in temperature that would be present in a typical pond.

We experimentally manipulated two factors in a fully crossed design with three replicates: predator treatment [no predators, two bluegill sunfish (*L. macrochirus*), two crayfish (*Orconectes* sp.), or two red-spotted newts (*N. viridescens*)] and chemical treatment (0, 3.5, or 7.0 mg/l carbaryl). We collected 18 bluegill sunfish (mean ±1 SE: 3.1±0.1 g) on 1 August from a small farm pond in Columbia, Boone County, Mo. that had been stocked with fish in 1987; 18 crayfish (1.4±0.1 g) on 4 August from a pond at the Baskett Wildlife Research Area near Ashland, Boone County, Mo. and 18 red-spotted newts (2.6±0.1 g) on 4–5 August from Three Creeks Conservation Area in Columbia, Boone County, Mo. We added all the predators to the experimental ponds on the same day that they were collected. Groups of 45 free-swimming bullfrog tadpoles (Gosner stage 25; Gosner 1960) were randomly assigned to ponds on 5 August (experimental day 0); these densities were within the range of tadpoles in natural communities (14–4,238 per 1,000 l; Morin 1983; Petranka 1989). We added carbaryl as liquid Sevin (21.3% carbaryl) on 8 August (day 3) at a nominal concentration of 3.5 mg/l (16.43 g Sevin added to 1,000 l water) or 7.0 mg/l (32.86 g Sevin added to 1,000 l water) which is near expected post-application levels in wetlands receiving direct overspray (≤4.8 mg/l; Norris et al. 1983; Peterson et al. 1994) and at levels known to alter behavior in many larval anurans (Bridges 1999a, 1999b). We mixed carbaryl with 5 l pond water and poured the mixture evenly across the pond surface with a watering can at 1200 hours Central Standard Time (CST); we added 5 l uncontaminated pond water to control ponds in the same manner to mimic the disturbance of chemical application. We did not stir ponds to minimize the potential of an algal bloom and because direct application in the natural environment would not involve vigorous mixing. In other studies, carbaryl has a half-life in these ponds of 1–4 days (e.g., Boone and Semlitsch 2002; Boone and James 2003).

Response variables and statistical analyses

We searched ponds daily for metamorphs, defined by the emergence of at least one forelimb (stage 42; Gosner 1960), but no metamorphs were collected during the experiment. Bullfrog tadpoles in this area typically overwinter in a pond and reach metamorphosis the following summer (Johnson 2000). We also checked tadpole activity and presence/absence of zooplankton on 22 August (day 17), 29 August (day 24), 5 September (day 31), 12 September (day 38), and 19 September (day 45; zooplankton levels were not recorded on this date only). All lids were removed from ponds 1 h prior to behavioral observations and the number of visible swimming and/or feeding tadpoles was counted; the number of active individuals was recorded three times from 1500–1600 CST, and this value was averaged for a mean number of active tadpoles for that pond on a given day. At the same time, we also visually searched the water column for the presence of any zooplankton, and presence or absence was recorded for each pond; zooplankton were readily visible or otherwise noted as absent. We terminated the experiment on 13–14 October (day 69) by draining the ponds and collecting all remaining tadpoles when it appeared that no individuals would reach metamorphosis before winter. We determined each tadpoles developmental stage (Gosner 1960) and mass to the nearest mg. For each predator species, we determined survival, mass before and after the experiment, and change in body mass during the study.

Body mass of tadpoles, Gosner developmental stage (Gosner 1960), and tadpole survival for each pond (i.e., experimental unit) were used to measure the response of bullfrog tadpoles to predators, carbaryl, and their interaction. Analyses for treatment effects and their interactions on body mass and developmental stage were performed using a multivariate analysis of covariance (MANCOVA; SAS 2000), using tadpole survival as a covariate because it explained significant proportions of the variation. Effects of treatments and their interactions on survival were analyzed with an analysis of variance (ANOVA). Predator survival, mass before and after the study, and change in mass were examined with an ANOVA to test for the effects of carbaryl treatment on each predator. We also analyzed for the effects of carbaryl, predators, and their interaction on tadpole activity with an analysis of covariance (ANCOVA), using tadpole survival in the pond as the covariate because it explained significant portions of the variation. The effects of carbaryl, predator, and their interaction on the presence or absence of zooplankton was determined using an ANOVA. To normalize data and stabilize variances, we angularly transformed proportion data, log transformed mass, and used a ranking procedure (PROC RANK; SAS 2000) on developmental stage and activity counts before analyses.

Results

The survival of predators was significantly influenced by the carbaryl treatment, which may have influenced the magnitude of the predator effect on bullfrog tadpoles. Survival of bluegill sunfish ($F_{2,6}=\infty$, $P<0.0001$) and crayfish ($F_{2,6}=\infty$, $P<0.0001$) was significantly and negatively affected by the presence of the carbaryl (Fig. 1), while red-spotted newts experienced 100% survival in all ponds. The mass of bluegill sunfish ($F_{2,6}=0.93$, $P=0.4440$), crayfish ($F_{2,6}=1.45$, $P=0.3056$), or red-spotted newts ($F_{2,6}=0.03$, $P=0.9703$) was not significantly different among carbaryl treatments at the beginning of the experiment, but the carbaryl treatment significantly reduced the change in mass of bluegill sunfish ($F_{1,4}=12.26$, $P=0.0249$). Bluegill sunfish in control ponds gained 5.7 ±0.7 g and those exposed to 3.5 mg/l carbaryl gained only 2.1±0.7 g. The change in mass of red-spotted newts during the study was not significantly affected by carbaryl treatments ($F_{2,5}=0.16$, $P=0.8576$), but on average newts exposed to carbaryl gained less weight than those in controls (0 mg/l: gained 0.225±0.354 g; 3.5 mg/l: lost 0.051±0.354 g; 7.0 mg/l: gained 0.032±0.433 g). Because no crayfish survived in ponds exposed to carbaryl, change in mass over the study could not be determined.

Carbaryl significantly influenced bullfrog tadpole survival ($F_{2,23}=9.22$, $P=0.0011$) and predator treatment moderately influenced their survival ($F_{3,23}=2.89$, $P=0.0572$); however, the interaction of carbaryl and predator did not affect survival ($F_{6,23}=1.47$, $P=0.2320$). Exposure to a low concentration of carbaryl increased survival, while exposure to a high concentration decreased survival relative to controls (Fig. 1). The presence of crayfish and red-spotted newts reduced bullfrog survival relative to controls, while the presence of fish appeared to facilitate bullfrog survival (Fig. 2). Although the interaction of carbaryl and predator was not significant, there was an interesting pattern. Across all predator treatments, the addition of a low level of carbaryl stimulated survival, while high concentrations reduced survival relative to the controls (Fig. 3). In the crayfish predator treatment, however, the addition of carbaryl resulted in the elimination of the crayfish, and tadpole survival was enhanced to levels near that in predator control ponds.

The multivariate response (i.e., mass and developmental stage) were significantly influenced by carbaryl (Wilks lambda =0.5968, $F_{4,42}=3.09$, $P=0.0256$) and predator treatments (Wilks lambda =0.3776, $F_{6,42}=4.39$, $P=0.0016$), but not by their interaction (Wilks lambda =0.7426, $F_{12,42}=0.56$, $P=0.8600$). Univariate analyses indicated that both bullfrog mass ($F_{2,22}=5.68$, $P=0.0103$)

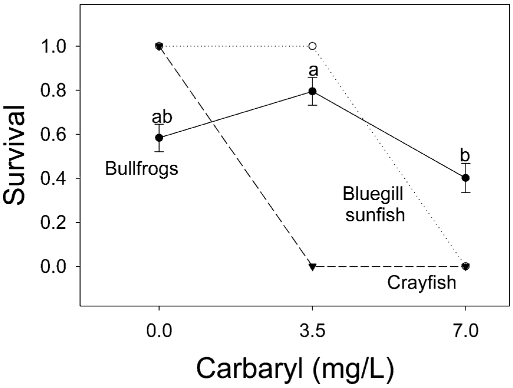

Fig. 1 Survival of bluegill sunfish ($P<0.0001$), crayfish ($P<0.0001$), and bullfrog tadpoles ($P=0.0011$) across carbaryl treatments. All of the newts survived across all carbaryl treatments. *Error bars* represent ±1 SE, but there was no variation in predator survival. *Differing letters* indicate significant differences among carbaryl treatments according to Scheffes multiple comparison test

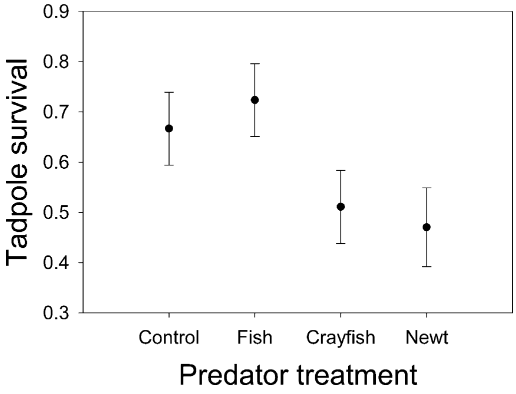

Fig. 2 Survival of bullfrog tadpoles reared with no predators (*control*), bluegill sunfish (*fish*), crayfish, or red-spotted newts (*newt*). The predator treatment was marginally significant ($P=0.0572$). *Error bars* represent ±1 SE

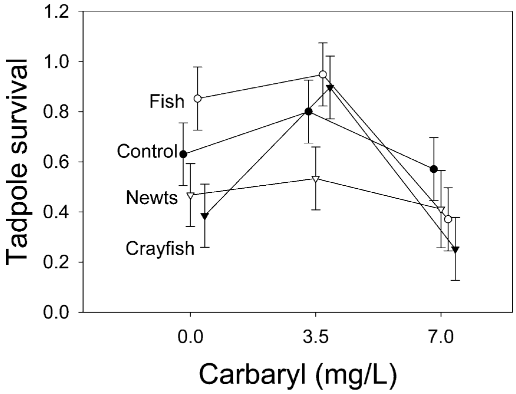

Fig. 3 Survival of bullfrog tadpoles exposed to no predators (*control*), bluegill sunfish (*fish*), crayfish, or red-spotted newts (*newt*) across carbaryl treatments. The interaction of carbaryl and predator treatments was not statistically significant ($P=0.2320$). *Error bars* represent ±1 SE and points are offset so that means and error bars are not obscured

and developmental stage ($F_{2,22}=4.42$, $P=0.0244$) contributed to the significant multivariate effect of carbaryl; mass and development were positively affected by carbaryl exposure (Fig. 4), with carbaryl resulting in enhanced development and larger size relative to tadpoles in control ponds. Developmental stage significantly contributed to the multivariate predator effect ($F_{3,22}=10.49$, $P=0.0002$) with the addition of bluegill sunfish and crayfish increasing developmental rates significantly over tadpoles in control ponds; presence of red-spotted newts slightly reduced developmental stage compared to controls (Fig. 5).

Bullfrog tadpole activity was not significantly influenced by time (Wilks lambda =0.9385, $F_{4,20}=0.33$, $P=0.8562$), or the interaction of time with the covariate (tadpole survival; Wilks lambda =0.9344, $F_{4,20}=0.35$, $P=0.8403$), with carbaryl (Wilks lambda =0.6072, $F_{8,40}=0.84$, $P=0.2196$), with predator treatment (Wilks lambda =0.6306, $F_{12,53}=0.84$, $P=0.6060$), or with the interaction of carbaryl and predator (Wilks lambda =0.4792, $F_{24,71}=0.69$, $P=0.8408$). On day 24 (21 days after carbaryl exposure), there was a moderate effect of

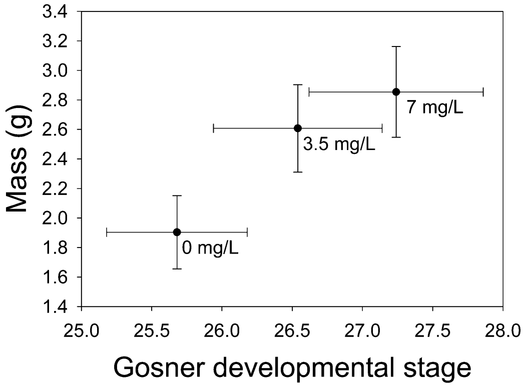

Fig. 4 Mass and developmental stage of bullfrog tadpoles exposed to 0, 3.5, or 7.0 mg/l carbaryl. Mass ($P=0.0103$) and developmental stage ($P=0.0244$) were significantly different among carbaryl treatments. *Error bars* represent ±1 SE

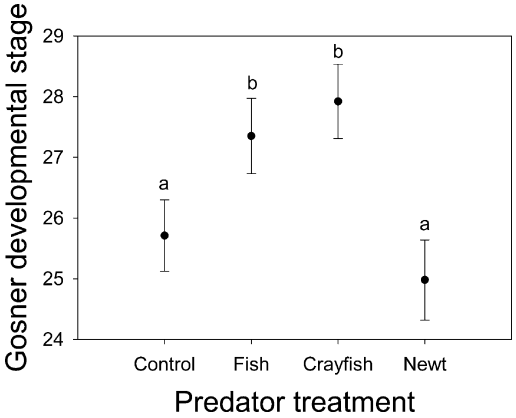

Fig. 5 Developmental stage of bullfrog tadpoles exposed to no predators (*control*), bluegill sunfish (*fish*), crayfish, or red-spotted newts (*newt*) averaged across all carbaryl treatments. Developmental stage was significantly different among predator treatments ($P=0.0002$). *Differing letters* indicate significant differences among carbaryl treatments according to Scheffes multiple comparison test. *Error bars* represent ±1 SE

carbaryl on tadpole activity ($F_{2,23}=3.22$, $P=0.0585$), with low levels of carbaryl reducing activity slightly in comparison to tadpoles in control ponds or in ponds exposed to 7.0 mg/l (0 mg/l: 2.5±0.6; 3.5 mg/l: 0.6±0.7; 7.0 mg/l: 2.8±0.7 active tadpoles/pond). Carbaryl would not be present at this time; however, carbaryl can increase food resources in the ponds (e.g., Boone and James 2003), which can influence tadpole activity (Bridges 1997). On day 42, predator treatment had a moderately significant effect on tadpole activity ($F_{3,23}=2.99$, $P=0.0518$) with tadpoles reared with no predators and newts having the highest activity levels (no predators: 9.5±1.5; bluegill fish: 5.8±1.5; crayfish: 7.2±1.5; red-spotted newts: 11.1 ±1.6 active tadpoles/pond).

The presence of zooplankton was significantly influenced by time (Wilks lambda =0.5749, $F_{3,81}=4.44$, $P=0.0168$) and its interaction with carbaryl (Fig. 6; Wilks lambda =0.4121, $F_{6,36}=3.35$, $P=0.0101$), but not the interaction of time and predator (Wilks lambda =0.7151, $F_{9,44}=0.72$, $P=0.6868$) or the interaction of

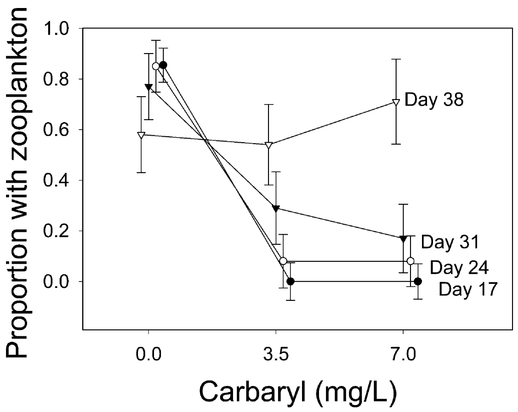

Fig. 6 Proportion of ponds with zooplankton present based of visual observations across carbaryl treatments. Presence of zooplankton was significantly affected by carbaryl exposure over time (P=0.0101). *Error bars* represent ±1 SE and points are offset so that means and error bars are not obscured

time, carbaryl, and predator (Wilks lambda =0.5165, $F_{18,51}$=0.69, P=0.7429). Carbaryl significantly reduced the likelihood of finding zooplankton in the ponds at day 17 ($F_{2,24}$=50.56, P<0.0001), day 24 ($F_{2,23}$=18.73, P<0.0001), and day 31 ($F_{2,24}$=5.76, P=0.0090), but by day 38 ($F_{2,21}$=0.28, P=0.7590) zooplankton levels were similar across all carbaryl treatments.

Discussion

Species differ in their sensitivity to biological and chemical stressors so that what is sublethal to one species may be lethal to another. Contaminant exposures, therefore, can disrupt or alter normal community function by removing vulnerable species, which will indirectly affect the species that remain. Given that the importance of predation in structuring an amphibian community has been found to both increase and decrease in the presence of environmental stress (reviewed in Sih et al. 1985), the exact effect of a chemical in nature may not be easily predicted unless the interactions among species in exposed environments are understood.

Carbaryl negatively affected survival of some of the predators used in our study, allowing for a potential release from predation risks for bullfrog tadpoles exposed to carbaryl. Carbaryl generally had a negative effect on predator survival, and those predators that survived gained less weight over the course of the study, presumably from a reduction in zooplankton food resources. Reductions in zooplankton, which can serve as food resources for all the predators used in our study, could have made bullfrogs more vulnerable to predation because of reduced abundance of alternative food resources; however, this does not appear to be the case. Reduced food resources could, in part, eliminate predators, although previously published LC50s suggest predator mortality was caused directly by carbaryl exposure (Mayer and Ellersieck 1986). In our study, crayfish were eliminated with any carbaryl exposure, fish were removed only from ponds with high levels of carbaryl, and red-spotted newt survival was not affected by carbaryl. The rank order of sensitivity of predators could be predicted from previous studies showing that invertebrates are highly sensitive to insecticides and that fish are generally more sensitive than amphibians (Mayer and Ellersieck 1986; Bridges 1997). At a high concentration of carbaryl, carbaryl exposure alone reduced tadpole survival regardless of any predator mortality. For instance, 7.0 mg/l carbaryl removed all crayfish and fish from ponds, but this carbaryl concentration also reduced tadpole survival more than predators did under control conditions, so that release from predation was not observed. Low levels of carbaryl exposure generally stimulated tadpole survival as mild stressors often do (i.e., hormesis: Forbes 2000). Yet this was particularly dramatic with crayfish predator treatments where tadpole survival was positively affected by exposure to 3.5 mg/l carbaryl; here, survival increased to levels slightly above those in ponds without predators. In this case, carbaryl released the bullfrogs from crayfish predation and had a positive effect on the bullfrog population. In this way, carbaryl may reduce or eliminate a whole class of predators (i.e., invertebrates), which can be a major source of predation, because bullfrogs have mechanisms (e.g., unpalatability) to avoid vertebrate predators.

Although fish are generally negatively associated with amphibian populations, presence of bluegill sunfish did not reduce the survival of bullfrog tadpoles and were (in effect) not actual predators, unlike newts and crayfish. If anything, presence of bluegill sunfish facilitated bullfrog survival. Although bluegill readily feed upon many tadpole species, bullfrog tadpoles are less palatable than other larval amphibians (Kruse and Francis 1977; Werner and McPeek 1994) and experience increased survival in the presence of fish (Hambright et al. 1986; Werner and McPeek 1994; Adams 2000; Adams et al. 2003). Werner and McPeek (1994) attributed facilitation of bullfrog survival in the presence of bluegill to an indirect interaction where bluegill remove odonates (significant predators on bullfrog tadpoles), which resulted in increased survival of bullfrogs. In our study, however, odonate predators were excluded from ponds, so the presence of bluegill facilitated bullfrogs even without removing significant insect predators. As planktivores, bluegill can suppress large zooplankton species, thereby enhancing phytoplankton (Hambright et al. 1986); therefore, the presence of bluegill may also facilitate bullfrogs through increasing algal food resources (which were not monitored in our study) or through some other mechanism such as enhancement of nutrient cycling (Bronmark et al. 1991).

Gosner development stage was also influenced by our predator treatment, with those tadpoles exposed to fish and crayfish showing the most rapid development. Both fish and crayfish may have had an indirect positive effect on algal resources for bullfrog tadpoles, because both species primarily feed upon invertebrates; however, our visual observations of presence/absence of zooplankton would not reveal subtle differences in zooplankton abundance.

Enhanced development of tadpoles in the presence of these two predators may arise from different causes, however. Bluegill did not appear to act as predators of bullfrog tadpoles, therefore, their presence may have stimulated bullfrog activity (which we did not detect) or enhanced nutrient cycling to the benefit of bullfrog tadpoles. Because larger tadpoles are generally less susceptible to predation (Formanowicz 1986; Semlitsch and Gibbons 1988) and because crayfish were proficient predators in predator controls, tadpoles that grew and developed the fastest in the presence of crayfish may have been the ones to escape predation, which could result in the observed pattern of greater development in these treatments. In general, however, differences in developmental stage were small, ranging only from Gosner stages 25 to 28.

The effect of carbaryl exposure alone significantly influenced tadpole survival, reduced the zooplankton community, and had positive effects on mass and developmental stage of tadpoles. Carbaryl has been found to stimulate growth in development of green frogs (Boone et al. 2001; Boone and Bridges 2003b), which has been hypothesized to result from indirect positive effects on the tadpoles food base or from increases in stress hormones that stimulate metamorphosis (Denver 1997). Stimulation of the development of bullfrogs further suggests that this response may be widespread and that the mechanism of this effect should be investigated. Additionally, carbaryl exposure has previously been found to result in greater mass in anurans (Boone and Semlitsch 2002; Boone and James 2003), mainly through indirect increases in algal food resources via reductions in zooplankton (Mills 2002). Seemingly positive effects on anuran size and development may be rife when effects of direct exposure are small.

In conclusion, our study demonstrates that the presence of a contaminant stress can alter interactions between predators and prey. Because bullfrogs may be detrimental to many other amphibian species, particularly in areas where they are exotic and associated with amphibian declines (Jennings and Hayes 1985; Hayes and Jennings 1986; Hecnar and MCloskey 1997), the presence of a contaminant capable of reducing or eliminating predators may bolster the ability of bullfrogs to invade new habitats and reduce community diversity. Furthermore, given that carbaryl exposure increased size and development of bullfrogs, the contaminant may further the success of this species, and help explain why highly managed areas often support bullfrog populations.

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