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The effect of community composition on persistence of prey with their predators in an assemblage of pond-breeding amphibians

Abstract We examined whether the species composition of a community influences the persistence of larval *Ambystoma maculatum* in assemblages composed of two larger intraguild predators (*A. opacum* and *A. jeffersonianum*) and an alternative prey species (tadpoles of *Rana sylvatica*). We predicted a priori that *A. maculatum* would have higher survival in more diverse communities containing alternative species of prey and top predators (*A. opacum*), the latter of which may lower the abundance of intermediate predators (*A. jeffersonianum*) via intraguild predation. In a factorial experiment, we manipulated the presence of larval *A. opacum*, *A. jeffersonianum*, and *R. sylvatica* in replicated artificial ponds containing larval *A. maculatum*. The presence of all three species significantly depressed biomass production in *A. maculatum*: biomass was highest in ponds lacking the other species and was zero in ponds initially containing all four species. Tadpoles severely reduced the growth of filamentous algae in the ponds. This, in turn, may have affected the abundance of some herbivorous prey of larval salamanders, although this possibility was not tested. The presence of congeneric predators severely restricted the presence in the water column of larval *A. maculatum*, which otherwise exhibited significant diel patterns of activity in the absence of predators. Together, the presence of tadpoles and a predator-mediated reduction in activity

patterns may have limited foraging opportunities for *A. maculatum*, thus exacerbating the direct impact of predation on survival in this species. These results suggest that diverse assemblages consisting of these particular species may actually inhibit, rather than promote, inclusion of *A. maculatum* in some communities of pond-breeding amphibians.

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Introduction

A fundamental concern in community ecology is how species of prey persist in assemblages with their predators. The answer to this question has broader implications in terms of understanding what influences community composition and, ultimately, species richness. Historically, a great deal of debate has focused on the relative importance of biotic versus abiotic factors in structuring communities. More modern syntheses have acknowledged that many ecological factors (and their interactions) simultaneously determine the patterns of coexistence that are observed in natural communities (e.g., Wilbur 1987; Hunter and Price 1992, and references therein). Moreover, the relative roles of different ecological factors are expected to vary from one biological system to another, as well as within the same system, when environmental heterogeneity and chance events are considered (Wilbur 1987; Dunson and Travis 1991; Hunter and Price 1992).

Another facet of this debate has been the issue of whether community organization is driven by "top-down" (e.g., predators) versus "bottom-up" (e.g., nutrient availability) forces (see reviews in Hunter and Price 1992; Power 1992; Strong 1992). Such models of trophic cascades and food webs have focused predominantly on interactions among species occupying different trophic levels. Often, however, potentially competing species occupying the same trophic level engage in predator-prey

interactions. This phenomenon, known as intraguild predation (Polis et al. 1989; Polis and Holt 1992), differs from classical predation because the act reduces potential competition. This recent realization that competitors may also interact as predators and prey has altered more traditional views of trophic cascades (e.g., Hairston et al. 1960; Slobodkin et al. 1967; Menge and Sutherland 1976) and their consequences for community structure.

The recognition of intraguild predation offers new insight into understanding how prey may persist with their predators. In general, coexistence between any type of predator and its prey is promoted by the presence of alternative species of prey (e.g., Paine 1966; Morin 1981), the presence of refugia (e.g., Holt 1987; Hixon and Menge 1991; Garvey et al. 1994), and/or the evolution of predator avoidance mechanisms (e.g., Sih 1987; Lima and Dill 1990). In the absence of these mediating factors, classical (i.e., noncompetitive) predator-prey systems typically result in predators supressing populations of their prey, even to the point of extinction. Alternatively, intraguild predators may paradoxically increase the abundance of their intraguild prey (Polis et al. 1989). By consuming a competitor that is exploitatively superior in its use of other, shared prey, an intraguild predator may actually relax the predation pressure on the shared prey, thus increasing its abundance (Polis and Holt 1992). In this way, an intraguild predator may indirectly facilitate its competitor on which it preys while concurrently exploiting it via direct consumption (Polis and Holt 1992). One possible outcome of such facilitation could be sustained coexistence.

The purpose of our study was to examine whether variation in the presence of particular species in an intraguild predation system influences the persistence of a focal prey species within assemblages. A useful system for such exploration is that of the aquatic larvae of amphibians that breed in temporary freshwater ponds. In the northeastern USA, a common amphibian assemblage found in such habitats includes the larvae of three species of salamanders belonging to the family Ambystomatidae [*Ambystoma opacum*, *A. maculatum*, and members of the *A. laterale-jeffersonianum* complex (henceforth referred to as *A. jeffersonianum*: Anderson and Graham 1967)] and at least one anuran (*Rana sylvatica*: Ranidae). Larval *Ambystoma* are generalist predators whose diets may include conspecifics and congeners in high-density and/or food-limited environments (Petranka 1989). In some fishless, temporary ponds, larval *A. opacum* may be the primary predator on the larvae of coexisting congeners and anuran tadpoles (e.g., Walters 1975; Stenhouse et al. 1983; Stenhouse 1985; Cortwright 1988; Cortwright and Nelson 1990; Walls 1995). *A. opacum* larvae become the top vertebrate predator in these communities because they hatch up to 4 months prior to the onset of breeding by other amphibians (S. Walls, personal observation), thus acquiring a size sufficient to prey on congeneric larvae and tadpoles after they hatch. In the spring, *A. jeffersonianum* generally begins to breed up to 1 week before *A. maculatum* (Nyman 1991). Larvae of

A. jeffersonianum and *R. sylvatica* often hatch synchronously, whereas larvae of *A. maculatum* are the last to hatch. Because of these differences in the timing of hatching, *A. maculatum* larvae are vulnerable as prey to *A. jeffersonianum* and *A. opacum*; developing embryos of *A. maculatum* may be prey to *R. sylvatica* tadpoles as well (Petranka et al. 1998). *A. jeffersonianum* are prey to *A. opacum*, and tadpoles of *R. sylvatica* are alternative prey to both *A. jeffersonianum* and *A. opacum*. In addition to preying on each other, larvae of the three *Ambystoma* species, as well as *R. sylvatica* (Petranka and Kennedy 1999), also feed on the same prey base consisting of microcrustaceans and other small invertebrates; thus, they constitute a group of intraguild predators.

Because *R. sylvatica* may cause high embryonic mortality in *A. maculatum* (Petranka et al. 1998) and larvae of *A. maculatum* are also vulnerable as prey to both *A. jeffersonianum* and *A. opacum*, we became interested in the means by which *A. maculatum* is able to persist in communities containing these predators. We examined the relative importance of each species component of the *Ambystoma-R. sylvatica* assemblage to the persistence of *A. maculatum* within the community. Specifically, we tested the hypothesis that the identity of the species present in a community influences the performance (measured as biomass produced) of larval *A. maculatum*. Two predictions can be made from this hypothesis. (1) Biomass production (a product of survival and mean body mass) in *A. maculatum* should be highest in communities with high species richness; i.e., the presence of a top predator (*A. opacum*) may reduce the abundance of intermediate predators (*A. jeffersonianum*) and, thus, alleviate the intensity of predation on *A. maculatum*. Moreover, predation on *A. maculatum* may be less intense when an alternative prey species (*R. sylvatica*) is present. (2) Biomass production in *A. maculatum* may be lower in communities with high species richness; i.e., the presence of two predator species (*A. opacum* and *A. jeffersonianum*) may lower the survival of larval *A. maculatum* more than when only one predatory species is present.

Materials and methods

Experimental treatments and design

We designed this experiment to assess whether the addition of particular species in an assemblage influences the performance of *A. maculatum* within that assemblage. We reared *A. maculatum* larvae alone and in all possible combinations with the larvae of *A. opacum*, *A. jeffersonianum*, and *R. sylvatica*. By simultaneously manipulating the presence and absence of these three species, our $2\times2\times2$ factorial design resulted in eight experimental treatments, each of which was replicated in five randomized complete blocks in a total of 40 artificial ponds.

Artificial ponds

Fiberglass cattle-watering tanks (1.2 m diameter, 0.62 m depth, 378 l volume, 1.04 m² surface area) were used as artificial ponds (Morin 1981). Tanks were fitted with L-shaped standpipes (open

end covered with fiberglass mesh screen to prevent loss of animals), which maintained constant water levels. We placed tanks in a rectangular array in a field at the Black Rock Forest near Cornwall, Orange Co., New York. Each tank was assigned randomly to a position in a spatial block, and treatments were assigned randomly to tanks within each block. From 21 February–1 March 1996, we filled each tank with filtered water from a nearby stream. An equal and homogeneous mixture of leaf litter (500 g) was added to the tanks in blocks 1 and 2 on 10 March, and to blocks 3–5 on 13 March 1996. A concentrated mixture of zooplankton and other microorganisms collected from several natural ponds was added in 1.0-l volumes to each tank on 20 March, 8 April, and 4 May 1996. Tanks were initially left uncovered (March–June) to facilitate their colonization by aquatic insects as an additional food source for larvae, but window-screen lids were placed on the tanks on 3–4 June to prevent the escape of metamorphosing animals. We scrutinized tanks at regular intervals for the presence of any predatory aquatic invertebrates that could have colonized the tanks; none were found.

We collected newly deposited eggs of *A. jeffersonianum* from a temporary woodland pond near Middletown, Orange Co., New York, on 20 March 1996; eggs of *A. maculatum* and *R. sylvatica* were collected from the same pond on 8 April, and free-swimming larval *A. opacum* were dip-netted from the pond on each date. Numerous egg masses (10–20) were collected for each species to insure genetic variation in the experimental population of each. As they were collected, five larval *A. opacum* were added sequentially, by block, to their designated tanks. Eggs of the other species were held in the laboratory in 38-l aquaria until hatching. On 17 April, 10 newly hatched *A. jeffersonianum* and 100 tadpoles of *R. sylvatica* were added to the tanks designated to receive them. The experiment began on 4 May when 20 hatchling *A. maculatum* were added to the all of the tanks.

We observed the activity of larval *A. maculatum* in the tanks at the following times: from 2100 to 2210 hours on 3 June, 0815–0910 hours on 4 June, 0035–0200 h and 0850–1010 h on 4 July. This schedule resulted in two nocturnal and two diurnal observation periods that occurred both before (3–4 June) and after (4 July) the metamorphosis of *A. opacum*. During each observation period, we counted the number of larval *A. maculatum* visible to a depth of 39 cm and used these data as an indication of larval activity. Starting in June, we checked all tanks two or three times per week for metamorphosing larvae. The date of metamorphosis was recorded for all individuals; in addition, for *A. maculatum* we recorded the mass (to the nearest 0.05 g, after patting the individual dry to remove excess moisture), and snout-vent length (tip of snout to posterior margin of the vent, to the nearest 0.5 mm) of each individual. We ended the experiment on 23–24 July (day 81), when all remaining larvae were removed from their tanks, weighed and measured. All surviving metamorphs and larvae were released at their pond of origin.

Response variables and statistical analyses

To assess the effects of species composition on the performance of *A. maculatum*, we calculated the biomass of this species as the number of survivors×the mean mass per tank. Survival of *A. maculatum* was zero in several tanks (see Results), which resulted in missing values of mass for those tanks. Thus, we used biomass, rather than other possible response variables, because it provided a composite measure of both survival and body size and also allowed us to maintain a balanced number of replicates for our statistical analysis. We then subjected these data to a type III SS ANOVA to determine the potential influence of each of the other species on the success of *A. maculatum*.

Repeated-measures MANOVA was used to test for treatment effects on the diel activity patterns of larval *A. maculatum* observed on the two different dates. For both analyses, we examined the data for departures from normality using normal probability plots; transformations were not required to improve the approximation of the data to a normal distribution. ANOVA was conducted using Systat for Windows 95, version 6.0 (SPSS). The repeated-measures MANOVA was conducted using the General Linear Models procedure of the Statistical Analysis System, version 8 (SAS 1999).

Results

Preliminary analyses of the effects of the five blocks showed no significant differences in our response variable for *A. maculatum*. The block sum of squares and degrees of freedom were, therefore, pooled into the residual term for all remaining analyses.

ANOVA indicated that the presence of all three of the manipulated species significantly lowered the biomass production of *A. maculatum* (Table 1, Fig. 1). The three-way interaction term was statistically significant (Table 1), indicating that the influence of each species on *A. maculatum* depended upon which other species were present. Biomass of *A. maculatum* was highest in those tanks in which no other species were present (Fig. 1). *A. opacum* lowered the biomass of *A. maculatum* by 14.8%, compared to when *A. maculatum* was alone. In contrast, *A. jeffersonianum* depressed the biomass of *A. maculatum* by 47.9%, indicating it had a much stronger negative effect on *A. maculatum* than did *A. opacum*. The combined presence of both *A. opacum* and *A. jeffersonianum* reduced the biomass of *A. maculatum* by an additional 26.7% relative to that in tanks where *A. jeffersonianum* was the only congener present. Thus, of the two congeneric predators, *A. jeffersonianum* had a stronger negative effect than *A. opacum* on *A. maculatum*.

The presence of *R. sylvatica* tadpoles substantially exacerbated the influence of predators on *A. maculatum*. In the absence of *A. opacum* and *A. jeffersonianum*, *R. sylvatica* lowered the biomass of *A. maculatum* (compared to those tanks in which no other species were present) only slightly (15.1%; Fig. 1). However, the addition of

Table 1 ANOVA of the biomass [number of survivors×mean mass (g) per replicate] of *Ambystoma maculatum* in all treatments

Source	df	SS	F	P
A. opacum	1	107.453	22.838	<0.0001
A. jeffersonianum	1	588.442	125.069	<0.0001
Rana sylvatica	1	365.058	77.590	<0.0001
A. opacum×*A. jeffersonianum*	1	45.284	9.625	0.004
A. opacum×*R. sylvatica*	1	12.792	2.719	0.109
A. jeffersonianum×*R. sylvatica*	1	3.457	0.735	0.398
A. opacum×*A. jeffersonianum*×*R. sylvatica*	1	42.477	9.028	0.005
Error	32	150.558		

either *A. opacum* or *A. jeffersonianum* in combination with *R. sylvatica* lowered biomass production by 67.9 and 98.3%, respectively, and the presence of all three species resulted in 0% survival of *A. maculatum* (Fig. 1). Thus, the impact of congeneric predators on *A. maculatum* strongly depended upon the presence of tadpoles of *R. sylvatica*.

Repeated-measures MANOVA revealed that larval *A. maculatum* exhibited significant diel patterns of activity that varied in a complex fashion with variation in the experimental treatments, time, and date of observation (Table 2, Fig. 2). Early in the larval period (observation period 1; Fig. 2), *A. maculatum* reared in the absence of congeners were more active during the day than at night; however, this pattern was reversed later in the larval period (Fig. 2). The presence of *R. sylvatica* tadpoles had no significant effect on the activity of *A. maculatum* (Table 2, Fig. 2). However, the two congeneric predators, both by themselves and in combination, significantly restricted *A. maculatum* activity (Table 2, Fig. 2). In those tanks in which *A. opacum* were initially present, *A. maculatum* showed no change in diel activity before *A. opacum* metamorphosed; afterwards, however, larval *A. maculatum* activity increased at night (Fig. 2). In contrast, larval *A. maculatum* reared in tanks containing *A. jeffersonianum* (both in combination with *A. opacum* and
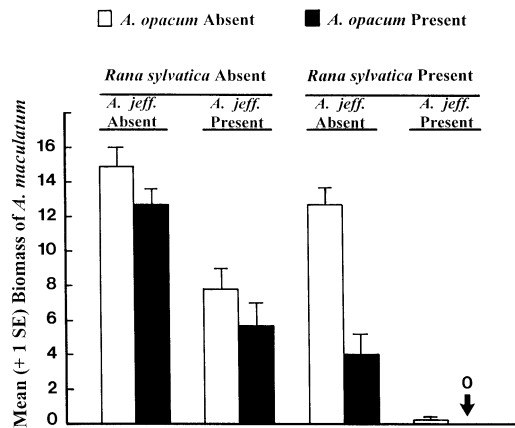
as the only predator present) showed no appreciable change in activity, either with a change in time of day or the date of observation (Fig. 2). Part of these differences in activity patterns may reflect a difference in overall survival of *A. maculatum*; i.e., in some cases, the low
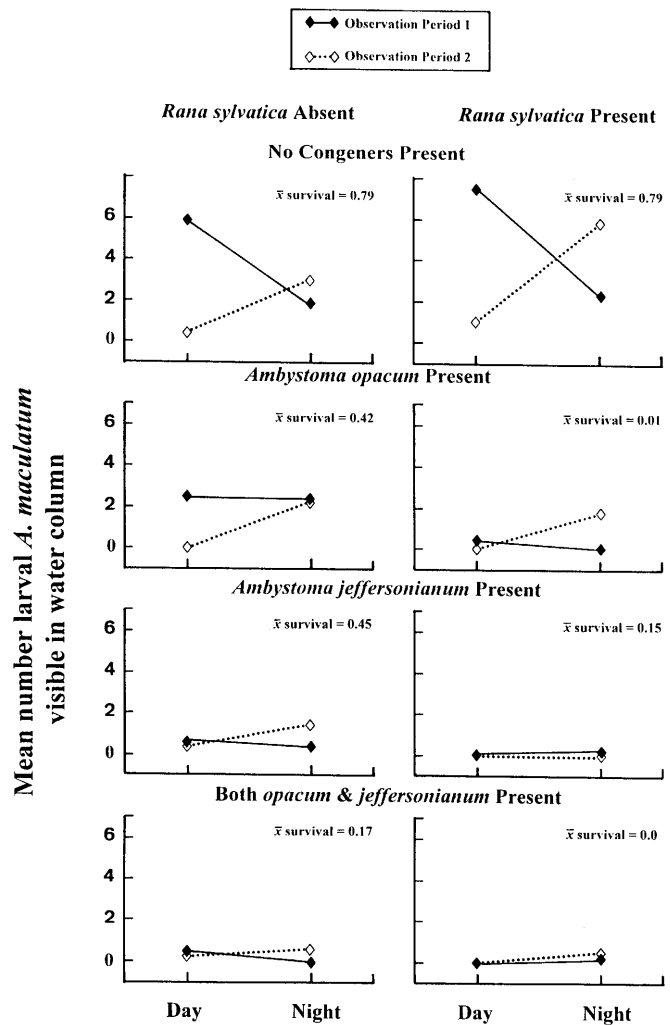

Fig. 2 The mean number of larval *A. maculatum* visible in the water column of the experimental tanks during diurnal and nocturnal observations. Each graph represents the responses in one of the eight experimental treatments. Tanks were observed on 3 June (*solid line*) and 4 July *(dotted line)* 1996, which preceded and followed the metamorphosis of *A. opacum*, respectively (*survival* the proportion of larval *A. maculatum* that survived to the end of the experiment)

Fig. 1 Mean biomass [number of survivors×mean mass (g) per replicate] of *Ambystoma maculatum* in each of the experimental treatments. The *arrow* indicates 0% survival in all replicates of the treatment in which all four species were present

Table 2 Repeated-measures MANOVA on the number of larval *A. maculatum* active in the water column of the experimental tanks [*period* observation period (3–4 June and 4 July 1996), *time of day* when observations were made (day or night)]

Source	Wilks' λ	df	F	P
Period×time of day	0.48859	1,32	33.49	<0.0001
Period×time of day×*A. opacum*	0.76359	1,32	9.91	0.0036
Period×time of day×*A. jeffersonianum*	0.57396	1,32	23.75	<0.0001
Period×time of day×*R. sylvatica*	0.99487	1,32	0.16	0.6873
Period×time of day×*A. opacum*×*A. jeffersonianum*	0.77522	1,32	9.28	0.0046
Period×time of day×*A. opacum*×*R. sylvatica*	0.98854	1,32	0.37	0.5467
Period×time of day×*A. jeffersonianum*×*R. sylvatica*	0.94837	1,32	1.74	0.1962
Period×time of day×*A. opacum*×*A. jeffersonianum*×*R sylvatica*	0.96248	1,32	1.25	0.2724

numbers of larvae visibly active in the water column may reflect a low number of survivors. However, in two treatments (*R. sylvatica* absent, *A. opacum* present; *R. sylvatica* absent, *A. jeffersonianum* present: Fig. 2), larval activity remained low even though survival at the end of the experiment averaged >40%. Thus, these data suggest that the effect of congeneric predators included restricting the activity (and, thus, foraging opportunities) of *A. maculatum*, in addition to directly lowering survival.

Discussion

The results of our study demonstrate that, under the quasi-natural conditions of our mesocosm experiment, the presence of a particular suite of species inhibited, rather than promoted, the coexistence of *A. maculatum* within larval amphibian assemblages. Biomass production in *A. maculatum* was highest in those ponds in which no other species were present and was zero in ponds containing all four species. This result appears to be a consequence of lowered survival due to (1) more intense predation in the presence of both congeneric predators; (2) a reduction in activity (and, thus, foraging opportunities) by *A. maculatum* when at risk of predation; (3) a possible indirect (or direct) effect of tadpoles on some prey items of *A. maculatum*, and (4) a synergistic negative effect of the combined presence of tadpoles and predators.

The effect of other community members
on *A. maculatum*

Our analysis revealed a significant three-way interaction effect (*A. opacum*×*A. jeffersonianum*×*R. sylvatica*) on the biomass production of *A. maculatum*; i.e., each of these other species strongly affected the performance of *A. maculatum*, but their effect depended upon the presence of each other. One a priori prediction that we made was that *A. opacum* would lower the densities of *A. jeffersonianum*, resulting in a concomitant decrease in the intensity of predation on *A. maculatum*; i.e., this latter species would be more successful in more diverse assemblages. Contrary to this prediction, we found that the combined presence of both *A. opacum* and *A. jeffersonianum* had a greater effect on *A. maculatum* than did either species alone; i.e., *A. opacum* exacerbated the negative impact of *A. jeffersonianum*, rather than alleviating it. Because our analyses focused solely on the responses of *A. maculatum*, we are presently unable to evaluate whether *A. opacum* was successful in suppressing populations of *A. jeffersonianum* as we originally predicted.

By themselves, the two predator species also differed in their effect on *A. maculatum*: *A. jeffersonianum* depressed biomass production in *A. maculatum* significantly more than did *A. opacum*. This asymmetric effect was most likely a consequence of a difference in the temporal overlap of these three species. In our study, all *A. opacum* had metamorphosed by 30 June 1996, whereas larval *A. jeffersonianum* persisted in the tanks with *A. maculatum* until the end of the experiment (24 July). Moreover, larval *A. jeffersonianum* and *A. maculatum* may be ecologically very similiar in some areas: they utilize similiar microhabitats and have been regarded as "competitive equals" (Brodman 1996). This effect of predators was manifested in two ways: a direct reduction in survival, as well as a reduction in activity and thus, possibly, feeding activity of *A. maculatum*. Our examination of *A. maculatum* activity patterns indicated that the presence of *A. opacum* and *A. jeffersonianum*, both alone and in combination, significantly restricted the activity of *A. maculatum* in the water column of the experimental tanks. Other studies (e.g., Semlitsch 1987) have demonstrated that predators may dramatically reduce the activity of larval *Ambystoma* and, furthermore, reduce the number of prey consumed by larvae. Thus, the presence of predatory congeners may have restricted foraging opportunities for *A. maculatum*, which would have contributed to a lower biomass production in treatments containing predators.

We also predicted that the presence of alternative species of prey, such as *R. sylvatica* tadpoles, would alleviate the intensity of predation on *A. maculatum*. Contrary to this prediction, we found that the negative effect of congeners was exacerbated by the presence of *R. sylvatica*: in experimental tanks in which all four species were initially present, no *A. maculatum* survived. There are at least three hypotheses for this synergistic effect of tadpoles and predators. First, in a similar study of competition and predation in an *Ambystoma-R. sylvatica* assemblage, Wilbur (1972) noted that larval *A. tigrinum* acted as a predator on three other species of *Ambystoma* if it acquired an initial size advantage by preying on *R. sylvatica* tadpoles; otherwise, *A. tigrinum* acted primarily as a competitor. In our study, the predatory abilities of *A. opacum* and *A. jeffersonianum* may have been improved by preying upon *R. sylvatica*, which further increased their size advantage over *A. maculatum*.

Second, our casual observations indicated that the growth of filamentous algae was neglible in those tanks in which *R. sylvatica* was present, compared to the excessive growth of algae in tanks lacking tadpoles. North American ranids are generalized tadpoles that filter suspended algae from the water column (Seale and Wassersug 1979), although epiphytic algal growth can be a large component of tadpole diets and is critical to their performance (Jennsen 1967; Hendricks 1973; Kupferberg et al. 1994). We did not quantify this apparent effect of tadpoles or its possible consequences to larval salamanders. However, our observations suggest that tadpoles altered the ecosystems within our mesocosms. We hypothesize that the reduction of periphytic algae by tadpoles limited the availability of this food resource for other herbivorous organisms that were prey of larval *Ambystoma*. Through possible competition with these organisms for periphytic algae, tadpoles may have negatively affected a portion of the prey base of larval salamanders, thus excacerbating the effect of predators on

the survival of *A. maculatum* by subjecting larvae of this species to food limitation as well. This hypothesis is strengthened by Wilbur's (1972) observation that *R. sylvatica* adversely affected three species of larval *Ambystoma* (including *A. maculatum*) by competing with invertebrate prey for periphyton and phytoplankton. Tadpoles of another anuran species (*R. temporaria*) have been shown to dramatically reduce the abundance of periphyton and to have competitive effects on a distantly related taxon (snails) that also feeds on this food resource (Brönmark et al. 1991). Similarly, Morin et al. (1988) demonstrated competition between tadpoles and herbivorous aquatic insects. Future studies are needed to examine whether *R. sylvatica* may have indirectly affected the survival of *A. maculatum* in a similar manner.

Third, as predators, *R. sylvatica* tadpoles may directly affect the survival of *A. maculatum* by preying upon embryos of this species (Petranka et al. 1998), as well as by competing with larval *A. maculatum* for micro- and macroinvertebrate prey, upon which these tadpoles also feed (Petranka and Kennedy 1999). *R. sylvatica* is unlikely to have caused embryonic mortality (via predation) in *A. maculatum*, because we added the latter species to our experimental tanks as hatchlings. However, at present, we cannot discount the possibility that competition for invertebrate prey may have occurred between these two amphibians.

Comparison with other assemblages

The phenomena that we are discussing here (i.e., intraguild predation and predator-mediated indirect effects) are widespread and have been observed in a diverse array of other assemblages (Polis et al. 1989; Lima and Dill 1990; Polis and Holt 1992; Relyea 2000). Intraguild predation is now recognized as being ubiquitous in nature and as having complex effects on community organization (e.g., see review of numerous systems in Polis et al. 1989). These effects may be counter to those expected in systems where intraguild predation links are weak or lacking in trophic cascades (Polis and Holt 1992). For example, in marine benthic communities, epibenthic intraguild predators exert a positive, rather than the expected negative effect on their nonpredaceous prey (Ambrose 1984). This counterintuitive effect occurs because epibenthic predators control the abundance of intermediate infaunal predators that, in turn, control the abundance of other infauna that are also consumed by epibenthic predators (Ambrose 1984). Similar direct and indirect compensating effects may explain why predator manipulations have often had unpredictable or undetectable impacts on freshwater benthic communities (Wissinger and McGrady 1993).

Both noncompeting and intraguild predators may induce behavioral changes in their prey (e.g., a reduction in foraging or other activity) which, in turn, may have far-reaching, complex effects on the community. For example, prey may reduce their activity or increase refuge use in the presence of predators, resulting in decreased foraging activity (e.g., Sih 1987; Lima and Dill 1990; Turner and Mittelbach 1990; Skelly 1992; Wissinger and McGrady 1993; Diehl and Eklöv 1995; Schmitz et al. 1997). A predator-induced reduction in foraging may have a positive indirect effect on resource levels and, thus, on competitors of the prey (Werner and Anholt 1996; Peacor and Werner 1997). Similarly, the addition of a competitor can reduce the availability of resources, causing individuals to increase their foraging and their susceptibility to predation (Peacor and Werner 1997). The addition of both competitors and predators can also alter prey morphology which, in turn, may cause trait-mediated indirect effects in the community (Relyea 2000). Thus, an understanding of the mechanisms of predator avoidance can provide invaluable insight into understanding the means by which predators and prey coexist.

Hypotheses for patterns of coexistence of larval amphibians

Throughout their overlapping ranges, as many as four species of *Ambystoma* frequently coexist, despite their propensity to prey on each other. The questions therefore remain as to how coexistence is accomplished among these intraguild predators and, furthermore, how species that are especially vulnerable because of their relatively smaller size (e.g., *A. maculatum*) are able to persist within these assemblages. Brodman (1996) proposed that *A. maculatum* is a behaviorally more variable species which, in general, may explain its broad geographic distribution and successful coexistence with other species. In particular, Brodman (1996) suggested that habitat partitioning and the use of refugia may contribute to the coexistence of *A. jeffersonianum* and *A. maculatum* in Ohio.

Alternatively, as Wilbur (1972) stated, coexistence may be a consequence of the relative advantages of various species in different years and their long adult life spans; i.e., *A. maculatum* may experience "booms" in population growth during "bust" years of no (or low) reproductive success experienced by congeneric species whose larvae act as predators on *A. maculatum*. For species such as *A. maculatum* that are long-lived, several years of low reproductive success may be more than offset by a single year of successful recruitment in years in which *A. opacum* and/or *A. jeffersonianum* do poorly; such cycles in the reproductive success of congeners may be sufficient to sustain long-term coexistence (a concept known as the "storage effect": Chesson 1983). When in assemblages with predatory congeners, *A. maculatum* may also represent "sink" subpopulations that would otherwise go extinct without continued immigration (Pulliam 1996). Sinks may, nevertheless, contribute to the survival of a species because on-going reproduction in these habitats produces young, some of which emigrate (along with adults) to other patches, including

source habitats. A synthesis of information on longevity, lifetime reproductive success, habitat usage, and migration patterns of *A. maculatum* would provide valuable insight into the potential for the storage effect and source-sink dynamics to promote species diversity in some assemblages of larval amphibians.

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