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TESTS OF FUNCTIONAL EQUIVALENCE: COMPLEMENTARY ROLES OF SALAMANDERS AND FISH IN COMMUNITY ORGANIZATION

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Abstract. We experimentally tested whether two similarly sized generalist predators found in different habitats had similar effects on prey community patterns. *Notophthalmus viridescens* (the red-spotted newt) occurs primarily in temporary ponds, while *Enneacanthus obesus* (the banded sunfish) is restricted to permanent ponds. Larval anurans are an important prey assemblage found in both kinds of ponds. We stocked both predators in artificial ponds together with six species of larval anurans, forming different species assemblages, to assess whether a similar abundance and biomass of each predator would have comparable impacts on community patterns. The predators differed in their effects on prey species composition but had similar impacts on composite community attributes, including prey species diversity and total prey biomass. *Enneacanthus* eliminated *Pseudacris crucifer*, *Hyla andersonii*, *Hyla versicolor*, and *Scaphiopus holbrookii*, creating a community dominated by *Bufo woodhousii* and *Rana sphenocephala*. *Notophthalmus* eliminated *Bufo*, creating an assemblage dominated by *Pseudacris* but also containing four additional species. Very few anurans survived in ponds containing both newts and fish. The different consequences of predation by newts and fish reflect different effectiveness of anuran antipredator defenses against these predators. Mechanisms that reduced predation by fish, such as unpalatability, were ineffective against newts. Our findings suggest that a patchy distribution of functionally distinct predators across a landscape of discrete habitats will contribute to predictable patterns of spatial variation in community composition and will create a mosaic of communities dominated by different prey species.

Key words: anurans; *Bufo woodhousii*; *Enneacanthus obesus*; fish; *Hyla andersonii*; *Hyla versicolor*; *Notophthalmus viridescens*; ponds; predation; *Pseudacris crucifer*; *Rana sphenocephala*; salamanders.

INTRODUCTION

Most studies of the influence of interspecific interactions on community structure focus on representative communities that consist of a few species found in a given location (Hairston 1989). Representative communities provide invaluable case studies of interactions in nature, but the general implications of patterns and processes within them are difficult to assess, because observed patterns and interactions may depend critically on the choice of species and location. For example, many studies of predation focus on the effects of a single predator species (Sih et al. 1985), and relatively few have compared the effects of two or more predators on the same community (Paine 1992, Wilbur and Fauth 1990, Morin 1995, Raffaelli and Hall 1996). Therefore, we seldom know whether different predator species are functionally equivalent (Lawton and Brown 1993), exerting similar effects on community organization, or whether they are functionally distinct (as in

Paine 1992), with unique or non-substitutable roles in community organization. If different predator species consistently affect communities in different ways, it will be difficult to make generalizations about how predation influences community structure. Numerous case studies show that predators can substantially affect prey community structure, either by offsetting competition among prey species (Paine 1966, Menge and Sutherland 1976, Lubchenco 1978, Morin 1983, Wilbur et al. 1983, Alford 1989), or by limiting species distributions via habitat selection or direct exclusions (Smith 1983, Woodward 1983, Spiller and Schoener 1988, Reseratis and Wilbur 1989, McPeck 1990). What remains uncertain is whether these studies describe general features of predator-prey interactions, or simply constitute a collection of special cases. One way to address this problem is to try to develop a predictive framework for the impact of generalist predators on prey assemblages.

Successful predictions about how different species will affect community patterns require knowledge of the factors that make species functionally similar or different. What factors should be considered? One possible starting point is body size, which affects both energy demands and morphological constraints that in-

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fluence predator-prey interactions. Within guilds, similarity in body size and morphology have long been considered to be predictors of ecological similarity (Hutchinson 1959, Pacala and Roughgarden 1982). Per capita effects often depend strongly on body size (see references in Ebenman and Persson 1988). Using this logic, different generalist predators of similar size might alter communities in similar ways, as long as they consume similar sets of prey species at comparable rates. Rates of prey consumption should reflect size-dependent energy requirements, and should scale with predator size within metabolically similar groups of organisms (Peters 1983), e.g., aquatic ectotherms like fish or salamanders. The outcomes of predator-prey encounters are also sensitive to the relative sizes of predators and prey (Paine 1976, Smith 1983, Stenhouse et al. 1983, Travis et al. 1985, Werner 1986, Semlitsch and Gibbons 1988). Rapid growth to a large size can enable prey to obtain a size-refuge against a suite of gape-limited predators with similar body sizes. Conversely, large differences in body size among predator species create situations where the same prey species may be invulnerable to smaller predators but not to larger ones.

Of course, predator-prey interactions can be influenced by factors other than size-related patterns of energy requirements and morphological constraints on the relative sizes of predators and prey. Different responses of predators to behavioral or chemical antipredator mechanisms can lead to selective consumption of different species, with corresponding consequences for community patterns. A priori, it is difficult to predict why one prey species might be unpalatable or unattractive to one generalist predator and not to another, but such specificity in antipredator mechanisms could render most predators functionally unique. Specificity of antipredator mechanisms seems much more likely to arise when specialized predators feed selectively on one or a few of closely related prey species. Specialized predators would be expected to affect communities in rather different ways, and the size-equivalence of their per capita effects seems unlikely.

Here we compare the community-level effects of two broadly sympatric aquatic predators with largely allopatric distributions, to see whether generalist predators of similar size have comparable impacts on community patterns. The red-spotted newt, *Notophthalmus viridescens*, is found primarily in temporary ponds, although it sometimes occurs in permanent ponds with fish. The banded sunfish, *Enneacanthus obesus*, is restricted to permanent ponds, since it cannot tolerate the drying of temporary ponds. Both species are generalist predators, and both can be similar in body size, although *Enneacanthus* can grow to be much larger than *Notophthalmus*. Both predators are limited by gape, since the functional morphology of the mouth limits maximum size of the prey that can be consumed. Newts and fish are visual predators with considerable dietary

overlap (Morgan and Grierson 1932, Wood and Goodwin 1954, Graham 1986, Bristow 1991), and they compete asymmetrically, with fish enjoying a distinct competitive advantage (Bristow 1991). This competitive asymmetry may account for the common restriction of newts to temporary waters without fish.

We used a common-environment approach (as in Clausen et al. 1948) to assess whether a similar density and biomass of *Notophthalmus* or *Enneacanthus* would generate similar communities of surviving prey. Comparisons of the influence of fish and salamanders on community composition are particularly interesting, because fish are often implicated as the primary factor determining the presence or absence of various amphibian species in temporary (fishless) or permanent (with fish) ponds (Heyer et al. 1975, Gascon 1992, Bronmark and Edenhamn 1994, Werner and McPeck 1994). It is unclear whether the apparent difference in the impact of predators from temporary ponds (salamanders, insects) and permanent ponds (fish) reflects their possible functional uniqueness or results from different net intensities of predation by species that are otherwise functionally similar on a per capita basis. Experimental manipulations of different predator species that hold predator density and biomass constant can directly evaluate whether fish and salamanders are functionally equivalent. Many studies describe predation on anurans by fish (Heyer et al. 1975, Kats et al. 1988, Semlitsch and Gibbons 1988, Bristow 1991, Gascon 1992) or by salamanders (Wilbur 1972, Morin 1983, 1986, 1987, Wilbur et al. 1983, Alford 1989, Wilbur and Fauth 1990, Fauth and Resetarits 1991). However, the relative impacts of fish and salamander predation remain poorly known, and the joint impacts of these two groups of common aquatic predators are essentially unexplored.

Functionally equivalent species of salamanders occur together in some temporary pond communities (Morin 1995). These species affect prey species composition similarly (Kurzava and Morin 1994, Morin 1995), especially after differences in predator biomass are accounted for. Other studies show that unrelated taxa, or predators from different habitats that typically encounter different sets of prey, can have different impacts on prey even when their influence is adjusted to account for differences in biomass (Wilbur and Fauth 1990, Fauth and Resetarits 1991). Both the taxonomic distance between salamanders and fish, and the use of different habitats with somewhat different prey assemblages, may make these predators functionally distinct.

MATERIALS AND METHODS

Artificial ponds

We studied how predation by the red-spotted newt (*Notophthalmus viridescens viridescens*) and the banded sunfish (*Enneacanthus obesus*) altered a prey assemblage consisting of six species of larval anurans.

Our experiments took place in 12 artificial ponds (0.61 × 1.52 m diameter cattle-watering tanks) located at the Hutcheson Memorial Forest of Rutgers University (Somerset County, New Jersey, USA). Following the protocol used in prior artificial pond studies (e.g., Kurzava and Morin 1994, Morin 1995), each tank initially contained filtered stream water (1000 L), a plankton inoculum (1 L of mixed phytoplankton and zooplankton collected from natural ponds), hay (500 g), commercial trout chow (20 g), and *Elodea* stems for cover and oviposition sites (30 g) on 14 May 1992. Additional trout chow (20 g/tank) was added on 23 July 1992 to offset nutrient depletion. Screen lids excluded frogs, insects, and other unwanted organisms, and retained metamorphosed amphibians until their collection and processing to define the final composition of the anuran assemblage.

Experimental design

We manipulated the presence of newts and fish using a two-way factorial design, with three replicates per treatment. The four treatment combinations were: a predator-free control (0 newts, 0 fish); a newt-only treatment (4 newts, 0 fish); a fish-only treatment (0 newts, 4 fish); and a newt-plus-fish treatment (4 newts, 4 fish). This design allowed us to test both statistical and biological interactions between the two predators; the choice of predator species allowed us to compare the effects of predators that were phylogenetically distant but of similar individual size (mass). Initial body mass (mean ± 1 SD) of the individual predators used in this experiment was 2330.94 ± 358.17 mg for *Notophthalmus v. viridescens* and 2191.42 ± 906.25 mg for *Enneacanthus obesus*. Average snout-vent length for *N. v. viridescens* was 43.34 ± 2.21 mm, while standard length for *E. obesus* (the distance from the most anterior point on the head to the caudal peduncle) was 36.84 ± 4.89 mm. Each experimental population of *N. v. viridescens* or *E. obesus* also had a similar aggregate biomass. The treatment containing both predators tested whether the impact of the two predator species was additive based on the separately measured effects of each predator species. Adult *N. v. viridescens* were collected from a pond in Warren County, New Jersey, on 11 May 1992. Newts were stocked at a 1:1 sex ratio on 21 May 1992. Adult *E. obesus*, which could not be sexed, were collected from ponds in Ocean County, New Jersey, on 26 May 1992. Fish were stocked on 28 May 1992.

We measured how a standard prey assemblage initially consisting of hatchlings of six anuran species (a total of 1000 hatchlings per tank) responded to the different combinations of predator species. Previous studies of *Notophthalmus* and *Enneacanthus* indicated that these prey densities would yield some survivors (Morin 1987, Bristow 1991). Anuran eggs were collected from ponds in Atlantic County, New Jersey, on 6–7 May 1992. After the eggs hatched, each tank was

stocked with hatchling larvae of 100 *Scaphiopus holbrookii* (eastern spadefoot toad), 200 *Hyla versicolor* (gray treefrog), 200 *H. andersonii* (pine barrens treefrog), 200 *Bufo woodhousii fowleri* (Fowler's toad), 200 *Pseudacris crucifer*, (spring peeper), and 100 *Rana sphenoccephala* (southern leopard frog) on 11, 12, and 14 June 1992. The densities of all species used were within the range of densities that occur in natural ponds, and all of these species can occur in the same ponds. Tanks were censused daily for metamorphs, which were collected and returned to the laboratory for enumeration and measurement of body mass. The experiment reaches a logical end point after the last anuran completes metamorphosis. In our climate, most tadpoles of the species used in this experiment have metamorphosed or died by late October. Differences in the intensity of competition experienced under different predator treatments can be inferred from differences in tadpole mass and larval period (Morin 1983). Competition among tadpoles leads to reduced mass at metamorphosis and prolonged larval periods (Morin 1983).

Response variables

For each anuran species in each tank we determined survival to metamorphosis, mean mass at metamorphosis, mean larval period, and relative abundance. Larval period is the mean number of days from initial stocking to metamorphosis. For each tank, we also calculated a measure of prey diversity, H' (Shannon-Wiener diversity [Magurran 1988]), and total anuran biomass (the sum of the mass of each metamorph across all six species), to see whether these composite measures of community properties would respond differently to our experimental manipulations.

To compare growth rates of the predators, we estimated K , the relative growth rate (on a mass basis), of newts and fish in the single-predator treatments. Initial newt masses were measured on 15–17 May 1992, and initial fish masses were measured on 27–28 May 1992. We measured final newt masses from 30 October to 12 November 1992, and final fish masses on 12–15 November 1992. Since individual fish could not be identified, a measure of change in individual mass could not be used. Therefore, mass-specific growth rate for each predator species was calculated as: $K = (\ln S_2 - \ln S_1)/(T_2 - T_1)$, where S_2 and S_1 are the mean predator masses (per replicate tank) at times T_2 and T_1 , respectively (Andrews 1982, Gerwien and John-Alder 1992).

Statistical analyses

We used two-factor multivariate analysis of variance (MANOVA), together with univariate two-factor ANOVAs, to analyze the effects of *Notophthalmus* and *Enneacanthus* on the survival and relative abundance of the six anuran prey species. Survival was determined for each species by the fraction of the initial number of hatchlings stocked in each replicate that was collected as metamorphosing froglets. Relative abundance

was determined by the fraction of the entire collection of froglets emerging from a replicate tank that belonged to each species. We used both multivariate and univariate tests because we were concerned that the low level of replication combined with the large number of response variables (six species) might make it difficult to assess differences using only the conservative multivariate test. Discriminant analysis determined which variables (species) contributed to significant differences detected by the multivariate tests (Morin 1983, Manly 1986, Scheiner 1993). Our analysis is similar to the protected ANOVA approach described by Scheiner (1993), in that ANOVA results for a particular factor, newts or fish, were not considered unless MANOVA results for that factor were significant. The two-factor analysis provides tests of three a priori hypotheses: (1) no effect of newts, (2) no effect of fish, and (3) an interaction between the effects of newts and fish. We also used a cluster analysis (unweighted pair-group method using arithmetic averages, or UPGMA [Pielou 1984]) as an alternate description of the similarity of anuran responses to the four treatments. We analyzed both survival and relative abundance in case the predators differed in their effects for one response but not the other. For example, if one predator tended to consume more prey than the other, but if attacks were distributed randomly among prey species, we might have observed differences in the effects of predator species on survival, but not on the relative abundance of different species of survivors.

In addition to the species-specific patterns of survival and relative abundance, we also measured composite responses for the entire anuran assemblage, including the total number of survivors summed over all six species; total anuran biomass, again summed over all six species; and anuran diversity. Two-factor ANOVAs tested the effects of newts and fish on anuran biomass and diversity. Orthogonal contrasts compared treatments containing an initially similar biomass of predators (the newt-only and fish-only treatments) to determine if the two predator species differed in their effects on the total number of survivors, total anuran biomass, and anuran diversity.

The effects of newts and fish on the mass and larval period of each anuran species were analyzed using univariate ANOVAs, since missing values of these responses for some species in some treatments precluded the use of multivariate analysis. Missing values arose when a species failed to survive in a replicate, and mass and larval period could not be estimated. For most species, these variables did not differ significantly among treatments, and the analysis is described here for completeness.

We compared the final mass of fish and newts in the single-predator treatments using one-way analysis of variance. One-way ANOVA also was used to compare K values for newts and fish. Since these two variables are not independent, significance levels of ANOVAs

were adjusted using Bonferroni corrections (Rice 1990, Scheiner 1993).

RESULTS

Prey survival

Newts and fish affected the survival of anuran species quite differently, and the two predators generated quite distinct assemblages of surviving prey (Fig. 1). Both predators significantly reduced anuran survival to metamorphosis (Fig. 1, Table 1), but they differed in their effects on different prey species. *Pseudacris crucifer* survived nearly as well in ponds where newts were the only predators as in the controls, while newts reduced the survival of *Bufo*, *Scaphiopus*, and *Hyla versicolor*. In contrast, in ponds where fish were the only predators, *Bufo* survived at levels similar to the controls, while *Pseudacris*, *Scaphiopus*, and both *Hyla* species were eliminated. The significant interaction between the effects of newts and fish on survival (Table 1) is a statistical artifact. Because fish and newts each reduced prey survival to <50% of the value in the controls (Fig. 1), their combined effect, if additive, would result in prey survival of <0, while survival has a lower bound of zero. This constraint accounts for the interaction in the MANOVA.

Discriminant analysis indicated that the survival of *S. holbrookii*, *H. versicolor*, and *H. andersonii* contributed to the significant effects of both newt and fish predation (Table 2). Newts also reduced the survival of *B. woodhousii*, but fish did not. In contrast, fish reduced the survival of *P. crucifer*, but newts did not (Fig. 1). Although newts and fish differed in their effects on survival of individual anuran species, they had similar effects on total number of anurans, summed across all six species, surviving to metamorphosis (two-sample t test: $t = -0.139$, $P > 0.90$, $df = 4$; mean anuran survival in the newt-only vs. fish-only treatment: 106.7 ± 91.5 and 117.0 ± 90.1 individuals, respectively).

A cluster analysis underscores the species-specific patterns of prey survival to metamorphosis that were generated by the different predators (Fig. 2). Initial clustering of the 4-newt treatment with the treatment with 4 newts plus 4 fish reflects the fact that both treatments resulted in low survival of many of the same species, differing primarily in the higher survival of *Pseudacris* in the 4-newt treatment. The 4-fish treatment clustered next with the other predator treatments, differing from both of them in the higher survival of *Bufo*. Finally the predator-free control clustered last, reflecting the higher survival of *Hyla versicolor*, *Hyla andersonii*, and *Scaphiopus* in ponds without predators (Fig. 2).

Prey relative abundance

Different predators also created different patterns of anuran relative abundance (Fig. 3). *Pseudacris crucifer*

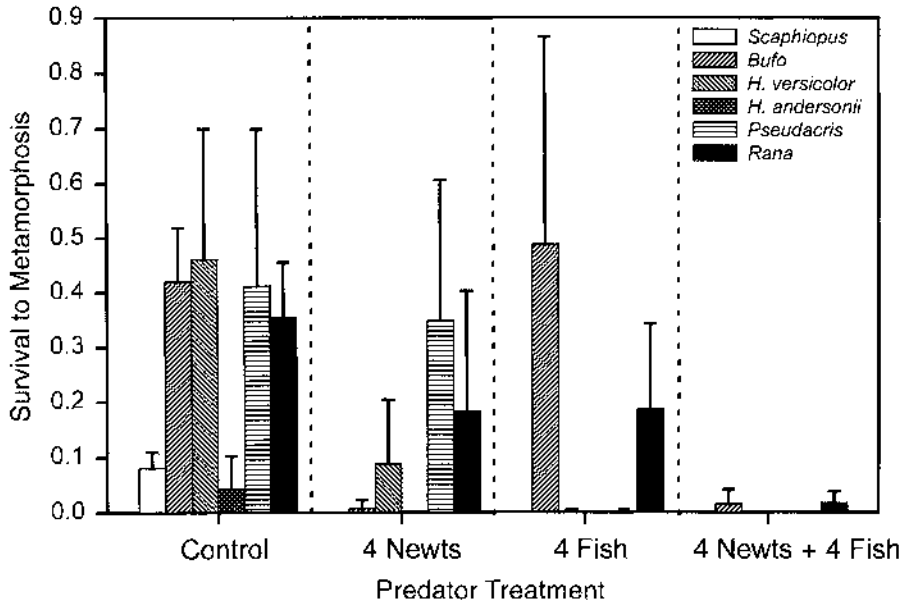


FIG. 1. Survival to metamorphosis (mean \pm 1 SD) for each anuran species in the four experimental treatments. Species are keyed by different shading patterns. Each value is the mean of three replicates.

TABLE 1. MANOVA and univariate ANOVAs for effects of newts and fish on anuran survival.

| a) Multivariate analysis | | | | | |
|------------------------------|---------------------|------|------------------|--------|---------------|
| | Source | df | Wilks' λ | F | P† |
| | Newts | 6, 3 | 0.014225 | 34.650 | 0.0073 |
| | Fish | 6, 3 | 0.015477 | 31.806 | 0.0083 |
| | Newts \times Fish | 6, 3 | 0.014048 | 35.090 | 0.0072 |
| b) Univariate analyses | | | | | |
| | Source | df | ss | F | P† |
| <i>Scaphiopus holbrookii</i> | Newts | 1 | 0.0048000 | 21.33 | 0.0017 |
| | Fish | 1 | 0.0048000 | 21.33 | 0.0017 |
| | Newts \times Fish | 1 | 0.0048000 | 21.33 | 0.0017 |
| | Error | 8 | 0.0018000 | | |
| <i>Bufo woodhousii</i> | Newts | 1 | 0.5896333 | 15.43 | 0.0044 |
| | Fish | 1 | 0.0044083 | 0.12 | 0.7429 |
| | Newts \times Fish | 1 | 0.0027000 | 0.07 | 0.7971 |
| | Error | 8 | 0.3056833 | | |
| <i>Hyla versicolor</i> | Newts | 1 | 0.1640833 | 6.04 | 0.0395 |
| | Fish | 1 | 0.2241333 | 12.72 | 0.0073 |
| | Newts \times Fish | 1 | 0.1045333 | 5.93 | 0.0409 |
| | Error | 8 | 0.1410000 | | |
| <i>Hyla andersonii</i> | Newts | 1 | 0.0013021 | 1.46 | 0.2609 |
| | Fish | 1 | 0.0013021 | 1.46 | 0.2609 |
| | Newts \times Fish | 1 | 0.0013021 | 1.46 | 0.2609 |
| | Error | 8 | 0.0071167 | | |
| <i>Pseudacris crucifer</i> | Newts | 1 | 0.0031688 | 0.09 | 0.7780 |
| | Fish | 1 | 0.4313021 | 11.57 | 0.0093 |
| | Newts \times Fish | 1 | 0.0028521 | 0.08 | 0.0712 |
| | Error | 8 | 0.2981000 | | |
| <i>Rana sphenoccephala</i> | Newts | 1 | 0.0867000 | 4.16 | 0.0758 |
| | Fish | 1 | 0.0833333 | 4.00 | 0.0807 |
| | Newts \times Fish | 1 | 0.0000000 | 0.00 | 1.0000 |
| | Error | 8 | 0.1668667 | | |

† Significance levels for ANOVAs should be compared against a conservative Bonferroni-corrected significance level of $\alpha = 0.009$ for six tests, one test for each prey species. ANOVA significance levels that satisfy the Bonferroni correction are highlighted in boldface type.

TABLE 2. Discriminant analysis for differences in anuran survival among predator treatments. Numerical table entries are discriminant function coefficients and correlations between discriminant scores and anuran survival.

| Species | Statistic | Newts | Fish | Newts × Fish |
|--------------------------|-------------|----------|---------|--------------|
| <i>S. holbrookii</i> | coefficient | 54.4283 | 67.6909 | 56.5406 |
| | correlation | 0.94357 | 0.94513 | 0.94907 |
| | P | 0.0001 | 0.0001 | 0.0001 |
| <i>B. woodhousii</i> | coefficient | 1.7844 | 0.6112 | 1.4091 |
| | correlation | 0.42335 | 0.38111 | 0.46953 |
| | P | 0.1703 | 0.2216 | 0.1235 |
| <i>H. versicolor</i> | coefficient | 18.1524 | 10.7659 | 17.9227 |
| | correlation | 0.84536 | 0.85953 | 0.83595 |
| | P | 0.0005 | 0.0003 | 0.0007 |
| <i>H. andersonii</i> | coefficient | -30.8853 | -5.4345 | -29.5798 |
| | correlation | 0.59577 | 0.59676 | 0.58057 |
| | P | 0.04090 | 0.0405 | 0.0478 |
| <i>P. crucifer</i> | coefficient | -3.6782 | -1.2697 | -3.6262 |
| | correlation | 0.48222 | 0.52891 | 0.47490 |
| | P | 0.1124 | 0.0770 | 0.1187 |
| <i>R. sphenoccephala</i> | coefficient | -4.8098 | -2.5647 | -4.7211 |
| | correlation | 0.57243 | 0.58129 | 0.60333 |
| | P | 0.0518 | 0.0474 | 0.0378 |

dominated in anuran communities where newts were the sole predators, while *Bufo woodhousii* predominated where fish were the only predators. In contrast, surviving froglets were more evenly distributed among the six species in ponds without predators than in the ponds with predators. These differences are emphasized by a cluster analysis of average anuran relative abundance patterns within communities (Fig. 4), which emphasizes the dissimilarity between the newt-only and fish-only treatments. The cluster analysis first

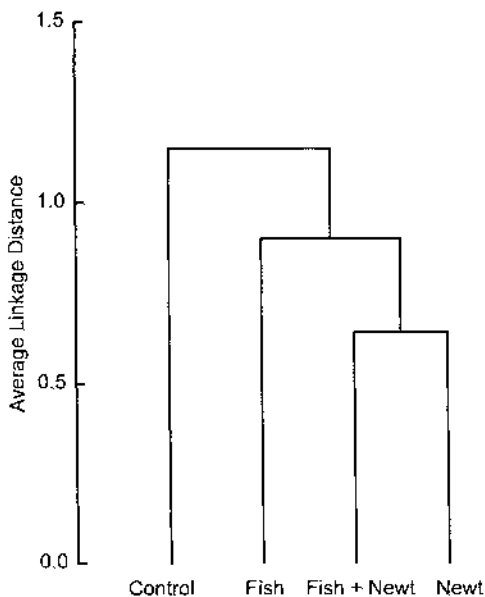


FIG. 2. An average linkage cluster analysis using the mean values of survival of each anuran species to metamorphosis in each treatment to describe the similarity of effects of predators on community processes.

grouped the control with the newt-only treatment, while the fish-only and the newt-plus-fish treatments were somewhat less similar (Fig. 4). This means that patterns of relative abundance in communities without fish (regardless of salamander presence) were more similar to each other than they were to communities with fish (regardless of salamander presence).

Fish significantly increased the relative abundance of *B. woodhousii* and significantly decreased relative abundances of *H. versicolor* and *P. crucifer*, while newts decreased the relative abundance of *B. woodhousii* and increased the relative abundance of *P. crucifer* (Tables 3-4, Fig. 3). MANOVA indicated a significant effect of fish, but not newts, on anuran relative abundance (Tables 3-4). The multivariate analysis was highly conservative because the number of variables tested was large relative to the number of experimental units; increased replication would probably have enhanced the ability to detect a significant effect of newts on anuran relative abundance. Furthermore, the predators had differing effects on only two of the six prey species, which may have contributed to the absence of an overall significant effect of newts in the multivariate case.

Larval performance

The predators only affected the larval performance of one prey species, *Rana sphenoccephala*. Metamorphs from the newt-only treatment were significantly larger than those from the predator-free controls (3.203 ± 1.896 vs. 1.517 ± 0.403 g, respectively (means ± 1 SD); $F_{1,10} = 17.13$, $P = 0.0044$). The effects of fish on body mass of *R. sphenoccephala* metamorphs (1.876 ± 0.811 g; $F_{1,10} = 5.08$, $P = 0.0588$) were also nearly significant. These results suggest that surviving *R.*

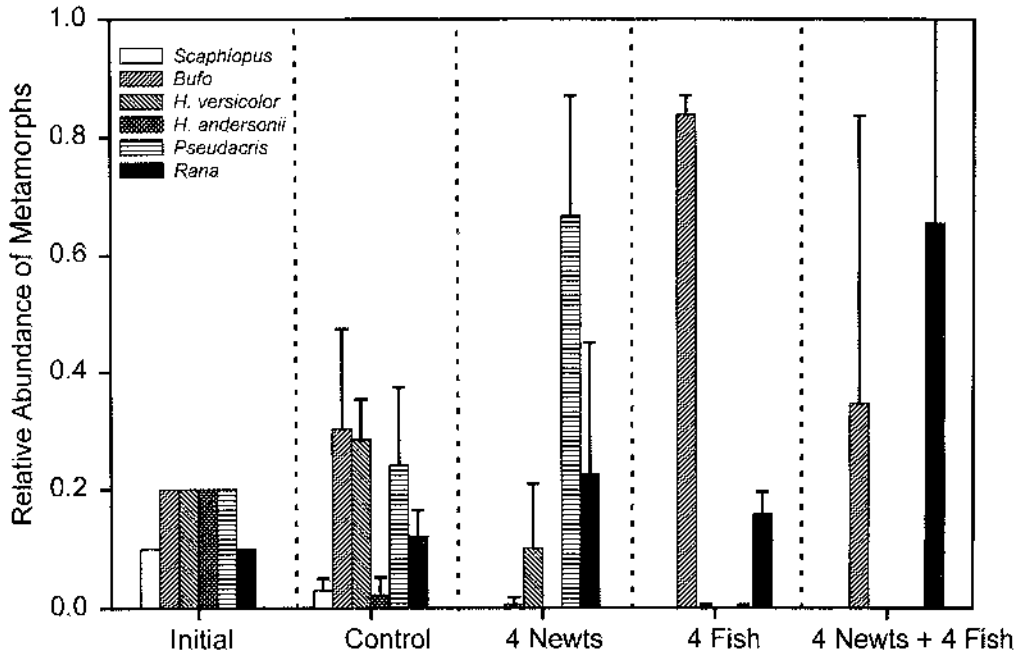


FIG. 3. Relative abundance of emerging metamorphs (mean \pm 1 SD), a measure of dominance, for each anuran species in each of the four experimental treatments. Each value is the mean of three replicates. Communities with fish were dominated by *Bufo* and *Rana*, while communities containing only newts were dominated by *Pseudacris*.

sphenocephala tadpoles experienced a release from competition in ponds with predators.

Prey diversity and biomass

Both predators decreased the diversity of anurans that survived through metamorphosis (Table 5; ANO-

VA main effect of newts, $F_{1,11} = 24.90, P = 0.0011$; main effect of fish, $F_{1,11} = 41.69, P = 0.0002$), but the two predators generated similar levels of anuran diversity (orthogonal contrast, fish-only vs. newt-only treatment: $F_{1,11} = 1.08, P = 0.33$). Although both predators reduced anuran diversity to a similar extent, the reductions resulted in part from different effects of each predator on different prey species.

Newts and fish significantly reduced the total biomass of anuran metamorphs emerging from ponds relative to the values obtained in the controls (Fig. 5; ANOVA main effect of newts, $F_{1,11} = 5.71, P = 0.0439$; main effect of fish, $F_{1,11} = 6.62, P = 0.0329$). The two predator species did not differ in their effects on total anuran biomass (orthogonal contrast: $F_{1,8} = 0.02, P = 0.90$).

Predator size and growth rate

Although the treatments initially established a similar biomass of each predator species, after several months of growth the mass of individual predators and predator populations diverged somewhat. Individual fish grew to a larger size than individual newts by the end of the experiment (6.99 ± 1.21 vs. 2.96 ± 0.63 g per individual, respectively; $F_{1,4} = 25.48, P = 0.0072$). Fish had greater estimated relative growth rates (0.0068 ± 0.0010 d⁻¹) than newts (0.0013 ± 0.0016 d⁻¹; $F_{1,4} = 26.56, P = 0.0067$).

DISCUSSION

Tests of functional equivalence

The answer to the question of whether newts and fish are functionally equivalent predators depends critically

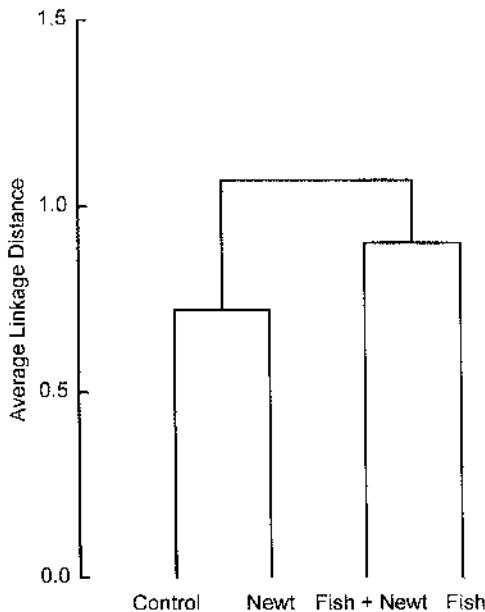


FIG. 4. An average linkage cluster analysis using the mean values of relative abundance for each anuran species to describe the similarity of effects of different predators on community processes.

TABLE 3. MANOVA and ANOVAs for effects of newts and fish on anuran relative abundance.

| a) Multivariate analysis | | | | | |
|--------------------------|---------------------|------|------------------|--------|---------------|
| | Source | df | Wilks' λ | F | P† |
| | Newts | 5, 3 | 0.009519 | 4.420 | 0.1255 |
| | Fish | 5, 3 | 0.034692 | 16.695 | 0.0213 |
| | Newts \times Fish | 5, 3 | 0.11365 | 4.679 | 0.1171 |
| b) Univariate analyses | | | | | |
| | Source | df | ss | F | P† |
| <i>S. holbrookii</i> | Newts | 1 | 0.00058583 | 5.29 | 0.0550 |
| | Fish | 1 | 0.00058583 | 5.29 | 0.0550 |
| | Newts \times Fish | 1 | 0.00058583 | 5.29 | 0.0550 |
| | Error | 8 | 0.00077533 | | |
| <i>B. woodhousii</i> | Newts | 1 | 0.41435857 | 9.66 | 0.0171 |
| | Fish | 1 | 0.51000364 | 11.89 | 0.0107 |
| | Newts \times Fish | 1 | 0.02544013 | 0.59 | 0.4665 |
| | Error | 8 | 0.3036478 | | |
| <i>H. versicolor</i> | Newts | 1 | 0.002284945 | 4.88 | 0.0629 |
| | Fish | 1 | 0.09775780 | 20.87 | 0.0026 |
| | Newts \times Fish | 1 | 0.02189723 | 4.67 | 0.0674 |
| | Error | 8 | 0.03279335 | | |
| <i>H. andersonii</i> | Newts | 1 | 0.00030914 | 1.24 | 0.3014 |
| | Fish | 1 | 0.00030914 | 1.24 | 0.3014 |
| | Newts \times Fish | 1 | 0.00030914 | 1.24 | 0.3014 |
| | Error | 8 | 0.00173862 | | |
| <i>P. crucifer</i> | Newts | 1 | 0.11953591 | 7.09 | 0.0323 |
| | Fish | 1 | 0.54629897 | 32.41 | 0.0007 |
| | Newts \times Fish | 1 | 0.12174717 | 7.22 | 0.0312 |
| | Error | 8 | 0.11797572 | | |
| <i>R. sphenoccephala</i> | Newts | 1 | 0.24099636 | 4.86 | 0.0632 |
| | Fish | 1 | 0.14396231 | 2.91 | 0.1320 |
| | Newts \times Fish | 1 | 0.10154366 | 2.05 | 0.1953 |
| | Error | 8 | 0.34680533 | | |

† Univariate ANOVAs indicate which variables contribute to overall multivariate differences. Univariate significance levels should be compared to the Bonferroni-corrected level of $P = 0.009$ for six tests, one for each species. Format is as in Table 1.

TABLE 4. Discriminant analysis for differences in relative abundance of anuran metamorphs among treatments with and without fish. Discriminant function coefficients and correlations between discriminant scores and anuran relative abundance are only given for the effects of fish, because this was the only factor that significantly affected relative abundance in the MANOVA.

| Species | Statistic | Fish |
|--------------------------|-------------|---------|
| <i>S. holbrookii</i> | coefficient | 67.32 |
| | correlation | 0.710 |
| | P | 0.0143 |
| <i>B. woodhousii</i> | coefficient | -0.812 |
| | correlation | -0.556 |
| | P | 0.075 |
| <i>H. versicolor</i> | coefficient | 3.156 |
| | correlation | 0.893 |
| | P | 0.0002 |
| <i>H. andersonii</i> | coefficient | 22.496 |
| | correlation | 0.510 |
| | P | 0.1087 |
| <i>P. crucifer</i> | coefficient | -2.277 |
| | correlation | 0.514 |
| | P | 0.1062 |
| <i>R. sphenoccephala</i> | coefficient | 0.0000 |
| | correlation | -0.3401 |
| | P | 0.3061 |

on the measure used to assess their community-level impacts. Despite their initially similar body sizes, and their general feeding habits, newts and fish changed the species composition of anuran assemblages in very different ways. In contrast, if the property of interest is prey diversity, or prey biomass (a component of secondary production), then newts and salamanders were functionally equivalent. One of our initial hypotheses, that a similar number of individual predators with a similar collective biomass might have similar effects on prey community composition, regardless of their specific identity, was refuted. Both predators reduced the survival of *S. holbrookii*, *H. versicolor*, *H. andersonii*, or *R. sphenoccephala* to a similar extent. Two

TABLE 5. Anuran species diversity (mean \pm 1 SD). "Initial" indicates the starting value of diversity for hatchlings stocked in all treatments.

| Treatment | H' |
|--------------|-------------------|
| Initial | 1.748 |
| Control | 1.614 \pm 0.099 |
| Newts | 0.685 \pm 0.360 |
| Fish | 0.492 \pm 0.221 |
| Newts + Fish | 0.105 \pm 0.314 |

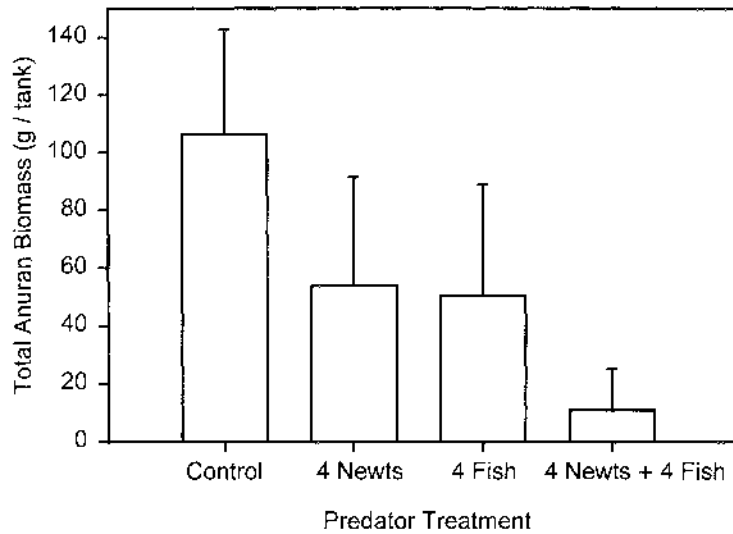


FIG. 5. Values of anuran biomass (mean and 1 SD), summed across all six species, as a function of different predator treatments. The two predators, when acting separately, generated communities with similar biomasses of metamorphosing anurans.

species, *S. holbrookii* and *Hyla andersonii*, were effectively eliminated by both vertebrate predators. This result is consistent with patterns seen in previous studies (Morin 1983, 1995) and suggests that both these anuran species require relatively ephemeral ponds that are unlikely to support populations of salamanders or fish. However, the predators had opposite effects on the survival of *B. woodhousii* and *P. crucifer*. These differences in strong interactions among predators and prey are summarized graphically in Fig. 6. This summary also clarifies why so few anurans managed to survive the joint onslaught of predation by newts and fish. For some reason, antipredator strategies that were effective against one predator species were ineffective against the other. We have observed that fish will taste and reject tadpoles of *Bufo woodhousii*, while newts readily consume tadpoles of this species. Apparently whatever the mechanism is that gives *Bufo* a defense against fish, unpalatability or toxicity, it is ineffective against newts. *Pseudacris crucifer* changes its microhabitat use and reduces its activity in the presence of newts (Morin 1986, Lawler 1989). Our results indicated that this behavioral defense was considerably less effective against fish than against newts. The reason for this difference is unclear, since both newts and fish are active predators that forage visually. The net result of the different effectiveness of antipredator strategies against these two predator species was that *P. crucifer* predominated in ponds with newts, while *B. woodhousii* predominated in ponds with fish. Other experiments examining the competition between *E. obesus* and *N. viridescens* (Bristow 1991) demonstrated similar effects of newts and fish on *B. woodhousii* and *P. crucifer*. This result also explains the well-known habitat preference of breeding *Bufo woodhousii* for permanent

ponds with abundant fish (Martof et al. 1980, Conant and Collins 1991).

Very few anurans survived to metamorphosis in the artificial ponds that contained both newts and fish. The virtual elimination of the entire anuran assemblage by the combined predation by salamanders and fish suggests that anurans use predator-specific defenses, rather than all-purpose defenses that are effective against a wide range of vertebrate predators. Few natural ponds contain both salamanders and fish, perhaps because of the strongly asymmetric negative interaction between the two groups (Bristow 1991). Ponds containing both fish and newts would probably be reproductive sinks for many anuran species, few of whose larvae would survive to metamorphosis.

Quantifying the extent to which changes in community composition or structure affect ecosystem function is an important goal of ecology and conservation biology (Lawton and Brown 1993, Naeem et al. 1994, Tilman and Downing 1994, Lamont 1995). Species interactions clearly drive some ecosystem properties (Paine 1966, 1992, Risser 1995), but it is difficult to decide a priori on the specific functions and aspects of biodiversity that should be measured (Risser 1995). Rather different predators may be deemed to be functionally similar if the measurement used to assess function is sufficiently aggregated across responding species to compensate for, or obscure, the unique responses of particular prey species to particular predators. Composite measures of ecosystems attributes, such as species diversity and standing stock of biomass, are more likely to blur the distinctions among species-specific responses to predators than are measures of community composition that emphasize the contributions of different species to overall patterns. Consequently, it

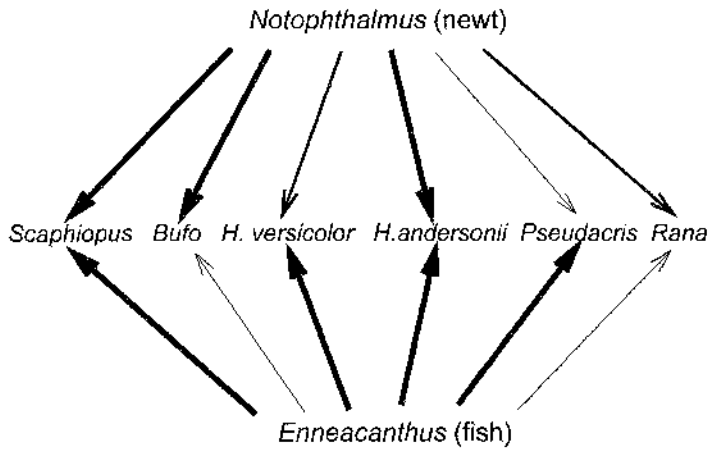


FIG. 6. Comparison of net effects of *Notophthalmus* and *Enneacanthus* on the anuran assemblage. The width of the arrows corresponds to the difference in survival of each prey species between predator-free controls and treatments containing each predator, with wider arrows corresponding to stronger negative interactions and greater reductions in survival.

seems likely that any assessment of functional redundancy will depend critically on the measure used to assess the impacts on species on the properties of communities and ecosystems. Our results show that it should not seem surprising that species may be redundant with respect to some measures, and not to others. This makes the choice of measure used to assess redundancy all the more critical.

Reduction of prey biomass to a similar extent by both predators demonstrates similar effects on a component of secondary production. It is unknown whether the differences in anuran species composition that occurred despite similar levels of secondary production affected either primary productivity or nutrient cycling. Larval anurans can alter both processes (Seale 1980, Leibold and Wilbur 1992), but interspecific differences among anurans in their effects on ecosystem processes remain little studied. Future experiments that include the monitoring of primary productivity and nutrient availability in ponds could determine whether knowledge of anuran diversity or biomass is sufficient to predict their impacts on ecosystem processes, or whether knowledge of species composition is required.

Predator biomass was a poor predictor of effects on species composition, although it appeared to work well enough for species diversity and prey biomass. Biomass may be an unreliable predictor of community level effects for distantly related or morphologically dissimilar predators from different habitats, perhaps because species-specific antipredator strategies are more likely to evolve in communities that consistently contain different predator species. Studies of closely related morphologically similar predators from similar habitats (temporary ponds) show that predators can have mass-equivalent effects on community structure (Morin 1995). Other studies suggest that distantly related predators from similar habitats may not be equivalent. Fauth and Resetarits (1991) examined the effects of the lesser siren, *Siren intermedia* (Sirenidae), and the broken striped newt, *N. v. dorsalis* (Salamandridae)

on anuran assemblages. Sirens and newts altered anuran species composition in different ways that could not be accounted for by predator biomass. Newts changed anuran species composition through selective predation on particular species, while nonselective predation by sirens did not alter prey species composition. Wilbur and Fauth (1990) compared the impacts of two even more distantly related predators, *Notophthalmus* and larvae of the odonate *Anax junius*. Although similar in mass and population density, *Anax* consumed more anurans than *Notophthalmus* and caused a greater shift in community composition relative to predator-free control ponds. Although the number of studies is small, the emerging pattern is that taxonomically similar predators within similar habitats can have functionally equivalent impacts on prey species composition, while more distantly related species may not. These distinctions may be less important if relatively coarse measures, such as prey biomass or prey diversity, are used to assess functional attributes of species.

Roles of predators in generating variation in species composition among habitats

Our results indicate that ponds structured by different predators, specifically newts or fish, will make different contributions to the adult amphibian assemblage that exploits a local constellation of breeding sites. Ponds without vertebrate predators produced the greatest diversity and highest survival of larval anurans, but the potential contribution of predator-free ponds to the local amphibian assemblage is probably offset by the rarity of such breeding sites (Morin 1983). Also, ponds without vertebrate predators are readily colonized by predatory insects (Roth and Jackson 1987) and seldom remain a safe haven for long. Others have noted the importance of fish in restricting some anuran species to fishless ponds (e.g., Heyer et al. 1975, Werner and McPeck 1994). Fish usually have very strong negative effects on anuran larvae (Heyer et al. 1975, Woodward 1983, Kats et al. 1988, Semlitsch and Gibbons 1988),

although the strength of this effect seems to vary considerably among systems (Gascon 1992). Rather less attention has been paid to the idea that nonfish predators in temporary ponds may be responsible for excluding prey species that typically co-occur with fish in permanent waters. Werner and McPeck (1994) have proposed that predation by salamanders and larval odonates may exclude *Rana catesbeiana* from fishless ponds, while *Rana* tadpoles appear to be well-protected from fish predation by unpalatability (Kruse and Francis 1977). Our results support a similar pattern for *Bufo woodhousii*, which persists well with fish but is readily excluded by newts in fishless ponds. These results suggest that fish and salamanders have rather different community level effects, despite earlier predictions to the contrary (Zaret 1980). Some of the differences between the species composition of natural anuran assemblages in ponds with and without fish are well known to herpetologists (Martof et al. 1980, Conant and Collins 1991). The differences in species composition probably have multiple causes, including habitat selection by adult anurans (Resetarits and Wilbur 1989), as well as the direct exclusions of larvae described in our study. Exclusions by predators presumably result from the failure of anuran antipredator strategies, which include unpalatability (Licht 1968, 1969, Kruse and Francis 1977, Formanowicz and Brodie 1982, Kats et al. 1988), behavioral mechanisms (Caldwell et al. 1980, Woodward 1983, Lawler 1989, Skelly and Werner 1990, Skelly 1995), and rapid growth to an invulnerable size (Smith 1983, Cronin and Travis 1986, Formanowicz 1986, Semlitsch and Gibbons 1988). Effectiveness of some of these strategies against one predator species may be a poor predictor of their effectiveness against others. This is more likely to be the case for chemical or behavioral defenses, which have a greater potential for species specificity, than for purely biomechanical defenses.

Differences in the final size of newts and fish that developed after ~6 mo of growth were not likely to be responsible for the observed differences in their effects on anurans. Other studies have shown that anuran larvae are most vulnerable to predators during the first 2–3 wk of development (Alford 1989), long before large differences in the sizes of the predators would occur. Also, the majority of the anurans in our study completed development within 1–2 mo, again well before large differences in predator size appeared. However, the fact that some fish (including *Enneacanthus*) can attain a much larger size than many salamanders makes it unlikely that anuran larvae can rely on rapid growth to a large size as an effective antipredator strategy in ponds containing fish.

This study adds to the large body of information documenting the extensive differences between aquatic communities that differ with respect to whether the dominant top predators are fish or other taxa. The presence or absence of fish, and the replacement of fish by

other predatory species, is correlated with profound shifts in the species composition of zooplankton (Brooks and Dodson 1965, Zaret 1980), and a variety of littoral and benthic invertebrates, including anisoptera (Morin 1984), zygoptera (McPeck 1990), and others (Hall et al. 1970, Crowder and Cooper 1982). These patterns suggest that fish are functionally distinct from the other kinds predators, such as salamanders or large aquatic insects, that replace fish in more ephemeral aquatic habitats. Fish may be more efficient predators than their amphibian or insect counterparts, and may therefore put greater pressure on some prey populations. One consequence of this greater efficiency might materialize as a consistently greater standing stock of fish in aquatic communities compared to the standing stock of other, less efficient predators in otherwise comparable communities.

Finally, although our experiments were conducted in artificial ponds, they suggest an important role for different predator species in maintaining anuran diversity within a complex landscape of ponds. The patchy distribution of functionally distinct predators across a landscape of discrete habitats should contribute to predictable patterns of spatial variation in community composition. As a consequence, studies of a single type of pond, whether temporary or permanent, or a single kind of predator, such as newts or fish, would not reveal the complementary contributions of different habitats and predators to prey species composition across an array of habitats.

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