Wetland Restoration for Amphibians: Should Local Sites Be Designed to Support Metapopulations or Patchy Populations?

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Abstract

Pond-breeding amphibians have been characterized as having metapopulation structure, and a goal of many local restoration projects is to establish viable metapopulations. However, recent studies suggest that metapopulation organization is unlikely at the local level because of high dispersal rates between neighboring ponds. Although many amphibians avoid ovipositing in habitats that pose high predation risk to their offspring, the spatial scale of avoidance is poorly resolved for natural systems and could involve wholesale movements between ponds. To determine the scale of avoidance, we monitored annual habitat use by the Wood frog (*Rana sylvatica*), American toad (*Bufo americanus*), and Spotted salamander (*Ambystoma maculatum*) at a restoration site in western North Carolina, U.S.A. Wood frogs consistently used most fish-free ponds, but rapidly curtailed use following fish invasions. American toads rarely used the same breeding site from year to year, and adults strongly avoided ovipositing in habitats with predatory Wood frog tadpoles. Spotted salamanders exhibited a predator avoidance response to fish that was weaker than the predator avoidance response of anurans. Our data indicate that the spatial scale of predator avoidance by ovipositing amphibians often exceeds that of an individual pond and that the focal species at this site are organized as patchy populations rather than as metapopulations. At local restoration sites, ponds that are placed in spatial arrays to create metapopulations may not accomplish their goal and may limit the extent to which ovipositing adults can express an adaptive antipredator behavior. We discuss an alternative design that is more likely to enhance the long-term persistence of local populations.

Key words: ***Ambystoma maculatum*, amphibians, *Bufo americanus*, habitat restoration, metapopulations, oviposition sites, predator avoidance, *Rana sylvatica*.**

Introduction

Amphibian populations have declined worldwide, and the loss or degradation of habitat is considered to be the most important contributing factor (Houlahan et al. 2000; Collins & Storfer 2003). In North America, small seasonal wetlands are the primary breeding habitats of many amphibians and have diminished at alarming rates (Semlitsch & Bodie 1998; Gibbs 2000; McCauley & Jenkins 2005). To compensate, restoration ecologists are increasingly creating ponds for amphibians as components of wetland restoration projects.

Ecologists have improved the design of wetlands for amphibians by incorporating information on natural history, community interactions, landscape ecology, and population dynamics (Richter 1997; Semlitsch 2000, 2002). At the local level, pond hydroperiod and terrestrial buffers are critical components of wetland design. The seasonal hydroperiod affects the probability of larvae surviving to metamorphosis, as well as the abundance and diversity of aquatic predators (Schneider & Frost 1996; Wellborn et al. 1996). These characteristics, when coupled with life history constraints, prevent most species from occupying the entire hydrologic gradient from highly seasonal to permanent ponds (Wellborn et al. 1996; Paton & Crouch 2002; Babbitt et al. 2003).

Because amphibians rarely disperse more than 2–3 km from their natal ponds (Smith & Green 2005), populations within local mitigation sites may have little connectivity to adjacent populations. Consequently, restoration ecologists often must restore local sites so that they function as self-sustaining systems. A common goal is to create a mitigation site with high amphibian diversity and that maximizes population resilience and persistence. Factors that may affect population resilience and long-term persistence include the invasion of predators, outbreaks of disease, and long-term drought (Petranka et al. 2003*b*; Pearl et al. 2005).

Pond-breeding amphibians have frequently been characterized as having strong site fidelity, low vagility, and metapopulation structure (Alford & Richards 1999; Smith & Green 2005). Although conservation guidelines have emphasized the need to establish habitats to support metapopulations (e.g., Semlitsch 2000), emerging research suggests than many amphibians are more vagile and less philopatric than previously suspected (Petranka et al. 2004; Smith & Green 2005). An alternative to metapopulation structure at the local level is the existence of patchy populations that treat local ponds as habitat patches. Under this

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scenario, movements between ponds occur at such high rates that local pond populations do not develop a significant degree of demographic independence and lack metapopulation structure (Harrison 1991; McCullough 1996; Smith & Green 2005).

When creating ponds on restoration sites, ecologists must decide on the appropriate number and spatial arrangement of habitats. This, in turn, will be strongly influenced by the nature of population organization at the local level. Consequently, whether amphibian populations that utilize local clusters of ponds function more as patchy populations or metapopulations is a fundamental issue that needs to be resolved in order to optimize restoration designs.

The "patchy population" model of organization has support from behavioral studies that show that many adult amphibians have evolved behavioral avoidance mechanisms in response to competitors, predators, or parasites in ponds (Resetarits & Wilbur 1989; Crump 1991; Kiesecker & Skelly 2000). In particular, gravid females may assess predation risk to their future offspring and avoid ovipositing in habitats of low quality (e.g., Petranka et al. 1994; Binckley & Resetarits 2002; Rieger et al. 2004).

Because most experimental studies of adult choice have been restricted to small systems such as wading pools, the spatial scale at which behavioral avoidance occurs in nature is poorly resolved. This could range from microhabitat shifts within a pond (e.g., laying in vegetated shallows vs. deep areas of a pond) to wholesale shifts of breeding populations between ponds. If the latter is typical, then it would strongly violate the assumption of low dispersal rates between local pond populations, which is essential for metapopulation organization (Smith & Green 2005).

Here, we provide multiyear data on breeding habitat use and reproductive effort for the Wood frog (*Rana sylvatica*), American toad (*Bufo americanus*), and Spotted salamander (*Ambystoma maculatum*) that provide evidence of wholesale shifting of populations among ponds in response to predators. All species have been tested experimentally for avoidance behavior using small-scale studies (Hopey & Petranka 1994; Petranka et al. 1994; Sexton et al. 1994), and all but *A. maculatum* show strong avoidance of pools with aquatic predators. Our primary goals were to determine (1) whether experimental results from small-scale behavioral experiments apply to natural systems that are more complex, (2) whether the spatial scale of avoidance in natural systems exceeds that of a single pond, and (3) whether ponds with fish are high-risk environments for future offspring.

Methods

Site Description and History

We conducted research at the Tulula Wetlands Mitigation Bank (TW), which is a 95-ha wetland restoration site in Graham County, western North Carolina, U.S.A. (lat 35°17′N, long 83°41′W; elevation range 784–800 m). Details of the site history are in Petranka et al. (2003*a*, *b*) and are only briefly summarized here. The area was severely degraded in the late 1980s when an attempt to construct a golf course failed. Site alterations included ditching and channelization of Tulula Creek, the filling of seasonal wetlands, timbering of approximately 40% of the forest, and cattle grazing. TW was purchased as a mitigation site, and restoration occurred from 1996 to 2002. Restoration entailed recreating the original stream channel, filling drainage ditches, creating ponds for aquatic organisms, removing fill from underlying wetland soils, and planting trees.

TW currently contains more than 50 seasonal and permanent ponds. Most were created in 1995–1996 and 1999 to provide breeding sites for the 10 species of resident pond-breeding amphibians. Many existing habitats are stream-fed ponds that contain fish, whereas others are fish-free seasonal or semipermanent ponds. The use of breeding habitats by amphibians has been monitored since 1994. Efforts have primarily focused on monitoring 10 ponds that were created in 1995–1996 for amphibian use, and 10 reference ponds that were used for comparison (Petranka et al. 2003*a*, *b*). All constructed ponds that were monitored had nearest neighboring breeding sites that were less than 80 m from the constructed ponds.

Annual seasonal hydroperiods have been influenced by annual precipitation and the invasion of Beavers (*Castor canadensis*). A drought occurred from 1998 to 2002, and Beavers invaded TW in 2000. Subsequent trapping and reinvasion altered annual hydroperiods and allowed fish to invade many ponds. Fish also invaded a few seasonal ponds during heavy rainfall events that resulted in pond overflow and temporary connectivity to Tulula Creek. Humans have occasionally introduced fish into seasonal ponds based on the presence of adult *Lepomis* spp. (sunfishes) in seasonal ponds with no connectivity to Tulula Creek.

Behavioral Responses of *Rana Sylvatica* and *Ambystoma Maculatum* to Fish

We examined the response of *R. sylvatica* and *A. maculatum* to fish invasions using data on the number of egg masses that were deposited in 10 constructed and 6 reference ponds during 10 consecutive breeding seasons (1996–2005). The constructed ponds were created from October 1995 to January 1996. The average surface area and maximum depth at full capacity (±1 SE here and throughout) were 480 ± 68 m^2 and 44 ± 5 cm. The reference ponds were the largest and most natural seasonal depressions on site in 1995 (mean surface area at full capacity = 82 ± 21 m^2; mean depth = 24 ± 3 cm). All ponds were fish free when the study began in 1995–1996, but eight ponds experienced fish invasions in subsequent years. The constructed ponds were rapidly colonized by *A. maculatum* and *R. sylvatica* during 1996 within a few months after the ponds first filled with water. Occupancy rates in 1996 were 100% for *R. sylvatica* and 90% for *A. maculatum* (Petranka et al. 2003*a*).

Annual reproductive effort was estimated using the cumulative number of egg masses that were deposited in each pond (see Petranka et al. 2003*b* for details). Both species lay large egg masses (one per female for *R. sylvatica*; one to four per female for *A. maculatum*) that can be accurately censused to assess changes in the size of female breeding populations. Egg mass censuses were conducted at 1- to 3-week intervals during the breeding season until no new masses were found. During each visit, researchers systematically waded through each pond and counted all egg masses that were observed. Because ponds were clear and shallow, almost all masses within each pond were presumably counted. Estimates of the cumulative number of masses that were laid during the season were then used in the analyses (Petranka et al. 2003*b*). Censuses were conducted for 10 consecutive years (1996–2005), except for two reference ponds that were destroyed during stream restoration and were monitored for only 4 years (pond 3C) or 5 years (pond 2C). Four reference ponds that were used irregularly during the 10-year monitoring period were excluded from the analysis.

Fish were detected during routine site visits to estimate larval survival, to obtain data on physiochemical parameters, and to compile lists of amphibians that were using each pond (Petranka et al. 2003*a*, *b*). Ponds were typically visited a minimum of 8–10 times per field season (February–October). Most ponds were shallow and clear, and fish could be directly observed in the water. Specimens were also collected while dipnetting or when sampling larvae with open-bottomed samplers (Petranka et al. 2003*b*). Ponds where fish were not observed or collected during the breeding season were considered to be fish free.

Fish that were found in ponds were Bluegill (*Lepomis macrochirus*), Redbreast sunfish (*L. auritus*), Largemouth bass (*Micropterus salmoides*), and unidentified minnows. *Lepomis* spp. were the most common occupants. *Micropterus salmoides* was observed in only two ponds over the 10-year period, whereas minnows were observed in two additional ponds. With the possible exception of *M. salmoides*, all species are gape limited and unable to feed on adult *R. sylvatica* or *A. maculatum*. However, *Lepomis* spp. are efficient predators on palatable amphibian hatchlings and larvae (Kats et al. 1988).

Behavioral Responses of *Bufo Americanus* to *R. Sylvatica*

Rana sylvatica tadpoles are generalist omnivores that forage on detritus, algae, and small invertebrates. They are also effective predators on the eggs and hatchlings of amphibians such as *B. americanus* and may engage in context-dependent intraguild predation (Petranka et al. 1994; Holbrook & Petranka 2004). Local ponds often have high densities of *R. sylvatica* tadpoles when *B. americanus* arrives to breed in March or April.

We examined whether adult *B. americanus* avoid local ponds with *R. sylvatica* tadpoles by surveying most ponds at TW and documenting breeding activity ($n = 41$–58 ponds annually). *Bufo americanus* lays long strings of eggs that hatch quickly, so egg mass counts similar to those for *R. sylvatica* and *A. maculatum* were not feasible. Instead, we documented the presence of calling adults, amplexed pairs, egg strings, or hatchlings in ponds during site visits that were made from March–May annually. We also recorded whether *R. sylvatica* tadpoles and fish were present during the time of breeding. We conducted pond surveys for six consecutive breeding seasons (2000–2005) to document annual patterns of habitat use.

Survival of *A. Maculatum* Hatchlings

Centrarchid fish are effective predators on the hatchlings of many amphibians that lack chemical defenses. To determine whether hatchlings of *A. maculatum* are at high risk of predation from fish, we compared survival of hatchlings in ponds with and without fish in 2005. We conducted egg mass censuses in reference and constructed ponds in March and April. We then sampled for hatchlings approximately 2–3 weeks after more than 95% (typically 100%) of the embryos had hatched. Sampling involved dipnetting within open-bottomed trashcans that were forced into the pond substrate to trap larvae (see Petranka et al. 2003*b* for details). We obtained 12–54 samples per pond and estimated the total larval population based on the mean catch per sample and the pond surface area. For comparative purposes, we expressed survival as the estimated number of hatchlings that survived per egg mass based on the cumulative number of masses deposited during the breeding season in each pond.

Statistical Analyses

Fish could reduce the size of local pond populations of *R. sylvatica* and *A. maculatum* either by chronically eliminating larvae annually (demographic effects) or by triggering short-term behavioral avoidance. To quantify the strength of behavioral avoidance, we calculated the percent change in number of egg masses for the first year following an initial fish invasion relative to the previous year when fish were absent. We then compared this set of data (“fish” group) with a matching set of data based on changes in the number of egg masses during 2 consecutive years when fish were absent from a pond (“no-fish” group).

To generate the no-fish dataset, we randomly selected 2 consecutive years when fish were absent (e.g., 2000 and 2001) from among all possible pairs of consecutive years between 1996 and 2005 when fish were absent. We then calculated the percent change in egg mass counts for year 2 relative to year 1. We selected a single pair of consecutive years for each pond. Respective sample sizes for fish and no-fish groups were 8 and 15 for *A. maculatum* and

8 and 12 for *R. sylvatica*. Our prediction was that breeding effort for the fish group should be significantly reduced relative to the no-fish group if adults actively avoided ponds with fish. We compared the two groups using a Wilcoxon test with a *t* approximation using Statistical Analysis System. We used a one-tailed test because these two species should not be attracted to ponds with dangerous predators.

We used Fisher's exact test to compare the frequency of pond use by *B. americanus* with respect to the presence or absence of *R. sylvatica*. The latter species strongly prefers fish-free habitats (see Results). However, *B. americanus* tadpoles have chemical defenses, and the adults use both fish-free and permanent ponds with fish. We analyzed 2 × 2 frequency tables for all ponds (seasonal and permanent) and for the subset of ponds that lacked fish (primarily seasonal ponds). To determine whether ponds are used repeatedly from year to year, we calculated turnover rates following Hecnar and M'Closkey (1996). We treated a pond as being unused if no breeding adults, egg strings, or larvae were observed during the breeding season at a site where breeding occurred the previous year. We calculated annual turnover rates as the percentage of used ponds that were unused the following year.

We compared the estimated number of *A. maculatum* hatchlings that survived per egg mass in ponds with and without fish using a one-tailed Wilcoxon two-sample test with a *t* approximation.

Results

Behavioral Responses of *Rana Sylvatica* and *Ambystoma Maculatum* to Fish

In the absence of fish, *R. sylvatica* used most ponds annually for the duration of the study (Fig. 1). Breeding adults largely abandoned traditional fish-free breeding sites following the invasion of fish (Fig. 1). The percent change in egg masses for randomly selected consecutive years when fish were absent (the no-fish group) increased slightly in year 2 relative to year 1 and averaged 33.1 ± 25.5% ($\bar{X} \pm 1$ SE here and throughout). In contrast, egg mass counts declined 97.4 ± 2.2% relative to the year that immediately preceded a fish invasion. No egg masses were laid in 62% of the ponds following a fish invasion. In 88% of ponds, the decline in the number of egg masses was greater than 98%. The percent change in egg mass numbers differed significantly between the fish and no-fish groups (Wilcoxon test; $p = 0.0008$). Adults appeared to avoid ponds annually whenever fish were present but rapidly recolonized if fish disappeared (e.g., pond 5X; Fig. 1).

Ambystoma maculatum showed a parallel response, but avoidance was not as strong (Fig. 2). Changes for randomly selected consecutive years when fish were absent (no-fish group) averaged 3.24 ± 18.5%. Following initial fish invasion, egg mass numbers decreased by 68.8 ± 17.2%. As with *R. sylvatica*, the percent change in egg mass numbers differed significantly between the fish and the no-fish groups ($p = 0.006$). In ponds where fish were present for several consecutive years, the breeding responses were inconsistent. In some instances (e.g., ponds 3X and 6X in Fig. 2), adults appeared to strongly avoid ovipositing during all years. However, in other ponds (e.g., ponds 7X and 4X), egg mass numbers increased after the first year of invasion.

Behavioral Responses of *Bufo Americanus* to *R. Sylvatica*

Bufo americanus strongly avoided ponds with *R. sylvatica* tadpoles. From 2000 to 2005 *R. sylvatica* bred in 61% of the fish-free habitats that were monitored ($n = 236$ pond observations during 6 years). *Bufo americanus* bred in 55 fish-free habitats, but bred in ponds with *R. sylvatica* tadpoles in only seven instances. Analyses of contingency tables indicate strong spatial segregation between *B. americanus* and *R. sylvatica* for most years (Table 1). The results were similar for the two analyses that involved either all ponds or only fish-free ponds that were the preferred habitat of *R. sylvatica*. *Bufo americanus* rarely used the same ponds from year to year and appeared to opportunistically exploit seasonal ponds that lacked *R. sylvatica* tadpoles (Fig. 3). They also used fish-filled ponds such as Beaver ponds that lacked *R. sylvatica*. Respective turnover rates for 2000–2004 were 100%, 100%, 93%, 75%, and 86%. On average, 91% of ponds that were used in a given year were not used the following year.

Survival of *A. Maculatum* Hatchlings

We did not capture a single *A. maculatum* hatchling from open-bottom samplers in five of six fishponds where egg masses were deposited. The only pond with hatchlings was a seasonal pond that had a small number of adult fish that were apparently introduced. In contrast, we captured hatchlings in eight of nine ponds that lacked fish. The mean number of hatchlings per egg mass differed significantly among groups (Wilcoxon test: $p = 0.009$) and averaged 32.1 ± 8.6 for fish-free ponds compared with 1.15 ± 1.15 hatchlings for fishponds. This represents an approximately 96% reduction in hatchling survival in fishponds relative to fish-free ponds.

Discussion

Restoration projects that enhance breeding habitats for pond-breeding amphibians are often of small scale and involve installing one or more ponds locally. Restoration ecologists must ultimately make decisions about the number, spatial arrangement, size, complexity, and appropriate hydroperiods of ponds to be created or enhanced on site. Although this decision is based on many factors such as the composition of the resident amphibian communities and budgetary constraints, a fundamental goal should be to renew the ecological integrity of degraded wetlands

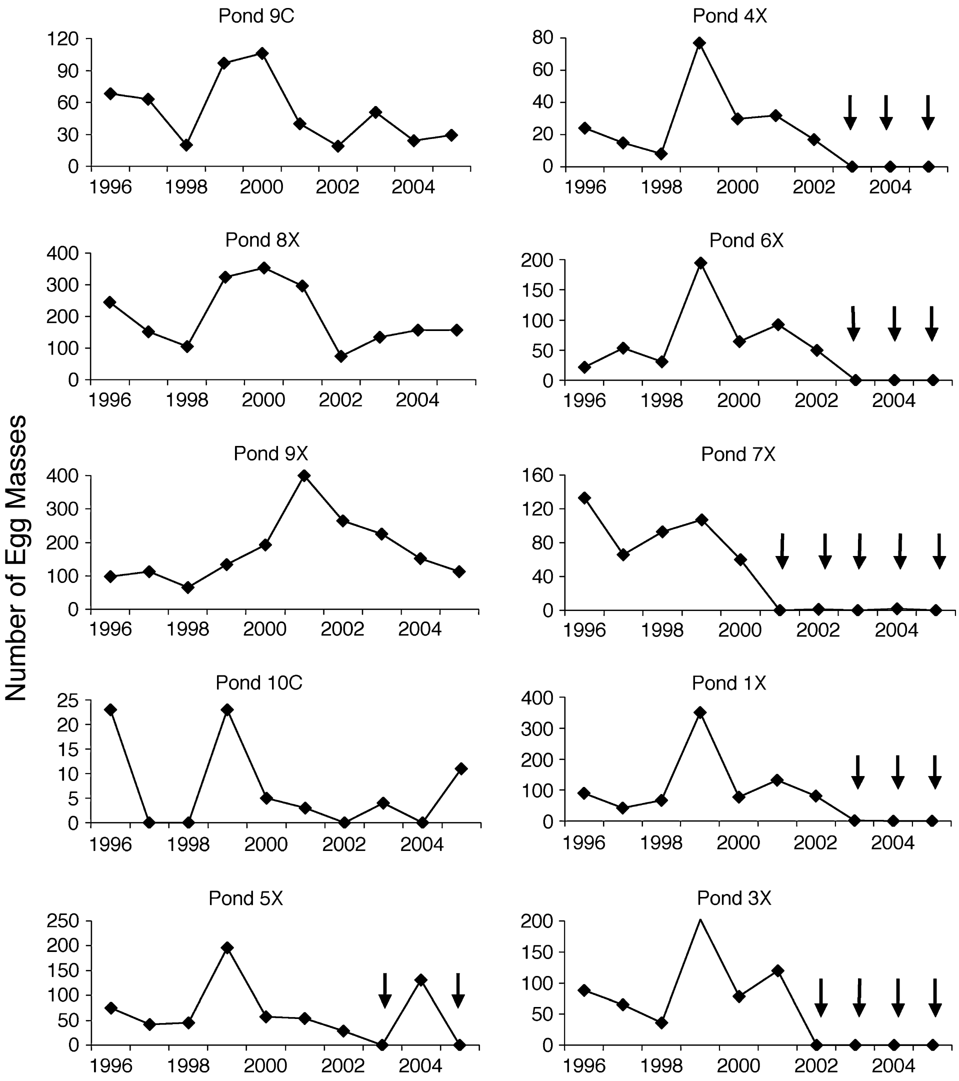

Figure 1. Number of egg masses deposited annually by *Rana sylvatica* in study ponds. Data are shown for 10 ponds that were monitored from 1996 to 2005. Arrows indicate years when fish were present at the time of breeding.

and to create self-sustaining systems that ensure the long-term persistence of resident populations. Paramount to achieving these goals is the need for a comprehensive understanding of population organization and dynamics at the local level. That is, should sites be designed to support local metapopulations or patchy populations?

Pond-breeding amphibians breed in spatially discrete habitats and have traditionally been characterized as having metapopulation structure where each local pond supports a local population. As such, a logical goal of restoration projects would be to establish viable metapopulations of resident species by creating several breeding ponds on site. However, the extent to which metapopulation organization occurs is strongly dependent on spatial scale and is greatly diminished when the dispersal rate between neighboring ponds is high (Marsh & Trenham 2001).

Based on published estimates of maximum dispersal rates of amphibians, Smith and Green (2005) concluded that metapopulation organization may be significantly compromised when pond populations are less than 10 km apart. This implies that metapopulation organization is unlikely within local restoration projects where neighboring breeding ponds are often separated by only a few hundred meters or less. Our study is consistent with this interpretation and provides strong evidence of weak site fidelity and the wholesale shifting of breeding populations among neighboring ponds that are in close proximity. We find no evidence that *Rana sylvatica*, *Bufo americanus*, or *Ambystoma maculatum* are organized as metapopulations within our 95-ha restoration site. Instead, the site is best viewed as supporting a single, patchy population of each species.

Petranka et al. (2004) conducted long-term studies of *R. sylvatica* and *A. maculatum* in local clusters of natural wetlands and found parallel evidence of high rates of local interpond movements in response to habitat disturbance

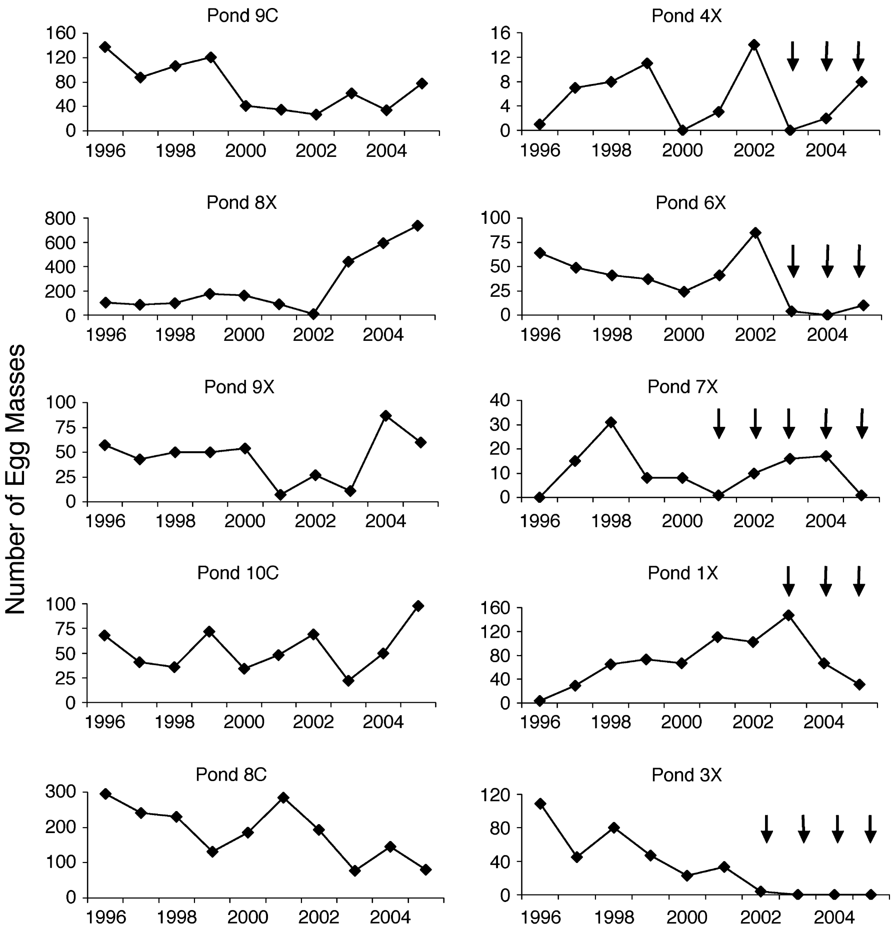

Figure 2. Number of egg masses deposited annually by *Ambystoma maculatum* in study ponds. Data are shown for 10 ponds that were monitored from 1996 to 2005. Arrows indicate years when fish were present at the time of breeding.

and invasions by fish. Although patterns may vary markedly among taxa (e.g., Jehle et al. 2005), emerging fine-scale genetic studies are providing additional evidence of lack of isolation and genetic differentiation for pond-breeding amphibians at this spatial scale (e.g., Newman & Squire 2001; Squire & Newman 2002).

At sites where ponds are in close proximity (e.g., <500 m apart), restoration success may be enhanced by creating spatial arrays of ponds that are designed to support patchy populations rather than metapopulations. For example, a metapopulation design would likely entail the installation of relatively few ponds that are spaced the maximum distance apart to increase demographic independence. In contrast, a patchy population design would likely incorporate more ponds, with many in close proximity to one another to facilitate adaptive habitat switching. At this scale, metapopulation designs will likely fail to establish local metapopulations (Smith & Green 2005) and may limit the extent to which ovipositing adults can express an adaptive antipredator behavior.

Pond-breeding organisms are subjected to complex spatiotemporal variation in predation risk that is often associated with winterkill of fish, Beaver activity, and annual-variation in seasonal rainfall and pond hydroperiods (Schneider & Frost 1996; Wellborn et al. 1996; Babbitt & Tanner 2000; Muller-Schwarze & Sun 2003). This has favored predator avoidance behavior by ovipositing amphibians and insects (Blaustein 1999), and data for our three focal species indicate that the scale of avoidance often exceeds that of an individual pond. That is, adults appear to treat local ponds within their normal activity range as habitat patches that are assessed for quality and opportunistically exploited (Blaustein 1999; Johnson & Semlitsch 2003; Petranka et al. 2004). Our data confirm that the results of small-scale experimental studies of adult choice of oviposition sites are applicable to more natural systems with larger and more distantly spaced breeding sites.

The two anurans responded more strongly to predators than *A. maculatum*. This may in part reflect the fact that anurans are more vagile and can readily move to neighboring ponds (Marsh et al. 2000; Johnson & Semlitsch 2003; Petranka et al. 2004). Hopey and Petranka (1994) and Petranka et al. (1994) found that the number of calling males of *R. sylvatica* and *B. americanus* was greatly

Table 1. Yearly summary statistics for breeding habitat selection by *Bufo americanus* with respect to presence or absence of *Rana sylvatica* tadpoles in ponds. *p* Values are for Fisher's exact test for analyses of both fish-free ponds and all ponds (fish free and fish filled combined). Analyses are for individual years and for all years combined (total).

	Number of Ponds		*% Used by Bufo*		
Year	*Rana*	*No Rana*	*Rana*	*No Rana*	*p*
Fish-free ponds					
2000	31	13	6.5	69.2	<0.0001
2001	28	11	3.6	36.4	0.02
2002	27	22	11.1	54.6	0.002
2003	26	4	0.0	100	<0.0001
2004	19	8	5.26	62.5	0.004
2005	14	16	0.0	25.0	0.10
Total	145	74	4.83	51.35	<0.0001
All ponds					
2000	31	14	6.5	71.4	<0.0001
2001	29	12	3.5	33.3	0.02
2002	28	22	10.7	54.6	0.001
2003	29	29	0.0	27.6	<0.005
2004	21	24	4.8	25.0	0.10
2005	14	38	0.0	21.0	0.09
Total	152	139	4.61	34.5	<0.0001

reduced in experimental ponds with predators relative to control ponds without predators. This suggests that the relative intensity of chorusing from specific ponds may create an acoustic landscape that indirectly signals the quality of breeding habitats to conspecifics.

Kats and Sih (1992) found that the Streamside salamander (*Ambystoma barbouri*) avoided local pools in streams that had predatory fish, which is consistent with our observations of moderate levels of avoidance of fishponds by *A. maculatum*. Our estimates of hatchling survival in fishpond and fish-free ponds show that the fitness reduction associated with ovipositing in fishponds is large for *A. maculatum*.

Although the pattern described above could be due to adults not breeding when fish are present in ponds, a more likely scenario is that most seek out alternate breeding sites and oviposit (Petranka et al. 2004). We observed shifts in the distribution of breeding *A. maculatum* that are consistent with this interpretation. For example, from 2002 to 2004, fish increasingly invaded many of the created ponds on site (from 10 to 80% occupancy). Egg mass counts in one large seasonal pond that remained fish free (pond 8X) increased markedly during this period (from 9 to 595 masses) even though annual larval mortality was near 100% from 1998 to 2004 due to outbreaks of ranaviral disease (Petranka et al. 2003*b*). This pattern is best explained by the wholesale immigration of adults from adjoining areas.

When restoring wetlands, we encourage restoration ecologists to implement designs that accommodate adult antipredator behaviors and adaptive habitat shifting. At TW, for example, we created a large array of wetlands (>50 ponds) that vary markedly in size, hydroperiod, and spatial proximity. One of our goals was to provide a complex of ponds that would provide each resident species with many potential breeding sites. Mitigation sites that contain one or only a few ponds with similar hydroperiods may severely constrain the ability of adults to seek out high-quality habitats that have low densities of predators. Having a diverse array of ponds on site increases spatiotemporal variability in predation risk and increases the likelihood that juveniles will be recruited annually into the adult population from one or more ponds that are of high quality. This, in turn, should enhance the long-term persistence of patchy populations.

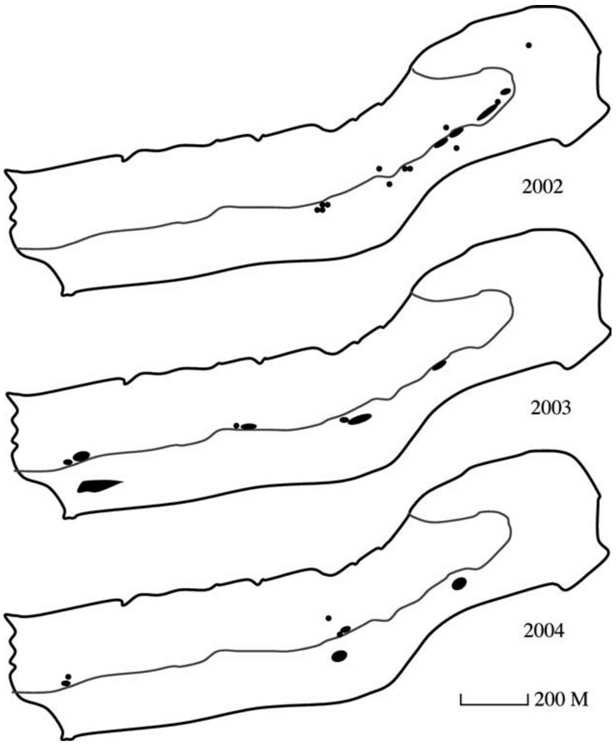

Figure 3. Examples of high turnover rates and opportunistic use of ponds by *Bufo americanus*. Maps show outlines of the site perimeter, Tulula Creek, and ponds (filled areas) that were used during 3 consecutive years. Toads primarily selected sites that were not used by Wood frogs in a given year.

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