Responses of a Pond-breeding Amphibian Community to the Experimental Removal of Predatory Fish

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ABSTRACT.—Introduced species have become one of the most important anthropogenic impacts in aquatic ecosystems and are implicated in the declines of many native amphibian populations. Despite the effects of introduced fish species on amphibian communities, there is little information concerning the responses of amphibians following the removal of introduced predatory fish. We present results of a 4-y field experiment designed to determine the amphibian community- and population-level responses to the removal of introduced predatory fish from two experimental ponds. We observed an increase in amphibian species diversity in experimental ponds following the removal of fish. We also observed temporal changes in smallmouth salamander (*Ambystoma texanum*) population dynamics. Although *A. texanum* size at metamorphosis was unaffected by introduced fish in experimental ponds, fish removal resulted in prolonged *A. texanum* larval period and improved reproductive success. We attribute these responses to increases in *A. texanum* larval densities, as we caught considerably more metamorphosed *A. texanum* juveniles from experimental ponds following the removal of fish. Collectively, these observations support previous studies indicating that introductions of predatory fish have adverse effects on amphibians at both the community and population levels. Furthermore, our results suggest that amphibian communities are capable of recovering from environmental perturbations.

INTRODUCTION

The effects of anthropogenic environmental perturbations on amphibian populations have received considerable attention, particularly the effects of introduced species (Collins and Storfer, 2003). In many aquatic systems introduced species constitute the most important anthropogenic impact (U.S. Congress, 1993). Whether native or exotic, human-assisted introductions of predatory fish into previously fishless aquatic habitats have had adverse effects on amphibian populations (Kiesecker, 2003). Introduced fish may serve as competitors and predators to pond-breeding amphibians (Kiesecker and Blaustein, 1998; Tyler *et al.*, 1998; Knapp and Matthews, 2000) and may be responsible for the extirpation of native amphibian populations (Bradford, 1989).

Predatory fish are important agents of amphibian community structure (*see* Hecnar and M'Closkey, 1997), capable of altering amphibian abundance and distribution via a number of mechanisms. Many fish species are capable of consuming amphibian eggs and larvae (Tyler *et al.*, 1998; Goodsell and Kats, 1999), directly influencing amphibian populations by decreasing reproductive success and subsequent juvenile recruitment. Furthermore, females of many amphibian species avoid breeding in bodies of water containing fish (Kats and Sih, 1992; Hopey and Petranka, 1994), indicating that the presence of fish may indirectly effect amphibian populations by limiting the number of potential breeding sites. Predatory fish also have adverse effects on amphibian larval behavior, growth, and survival (Petranka *et al.*, 1987; Kats *et al.*, 1988; Hoffman *et al.*, 2004), which may compromise the fitness of surviving amphibian larvae and future amphibian population viability (Semlitsch *et al.*, 1988; Berven, 1990; *but see* Boone, 2005).

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The smallmouth salamander (*Ambystoma texanum*) is distributed throughout the midwestern United States and exhibits geographic variation in its mode of reproduction (Petranka, 1998). In some populations in Kentucky, Indiana and Ohio, *A. texanum* may breed in streams (Petranka, 1983), whereas most *A. texanum* populations in Illinois breed in woodland ponds (Phillips *et al.*, 1999). Larval *A. texanum* are important in structuring amphibian communities by depredating zooplankton and larval anurans (Wilbur, 1997). Because *A. texanum* larvae are susceptible to predation by native fish species (Kats, 1988), their distribution is often limited to fishless aquatic habitats (Petranka, 1983; Phillips *et al.*, 1999). Although the larval distributions of most Ambystomatid salamander populations are influenced by predatory fish, previous studies have shown that a small proportion of salamander larvae are capable of surviving to metamorphosis in the presence of fish (Petranka, 1983; Figiel and Semlitsch, 1990; Tyler *et al.*, 1998; Hoffman *et al.*, 2004). Therefore, low rates of juvenile recruitment might allow *A. texanum* populations exhibit a minimum level of viability in habitats occupied by fish. At the landscape level, these populations might also be augmented from the colonization of individuals from nearby source populations (Semlitsch, 2002).

Despite the numerous reports describing the negative effects of introduced fish on amphibian populations, there is a growing body of evidence indicating that these impacts can be reversed (Knapp *et al.*, 2001; Hoffman *et al.*, 2004; Vredenburg, 2004). Following the removal of predatory fish, researchers have observed increased rates of colonization by pond-breeding amphibian species to restored wetlands, as well as shifts in larval behavior that benefit amphibian larval growth and survival (Knapp *et al.*, 2001; Hoffman *et al.*, 2004; Vredenburg, 2004). However, no study has examined amphibian community-level responses following the removal of predatory fish. In this study, we elucidate the community- and population-level responses of amphibians following the removal of predatory fish from two permanent ponds in east-central Illinois by quantifying amphibian community and population dynamics during periods before and after the experimental removal of fish. We then compare these observations to those recorded at two nearby fishless ponds. The objectives of this study were to: (1) determine the effects of introduced fish on amphibian species diversity, and (2) describe the responses of *Ambystoma texanum* to the presence and absence of fish.

METHODS

Study site.—We conducted our study at Warbler Woods Nature Preserve (WWNP; 39°26′N; 88°8′W), an 81.5 ha parcel of land in Coles County, Illinois managed by the Illinois Nature Preserves Commission. The site is dominated by a mixture of oak-hickory hardwood forests and old-field upland habitat (primarily goldenrod *Solidago* spp.). Four woodland ponds, ranging between 0.05 and 0.10 ha in size, were created in the early 1980's (K. Kruse, pers. comm.). We labeled these ponds east to west alphabetically: A, B, C, and D. Vegetation in and immediately peripheral to all four ponds included green algae, common duckweed (*Lemna minor*), Dudley's rush (*Juncus dudleyi*), stinging nettle (*Urtica dioica*), as well as a few other aquatic macrophytes. All ponds were of permanent hydroperiod except for Pond D, which filled in late winter and dried before 2 Aug. of each year of this study.

Centrarchids (*Lepomis macrochirus* and *L. cyanellus*) were introduced into Pond C and black bullhead catfish (*Ameiurus melas*) were introduced into Pond B between 1985 and 1986 (K. Kruse, pers. comm.). Centrarchids and black bullhead catfish are capable of depredating amphibian larvae (Kruse and Francis, 1977; Figiel and Semlitsch, 1990; Adams, 2000), and laboratory trials have revealed that the centrarchids and black bullhead catfish

captured from the ponds at WWNP depredate syntopic larval amphibians (S. Mullin, unpubl.). Therefore, we speculated that the introductions of these fish species into Ponds B and C at WWNP likely had adverse effects on amphibian community and population dynamics. Fish were observed in both ponds during intermittent field visits between the mid-1980's and late-1990's (K. Kruse, pers. comm.), and fish were still inhabiting the two ponds in the spring of 2000 when this study commenced.

Sampling.—Drift fence/pitfall trap arrays were constructed around each pond in May 2000 to census the amphibian community (Corn, 1994). The drift fence consisted of plastic-weave silt fence material, approximately 45 cm high with 10 cm buried beneath the soil surface. Pitfall traps (3-L plastic tubs, 20-cm deep) were placed on both sides of the fence at 7.5-m intervals. Due to inter-pond size variation, there were unequal numbers of pitfall traps among ponds. In total, there were 19, 23, 14 and 12 pairs of pitfall traps for Ponds A, B, C and D, respectively. Small (<2 mm diameter) holes were drilled in the bottom of the pitfalls to allow water to drain and prevent captured organisms from drowning. Pitfall traps were checked during the amphibian activity season (early Feb. through early Dec.) at least once every 48 h. We placed lids on the buckets during periods of inactivity to prevent mortality of non-target organisms such as small mammals. We were unable to obtain complete census data for all of 2000; therefore, only data collected from 2001 through 2004 were used in this study.

For all amphibians captured, we measured the snout-vent length (SVL; ±1 mm) and determined the sex of adult amphbibians captured during the breeding season by inspecting the swollen cloacae of male salamanders (*Ambystoma*) and the swollen nuptial pads on the fore-feet of male anurans. We identified juvenile amphibians as those that were captured the same year in which metamorphosis occurred. We marked all captured amphibians to a year-by-pond specific cohort using a pre-determined pattern of toe clipping (*from* Donnelly *et al.*, 1994). All recaptures were omitted from analyses.

In Dec. 2001, Rotenone, a plant-based isoflavonoid pesticide commonly used in fish management (McClay, 2000), was experimentally applied to Ponds B and C to eradicate all fish (*see* Mullin *et al.*, 2004). Although Rotenone can be toxic to non-target organisms including amphibians (Fontenot *et al.*, 1994), there is evidence that amphibians might be less sensitive to the pesticide than fish and are capable of recovering from exposure (Mullin *et al.*, 2004). Rotenone has a greater half-life in colder water (Gilderhus *et al.*, 1988) and is, therefore, most effective in lentic habitats when applied during the winter while most pond-breeding amphibians are dormant and utilizing the terrestrial habitats surrounding the ponds. We presumed that the poison was effective for less than 30 d (*from* Gilderhus *et al.*, 1988), becoming inert before amphibian activity resumed the following spring. Bullfrog (*Rana catesbeiana*) tadpoles were the only amphibian to overwinter in the WWNP ponds and were thus the only amphibian species exposed to Rotenone during application. However, *R. catesbeiana* were ubiquitous throughout WWNP and we assumed recolonization to the treated ponds was likely should the poison have adversely affected overwintering tadpoles. The application of Rotenone in December 2001 did not completely remove all black bull-head catfish from Pond B and a second dose was applied to only that pond in January 2003, approximately 40 d before amphibian breeding activity for the 2003 season commenced.

We grouped the four ponds into two categories: experimental ponds, ponds in which fish had been present and subsequently removed (Ponds B and C); and reference ponds, ponds in which fish had never been present (Ponds A and D). Temporal periods were determined with respect to Rotenone application (pre-application or post-application). The post-application period commenced after the 2001 season for Pond C and after the 2002 season

for Pond B because these were the first years in which fish were completely removed from the respective experimental pond. The period between the 2002 and 2003 field season was used to distinguish temporal periods in reference ponds, as this was the final period in which Rotenone was applied to any of the experimental ponds.

Statistical analyses.—We determined the annual relative abundance of all amphibian species captured at each WWNP pond. To characterize temporal changes in amphibian community composition between pond types, we used the Shannon-Weiner Diversity Index ($H' = \Sigma p_i \log_{10} p_i$) to calculate amphibian species diversity within each pond for every year. We tested for the effects of temporal period and pond type on amphibian species diversity by performing a nonparametric Friedman two-way analysis of variance by ranks test (PROC GLM; SAS Institute, 1989).

We assessed *Ambystoma texanum* population-level responses to the presence and absence of fish by examining the temporal changes in larval period (amount of time for an individual larva to reach metamorphosis), size at metamorphosis, and juvenile recruitment. To calculate larval period, we used the Julian date at which metamorphosed juvenile *A. texanum* were captured. Size at metamorphosis was quantified as the SVL (± 1 mm) of all juvenile *A. texanum* emigrating from each pond. Because *A. texanum* size and date at metamorphosis were not independent, we analyzed the effects of temporal period and pond type on *A. texanum* size and date at metamorphosis using multivariate analysis of variance (MANOVA; PROC GLM; SAS Institute, 1989) followed by univariate analyses of variance (ANOVA). We determined annual juvenile recruitment at each pond as the proportion of metamorphosing juveniles to the number of breeding female *A. texanum* that visited the pond during the breeding season and tested for the effects of fish on *A. texanum* juvenile recruitment by performing a nonparametric Friedman two-way analysis of variance by ranks test (PROC GLM; SAS Institute, 1989) between both pond types and temporal periods.

We followed all significant univariate interactions with a Tukey-Kramer Multiple Comparison Test. Due to unequal sample sizes among treatments, all analyses are reported using type III sums of squares. All analyses were performed using SAS 9.1 (SAS Institute, 1989).

<div align="center">RESULTS</div>

Fish have not been documented in either of the two experimental ponds since the final application of Rotenone to Pond B in Jan. of 2003. We observed a total of 10 amphibian species among the four WWNP ponds during our study (Table 1). There was no effect of pond type ($F_{1,15} = 0.03$; $p = 0.86$) or temporal period ($F_{1,15} = 1.19$; $p = 0.30$) on amphibian species diversity; however, there was a significant pond type-by-temporal period interaction ($F_{1,15} = 11.42$; $p = 0.005$). Prior to the removal of fish from the experimental ponds, amphibian species diversity was 3.5 times greater in the reference ponds than in the experimental ponds (Table 1). American toads (*Bufo americanus*) were the most abundant amphibian species during this temporal period, accounting for 90.5% and 66.8% of the captures at experimental and reference ponds, respectively. Amphibian community composition changed for both pond types following the removal of fish from the experimental ponds. *Ambystoma texanum* became the most abundant species, accounting for 40.6% and 54.0% of all amphibians in experimental ponds and reference ponds, respectively. Results of the Tukey-Kramer Multiple Comparisons Test revealed that only the species diversity of the experimental ponds changed between temporal periods ($p = 0.01$). Following the removal of fish, amphibian species diversity within experimental ponds increased by 341%, whereas amphibian species diversity increased by 9.6% within reference ponds (Table 1).

TABLE 1.—Mean relative abundance (percent) of amphibians captured in experimental (n = 2) and reference (n = 2) ponds at Warbler Woods Nature Preserve, Coles County, Illinois, during each temporal period (pre-application or post-application). Mean annual Shannon-Weiner Diversity Index values (H′; ±1 SE) are displayed for both pond types during each temporal period

Species	Pre-application		Post-application	
	Experimental ponds	Reference ponds	Experimental ponds	Reference ponds
Ambystoma texanum	2.55	16.82	40.60	53.96
Bufo americanus	90.50	66.78	12.03	2.32
Bufo fowleri	0.08	0.07	–	0.14
Acris crepitans	0.19	0.07	0.30	0.08
Hyla versicolor × *chrysoscelis*	–	0.34	8.81	1.11
Pseudacris crucifer	0.16	1.17	14.10	4.69
Pseudacris triseriata	–	–	0.24	0.05
Rana catesbeiana	4.84	4.14	6.81	7.43
Rana sylvatica	0.98	7.72	2.17	16.18
Rana utricularia	0.71	2.89	14.94	14.11
Mean H′ (±1 SE)	0.15 (0.03)	0.52 (0.08)	0.66 (0.04)	0.57 (0.04)

We captured 1302 emerging juvenile *Ambystoma texanum* from both pond types during the study period. Twelve juveniles were captured at the experimental ponds during the years when fish were present, whereas 861 juveniles were captured during the years following fish removal. Twenty-nine juveniles were captured at the reference ponds prior to the removal of fish from the experimental ponds, whereas 400 juveniles were captured after fish removal. There was an effect of pond type, temporal period, and their interaction on *A. texanum* larval period and size at metamorphosis (Wilks' $\lambda > 0.93$; $F_{2,1297} > 4.38$; $p < 0.01$). Throughout the study, juvenile *A. texanum* from the experimental ponds metamorphosed earlier than juveniles from the reference ponds ($F_{1,1298} = 23.47$; $p < 0.001$) and there was a significant pond type-by-temporal period interaction on *A. texanum* larval period ($F_{1,1298} = 5.96$; $p = 0.015$; Fig. 1). Tukey-Kramer Multiple Comparisons Tests revealed that *A. texanum* larval period changed only in the experimental ponds following fish removal ($p = 0.025$). Following the removal of fish, *A. texanum* larval period from experimental ponds increased by 12.0%, whereas larval period length from reference ponds decreased by 6.6% (Fig. 1).

Throughout the study period, juvenile *Ambystoma texanum* emerging from experimental ponds were larger than juveniles emerging from reference ponds ($F_{1,1298} = 48.15$; $p < 0.001$; Fig. 1). The average size of juvenile *A. texanum* at metamorphosis was 36.3 ± 0.3 mm and 30.5 ± 0.1 mm for experimental and reference ponds, respectively. Overall, *A. texanum* size at metamorphosis decreased in the years following fish removal ($F_{1,1298} = 133.95$; $p < 0.001$; Fig. 1), decreasing by 19.3% and 18.7% for experimental and reference ponds, respectively. There was no pond type-by-temporal period interaction on *A. texanum* size at metamorphosis ($F_{1,1298} = 2.41$; $p = 0.12$).

There was no effect of pond type on *Ambystoma texanum* juvenile recruitment ($F_{1,12} = 2.21$; $p = 0.163$). However, juvenile recruitment was affected by temporal period ($F_{1,12} = 13.52$; $p = 0.003$), and there was a significant pond type-by-temporal period interaction ($F_{1,12} = 16.35$; $p = 0.002$; Fig. 2). Results of the Tukey-Kramer Multiple Comparisons Tests showed that *A. texanum* juvenile recruitment increased only for the experimental ponds following the removal of fish ($p = 0.017$). After the removal of fish, *A.*
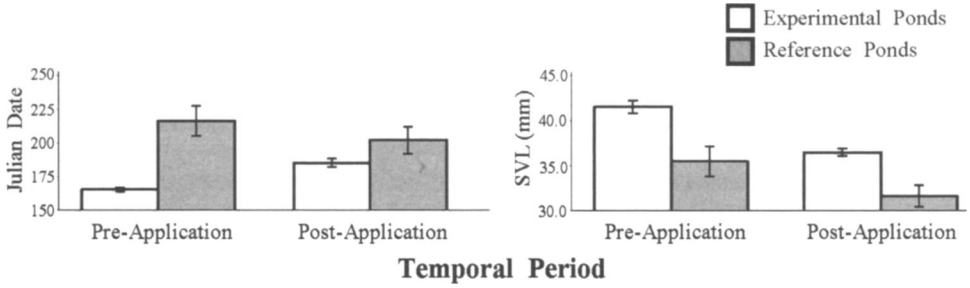
FIG. 1.—Changes in larval smallmouth salamander (*Ambystoma texanum*) larval period (date of metamorphosis) and size at metamorphosis between temporal periods and pond types at Warbler Woods Nature Preserve, Coles County, Illinois. All data are presented as means ± 1 SE

texanum juvenile recruitment increased 73-fold at the experimental ponds, whereas juvenile recruitment at the reference ponds increased 6-fold (Fig. 2). There was no temporal change in *A. texanum* juvenile recruitment at the reference ponds (p = 0.20)

DISCUSSION

This study demonstrates that the presence of introduced fish in the WWNP experimental ponds had adverse effects on native amphibians at the community and population levels. Differences in amphibian species diversity at WWNP were likely due to changes in species relative abundance rather than changes in species composition, as species richness within and between pond types did not vary considerably over the entire study period (Table 1). Our findings are consistent with previous studies describing the negative association between fish presence and amphibian community structure. Hecnar and M'Closkey (1997) discovered that amphibian species richness was lower in ponds containing predatory fish
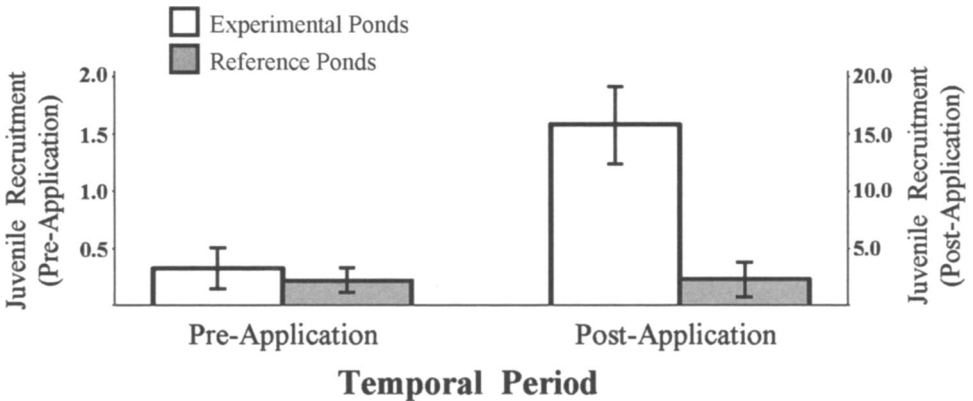

FIG. 2.—Changes in *Ambystoma texanum* juvenile recruitment (proportion of metamorphosing juveniles to number of breeding females) in experimental and reference ponds between temporal periods at WWNP. Note: the scale for post-application recruitment (right-axis) is ten times greater than the pre-application recruitment (left-axis). All data are presented as means ± 1 SE

than in ponds lacking predatory fish. Semlitsch (1988) also noted that the distributions of some *Ambystoma* communities are influenced by fish predation. During the years when fish were present at WWNP, the amphibian species diversity of reference ponds was (on average) 3.5 times greater than the diversity of experimental ponds. Following the removal of fish, amphibian species diversity improved only for experimental ponds, indicating that introduced fish were primarily responsible for the low amphibian species diversity at experimental ponds during the pre-application period. Thus, our before-and-after investigation provides causal evidence that introduced fish had negative effects on the amphibian community at the WWNP ponds, and that the removal of predatory fish improved amphibian species diversity.

The interaction between predation and interspecific competition is an important factor that regulates many amphibian communities (Wilbur, 1987) and is one plausible explanation for the temporal shifts in amphibian species diversity observed at the WWNP experimental ponds. During the years when fish were present, American toads (*Bufo americanus*) were the most abundant amphibian species at the experimental ponds, and metamorphosing juveniles accounted for 76.8% of all *B. americanus* captured during this study. Hence, the changes in *B. americanus* relative abundance likely occurred at the larval stage. Previous studies have demonstrated the relative unpalatability of *B. americanus* tadpoles compared to competing larval anurans (Kruse and Stone, 1984; Smith *et al.*, 1999). The presence of fish might have had positive indirect effects on *B. americanus* abundance by depredating and reducing the abundance of competing amphibians. However, *B. americanus* tadpoles are also inferior competitors (Wilbur, 1987). Therefore, the observed decline in *B. americanus* relative abundance after the removal of fish might be attributable to increased levels of interspecific competition following the release of predation pressure on other larval amphibians.

During the years when fish were present, juvenile *Ambystoma texanum* at the experimental ponds metamorphosed an average of 51 d earlier and were 17.5% larger than juveniles metamorphosing from fishless reference ponds. Following fish removal, juvenile *A. texanum* from the experimental ponds metamorphosed an average of 17 d earlier and were 15.5% larger than juveniles metamorphosing from reference ponds (Fig. 1). We found that the presence of fish in the experimental ponds reduced *A. texanum* larval period, as juvenile *A. texanum* at the experimental ponds metamorphosed earlier than juveniles from reference ponds during the years of fish presence. Others have discovered similar developmental responses of *Ambystoma* to predation risk. For example, larval Jefferson salamanders (*A. jeffersonianum*) increase development rate, metamorphosing earlier and at a larger body size when in the presence of aquatic predators (Cortwright, 1988; Wells and Harris, 2001). Reduced salamander larval period in the presence of predators may be due to decreased rates of intraspecific competition resulting from reduced larval density (Skelly, 1992; Wells and Harris, 2001). Increased amphibian larval densities often result in delayed metamorphosis (Scott, 1990), and may explain the prolonged larval period for *A. texanum* following the removal of fish from WWNP experimental ponds (Fig. 1). We captured considerably more juvenile *A. texanum* during the years following fish removal, and during this temporal period we captured over twice as many juvenile *A. texanum* at the experimental ponds (n = 861) than at reference ponds (n = 400). Although we were unable to directly quantify *A. texanum* larval densities in this study, we assumed that the increased number of juveniles captured following the removal of fish is attributable to increased larval densities.

Over the course of this study, juvenile *Ambystoma texanum* emerging from the experimental ponds were 15.7% larger than those emerging from the reference ponds. However,

the presence of fish had no apparent effect on *A. texanum* growth, as the size of juveniles emerging from both pond types decreased following the removal of fish (Fig. 1). The decrease in *A. texanum* size at metamorphosis for juveniles at both pond types might be due to increased *A. texanum* larval densities. Among other abiotic and biotic factors, amphibian larval growth is density-dependent (Wilbur, 1987; Werner, 1986) and increased amphibian larval densities often result in slower growth (Scott, 1990). Therefore, the temporal variability in *A. texanum* larval densities may also explain the between pond-type similarity in *Ambystoma texanum* size at metamorphosis.

Following the removal of fish, *Ambystoma texanum* juvenile recruitment increased only within experimental ponds (Fig. 2). Field and laboratory experiments have demonstrated the adverse effects of introduced fish on the reproductive success of other native amphibian species (Goodsell and Kats, 1999; Smith *et al.*, 1999). Although the fish species introduced into the WWNP experimental ponds are capable of consuming amphibian egg masses and larvae (Kruse and Francis, 1977; Figiel and Semlitsch, 1990; Adams, 2000), we did not directly observe predation of *A. texanum* larvae by the introduced fish during this study. However, the increase in juvenile recruitment at the experimental ponds coincided with fish removal, indicating that fish presence likely suppressed *A. texanum* juvenile recruitment. These observations support those of previous studies that have documented rapid (*i.e.*, <5 y) improvement in amphibian reproductive success following the removal of introduced fish, providing further evidence that some amphibian populations are capable of recovery following the removal of predatory fish (Knapp *et al.*, 2001; Hoffman *et al.*, 2004; Vredenburg, 2004).

We observed significant changes in the amphibian community at WWNP in less than 2 y after the removal of fish from the experimental ponds. These observations indicate that the application of Rotenone might be an effective management strategy for future amphibian conservation efforts (*see* Mullin *et al.*, 2004). The quick recovery of amphibians at the experimental ponds was likely due to colonization of amphibians from the nearby reference ponds, despite low levels of juvenile recruitment for most amphibian species at the experimental ponds during the years when fish were present. Although improvements in amphibian species diversity and *Ambystoma texanum* larval dynamics at WWNP coincided with, and are most likely attributable to, the presence and absence of fish, some of our results might be explained by abiotic processes such as variation in precipitation, temperature, or pond hydroperiod (Semlitsch, 1985; Phillips *et al.*, 2002). However, analyses of daily climatic data obtained from Coles County Regional Airport, approximately 12 km from WWNP, revealed no differences in mean daily precipitation or temperature patterns between temporal periods (MANCOVA; $F_{2,1450} = 0.600$; p = 0.549). As such, our 4-y study provides evidence that amphibian communities are capable of recovering from environmental perturbations over an ecologically relevant time scale. Because amphibian population sizes and reproductive output naturally fluctuate among years (Pechmann and Wilbur, 1994), long-term studies will be vital for accurately determining the effects of anthropogenic perturbations on amphibian communities.

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