Contributed Paper

Suitability of Golf Course Ponds for Amphibian Metamorphosis When Bullfrogs Are Removed

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Abstract: *Managing areas designed for human recreation so that they are compatible with natural amphibian populations can reduce the negative impacts of habitat destruction. We examined the potential for amphibians to complete larval development in golf course ponds in the presence or absence of overwintered bullfrog tadpoles (*Rana catesbeiana*), which are frequently found in permanent, human-made ponds. We reared larval American toads (*Bufo americanus*), southern leopard frogs (*R. sphenocephala*), and spotted salamanders (*Ambystoma maculatum*) with 0 or 5 overwintered bullfrog tadpoles in field enclosures located in ponds on golf courses or in experimental wetlands at a reference site. Survival to metamorphosis of American toads, southern leopard frogs, and spotted salamanders was greater in ponds on golf courses than at reference sites. We attributed this increased survival to low abundance of insect predators in golf course ponds. The presence of overwintered bullfrogs, however, reduced the survival of American toads, southern leopard frogs, and spotted salamanders reared in golf course ponds, indicating that the suitability of the aquatic habitats for these species partly depended on the biotic community present. Our results suggest that ponds in human recreational areas should be managed by maintaining intermediate hydroperiods, which will reduce the presence of bullfrog tadpoles and predators, such as fish, and which may allow native amphibian assemblages to flourish.*

Keywords: amphibian metamorphosis, competition, golf course ponds, predation, *Rana catesbeiana*

Beneficio de la Charcas en Campos de Golf para la Metamorfosis de Anfibios cuando son Removidas las Ranas

Resumen: *El manejo de áreas diseñadas para la recreación humana de manera que sean compatibles con las poblaciones naturales de anfibios puede reducir los impactos negativos de la destrucción del hábitat. Examinamos el potencial de anfibios para completar el desarrollo larvario en lagos en campos de golf en presencia o ausencia de renacuajos de* Rana catesbeiana*, que frecuentemente son encontrados en charcas artificiales permanentes. Criamos sapos (*Bufo americanus*), ranas (*R. sphenocephala*) y salamandras manchadas (*Ambystoma maculatum*) con cero o cinco renacuajos de* R. catesbeiana *en encierros localizados en charcas en campos de golf o en humedales experimentales en un sitio de referencia. La supervivencia hasta la metamorfosis de* B. americanus, R. sphenocephala *y* A. maculatum *fue mayor en los campos de golf que en los sitios de referencia. Atribuimos este incremento en la supervivencia a la baja abundancia de insectos depredadores en las charcas de los campos de golf. Sin embargo, la presencia de renacuajos de* R. catesbeiana *redujo la supervivencia de* B. americanus, R. sphenocephala *y* A. maculatum *en los campos de golf, indicando que el beneficio de los hábitats acuáticos para estas especies dependía parcialmente de la comunidad biótica presente. Nuestros resultados sugieren que las charcas en áreas recreativas deberían ser manejadas manteniendo hidroperíodos intermedios, que reducirían la presencia de renacuajos de* R. catesbeiana *y de depredadores, como peces, y que permitirían que florezcan ensambles de anfibios nativos.*

Palabras Clave: charcas en campos de golf, competencia, depredación, metamorfosis de anfibios, *Rana catesbeiana*

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Introduction

The impact of habitat destruction can be mitigated with outright habitat protection, but the increasing human population limits the feasibility of this solution. Sustainable remedies should focus on reducing impacts of habitat destruction and alteration so that humans and other organisms can coexist. Suitable habitat for wildlife and human use are not necessarily mutually exclusive, even in habitats that show high degrees of management and heavy use, if factors critical to wildlife are known and integrated into management plans (Semlitsch 2002; Hodgkison et al. 2007).

Golf courses are green spaces where the compatibility between human use and biodiversity can be tested. In the United States there are more than 17,000 golf courses covering some 610,000 ha (Kenna & Snow 2002), which encompass areas managed as fairways and tees, forests, grasslands, and wetlands. In addition, golf course organizations appear motivated to manage these areas in ways that reduce impacts on natural communities. For example, approximately 2300 golf courses in the United States and 24 other countries participate in Audubon International's Cooperative Sanctuary Program for Golf Courses, which helps golf courses manage their natural areas in ways that benefit wildlife.

Although managed green spaces are inadequate surrogates for protected land and ecosystems, areas such as golf courses can include suitable habitat for species native to the area. When natural areas on golf courses are maintained for suitable habitat, bird and butterfly populations use these areas for critical portions of their life cycles (e.g., Porter et al. 2004; Rodewald et al. 2004; Merola-Zwartjes & DeLong 2005). When management of green spaces considers use by both humans and wildlife, population extinctions in urban areas may be prevented or reduced. In contrast, when management of green spaces does not consider wildlife needs, these areas can hasten population extinctions or allow exotic or opportunistic species to spread to surrounding areas.

Management practices on golf courses can promote, rather than discourage, diverse native amphibian communities. One important consideration for any habitat designed to promote amphibian diversity is pond hydroperiod (i.e., the amount of time a pond holds water). Although amphibians breed in wetland habitats that range from ephemeral to permanent, maximum diversity is associated with intermediate hydroperiods (Heyer et al. 1975; Wellborn et al. 1996). Aquatic environments on golf courses are often permanent, which sets the stage for the biotic community that can exist there. Permanent ponds typically favor fish and anuran species such as green frogs (*Rana clamitans*) and bullfrogs (*R. catesbeiana*) that have larval periods that often exceed 1 year (Wellborn et al. 1996). Bullfrogs and green frog tadpoles are larger after overwintering than larvae of other anurans and can exert asymmetrical competitive effects (Werner 1994; Kupferberg 1997).

Bullfrogs, in particular, have been associated with amphibian population declines in areas where they are exotic (Hayes & Jennings 1986; Lawler et al. 1999) through their competitive and predatory effects (Blaustein & Kiesecker 2002) and potentially by carrying pathogens (Daszak et al. 2004). Bullfrog tadpoles reduce algal food resources (Kupferberg 1997; Boone et al. 2004*a*), and thus interfere with the feeding of other anurans when resources are clumped (Kiesecker et al. 2001); alter activity and feeding behaviors of other tadpoles (Kiesecker et al. 2001; Monello et al. 2006; Walston & Mullin 2007); and prey on recently hatched tadpoles of other species (Kiesecker & Blaustein 1997; Boone et al. 2004*a*). Adult bullfrogs also negatively affect amphibian populations because they eat tadpoles, metamorphs, and adults (Bury & Whelan 1984; Pearl et al. 2004; Wu et al. 2005), amplex with other species of anurans (Pearl et al. 2005), and their food resources overlap with those of other terrestrial amphibians (Bury & Whelan 1984; Wu et al. 2005).

Permanent ponds that support bullfrog populations can also support fish and predatory insect populations that reduce or eliminate many other amphibian species (Wilbur 1980; Wellborn et al. 1996; Porej & Hethrington 2005), and bullfrogs have greater survival in the presence of fish (Werner & McPeek 1994; Adams et al. 2003; Boone & Semlitsch 2003). A survey of golf course ponds in the southeastern United States showed that golf course ponds are areas where bullfrogs and green frogs are abundant (Paton & Egan 2002; Scott et al. 2002), likely because of a prevalence of permanent ponds.

A second consideration for amphibians is the presence of chemical contaminants that could affect amphibians and their food webs. Application of chemicals on golf courses is often heavy and may vary from spot application to regular, universal application of pesticides and fertilizers. Large amounts of contaminants, or frequent application, could alter aquatic and terrestrial food webs. Environmental concentrations of contaminants directly affect behavior (Bridges 1997), activity (Bridges 1999; Hatch & Blaustein 2000), metabolism (Rowe et al. 1998), and survival (Relyea & Mills 2001) in ways that could negatively affect population persistence. Contaminants may indirectly affect amphibians by altering algal and zooplankton food resources (Boone & James 2003) or predator communities (Boone & Semlitsch 2003; Relyea et al. 2005). Golf course operations can alter the algal communities present in stream systems (Winter et al. 2003) via nutrient enrichment and chemical contamination. Furthermore, combinations of contaminants even at sublethal levels could have more-severe effects than anticipated. Effects of chemical mixtures are poorly understood, but sublethal concentrations of contaminants that have no effects alone can have surprising effects in combination with other factors. For instance, Relyea and

Mills (2001) found that concentrations that have no effect alone become lethal in the presence of a predator. Hayes et al. (2006) found that frogs exposed to a chemical mixture became susceptible to a bacterial infection, whereas those exposed to one or 2 contaminants did not. Such responses suggest that places where chemical mixtures occur could severely compromise habitat integrity.

We examined effects on survival and growth of amphibians reared in the presence or absence of large overwintered bullfrog tadpoles in ponds on golf course and reference sites. Because of the potential negative effects of intense management on golf courses, presence of fish, and potential for contamination of ponds, we anticipated that amphibians reared in golf course ponds would suffer reduced survival, smaller mass at metamorphosis, and longer time to metamorphosis compared with references ponds. We anticipated that the presence of bullfrogs would also negatively affect amphibian metamorphosis.

Methods

Amphibians

We collected 20 egg masses of spotted salamanders (*Ambystoma maculatum*) on 5 April 2004 and 3–5 egg masses of southern leopard frogs (*R. sphenocephala*) and American toads (*Bufo americanus*) on 21 April from the University of Missouri's Baskett Wildlife Area near Ashland, Missouri (U.S.A.). We held spotted salamander eggs until use in outdoor cattle-tank ponds containing leaf litter, water, and abundant zooplankton populations from natural ponds. We kept southern leopard frog and American toad eggs in the laboratory until use in the study and fed them TetraMin fish flakes ad libitum. We collected overwintered bullfrog tadpoles from a pond at the U.S. Geological Service Columbia Environmental Research Center in Columbia, Missouri, on 12 May and held them overnight before use in the study.

We used 2 types of ponds in our study: 2 control references ponds and 2 ponds located on golf courses. Reference ponds (approximately 0.2 ha) were located at the Columbia Environmental Research Center experimental pond facility. Golf course ponds were located at the L. A. Nickell Golf Course (approximately 0.8 ha) managed by the City of Columbia Parks And Recreation Division and at the A. L. Gustin Golf Course (approximately 0.2 ha) managed by the University of Missouri-Columbia. Reference and golf course ponds were structurally similar in that they were all human-made, permanent ponds, and surrounded by mowed lawn. Nevertheless, the ponds at Nickell and Gustin golf courses were partially surrounded by deciduous forest and willows, respectively.

On 4 May we placed 10 field enclosures into each of the 4 ponds. Field enclosures were made of untreated lumber and were approximately 1.2 × 0.6 × 0.9 m and covered with fiberglass window screening (mesh size, 1 × 1.5 mm) secured with staples. Each enclosure had a removable fiberglass lid that was secured with a bungee cord. We anchored enclosures along the shore line of ponds with wooden stakes.

We randomly assigned each enclosure to a treatment containing either 0 or 5 overwintered bullfrog tadpoles (mean [±SE], Gosner [1960] developmental stage: 26.4 [±0.1]; mass: 3.320 g [±0.252]), which is within the range of natural bullfrog densities (0.72-10.6/1000 L; Cecil & Just 1979). Each treatment was replicated 5 times in each pond (i.e., 10 enclosures/pond and 40 enclosures total in all ponds).

On 13 May, we added 3 spotted salamander larvae, 15 southern leopard frog tadpoles, and 30 American toads to each enclosure after dip netting each enclosure to remove insect predators that may have entered the enclosure during conditioning. These amphibian larval densities are within the range found in nature (Morin 1983; Petranka 1989). In a strict sense we did not have a density control because enclosures with and without bullfrogs differed in total density by 5 individuals. Nevertheless, we believe any density control would be inadequate in this case. A "control" with an equal density of native amphibians relative to treatments with bullfrogs would increase density only slightly (i.e., increase density by 5 recently hatched larvae) and would not serve as a real control for overwintered bullfrog tadpoles. A control that included an equivalent mass of native amphibian larvae to bullfrog tadpole mass would have required the addition of a huge number of small native larvae. This manipulation would still not serve as an adequate bullfrog density control because the native larval mass, as well as survival, would be constantly changing over the course of the study. Our manipulation represented 2 distinct types of communities, those with and without bullfrogs, and a realistic way to examine how presence of overwintered bullfrogs affects a community of native amphibian larvae.

We checked ponds every other day for metamorphosed amphibians, defined as emergence of forelimbs for anurans (Gosner stage 42; Gosner 1960) and absorption of gills for salamanders (Donavan stage 56; Donavan 1980). We collected the metamorphs with a net and placed individuals from the same enclosure in a container with some water. Metamorphs were returned to the lab (thus, permanently removed from the enclosure) so that mass at metamorphosis and time to metamorphosis could be recorded.

Plankton and Invertebrates

On 19 May, 3 June, and 30 June we collected water samples from the ponds near enclosures from which 100 mL was filtered to measure phytoplankton abundance as an estimate of food abundance in ponds for anurans. Water was filtered onto glass filter paper and placed in buffered acetone solution, which was refrigerated for 24 hours before measuring by fluorometry. In addition, we filtered a 1-L water sample from each pond near enclosures to collect zooplankton as an estimate of food abundance for salamanders. We later analyzed the samples for the number of cladocerans, copepods, ostracods, and total zooplankton. On these sampling dates we also measured pond pH, temperature, and dissolved oxygen for each pond (mean [SE], Nickell: pH 7.2 [±0.1], 23.9 °C [±1.1], 4.1 mg/L oxygen [±1.5] ; Gustin: pH 7.8 [±0.2], 24.4 °C [±0.9], 8.8 mg/L oxygen [±0.3]; reference pond 1: pH 8.8 [±0.3], 25.8 °C [±2.0], 9.5 mg/L oxygen [±1.9]; reference pond 2: pH 8.8 [±0.6], 28.6 °C [±3.6], 9.6 mg/L oxygen [±0.2]).

On 9 July we sampled for invertebrates around and near the enclosures by taking 3, 2-m sweeps in each reference pond and 6 sweeps in each golf course pond because nothing was collected in the first 3 sweeps. We recorded the taxonomic groups we found. We terminated the study on 27 July, at which time we collected the remaining larvae to determine total survival.

On 1 August we took water samples at each site and measured for the following contaminants associated with golf courses: azoxystrobin, chlorothalonil, dithiopyr, diquat dibromide, trichlorfon, and mercury. We selected the contaminants based on common usage on golf courses (Mississippi State Chemical Laboratory, personal communication); nevertheless, because chemical analyses were too expensive, we sampled only once at the conclusion of the study, when normal chemical application was still ongoing at the golf course sites. None of these contaminants were detected in the water samples, which does not mean these or other contaminants were not present over the course of the study; it only means they were not detected at this single sampling time.

We collected amphibians at metamorphosis to determine length of the larval period (time at metamorphosis), mass at metamorphosis, percent survival to metamorphosis, and percent total survival (larval + metamorph survival) for each enclosure. Total survival was used as a covariate for time and mass at metamorphosis so that effects related to survival (and thus density) could be removed and treatment manipulations could be examined unconfounded. We analyzed the data with a nested analysis of variance (ANOVA) with golf course treatment nested within pond (i.e., pond[golf]). Because golf course treatments were replicated twice (4 ponds total), we used the mean square of pond[golf] as the denominator to calculate the F statistic for golf course treatment ($df_{numerator} = 1$, $df_{denominator} = 2$) and to avoid pseudoreplication. To examine the effects of bullfrog treatments and the interaction of bullfrogs and golf course treatments, we used the mean square error as the denominator to calculate the F statistics ($df_{numerator} = 1$, $df_{denominator} \leq 34$). The interaction of golf and bullfrog treatments could not be tested on time or mass to metamorphosis for any amphibians because of missing cells due to no survival in some treatment combinations. We analyzed phytoplankton and zooplankton data with a repeated measure ANOVA to test for differences between golf course treatments over time; ponds were the experimental unit.

Results

Amphibian Species

Survival to metamorphosis and total survival of toads, which were identical for this species, were significantly greater in golf course ponds than in reference ponds ($F_{1,2} = 43.14$, $p = 0.0224$), but survival in golf course ponds was reduced if overwintered bullfrog tadpoles

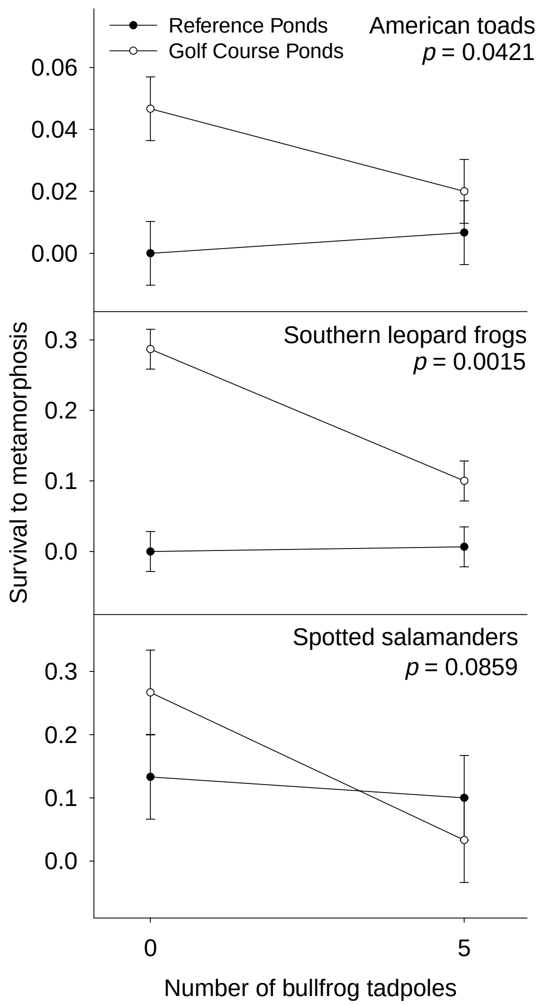

Figure 1. Survival of American toads, southern leopard frogs, and spotted salamanders reared in golf course and reference ponds with 0 or 5 overwintered bullfrog tadpoles. The p *values are for treatment interactions (error bars ± 1 SE).*

($F_{1,34} = 4.46$, $p = 0.0421$) were present (Fig. 1). Toads had shorter larval periods in golf course ponds relative to reference ponds ($F_{1,2} = 18.79$, $p = 0.0493$), but mass at metamorphosis was not significantly different between pond types ($F_{1,2} = 2.22$, $p = 0.2749$; Fig. 2). Neither time nor mass at metamorphosis were significantly affected by presence of overwintered bullfrogs.

Presence of bullfrog tadpoles significantly reduced survival of southern leopard frogs to metamorphosis ($F_{1,34} = 8.35$, $p = 0.0067$) and total survival ($F_{1,34} = 10.94$, $p = 0.0022$). In addition, survival of southern leopard frogs was greater in golf course ponds relative to reference ponds (survival to metamorphosis: $F_{1,2} = 239.56$, $p = 0.0041$; total survival: $F_{1,2} = 943.23$, $p = 0.0011$), but survival was reduced when bullfrogs were present in enclosures on golf course ponds (metamorphosis: $F_{1,34} = 11.99$, $p = 0.0015$; total: $F_{1,34} = 10.94$, $p = 0.0022$; Fig. 1). Presence of overwintered bullfrogs also resulted in a trend of southern leopard frogs metamorphosing at larger sizes ($F_{1,13} = 3.86$, $p = 0.0711$; mean [SE] zero bullfrogs: 1.388 g [±0.213], 5 bullfrogs: 1.847 g [±0.206]) and having slightly longer larval periods ($F_{1,13} = 2.38$, $p = 0.1470$; 0 bullfrogs: 61.5 days [±3.0], 5 bullfrogs: 66.2 days [±2.9]).

Spotted salamanders showed reduced survival to metamorphosis in the presence of bullfrogs ($F_{1,34} = 3.35$, $p = 0.0760$) and were moderately affected by an interaction of bullfrog presence and pond type ($F_{1,34} = 3.13$, $p = 0.0859$; Fig. 1). Although these effects were not significant, they showed the same pattern as American toads and southern leopard frogs. Total survival was also marginally affected by an interaction of bullfrog presence and pond type ($F_{1,34} = 4.05$, $p = 0.0521$), showing the same trend as survival to metamorphosis. Salamanders collected from golf course ponds showed a trend of reduced mass at metamorphosis ($F_{1,1} = 93.72$, $p = 0.0655$) and no difference in time to metamorphosis ($F_{1,2} = 3.13$, $p = 0.2189$; Fig. 2).

Larval development in a reference or golf course pond did not significantly affect survival to metamorphosis ($F_{1,2} = 1.09$, $p = 0.4062$), total survival ($F_{1,2} = 0.01$, $p = 0.9338$), mass at metamorphosis ($F_{1,2} = 0.11$, $p = 0.7670$), or time to metamorphosis ($F_{1,2} = 2.21$, $p = 0.2756$) for overwintered bullfrog tadpoles.

Plankton and Invertebrates

Phytoplankton abundance was not significantly different between pond types ($F_{1,2} = 0.82$, $p = 0.6163$), although on average reference ponds had lower phytoplankton abundances (mean μg/L ± SE; 19 May: reference ponds, 53.95 ± 30.37; golf course ponds, 83.25 ± 30.37; 3 June: reference ponds, 40.65 ± 13.28; golf course ponds, 105.20 ± 13.28; 30 June: reference ponds, 49.15 ± 6.93; golf course ponds, 55.20 ± 6.93). Total zooplankton did not differ between reference and golf course ponds ($F_{1,2} = 0.69$, $p = 0.6478$) or over time ($F_{1,2} = 3.04$, $p = 0.3759$). Nevertheless, cladoceran abundance did vary over time ($F_{1,2} = 472.04$, $p = 0.0325$) and with the interaction of time by pond type ($F_{1,2} = 360.99$, $p = 0.0372$; Fig. 3). At 2 sample times golf course ponds had greater abundance of cladocerans.

In general we found more invertebrate predators in reference ponds than in golf course ponds, despite twice the sampling effort in golf course ponds. In one reference pond we collected >43 dytiscid beetles, 4 crayfish, 4 aeshnid larvae, and 7 notonectids. In the other reference pond we found >31 dytiscid beetles, 2 crayfish, 5 aeshnid larvae, and 3 notonectids. In the Nickell golf course pond we found no arthropods, and in the Gustin golf course pond we collected one water glider.

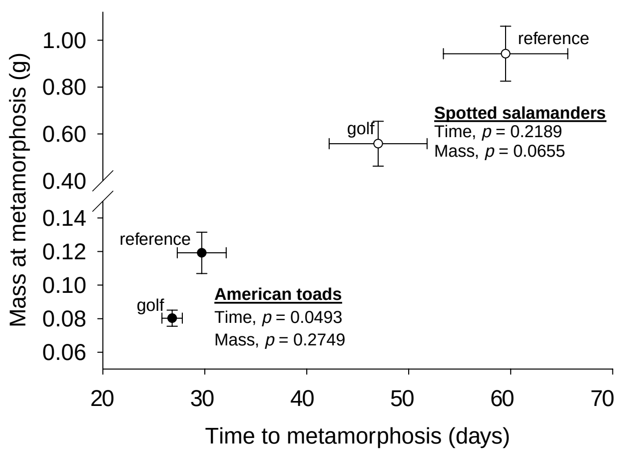

Figure 2. Time to metamorphosis and mass at metamorphosis of American toads and spotted salamanders reared in golf course and reference ponds (error bars ± 1 SE).

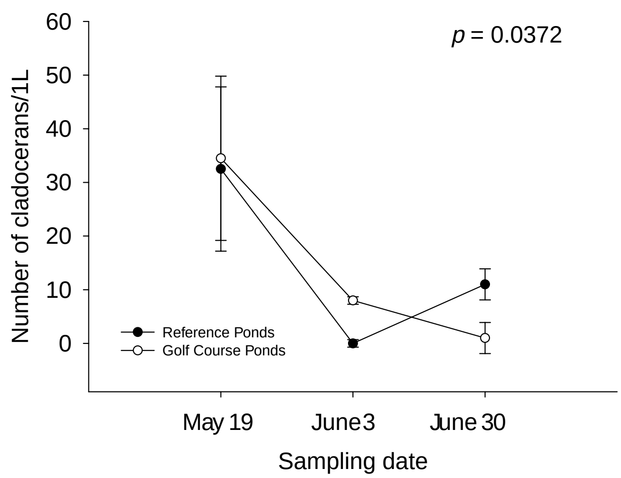

Figure 3. Abundance of cladocerans for golf course and reference ponds over sampling times (error bars ± 1 SE).

Discussion

On the basis of our results we concluded that aquatic environments on golf courses might be used by local native amphibian species if they are managed in a way that promotes diversity. Although we anticipated that amphibians would fare less well in golf course than in reference ponds because fertilizers and pesticides can readily move into aquatic environments on golf courses (Odanaka et al. 1994; Ryals et al. 1998; Ma et al. 1999), amphibians had greater survival in golf course ponds than reference ponds. This result could in part be attributed to a reduction in the number of insect predators in the golf course ponds. Midway through the study we noticed a large number of notonectids in enclosures in reference ponds, which must have entered cages as small larvae through the fiberglass screen. Predation in reference enclosures may have resulted in greater than normal mortality rates because of limited refugia (i.e., mud); nevertheless, survival in natural ponds to metamorphosis ranges between 2% and 5% (Semlitsch 1987; Berven 1990; Boone et al. 2004*b*), so survival in reference enclosures was near what one would expect to find in nature.

Nevertheless, the qualitative differences between golf course and reference ponds in the relative number of invertebrates highlights the fact that water quality, as it pertains to nutrient enrichment or chemical contaminants, potentially may release amphibians in golf course ponds from predation (as in Boone & Semlitsch 2003), although our limited chemical sampling did not reveal chemical contaminants. Because invertebrates are generally more sensitive to insecticides than vertebrates (Mayer & Ellersieck 1986), this class of amphibian predators may be reduced or eliminated in ponds exposed to intermittent levels of chemical contamination.

Although pesticide and fertilizers sometimes have negative effects on amphibians (e.g., Hatch & Blaustein 2000; Boone & James 2003; Boone et al. 2005; Hayes et al. 2006), there are a number of studies that show amphibians are not more sensitive than fish (Mayer & Ellersieck 1986; Bridges et al. 2002) and that expected environmental concentrations of contaminants can have apparent positive effects on anurans due to trophic cascades (e.g., Boone & Semlitsch 2001, 2002; Boone et al. 2004*b*). In addition, amphibian populations also appear to persist in agricultural areas, such as the Midwestern United States, despite heavy pesticide and fertilizer use. Best-management practices, such as vegetative buffers and careful timing of contaminants, could reduce impacts on the food web (Davis & Lydy 2002). Although the absence of some natural predators may indicate that aquatic food webs are not being fully maintained on either golf course used in our study, amphibians may still be able to complete larval development in these environments.

Nevertheless, amphibians did not do well under all conditions in golf course ponds. The presence of overwintered bullfrog tadpoles reduced survival of amphibians in golf course ponds to levels found in reference ponds, where predation rates were predicted to be greater. Overwintered bullfrog tadpoles could act as competitors, predators, or disease vectors. Overwintered bullfrog tadpoles have negative effects on other anurans inside (Boone et al. 2004*a*; Boone et al. 2007) and outside of their historic range (Kupferberg 1997; Adams 1999, 2000; Lawler et al. 1999) because of exploitative competition for algal resources (Kupferberg 1997; Pryor 2003) and in some cases because of interference competition (Kiesecker et al. 2001). Increased competition with larger bullfrogs could explain reduced survival; nevertheless, larval period or metamorph mass was generally not negatively affected.

There is some evidence that bullfrog tadpoles can prey on other amphibian larvae, whether through accidental or intentional predation while grazing algae (Kiesecker & Blaustein 1997). Therefore, the reduced survival we saw could also result from predation early in larval development. Predation by overwintered bullfrog tadpoles on other anurans has been low (6–29%, Kiesecker & Blaustein 1997; 4–6%, Boone et al. 2004*a*) in laboratory studies, which suggests that predation by bullfrog tadpoles is not the only or main effect. Metamorphosed bullfrogs may also have potentially fed on other amphibian larvae that had not transformed before being collected because bullfrog metamorphs are highly aquatic and will prey on metamorphs and tadpoles of other species (Bury & Whelan 1984; Pearl et al. 2004).

Furthermore, bullfrogs can carry pathogens and diseases (Bury & Whelan 1984; Daszak et al. 2004), which can reduce larval growth of some anurans (Parris & Cornelius 2004) and lead to reduced survival in juveniles (Berger et al. 1998). Nevertheless, this mechanism seems unlikely in our study given that the fiberglass mesh would have allowed for disease transfer among enclosures. The most likely explanation for the negative impact of overwintered bullfrogs on other amphibians in golf course ponds was competition for similar food resources (Altig et al. 2007) within the enclosure, although other mechanisms may have contributed to this effect.

Whatever the mechanism, absence of bullfrogs from enclosures allowed for the greatest larval survival and suggests that elimination of bullfrogs would be an important management strategy. Effects of bullfrogs can be reduced by creating aquatic habitat conditions that do not favor their presence, primarily by maintaining ponds with intermediate hydroperiods that dry in late summer or early fall. Changing hydroperiods from permanent to temporary hydroperiods eliminates bullfrog populations and thus is a useful management tool for controlling bullfrogs (Maret et al. 2006). Drying ponds in the late summer will permit other amphibians to metamorphose earlier in the summer but will eliminate bullfrog tadpoles and predatory fishes (Wellborn et al. 1996). If native species are present at locations that bullfrogs begin using for larval development, bullfrogs may be able to exclude other amphibians from the community.

Our results indicate the potential for ponds in golf courses to be managed in a way that supports native amphibian populations. By managing ponds to dry in late summer or early fall, predatory fishes that negatively affect amphibians (Vredenburg 2004) and large competitors, such as bullfrogs, can be eliminated, thereby increasing the probability for native amphibian populations to successfully complete the aquatic portion of their life cycle.

Amphibians require sufficient terrestrial habitat for feeding, overwintering, and connectivity among ponds to complete their life cycle (Semlitsch 2002; Semlitsch & Bodie 2003; Birchfield & Deters 2005). Although many golf courses have habitat patches that may serve this function (70% of the area is not played on), it is not currently known whether populations can be supported in both portions of their life cycle on golf courses. Nevertheless, because our results indicate that intensely managed habitats such as golf courses could be compatible with the conservation of native amphibians with appropriate management, studies in the terrestrial environment are needed to evaluate whether such recreational areas could support amphibian populations and help buffer local amphibians from extinction.

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