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Overwintered Bullfrog Tadpoles Negatively Affect Salamanders and Anurans in Native Amphibian Communities

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We examined the interactive effects of overwintered Bullfrog (*Rana catesbeiana*) tadpoles and pond hydroperiod on a community of larval amphibians in outdoor mesocosms including American Toads (*Bufo americanus*), Southern Leopard Frogs (*Rana sphenocephala*), and Spotted Salamanders (*Ambystoma maculatum*)—species within the native range of Bullfrogs. Spotted Salamanders and Southern Leopard Frogs were negatively influenced by the presence of overwintered Bullfrogs. Spotted Salamanders had shorter larval periods and slightly smaller masses at metamorphosis, and Southern Leopard Frogs had smaller masses at metamorphosis when reared with Bullfrogs than without. Presence of overwintered Bullfrogs, however, did not significantly affect American Toads. Longer pond hydroperiods resulted in greater survival, greater size at metamorphosis, longer larval periods, and later time until emergence of the first metamorphs for Southern Leopard Frog tadpoles and Spotted Salamander larvae. Our study demonstrated that overwintered Bullfrog tadpoles can respond to changing pond hydroperiods and can negatively impact metamorphosis of native amphibians.

INVASIVE species are those with the ability to infiltrate and increase in new habitats easily or during times of environmental change, and they can be either native or exotic (i.e., a nonnative). Female Bullfrogs (*Rana catesbeiana*) have large reproductive capabilities and can produce clutches with more than 20,000 eggs (Johnson, 2000). Bullfrogs are often found in newly created permanent wetlands, are an exotic species that has spread in the western United States and Europe (Stumpel, 1992), are implicated in amphibian declines in the western United States (Hayes and Jennings, 1986; Hecnar and M'Closkey, 1997), and are listed as one of the 100 worst invasive alien species by the International Union for Conservation of Nature (IUCN, 2003). For these reasons, the Bullfrog may be considered an invasive that could have serious effects on populations both within and outside of its range. Research with Bullfrogs, however, has focused on their effects outside their native range (i.e., as exotic invasive species), rather than within.

In the western United States where Bullfrogs are exotic, declines of ranid anurans have coincided with Bullfrog introduction and invasion (Bury and Luckenback, 1976). Bullfrogs may eliminate native amphibians directly through predation or interference competition, or indirectly through exploitative competition, behavior modification, habitat alteration, or introduction of disease or parasites. Experiments have demonstrated that overwintered Bullfrog tadpoles can affect development and survival of other anuran species via competition and predation (e.g., Kupferberg, 1997; Lawler et al., 1999; Kiesecker et al., 2001) and can be competitively superior to anurans with larval periods less than one year (Werner and Anholt, 1996). For instance, overwintered Bullfrog tadpoles decreased survival and delayed time to metamorphosis of Red-Legged Frogs (*Rana aurora*), presumably by reducing food resources (Lawler et al., 1999) and altered the composition and abundance of aquatic algal communities (Kupferberg, 1997). Although these effects were found where Bullfrogs are exotic, Bullfrogs could have similar effects in their natural range and could alter amphibian communities where environmental changes may promote the infiltration of Bullfrogs into habitats they were previously excluded from or in human-made ponds.

Pond hydroperiod is known to regulate some amphibian communities (e.g., Semlitsch et al., 1996) and may mediate the impact Bullfrogs have on amphibians. The pond hydroperiod gradient may be the main means of separating Bullfrogs from other amphibian species (Wellborn et al., 1996). Bullfrogs are typically found in permanent ponds, whereas most other amphibians inhabit temporary ponds. Generally, permanent ponds often accommodate fish populations, and fish will eliminate many larval amphibian species (but Bullfrogs often persist). Bullfrogs are often excluded from temporary ponds because they have larval periods exceeding one year, although they can reach metamorphosis in a single season (including Missouri, MDB, pers. obs.; South Carolina, Pechmann et al., 2001); additionally, Bullfrog tadpoles are sensitive to aquatic predators, which are more prevalent in temporary ponds in the absence of fish (Werner and Anholt, 1994). However, when Bullfrogs are present in the landscape, overwintered Bullfrog tadpoles may occur in temporary wetlands in years when ponds periodically fail to dry. Intentional release of bullfrog adults or tadpoles, as well as natural flooding events, may also introduce overwintered Bullfrog tadpoles in temporary ponds. For these reasons, the presence of bullfrogs in temporary or semipermanent wetlands represents a realistic scenario. Predatory and competitive relationships among Bullfrogs and other amphibian species may further explain their separation across a hydroperiod gradient and will have relevance to populations that may be invaded by Bullfrogs within or outside the Bullfrog's native range. To understand the interaction between the presence of Bullfrogs and pond hydroperiod, we examined the impact of overwintered Bullfrog tadpoles on an amphibian assemblage in communities with different pond hydroperiods.

Materials and Methods

We collected 15 egg masses of the Spotted Salamander (*Ambystoma maculatum*), five egg masses of the Southern Leopard Frog (*Rana sphenocephala*), and six egg strings of the American Toad (*Bufo americanus*) from the Baskett Wildlife Research Area near Ashland (Boone County), Missouri on 8, 23, and 24 April 2002, respectively. We maintained egg masses of Spotted Salamanders in a single cattle tank pond (containing well water, leaf litter, and plankton) until hatching at the University of Missouri-Columbia's Research Park in Boone County. We kept egg masses of all anurans in the laboratory at 23–25 C until hatching. We mixed multiple egg masses within each species before adding them to the ponds to homogenize genetic differences among families. We collected overwintered Bullfrog (*Rana catesbeiana*) tadpoles from the Baskett Wildlife Research Area on 30 April 2002. Bullfrogs had not yet bred in Missouri at the time we made our collections; therefore, Bullfrogs that we collected would have hatched presumably in the previous year. Bullfrog tadpoles weighed an average of 12.94 $\pm$ 0.39 g (mean $\pm$ 1 SE) and did not have prominent hind limbs (Gosner stage $\leq$ 35; Gosner, 1960).

Laboratory experiment.—We held 15 overwintered Bullfrog tadpoles in the laboratory for 48 h without food, each in separate plastic containers (5.1 liters total volume) with 3 liters of charcoal-filtered water. After 48 h on 2 May 2002 at 1400 CST, water was replaced and groups of 20 recently hatched tadpoles of Southern Leopard Frogs or American Toads, or three larvae of Spotted Salamanders were randomly added to containers to determine whether or not overwintered Bullfrog tadpoles would prey upon amphibian larvae used in our study. Six replicate containers (i.e., experimental units) were used for anurans and three replicate containers were used for salamanders. Six additional containers that had no overwintered Bullfrog tadpoles were set up with three containing 20 recently hatched tadpoles of Southern Leopard Frogs and three containing 20 recently hatched tadpoles of American Toads. All containers were held at 22–24 C in the laboratory under light conditions. After 24 h, each container was examined for dead or missing larvae, and survivors were counted.

Mesocosm experiment.—We established amphibian communities in 45 cattle tank mesocosms (1.85 m in diameter; 1480-liter volume) containing 1000 liters of well water, 1 kg of leaf litter, and plankton from natural ponds (500 mL of plankton suspension was added to each pond at four different times) in mid-March 2002. Screenmesh lids made of window screen covered each pond to exclude unwanted predators and anuran colonists. The ponds were located outdoors at the University of Missouri-Columbia Research Park (Columbia [Boone County], MO). We manipulated two factors in a fully crossed design with five replicates: relative length of the pond hydroperiod (fast-drying [43 days], slow-drying [64 days], or constant water level [89 days, the duration of the experiment]), and density of overwintered Bullfrogs (0, 2, or 6 Bullfrog tadpoles per pond). We selected hydroperiods encompassing the range of ephemeral to permanent ponds amphibians inhabit (Heyer et al., 1975; Wellborn et al., 1996). All species used in this study can be found in these wetland types. We randomly assigned anurans and salamanders to the ponds at realistic field densities (14–4238 per 1000 liters; e.g., Morin, 1983) when larvae were free-swimming. Bullfrog tadpoles were added to ponds on 30 April at realistic densities (0.72–10.6/1000 liters; calculated from Cecil and Just, 1979). To each pond, we added 45 American Toad tadpoles on 1 May, and 45 Southern Leopard Frog tadpoles and 10 Spotted Salamander larvae on 2 May (experimental day 0). In drying treatments, water level was lowered every third day for 36 days by following the drying regime of a natural pond (after Semlitsch, 1987) after an early or late initiation of drying for fast-drying and slow-drying ponds, respectively. The water level was reduced by bailing water with a bucket; ponds that were not being actively dried were also manipulated in a similar manner with water slowly added back into the pond. We made every effort to minimize the physical disturbance in the ponds while lowering water levels. We began reducing water levels in fast-drying treatments on 9 May (day 4) and slow-drying treatments on 30 May (day 25) until water levels reached 8 cm. Ponds were emptied three days after reaching 8 cm on 14 June (day 43) in fast-drying ponds and 5 July (day 64) in slow-drying ponds. Ponds with constant water levels were emptied on 6 August (day 89) after all amphibians had metamorphosed.

To determine whether treatments influenced plankton resources of amphibians, we measured periphyton and zooplankton levels in each pond three times; however, treatments had no statistical effect on zooplankton ($P > 0.15$) or periphyton ($P > 0.08$). We also measured the number of swimming and feeding amphibian larvae three times before they began metamorphosing; however, treatments had no statistical effect on the behavior of amphibians ($P > 0.19$).

Response variables and statistical analyses.—We searched ponds daily for metamorphs (defined by the emergence of at least one forelimb for anurans [Gosner stage 42] and by absorption of gills for salamanders [Donavan stage 56]). Average time to metamorphosis, mass at metamorphosis, and survival to metamorphosis were determined for each species in each pond. Because time to metamorphosis may be artificially truncated in drying treatments due to elimination of individuals with longer larval periods, the analysis could be biased; to account for this possibility, we also analyzed time to emergence of the first metamorphs (based on the average time the first three metamorphs of each species were collected in each pond), which should be unbiased. If results for time to metamorphosis and time to emergence of first metamorphs are in agreement, then significant differences in time to metamorphosis indicate that amphibians were developing at different rates, rather than this effect resulting from a statistical artifact.

Between 8 and 22 May, 12 ponds developed large amounts of filamentous algae. Presence of the filamentous algae corresponded with near total elimination of anurans in these ponds; however, survival of Spotted Salamanders appeared to be unaffected. Blue-green filamentous algae can be toxic (Bold and Wynn, 1985) and may be especially dangerous for small tadpoles that feed upon it; presence of blue-green algae may explain the mortality found in some of our ponds and why only anurans were affected. The 12 ponds with filamentous algae included all of the ponds with constant hydroperiods and no Bullfrogs, and one to two replicates from six other treatments. Presence of algae was low in all slow- and fast-drying ponds; however, in ponds with constant hydroperiods, bullfrogs reduced the occurrence of algae (proportion of ponds with constant hydroperiods with filamentous algae: 0 bullfrogs: 1.0 ± 0.2; 2 bullfrogs: 0.40 ± 0.18; and 6 bullfrogs: 0 ± 0.2). For this reason, the 12 ponds with filamentous algae were excluded from our analyses to assess the treatment level effects on American Toads and Southern Leopard Frogs. Because preliminary analyses with and without these ponds did not differ substantially for Spotted Salamanders, all ponds were used in analyses for salamanders.

We tested for the effects of hydroperiod, Bullfrog number, and their interaction on the mass and time to metamorphosis of Spotted Salamanders using multivariate analyses of covariance (MANCOVA), followed by univariate analyses of covariance (ANCOVA). Because American Toads and Southern Leopard Frogs did not survive in ponds with constant hydoperiods and no Bullfrogs, we could not test for the interaction of treatments for mass at and time to metamorphosis for these species. Therefore, analyses were limited to the main effects of hydroperiod and Bullfrog number for American Toads and Southern Leopard Frogs. Survival to metamorphosis of each species was used as a covariate in MANCOVAs and ANCOVAs, because this parameter explained significant proportions of the variation in analyses. We analyzed the effects of hydroperiod, Bullfrog number, and their interaction on survival to metamorphosis and time to emergence of first metamorphs of Spotted Salamanders with an ANOVA; we tested for effects of hydroperiod and Bullfrog number on survival to metamorphosis and time to emergence of first metamorphs of American Toads and Southern Leopard Frogs with an ANOVA. We also analyzed the effects of hydroperiod, Bullfrog number, and their interaction on survival to, mass at, and time to metamorphosis and time to emergence of first metamorphs of Bullfrogs themselves. In all analyses, proportion surviving was angularly transformed; mass and time to metamorphosis, and time to emergence of first metamorphs were log-transformed to normalize data.

Results

Laboratory experiment.—In the presence of an overwintered Bullfrog for 24 h, 6 ± 4% (mean ± 1 SE) of the Southern Leopard Frog tadpoles and 4 ± 2% (mean ± 1 SE) of American Toad tadpoles were missing and presumed eaten by Bullfrogs. This result indicated overwintered Bullfrog tadpoles could directly affect anurans in mesocosms through predation. Spotted Salamanders suffered no mortality in the presence of Bullfrogs. All Southern Leopard Frog or American Toad tadpoles reared in the absence of Bullfrog tadpoles survived the laboratory experiment.

Mesocosm experiment.—The multivariate response (i.e., mass and time to metamorphosis) of American Toads was not significantly affected by hydroperiod (Wilks' lambda = 0.8271, $F_{4,44}$ = 1.10, P = 0.3709) or Bullfrog number (Wilks' lambda = 0.7634, $F_{4,44}$ = 1.59, P = 0.1940); American Toad survival was used as a covariate and explained a significant proportion of the variation (Wilks' lambda = 0.6963, $F_{2,22}$ = 4.80, P = 0.0187). Time of emergence of first metamorphs was not significantly affected by hydroperiod ($F_{2,22}$ = 0.18, P = 0.8372). Survival to metamorphosis of American Toads was not significantly influenced by Bullfrog number ($F_{2,24}$ = 0.11, P = 0.8935) or hydroperiod treatment ($F_{2,24}$ = 0.32, P = 0.1581).

The multivariate response (i.e., mass and time to metamorphosis) of Southern Leopard Frogs was significantly influenced by pond hydroperiod (Wilks' lambda = 0.1648, $F_{4,46}$ = 6.83, $P < 0.0001$) and the covariate (survival to metamorphosis of Southern Leopard Frogs; Wilks' lambda = 0.6897, $F_{4,23}$ = 5.17, P = 0.0140) but not by Bullfrog number (Wilks' lambda = 0.7483, $F_{4,46}$ = 1.79, P = 0.1463). Increased hydroperiod length significantly increased mass at and time to metamorphosis of Southern Leopard Frogs (mass: $F_{2,24}$ = 11.54, P = 0.0003; time: $F_{2,25}$ = 14.28, $P < 0.0001$; Fig. 1A). Time of emergence of first metamorphs was significantly later with longer pond hydroperiods ($F_{2,23}$ = 11.63, P = 0.0003; fast-drying: 43.6 ± 1.0; slow-drying: 50.2 ± 0.8; constant: 50.4 ± 0.9 days). Increasing Bullfrog numbers moderately reduced mass at metamorphosis of Southern Leopard Frogs ($F_{2,25}$ = 3.27, P = .0556; mass [mean ± 1 SE] with 0 Bullfrogs: 1.878 ± 0.167; 2 Bullfrogs: 1.660 ± 0.133; 6 Bullfrogs: 1.232 ± 0.149). A fast-drying hydroperiod had a negative effect on survival to metamorphosis of Southern Leopard Frogs ($F_{2,25}$ = 13.60, P = 0.0001; Fig. 1B), but Bullfrog number did not ($F_{2,25}$ = 2.59, P = 0.0878).

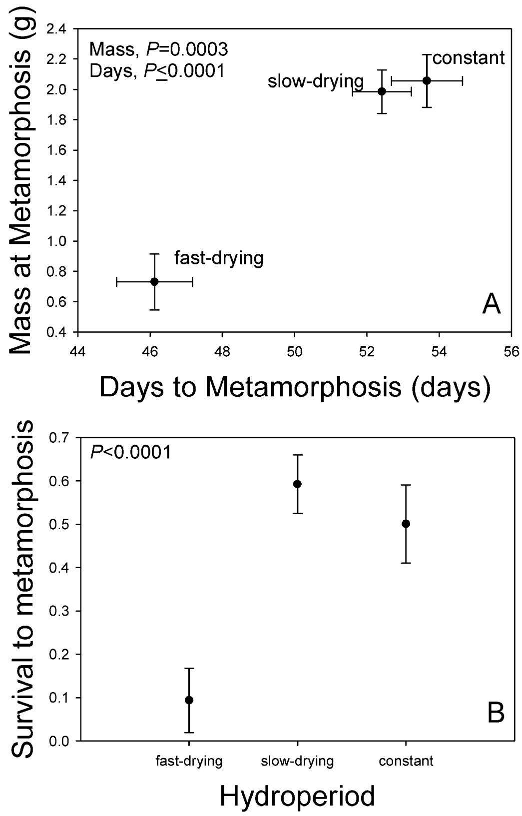

Fig. 1. The effect of pond hydroperiod on Southern Leopard Frog (A) mass at and time to metamorphosis, and (B) survival to metamorphosis. Error bars represent ± 1 SE.

The multivariate response (i.e., mass at and time to metamorphosis) of Spotted Salamanders was significantly affected by hydroperiod (Wilks' lambda = 0.1380, $F_{4,64}$ = 27.08, $P <$ 0.0001) and the covariate (survival of Spotted Salamanders to metamorphosis; Wilks' lambda = 0.6011, $F_{2,32}$ = 10.62, P = 0.0003); Bullfrog number (Wilks' lambda = 0.7630, $F_{4,66}$ = 2.32, P = 0.0666) moderately affected the multivariate responses, while the interaction of Bullfrog number and hydroperiod did not (Wilks' lambda = 0.8772, $F_{8,64}$ = 0.54, P = 0.8209). Lengthening pond hydroperiod resulted in significantly longer larval periods and larger size at metamorphosis for Spotted Salamanders (mass: $F_{2,33}$ = 12.50, $P < 0.0001$; time: $F_{2,33}$ = 100.32, $P <$ 0.0001; Fig. 2A). Time of emergence of first metamorphs was also later in ponds with longer hydroperiods ($F_{2,33}$ = 46.33, $P < 0.0001$; fast-drying: 38.0 ± 0.9; slow-drying: 45.9 ± 0.9; constant: 49.4 ± 0.9 days). Spotted Salamanders

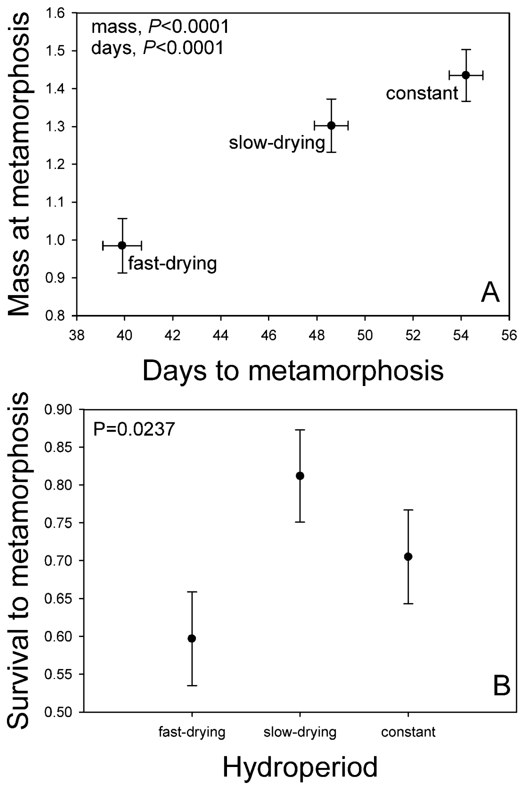

Fig. 2. The effect of pond hydroperiod on Spotted Salamander (A) mass at and time to metamorphosis, and (B) survival to metamorphosis. Error bars represent ± 1 SE.

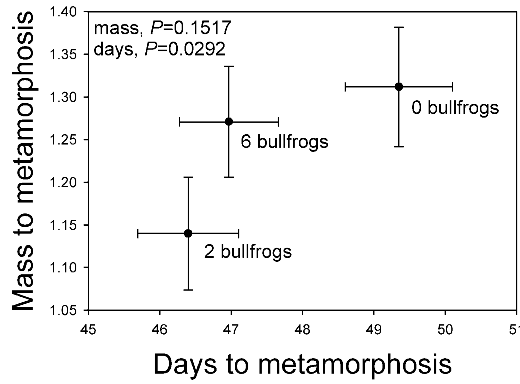

Fig. 3. The effect of Bullfrog number on Spotted Salamander mass at and time to metamorphosis. Error bars represent ± 1 SE.

reared in ponds without Bullfrogs had longer larval periods and had a slightly greater mass at metamorphosis than those reared with Bullfrogs (mass: $F_{2,33}$ = 2.00, P = 0.1517; time: $F_{2,33}$ = 3.94, P = 0.0292; Fig. 3). Lengthening pond hydroperiod significantly increased survival to metamorphosis ($F_{2,34}$ = 4.19, P = 0.0237; Fig. 2B), but survival was not affected by Bullfrog number ($F_{2,34}$ = 0.04, P = 0.9574) or the interaction ($F_{4,34}$ = 2.13, P = 0.0986).

We also analyzed the effects of hydroperiod, Bullfrog number, and their interaction on Bullfrogs. Length of the hydroperiod (Wilks' lambda = 0.1651, $F_{4,46}$ = 16.80, $P < 0.0001$) and Bullfrog number (Wilks' lambda = 0.5397, $F_{2,23}$ = 9.81, P = 0.0008) significantly affected the multivariate response (i.e., mass and time to metamorphosis) of overwintered Bullfrog tadpoles, although the interaction of hydroperiod and Bullfrog number did not (Wilks' lambda = 0.8684, $F_{4,46}$ = 0.84, P = 0.5066). The hydroperiod effect on Bullfrogs was mainly attributable to its effects on time to metamorphosis (mass: $F_{2,24}$ = 0.05, P = 0.9478; time: $F_{2,24}$ = 60.29, P = 0.0001) with lengthening hydroperiods resulting in longer time to metamorphosis (fast-drying hydroperiod: 42.5 ± 1.0 days; slow-drying hydroperiod: 50.6 ± 0.9 days; constant water level: 58.4 ± 0.9). Time of emergence of first metamorphs was significantly later in ponds with longer hydroperiods ($F_{2,18}$ = 20.74, $P <$ 0.0001; fast-drying: 42.4 ± 1.2; slow-drying: 47.2 ± 1.2; constant: 52.9 ± 1.2 days). Size at metamorphosis of Bullfrogs declined and time to metamorphosis increased as Bullfrog number increased (mass: $F_{1,24}$ = 6.34, P = 0.0189; time: $F_{1,24}$ = 12.89, P = 0.0015; Fig. 4A). Bullfrog survival to metamorphosis was significantly affected by hydroperiod ($F_{2,24}$ = 19.30, $P < 0.0001$), Bullfrog number ($F_{1,24}$ = 25.12, $P < 0.0001$), and their interaction ($F_{1,24}$ = 7.91, P = 0.0023). Shortening the pond hydroperiod and increasing the Bullfrog number resulted in reduced survival of Bullfrog tadpoles. Bullfrogs in ponds with a high density of Bullfrogs were less likely to survive to metamorphosis as the pond hydroperiod shortened than were Bullfrogs in ponds containing a low density of Bullfrogs (Fig. 4B).

Discussion

A fundamental goal in ecology is to understand how community assemblages are maintained and how they change with the invasion of new species (Elton, 1958). In our study, overwintered Bullfrog tadpoles were added to aquatic amphibian communities and, regardless of hydroperiod treatment, they had negative effects on responses correlated with amphibian fitness. The presence of overwintered Bullfrog tadpoles reduced the mass at metamorphosis of Southern Leopard Frog and shortened the larval period and reduced mass at metamorphosis

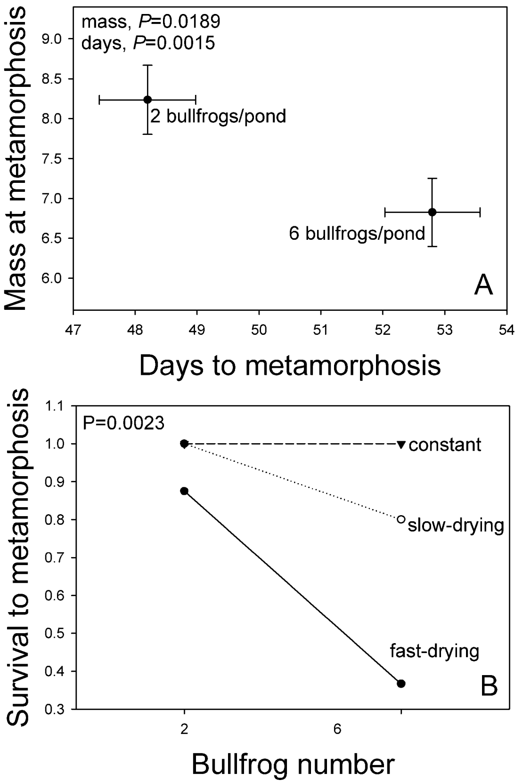

Fig. 4. (A) The effect of Bullfrog number on overwintered Bullfrog tadpoles mass at and time to metamorphosis. Error bars represent ± 1 SE. (B) The interaction of Bullfrog number and pond hydroperiod on overwintered Bullfrogs survival to metamorphosis.

for Spotted Salamanders; American Toad tadpoles, however, were not significantly affected by the presence of Bullfrogs. We expected that the presence of Bullfrogs would also reduce algal resources (food resources of anurans) and, potentially, zooplankton (food resources for salamanders) through accidental ingestion. However, we did not detect any differences among Bullfrog treatments in periphyton levels or zooplankton abundance. Effects such as reduced mass for Southern Leopard Frogs, suggest that food resources may have been affected, however. Studies by Kupferberg (1997), Lawler et al. (1999), and Adams (2000) in the western United States all found anurans and algal resources were negatively affected by overwintered Bullfrog tadpoles; although these studies had a greater relative density of overwintered Bullfrogs than our study, our outcomes were similar.

Pond hydroperiod is an important regulator of amphibian community dynamics (Werner and McPeek, 1994; Semlitsch et al., 1996; Skelly, 1996) and has been found to influence the effect of overwintered Bullfrogs on amphibian species in the western United States (Adams, 2000). Our study reiterates the importance of pond hydroperiod, with survival of Southern Leopard Frogs and Spotted Salamanders being significantly influenced by it. Southern Leopard Frogs and Spotted Salamanders had their greatest survival in slow-drying ponds, which allowed ample time to reach metamorphosis. Southern Leopard Frogs and Spotted Salamanders in ponds with longer pond hydroperiods stayed in the aquatic environment longer and were able to reach larger mass at metamorphosis than those in fast-drying environments. We could not test for an interaction between bullfrog number and pond hydroperiod for anurans (because of missing cells), but the effect of bullfrogs did not change with hydroperiod treatments for Spotted Salamanders.

The addition of a species in a community may alter the dynamics of a system, or the effects may be minimal. For amphibian species that have evolved with Bullfrogs, the presence of Bullfrogs may be less serious than for species that have not. All of the effects of overwintered bullfrog tadpoles in our study, however, were neutral or negative, affecting time to and/or mass at metamorphosis. Studies with bullfrogs outside of their range have shown similar results on metamorphosis and additionally found that bullfrog tadpoles have negative effects on survival. Kiesecker and Blaustein (1997) found tadpoles of Red-Legged Frogs (*Rana aurora*) syntopic with Bullfrogs increased their survival by altering their behavior in the presence of Bullfrogs. Populations of Red-Legged Frogs allopatric (i.e., evolutionarily naïve) to Bullfrogs, however, suffered increased mortality because tadpoles did not alter their behavior in the presence of Bullfrogs. Past or intermittent exposure to Bullfrogs in their evolutionary history may have permitted amphibians within the Bullfrog's range to develop innate or learned strategies to tolerate and coexist more successfully with Bullfrogs than those outside their range. Additionally, the presence of fish (via introduction) may further facilitate invasion of Bullfrogs (Adams et al., 2003; Boone and Semlitsch, 2003) and decrease the persistence of amphibian populations in a pond community, thereby affecting community dynamics of amphibians (Werner et al., 1995).

Bullfrogs have proven themselves invasive by spreading in the western United States and in Europe. Anthropogenic changes (e.g., creating wetlands with longer hydroperiods [e.g., farm ponds, sediment basins, golf course ponds], chemical contamination, and fish introduction) may facilitate the movement of invasive species like Bullfrogs by increasing the amount of suitable habitat and speed their distribution throughout the landscape. Increasing suitable bullfrog habitat by adding permanent ponds to a landscape could augment the number of Bullfrog populations and their abundance, thereby boosting the potential for Bullfrogs to inhabit and breed in ponds from which they were previously excluded. Our study is unique in its examination of the effects of an invasive species within its native range. We demonstrated Bullfrogs at naturally low densities can have negative effects on Southern Leopard Frogs' mass at metamorphosis and Spotted Salamanders' mass at and time to metamorphosis. Additionally, overwintered Bullfrog tadpoles could respond to changing pond hydroperiod and stimulate metamorphosis, suggesting they have environmental flexibility to take advantage of new or suboptimal environments on the landscape.

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