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Effects of an Invasive Plant, Chinese Tallow (*Triadica sebifera*), on Development and Survival of Anuran Larvae

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ABSTRACT.—Amphibians are considered one of the most threatened vertebrate groups. Although numerous studies have addressed the many causes of amphibian population decline, little is known about effects of invasive plants. Chinese tallow (*Triadica sebifera*) is an exotic deciduous tree that has invaded the southeastern United States. Amphibian larvae in environments invaded by *T. sebifera* may be impacted negatively as autumn leaf litter decomposes in natal areas. We compared effects of leaf litter decomposition from *T. sebifera* and two native tree species on survival and development of four species of anuran larvae from eastern Texas. Larvae from *Pseudacris fouquettei*, *Lithobates (Rana) sphenoccephalus*, *Hyla versicolor*, and *Incilius (Bufo) nebulifer* were introduced into mesocosms containing leaf litter from one of the three tree species. *Pseudacris fouquettei* and *L. sphenoccephalus*, species that breed earlier in the year, had lower survival within the *T. sebifera* pools. *Pseudacris fouquettei* were smaller in *T. sebifera* mesocosms compared with native tree mesocosms, whereas *L. sphenoccephalus* were larger in *T. sebifera* mesocosms. *Hyla versicolor* showed significant developmental and morphological differences in *T. sebifera* mesocosms; however, survival was not significantly different among treatments. Leaf litter treatment did not affect survival or development in *I. nebulifer*. Our results suggest that breeding season may determine how each species survives and develops in an environment with *T. sebifera* leaf litter. *Triadica sebifera* leaf litter breaks down faster than native species; therefore, negative effects may be short lived but pose a greater threat to species that breed soon after leaf fall.

Amphibians are considered, perhaps, the most threatened of all vertebrate groups, with recent estimates that 43% of all amphibian species are experiencing population declines (Semlitsch, 2003; Stuart et al., 2004; Cushman, 2005; Mendelson et al., 2006). These declines do not seem to result from a single variable common to all species. Rather, threats include pollution, habitat loss and fragmentation, climate change, and disease (Blaustein et al., 1994; Berger et al., 1998; Alford and Richards, 1999; Andersen et al., 2004; Relyea, 2005; Becker et al., 2007). Amphibians seem especially susceptible because of their habitat requirements for both aquatic and terrestrial environments. Aquatic threats might be particularly dangerous because they could presumably affect adults, eggs, and larvae. For example, detrimental effects on larvae by a widely used herbicide, atrazine, have been documented previously (e.g., Hayes et al., 2002, 2003), although effects on larvae survival are equivocal (Diana et al., 2000; Allran and Karasov, 2001; Storrs and Kiesecker, 2004; LaFiandra et al., 2008).

Amphibian declines also can be attributed to invasive species (Kiesecker, 2003; Maerz et al., 2009). Negative effects of invasive animals, especially anurans and fishes, on amphibian communities are well documented (Moyle, 1973; Lawler et al., 1999; Adams, 2000; Knapp and Matthews, 2000; Hamer et al., 2002; Doubledee et al., 2003). Impacts of invasive plant species on vertebrate populations are not as well known (Soulé and Orians, 2001), but they are beginning to receive more attention. Detrimental effects from exotic plant invasions have been demonstrated for a variety of vertebrates (Schmidt and Whelan, 1999; Borgmann and Rodewald, 2004), and some evidence indicates they impact amphibian species. Garlic mustard (*Alliaria petiolata*) invasion is associated with declines in terrestrial woodland salamanders and Japanese knotweed (*Fallopia japonica*) reduces adult amphibian foraging success (Maerz et al., 2005a,b, 2009). Purple loosestrife (*Lythrum*

salicaria) affects survival and development in larvae of American Toads (*Anaxyrus americanus*, Frost et al., 2006); tadpoles exposed to the exotic species developed slower and had lower survival than those exposed to native plants (Brown et al., 2006). These detrimental effects may result from direct toxicity from high tannin concentrations produced by the exotic species and from indirect impacts on the aquatic ecosystems (Brown et al., 2006).

The invasive exotic tree Chinese tallow (*Triadica sebifera*) is a member of the family Euphorbiaceae native to southeastern Asia (Webster, 1994; Bruce et al., 1997). *Triadica sebifera* was introduced to the United States in the 1700s as an ornamental, and it could be found from the Texas Gulf Coast to the Atlantic coast of North Carolina by the 1800s, often as monocultures (Brown, 1956; Radford et al., 1964). *Triadica sebifera* is a deciduous species with extremely rapid growth; trees can reach 2.8 m just 2 yr after germination (Scheld and Cowles, 1981).

Triadica sebifera's range expansion potential is limited by cold weather and the availability of water (Jones and Sharitz, 1990; Barrilleaux and Grace, 2000). In Texas, the tree has become prolific in bottomlands and coastal areas (Correll and Johnston, 1970), and it overlaps with habitat of more than 20 species of amphibians (Conant and Collins, 1998; Dixon, 2000); yet, impacts of this tree on anuran species found within its range are virtually unknown. Because *T. sebifera* thrives in wet habitats, it is often found at sites where anurans deposit eggs and larvae develop. At these sites, *T. sebifera* may affect anuran populations through considerable amount of leaf litter added to the water. Decomposition of *T. sebifera* leaf litter could impact anuran larvae development or survival by changing water chemistry, such as pH and oxygen levels, or by adding novel tannins to the water (Schmitz et al., 1997; Maerz et al., 2005b; Brown et al., 2006). If leaf litter from *T. sebifera* has detrimental effects on larvae, potential impact on anuran populations could be considerable, given the rapid spread of this invasive plant.

Objectives of this study were to determine whether (1) *T. sebifera* leaf litter affects anuran development compared with two native tree species, (2) *T. sebifera* leaf litter reduces survival in anuran larvae compared with the leaf litter from two native

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tree species, and (3) survival differs among species in different treatments.

MATERIALS AND METHODS

Study Species.—Four anuran species (Cajun Chorus Frog, *Pseudacris fouquettei*; Gray Treefrog, *Hyla versicolor*; Southern Leopard Frog, *Lithobates sphenoccephalus*; and Gulf Coast Toad, *Incilius nebulifer*) were selected for the study to represent a broad ecological and taxonomic range, including two hylids, one ranid, and one bufonid. Two species, in this study, are considered winter breeders in eastern Texas. The Cajun Chorus Frog is a small species (2–3 cm) commonly found in moist woodlands, grassy swales, and river bottoms. They breed from January to March and deposit 100–1,500 eggs per female in several small clusters attached to substrate or along the bottom of ephemeral pools (Correll and Johnston, 1970; Conant and Collins, 1998; Saenz, 2004). Southern Leopard Frogs average 8 cm and are common in most shallow freshwater habitats. They breed year-round in Texas (Saenz et al., 2006), with peaks in fall and late winter to early spring, producing 3,000–5,000 eggs per female in a single large clutch (Smith, 1961; Correll and Johnston, 1970; Conant and Collins, 1998).

The other two study species are spring–summer breeders. Gray Treefrogs average 3–5 cm in length and deposit 600–4,200 eggs per female in several clusters, either attached to vegetation or often in floating masses from March to July (Saenz et al., 2006). They inhabit wooded areas near both temporary and permanent waters, spending most of their times in the trees and only coming to the water to breed (Ritke et al., 1990). The Gulf Coast Toad (Frost et al., 2009) averages 5–10 cm and breeds in diverse habitats that can include heavily disturbed areas from March to September (Conant and Collins, 1998; Saenz et al., 2006). Females deposit an average of 4,100 eggs in long strings often coiled around vegetation (Limbaugh and Volpe, 1957; Conant and Collins, 1998).

These four ecologically and phylogenetically diverse species (four genera and three families) overlap the range of *T. sebifera*, red maple (*Acer rubrum*), and swamp chestnut oak (*Quercus michauxii*) and are potentially affected by detritus from these trees (Correll and Johnston, 1970; Conant and Collins, 1998). *Acer rubrum* is a common bottomland hardwood species within the range of both *T. sebifera* and the amphibians being tested. *Acer rubrum* has a more rapid decomposition rate than other native species, but it is not as fast as *T. sebifera* (Leonard, 2008). Similar effects on tadpoles in both *T. sebifera* and *A. rubrum* may suggest a function of rapid leaf decay. *Quercus michauxii*, another common bottomland hardwood species within the range of the anurans tested in this study, has an extremely slow decomposition rate that may affect water chemistry differently than that of a species that decomposes rapidly.

Mesocosm Design.—Freshly fallen leaves from *T. sebifera*, *A. rubrum*, and *Q. michauxii* were collected before they had a chance to begin decomposition, or for *T. sebifera*, by cutting down the trees and stripping loosely attached leaves from branches. Leaves were collected from trees on the campus of Stephen F. Austin State University and in the Stephen F. Austin Experimental Forest (SFAEF), part of the Angelina National Forest, in Nacogdoches County, Texas. All leaf collection took place during the first 3 weeks of November 2007. All leaves collected were then air-dried. An oven was not used for drying to simulate natural conditions of leaf fall without compromising the experimental design.

Ninety mesocosms were created by adding 150 g of dry leaf litter to 30 100-liter plastic wading pools for each of the three tree species. On 13 December 2007, each pool was filled with 80 liters of well water from the SFAEF to produce approximately 1.875 g of leaf litter per liter of water. Holes were drilled in the pools just above the water line to prevent tadpoles from possibly spilling over the tops during heavy rainfall. To simulate natural ponds, primary producers and other microscopic organisms were collected with a 150- μ m mesh plankton net from nearby natural ponds within the SFAEF and divided evenly between all mesocosms 24 h after water was added. Mesocosms were allowed to overwinter in the field before the first tadpoles were introduced. Introducing leaf litter well in advance of the tadpoles mimicked the process of fall deciduous leaf shed and rainfall, followed by primary production. The first frog species was introduced 51 days after the pools were filled. Pools were covered with mesh shade cloth to prevent colonization from invertebrate predators or unintended breeding amphibians. All pools received the same light cycle, temperature, and rainfall.

Anuran Collection and Introduction.—Breeding pairs of *P. fouquettei*, *H. versicolor*, and *I. nebulifer* were captured in amplexus and returned to the laboratory in buckets containing water from their breeding sights, where they were allowed to deposit their eggs in the laboratory before being released. Early developmental *L. sphenoccephalus* egg clutches were collected from breeding sites the day after breeding behavior was observed. Fifteen clutches from 15 different breeding pairs were collected for each species. Tadpoles were allowed to develop in plastic tubs inside the laboratory for 3 days after hatching until the entire yolk had been absorbed to ensure larvae were healthy before introduction into mesocosms. Three groups of 50 tadpoles, one group for each of the three leaf treatments, were separated from each clutch and introduced to randomly assigned mesocosms. Introduction dates for each species depended on breeding times (Table 1). Each mesocosm contained 0.625 tadpoles/L water to minimize impacts from higher tadpole densities (Girish and Saidapur, 2003). Only a single species was in each mesocosm at a time, and leaf litter was not changed during the duration of the study.

Sampling.—Based on the earliest possible time to metamorphosis, according to the literature, three sampling periods were determined for each species (Table 1). Accordingly, each mesocosm was sampled by removing five individuals at a point early in development (t1), at an intermediate point (t2), and then at the end of development (t3; Table 1). All collected tadpoles were anesthetized in MS-222 and then preserved in 10% formalin in accordance with guidelines of the American Society of Ichthyologists and Herpetologists, Herpetological Animal Care and Use Committee. Tadpoles were deposited in the Stephen F. Austin State University Vertebrate Museum (4925–4989 and 5045–5092). The three sampling time periods were selected to prevent metamorphs from dispersing out of the pools. Gosner stage (GS; Gosner, 1960) was recorded and total length (millimeters), tail length (millimeters), tail depth (millimeters) and head length (millimeters) were measured for each individual sampled using digital calipers. Mean values were calculated for each mesocosm at each sample period. At the final sampling period (t3), all surviving tadpoles (including the five collected for t3) were collected and counted to determine survival.

Data Analyses.—All size (total length) and GS data were adjusted to account for clutch effects by subtracting clutch means (at time of measurement) from pool values. Therefore, every value is a residual that represents either positive or negative

TABLE 1. Minimum days to metamorphosis, approximate time period (t1, t2, and t3) for sampling each anuran species as determined by average larval time periods, dates of tadpole introduction, and final sample date.

Species	Days to metamorphosis	t1	t2	t3	Introduction dates	Final sample taken
<i>Pseudacris fouquettei</i>	55 days (Smith, 1983)	Day 15	Day 30	Day 55	3–14 February 2008	10 April 2008
<i>Lithobates sphenocephalus</i>	67 days (Wright and Wright, 1949)	Day 15	Day 40	Day 67	9–14 February 2008	22 April 2008
<i>Hyla versicolor</i>	35 days (Ritke et al., 1990)	Day 15	Day 25	Day 35	10 April–22 May 2008	26 June 2008
<i>Incilius nebulifer</i>	20 days (Garrett and Barker, 1987)	Day 6	Day 12	Day 20	15–26 May 2008	1 June 2008

differences in size or GS from expected clutch values. These clutch-adjusted residuals were used to test for differences among treatments, at each time measurements were taken. Because initial examination of the morphometric measures revealed they were highly correlated (all Pearson $r > 0.97$), only total length was used in subsequent analyses as a metric of frog size. Although the experiment was a repeated-measures design, parametric repeated measures analysis of variance is problematic because some pools lost all tadpoles before the experiment ended (i.e., produced missing values). Therefore, nonparametric permutation procedures (randomization tests) were performed to test the null hypothesis of no differences among treatment means. The 45 pools were considered fixed (experimental) units that were randomly shuffled to different treatments in every random permutation. In each permutation, mean size and GS were calculated for each treatment, as well as all pairwise differences between treatment means. This procedure was repeated 10,000 times for each species (the observed differences accounted for one random permutation) to produce empirical null distributions of treatment differences at each time of measurement. The percentile of the observed value in any distribution was the P value of the test (the probability of finding a greater difference than the observed case by chance alone). We considered a pairwise difference significant if $P < 0.05$.

Likewise, survival data were clutch adjusted by subtracting the average number of survivors (of 50) from a clutch from each pool in which the clutch was introduced. In this case, every value is a residual which expresses the expected number of survivors above or below the clutch mean when that clutch was introduced to the different treatment types. The same permutation procedure was performed to test the null hypothesis of no difference in survival among the different treatments. In each iteration, survival disparity was calculated as $\Sigma d^2 / \binom{n}{2}$, where d is a pairwise difference in survival, n is the number of groups compared, and $\binom{n}{2}$ is the number of possible comparisons (in this case, equal to 3 for the three treatments). The expected value of survival disparity is 0 under the null hypothesis. The 10,000 random permutations performed for each anuran species produced empirical null distributions of survival disparity, from which the percentile of the observed disparity was the P value of the test. We considered a pairwise difference significant if $P < 0.05$.

To consider whether size and GS were associated with survival, partial Mantel (1967) tests were performed. This method calculates the correlation between matrices of the same rank (usually, square symmetrical matrices) and tests the strength of the correlation with a permutation test, where cells of one matrix are randomly shuffled. We performed this test restricted to matrices of within-species intertreatment pairwise difference, for both size and survival. Plots of size and GS differences vs. survival differences were produced to facilitate an understanding of any significant ($P < 0.05$) correlation.

RESULTS

Triadica sebifera, rather than *A. rubrum* or *Q. michauxii*, had significant effects on size differences among treatments but only during the late measurement period (Fig. 1). However, the effect of *T. sebifera* on anuran size was not consistent among species. *Pseudacris fouquettei* tadpoles exposed to the tallow treatment had significantly reduced growth, noticeable by the third measurement (Fig. 1; $P = 0.0001$ for *T. sebifera*–*A. rubrum* comparison; $P = 0.0107$ for *T. sebifera*–*Q. michauxii* comparison). However, *L. sphenocephalus* tadpoles exposed to the *T. sebifera* treatment had significantly increased growth, noticeable by the third measurement (Fig. 1; $P = 0.0010$ for *T. sebifera*–*A. rubrum* comparison; $P = 0.0001$ for *T. sebifera*–*Q. michauxii* comparison). *Hyla versicolor* tadpoles had slight but significant increased growth in the tallow treatment compared with the oak treatment in the third measurement (Fig. 1; $P = 0.0241$) but not compared with the maple treatment ($P = 0.1628$). No significant size differences were observed among treatments for *I. nebulifer*.

For *P. fouquettei* and *L. sphenocephalus*, differences in GS were consistent with growth (Fig. 2). Tadpoles of *P. fouquettei* were comparatively less developed in the *T. sebifera* treatment, but only in the third measurement (Fig. 2; $P = 0.0044$ for *T. sebifera*–*A. rubrum* comparison; $P = 0.0004$ for *T. sebifera*–*Q. michauxii* comparison). Tadpoles of *L. sphenocephalus* were comparatively more developed in the *T. sebifera* treatment, but also only in the third measurement (Fig. 2; $P = 0.0002$ for *T. sebifera*–*A. rubrum* comparison; $P = 0.0001$ for *T. sebifera*–*Q. michauxii* comparison). Size differences among treatments for tadpoles of *H. versicolor* were only observed in the third time measurement, although differences in developmental rate were observed throughout the experiment (Fig. 2). Tadpoles in *T. sebifera* treatments were comparatively more developed than those in *Q. michauxii* or *A. rubrum* treatments at every time measurement ($P < 0.0088$ and $P < 0.0184$, respectively), but tadpoles in *Q. michauxii* or *A. rubrum* treatments did not differ in GS ($P > 0.4451$). Tadpoles of *I. nebulifer* in *T. sebifera* treatments were comparatively more developed than tadpoles in either *Q. michauxii* or *A. rubrum* treatments, but these differences were marginally significant ($P = 0.0298$ and 0.0329 , respectively).

Triadica sebifera treatments negatively affected survival for *P. fouquettei* and *L. sphenocephalus*, but not the other two species (Table 2). Interestingly, *P. fouquettei* seemed to survive better in *A. rubrum* treatments and *L. sphenocephalus* seemed to survive better in *Q. michauxii* treatments, although both species survived better in either of these treatments compared with *T. sebifera*.

Survival (apparent density) was not associated with development, because survival differences were not correlated with GS differences (Fig. 3; Mantel $r = 0.0469$, $P = 0.4496$). However, size and survival were associated (Fig. 3; Mantel $r = 0.6458$, $P = 0.0213$). This association was largely influenced by the results from *L. sphenocephalus*. After removing the values for *L.*

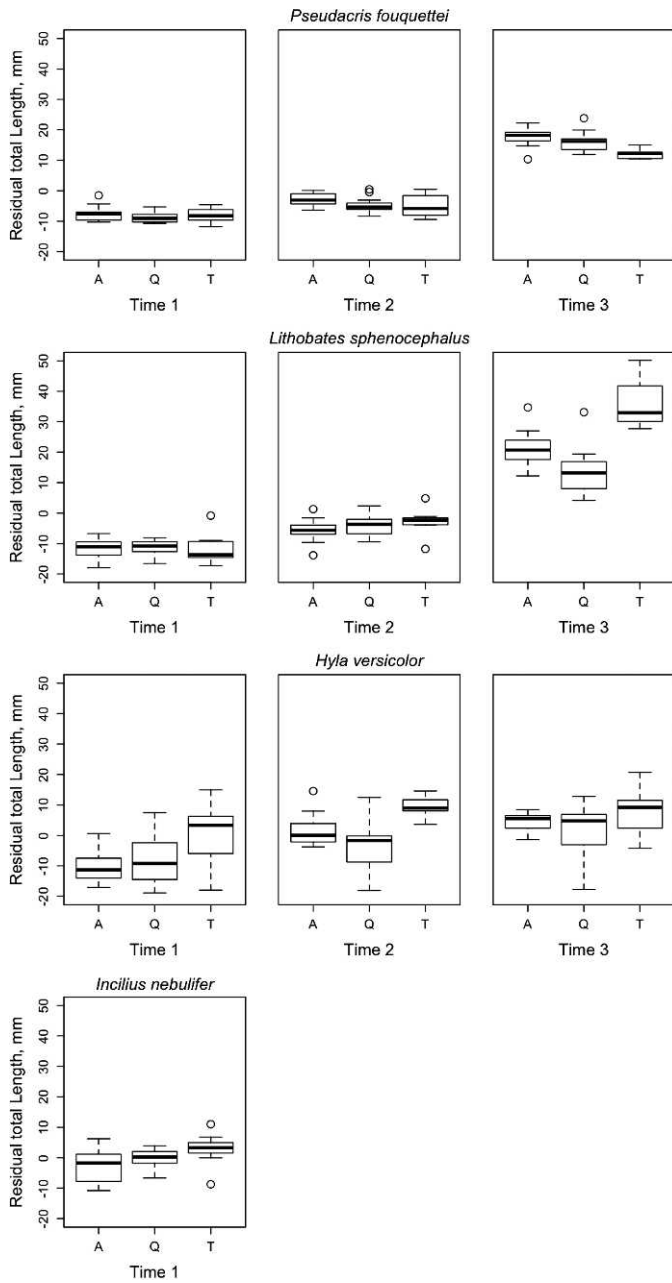


FIG. 1. Box plots of residual (clutch-adjusted) total length for species \times treatment \times time comparisons. Boxes represent the interquartile range. Whiskers represent either the full range of the data or 1.5 times the interquartile range, in which case outliers are shown as open circles. Bolded lines within boxes are medians. Treatment types are noted within time periods with A = *Acer rubrum* (red maple), Q = *Quercus michauxii* (swamp chestnut oak), and T = *Triadica sebifera* (Chinese tallow).

sphenoccephalus, comparisons between *T. sebifera* treatments and other treatments were no longer significant (Mantel $r = 0.2982$, $P = 0.2063$).

DISCUSSION

Effects of *T. sebifera* on tadpole development, morphology, and survival were species specific. The two species that breed early in the year, *P. fouquettei* and *L. sphenoccephalus*, had lower survival in the *T. sebifera* treatment. However, tallow impacted their development differently; *P. fouquettei* were smaller and less

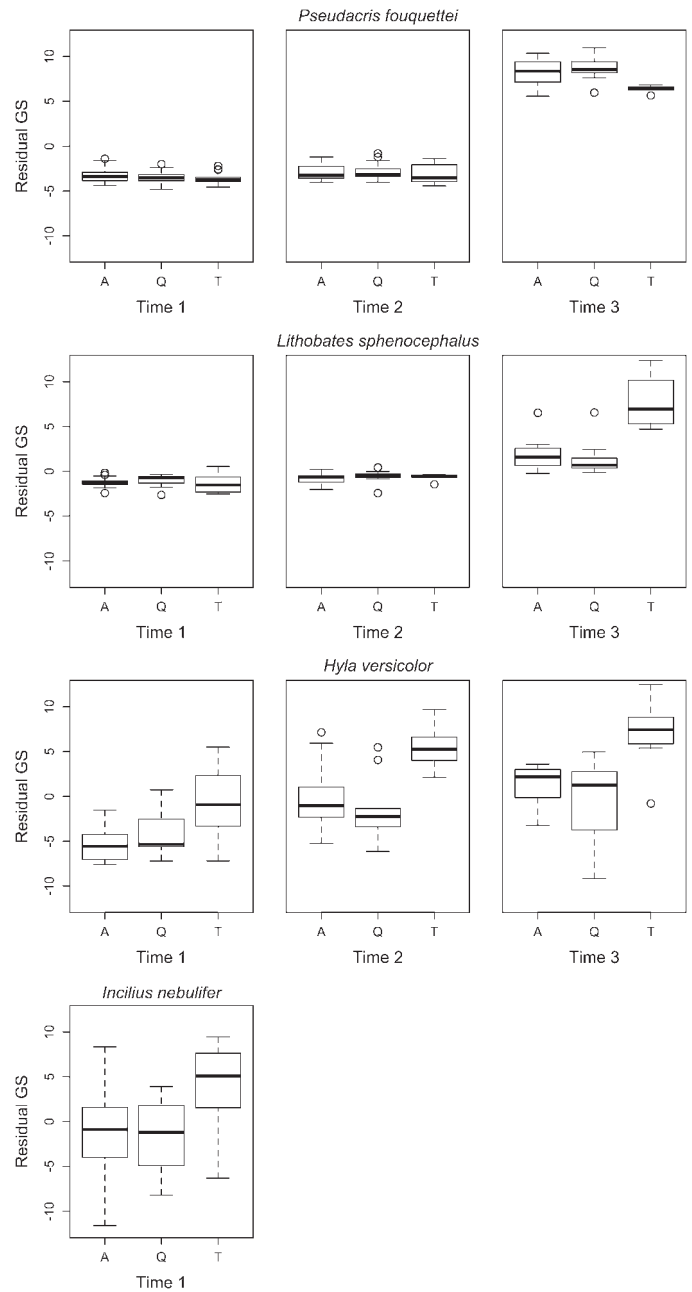


FIG. 2. Box plots of residual (clutch-adjusted) Gosner stage for species \times treatment \times time comparisons. Boxes represent the interquartile range. Whiskers represent either the full range of the data or 1.5 times the interquartile range, in which case outliers are shown as open circles. Bolded lines within boxes are medians. Treatment types are noted within time periods with A = *Acer rubrum* (red maple), Q = *Quercus michauxii* (swamp chestnut oak), and T = *Triadica sebifera* (Chinese tallow).

developed and *L. sphenoccephalus* were larger and more developed with tallow. The larger size of *L. sphenoccephalus* was, in part, attributable to the low density of individuals by the third time period, although previous studies also associated slower development with lower density (Dash and Hota, 1980; Girish and Saidapur, 2003). For the two species that breed later in the year, *H. versicolor* and *I. nebulifer*, survival did not differ among the treatments. However, *T. sebifera* seemed to affect growth and development in *H. versicolor*. Larvae in the *T. sebifera* treatment were larger and developed more rapidly than in the

TABLE 2. Survival of four species of anurans in experimental mesocosms. Values are average numbers of individuals (per 50) surviving the experiment, relative to clutch strength (i.e., positive values mean better survival and negative values mean poorer survival for any clutch exposed to the three treatments). Disparity is sum of squared differences divided by the number of comparisons. *P* values are percentiles of observed values from empirical null distributions, generated from 10,000 random permutations of a permutation test.

Species	Oak	Maple	Tallow	Disparity	<i>P</i>
<i>Pseudacris fouquettei</i>	3.07	7.53	-10.60	178.52	0.0001
<i>Lithobates sphenoccephalus</i>	9.40	0.80	-10.20	193.04	0.0001
<i>Hyla versicolor</i>	0.44	1.18	-1.62	4.22	0.6036
<i>Incilius nebulifer</i>	-0.69	-1.02	1.71	4.45	0.6595

other treatments, similar to what was seen with *L. sphenoccephalus*. In a similar study investigating the impacts of *T. sebifera* on amphibians, Leonard (2008) found that larvae of some anuran species exhibited lower survival when exposed to leaf litter from *T. sebifera*, whereas other species did not show a negative effect.

Anuran Breeding Phenology and Survival.—There was a distinct difference in the effect of *T. sebifera* on survival between early and late-breeding species. *Triadica sebifera* leaf litter breaks down rapidly, faster than native species (Cameron and Spencer, 1989; Leonard, 2008), perhaps breaking down so quickly that later breeding amphibians experience less detrimental effects from rapid *T. sebifera* decomposition in their breeding sites. Brown et al. (2006) investigated the effects of the exotic invasive plant *Lythrum salicaria* on survival and development of tadpoles of *A. americanus*. They found that tadpoles exposed to the exotic species developed slower and had lower survival and suggested leached tannins from the plants were the cause. With the rapid breakdown of *T. sebifera* in aquatic environments, a similar scenario could have occurred in this experiment.

Alternatively, the difference in larvae survival between early and late breeders may have resulted from lower dissolved oxygen levels in the early treatments. Although abiotic factors within each mesocosm were not measured in this study, rapid breakdown of *T. sebifera* leaf litter would lead to low dissolved oxygen during that period (Leonard, 2008; Saenz, unpubl. data). Anecdotal observations suggested that *P. fouquettei* tadpoles exposed to leaf litter from *T. sebifera* had enlarged hearts. Enlarged hearts in tadpoles suggests an increase in stress on the cardiovascular system, possibly due to decreased oxygen levels (Pronych and Wassersug, 1994). However, *I. nebulifer* tadpoles showed no difference in survival between the three leaf litter treatments, yet they are obligate gill breathers (Ultsch et al. 1999) and therefore should have been more affected by low oxygen levels than the other species that develop lungs and gulp air much sooner. Survival of gill-breathing *A. americanus* tadpoles was negatively affected by aqueous extracts from the invasive plant *L. salicaria*, whereas these extracts had no effect on *H. versicolor* tadpoles that develop lungs sooner (Maerz et al., 2005b). Maerz et al. (2005b) suggested that phenolics from the *L. salicaria* extracts may cause damage to the toad gills. Survival in *I. nebulifer* in this study was not affected by treatment. Adequate rainfall may have diluted any harmful extracts from the *T. sebifera* as well as increased oxygen levels by the time *I. nebulifer* tadpoles were introduced. Without introducing new leaf litter, compounds from leaf decomposition would have been far less concentrated by the time *H. versicolor* and *I. nebulifer* tadpoles were introduced, either from dilution by rainfall or by decomposition over time. Although development was significantly different in the *T. sebifera* treatment for *H. versicolor*, it seems that later breeding amphibians were introduced to more similar conditions among the three treatments such that tadpole survival was not differentially influence in *H. versicolor* and *I. nebulifer*. Leaf litter concentration for pools in this investigation was determined based on data in a previous study where litter accumulation on the bottom of natural ponds was measured (Leonard, 2008). Attempts to manipulate this approach may clarify what concentration of leaf litter may be harmful to a

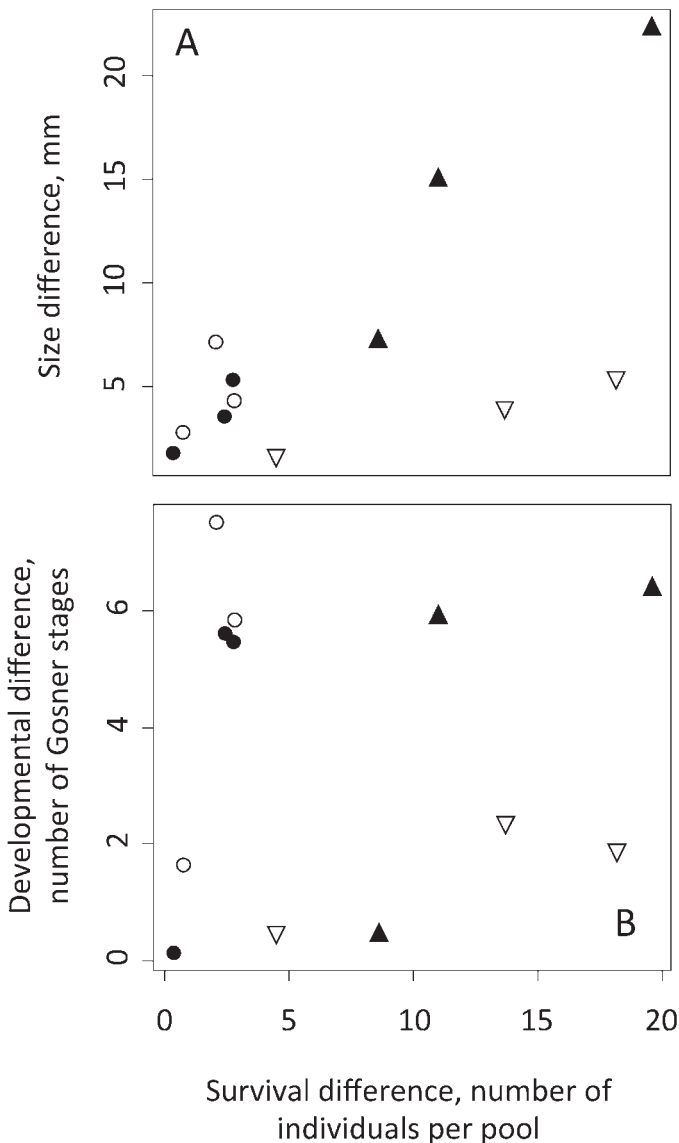


FIG. 3. Association of average species \times treatment size differences (A) and Gosner stage differences (B) with survival differences. Open triangles pointed down represent Chorus Frogs; filled triangles pointed up represent Leopard Frogs; open circles represent Gray Tree Frogs; and filled circles represent Gulf Coast Toads.

species and provide information useful in developing management protocols to control this invasive species.

An alternative explanation for the difference in larvae survival between early and late breeders is that species such as *I. nebulifer* and *H. versicolor* may be better adapted to dealing with unpredictable aquatic environments, such as rapid aquatic habitat evaporation from summer heat, and increased invertebrate predator densities. By being accustomed to unpredictable environmental conditions, these species may be better able to handle stress introduced from the leaf litter than *P. fouquettei* and *L. sphenoccephalus* that breed earlier in the year. Accordingly, breeding phenology for each species may influence how well each species survives within *T. sebifera* leaf litter.

Effects of Morphology and Development.—Morphology and developmental rate of tadpoles have impacts on survival and performance of adult anurans after metamorphosis. For example, predation of anurans is most intense during the larval stage, during metamorphosis, and in early juvenile life (Arnold and Wassersug, 1978). Hence, fast growth and development allow tadpoles to escape predation from aquatic predators and drying ephemeral ponds, thereby increasing their chances of survival and reaching breeding size early (Travis et al., 1985; Smith, 1987; Newman, 1988; Ficetola and De Bernardi, 2006). Rapid larval growth and development, such as observed with *H. versicolor* and *L. sphenoccephalus* tadpoles in *T. sebifera* mesocosms, have been suggested to increase growth rate and survival in postmetamorphic stages directly (Pechenik et al., 1998; Altwegg and Reyer, 2003). However, rapid aquatic development can lead to shorter legs in early metamorphic frogs and may decrease jumping performance and the ability to escape terrestrial predators, whereas tadpoles in environments without predators produced adult frogs with relatively longer legs (Relyea, 2001; Ficetola and De Bernardi, 2006). Several other studies also have suggested that body size affects jumping performance of frogs and their ability to escape predation as adults (John-Alder and Morin, 1990; Miller et al., 1993). Furthermore, Beck and Congdon (2000) found that larger tadpoles had higher metabolic rates as adults, faster sprint speeds, and greater endurance than those that had a lower mass. Hence, rapid development (a consequence of the size needed to escape an aquatic habitat) may decrease survival of adult frogs. This ultimately produces a trade-off for developing amphibians for which a longer larval period produces a more robust adult frog with greater fitness; however, the tadpole is more likely to succumb to predation or be affected by another aquatic stressor. *Triadica sebifera* could be stimulating certain species (*L. sphenoccephalus* and *H. versicolor*) to develop more quickly to escape the aquatic environment, but these tadpoles may have greater difficulty escaping predation as adults. If frogs are leaving aquatic environments sooner triggered by stress due to *T. sebifera* litter, and they are being preyed upon more heavily as adults, this may lead to population declines for *L. sphenoccephalus* and *H. versicolor* where their range overlaps with this invasive plant.

Consequences of Invasive Plants on Anurans.—Invasive species are thought to create an “evolutionary trap” scenario where species adapted to natural habitats are unable to adapt to the rapid invasion of a nonnative species, leading to decreases in population size (Kokko and Sutherland, 2001; Schlaepfer et al., 2005; Miner et al., 2005; Strauss et al., 2006). This may be the situation *T. sebifera* is creating for native amphibian populations. Species such as *P. fouquettei* and *L. sphenoccephalus* that had lower survival in *T. sebifera* may not be able to overcome their adaptive trap as *T. sebifera* encroaches rapidly on native habitat. *Triadica sebifera* also may create an ecological trap scenario that adversely

affects breeding behavior. *Hyla versicolor* seems to avoid calling in *T. sebifera* compared with native deciduous trees (Kwiatkowski, unpubl. data). If anuran species are found to avoid areas with *T. sebifera*, this may lead species to select for lower quality habitats.

Although there is evidence of detrimental impacts to amphibian populations from introduced vertebrates such as fishes and other amphibians (Lawler et al., 1999; Rosen and Schwalbe, 2002; Baber and Babbitt, 2003; Kiesecker, 2003), bottom-up effects of an invasive species on amphibian abundance are lacking (Maerz et al., 2009). Encroachment from invasive plants may alter nutrient characteristics, chemical and physical habitat features, and trophic composition of native habitats (Wedin and Tilman, 1990; Chapin et al., 1997; Knops et al., 2002). Forests of *T. sebifera* contained significantly higher quantities of Ca, N, K, Mg, and P than in adjacent native temperate deciduous habitat. Cameron and LaPoint (1978) noted that fall leaf litter readily leached tannins and phenolics during rainfall; this leaching, along with rapid decay, could potentially affect aquatic environments in which *T. sebifera* is found. Tannins and other materials leached from *T. sebifera* leaf litter into aquatic ecosystems were found to inhibit the performance of aquatic reducers (invertebrates) and reduce the recycling of nutrients within ephemeral ponds (Cameron and LaPoint, 1978). Combined with other threats to amphibian populations, plant invasions could intensify the effects on already threatened species.

With proper management techniques, such as creating buffer zones free of the invasive around critical habitat, the impacts of an invasive on native populations can be reduced (Semlitsch, 2003). Invasive plants have been found to negatively affect amphibian larval performances and the foraging success of adults; however, there is no research connecting an invasive plant directly to population level declines (Maerz et al., 2005a,b, 2009; Brown et al., 2006). With global amphibian populations threatened, it is important to investigate and consider all possible factors contributing to population losses, including possible interactions between *T. sebifera* and other known contributors to amphibian population decline, such as pollutants or disease.

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