The Effects of Crayfish Predation and Vegetation Cover on Tadpole Growth, Survival, and Nonlethal Injury

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Abstract.—Predator–prey interactions play an important role in structuring larval anuran communities in ephemeral wetlands. The type of interaction often depends on the predator species and the complexity of the aquatic habitat. We experimentally evaluated the effects of Panhandle Crayfish (*Procambarus evermanni*) predation on larval Southern Leopard Frogs (*Lithobates sphenocephalus*) and larval Ornate Chorus Frogs (*Pseudacris ornata*). We performed separate experiments for each anuran species and used multiple vegetation treatments to examine whether vegetation could provide refugia from crayfish predation. Our results indicate that crayfish are effective predators of anuran larvae regardless of the amount of vegetation present. Encounters between tadpoles and crayfish often resulted in nonlethal tail injury for tadpoles, suggesting that crayfish predation is prominent in ephemeral wetland communities. Leopard frog tadpoles in predator treatments also grew larger than their counterparts in nonpredator treatments, suggesting a reduction in intraspecific competition. Reduced competition and higher growth rates may allow anuran larvae to develop and metamorphose faster, allowing them to escape aquatic predators, drying wetlands, or both.

In freshwater ecosystems, community structure is determined by a complex set of biotic and abiotic interactions. Predation is an important biotic interaction in aquatic systems, and its effects on community structure and composition have been well documented (Welbourn et al., 1996; Wilbur, 1997; Rudolf and Rasmussen, 2013). Predators actively remove prey from the environment, lowering their abundance and even completely eliminating them from the environment (Smith, 1983); however, a decrease in prey abundance from predation can be positive for other members of the community. Reduced competition (both intra- and interspecific) can change community structure and increase the success of other species or individuals (Morin, 1983; Wilbur, 1997). Predator presence also can affect prey behavior and morphology, usually through a response to chemical stimuli (Relyea, 2001). For example, many species of tadpoles, including Southern Leopard Frogs (*Lithobates sphenocephalus*), will reduce activity in the presence of predators, which can decrease growth rates and increase time to metamorphosis (Feminella and Hawkins, 1994; Bishop et al., 2012).

Vegetation type and structure also can influence aquatic communities. Aquatic vegetation can increase the surface area on which biofilm and periphyton can grow (Cattaneo and Kalff, 1979; Morris and Monier, 2003), alter nutrient cycling (Granéli and Solander, 1988), modify dissolved oxygen (DO) levels, and create refugia for many species, which can alter predator–prey interactions. Many prey species can avoid predation attempts by using dense vegetation as refugia (Lefcort and Eiger, 1993; Kopp et al., 2006), but some predators will alter their hunting strategies depending on habitat complexity (Savino and Stein, 1989; Davis et al., 2012). Furthermore, litter inputs from aquatic vegetation can also strongly influence anuran growth and development rates (Williams et al., 2008). The potential for vegetation to affect predator–prey interactions suggests that changes to vegetation structure as a result of anthropogenic disturbances are likely to impact biotic interactions within aquatic communities.

Ephemeral wetlands often support a diverse amphibian assemblage (Dodd and Cade, 1998). Typically, many anuran species breed in the same wetland with at least partial overlap in their breeding phenology, resulting in a complex tadpole community. The predation pressure in ephemeral wetlands is generally considered to be lower than in more-permanent water bodies because of the regular drying events that exclude slow-developing predators such as fish (Skelly, 1996, 1997). Some predators (e.g., salamanders and crayfish), however, are adapted to persist through drying events or to colonize wetlands shortly after they fill (Wilbur, 1997). Several studies have demonstrated that these predators can directly influence anuran breeding success and the structure of tadpole communities in ephemeral wetlands (Morin, 1983; Van Buskirk, 1988; Alford, 1989).

Even though predation is an important ecological process, direct measures of predation often are difficult to obtain because predation events (successful or unsuccessful) are rarely observed (Morin, 1985). Tail injury of larval anurans commonly results from unsuccessful predation attempts by many predators including newts, turtles, crayfish, and dragonfly larvae (Morin, 1985; Semlitsch, 1990; Wilbur and Semlitsch, 1990). Unsuccessful predation attempts tend to increase as predator density increases (Morin, 1985), and tail injury can make larval anurans more susceptible to future predation events (Semlitsch, 1990; Figiel and Semlitsch, 1991). An increased susceptibility to future predation events allows nonlethal injury to act as a regulating mechanism within a population (Harris, 1989). Therefore, tail injury has important ecological consequences for individuals and is a useful metric for measuring predation intensity on tadpoles, especially when survival until metamorphosis cannot be recorded.

Pine flatwoods are found in low-lying, poorly drained areas of the southeastern United States (Means, 1996). Ephemeral wetlands embedded in pine flatwoods are typically characterized by an open canopy and abundant herbaceous vegetation (Kirkman, 1995; Gorman et al., 2013). Pine flatwoods wetlands provide important breeding habitat for multiple anuran species, including Ornate Chorus Frogs (*Pseudacris ornata*), now declining across much of their range, and Southern Leopard Frogs. These wetlands are fire dependent and often lose their characteristic vegetation structure in the absence of regular growing-season fires (Kirkman, 1995; Gorman et al., 2013). Fire regimes across the southeastern United States have been extensively altered by anthropogenic disturbance, and fire suppression became widespread after the 1930s (Southard, 2011). The loss of historic fire regimes has already affected vegetation structures in many ephemeral wetlands, reducing herbaceous cover as woody cover encroaches (Gorman et al.,

2013), and is thought to have contributed to the decline of native amphibians (Bishop and Haas, 2005; Gorman et al., 2009). This includes Ornate Chorus Frogs, which more-commonly occupy wetlands with high herbaceous vegetation cover (Gorman et al., 2013). The goal of this study was to examine the effects of a shifting habitat structure on tadpole predation by a common crayfish species. We experimentally tested whether a reduced percent cover of herbaceous vegetation decreased tadpole survival or growth of two anuran species in the presence of a crayfish predator.

MATERIALS AND METHODS

For this study, we conducted two experiments. The main experiment used Southern Leopard Frogs as the focal species and the second experiment used Ornate Chorus Frogs. Both experiments were conducted on Eglin Air Force Base (AFB), a large military installation in the Panhandle of Florida, USA. Eglin AFB contains over 146,000 ha of actively managed longleaf pine (*Pinus palustris*) forests, including pine flatwoods. All animals used in both experiments were collected from altered habitats (e.g., borrow pits and roadside ditches) on Eglin AFB.

Experiment 1.—We used Southern Leopard Frogs as our focal species. We originally intended to use Ornate Chorus Frogs because they are habitat specialists and declining across much of their range. We used leopard frogs instead because sufficient numbers of Ornate Chorus Frog eggs–tadpoles could not be located. Southern Leopard Frogs are common throughout the southeastern United States and lay eggs in large egg masses, which makes them an ideal species for large-scale experiments. We collected four leopard frog egg masses from a borrow pit on Eglin AFB. We housed egg masses individually in 10-gal (~38 L) aquaria filled with approximately 6 cm of water from the borrow pit until tadpoles emerged. The water in each aquarium was aerated with a small aerator, and we fed tadpoles a small amount of fish food approximately 24 h prior to starting the experiment.

We selected the Panhandle Crayfish (*Procambarus evermanni*) as the predator of our experiment. Panhandle Crayfish are the most-common crayfish species in pine flatwoods ephemeral wetlands on Eglin AFB (Chandler, unpubl. data). We collected 15 male *P. evermanni* from inundated areas on Eglin AFB (carapace length 25–30 mm). We housed crayfish in small plastic containers (approximately 20 × 20 cm) prior to adding them to the experiment, and all crayfish were fed tadpoles before being placed in experimental tanks.

We used a completely randomized design in which our experimental units were 30, 150-L oval plastic mesocosms (82 × 54 × 32 cm; Tuff Stuff Products, Terra Bella, California). We arranged experimental mesocosms in a 5 × 6 array in an open field at Eglin AFB, Niceville, Florida. Mesocosms were randomly assigned one of six possible treatment combinations that were each replicated five times. We manipulated the amount of herbaceous vegetation cover (zero, low, and high) and the presence (present–absent) of a predator (a single crayfish) in each mesocosm. To examine the effect of vegetation structure, without the confounding effects of litter production or effects on DO, we simulated the herbaceous vegetation commonly found in ephemeral wetlands in northwestern Florida using plastic grass mats designed for aquaria. Each mat was 25 × 25 cm with 100 clumps of plastic vegetation that were approximately 15 cm tall. Mesocosms assigned to the low vegetation treatment received two mats placed in the center of the mesocosm (34% coverage), and mesocosms assigned to the high vegetation treatment received four mats placed in the

center (68% coverage). Percent cover was representative of the herbaceous vegetation cover observed in natural flatwoods wetlands with varying habitat quality (Gorman et al., 2013). We placed the vegetation mats together in the center of the mesocosm to form one continuous patch of vegetation.

We added approximately 2 cm of sand to the bottom of each mesocosm to act as substrate. Also, we added 30 g of dried grass litter collected from the edge of a natural wetland and filled each mesocosm to a depth of 20 cm (135.5 L) using dechlorinated tap water. In addition to the dried grass litter, we added 10 g of crushed rabbit chow to each mesocosm to promote algal and bacterial growth. We inoculated each mesocosm with 200 ml of water taken from three natural wetlands (combined sample) on the day mesocosms were filled and 1 wk later. Water samples were screened prior to inoculating mesocosms to remove any aquatic invertebrates or amphibian larvae. We also added two iButton temperature data loggers (one on each end of the mesocosm; Maxim Integrated, San Jose, California) sealed inside small plastic bags filled with sand. We drilled small holes at one end of each mesocosm to ensure water levels remained close to 20 cm even during precipitation events. Finally, each mesocosm was covered with a lid made of fiberglass window screen to eliminate the possibility of colonization by unwanted predatory invertebrates or other amphibians (none were found during destructive sampling at the end of the study). We allowed mesocosms to acclimate for 2.5 wk before adding animals.

A combination of newly hatched leopard frog tadpoles from different egg masses was used in our experiment to reduce the possibility of genetic influences. We added 20 tadpoles (Gosner stage 25; Gosner, 1960) to each mesocosm on 19 February 2014 (approximately one tadpole per 7 L). This density is well within the range of larval densities for this species in natural wetlands (Morin, 1983). We measured the snout to vent length (SVL, mm) and total length (TL, mm) of five tadpoles from each treatment prior to adding them to the tanks. We randomly assigned one Panhandle Crayfish to each mesocosm in the predator treatment on the same day as the tadpoles.

We sampled the tadpoles in each mesocosm once a week for 10 wk. Before sampling, we removed the artificial vegetation from each mesocosm while being careful to ensure that tadpoles and crayfish were not in the vegetation. If the treatment had a crayfish present, we removed it before catching any tadpoles to reduce the chances of inadvertently causing a predation event. We recorded the number of surviving tadpoles in each mesocosm. We then randomly selected 10 tadpoles and measured their SVL and TL (in cases where there were fewer than 10 surviving tadpoles, we measured all tadpoles). Tail injury (an indicator of failed predation attempts; Morin, 1985; Semlitsch, 1990; Wilbur and Semlitsch, 1990) was recorded in all surviving tadpoles from weeks 6–10. We returned artificial vegetation and crayfish to their respective mesocosm prior to returning tadpoles. All surviving tadpoles were returned to the middle of the mesocosm at the same time.

During the 10 wk of the experiment, several crayfish were found dead. All dead crayfish were replaced either the same or the following day, and no mesocosm had a dead crayfish on more than one occasion. We think these deaths were likely related to the cold weather in late February and early March (i.e., water temperatures in most mesocosms fell to approximately 5°C on 27 and 28 February) and the initial stress of being kept in the lab prior to being added to mesocosms. On 30 April 2014, we destructively sampled all mesocosms and obtained final measurements of tadpoles and crayfish. We euthanized all

surviving tadpoles in a buffered solution of tricaine methane sulfonate (MS-222).

Experiment 2.—For this experiment, we used Ornate Chorus Frog tadpoles collected from borrow pits and ditches on Eglin AFB. We collected 75 tadpoles and housed them overnight in a large aquarium filled with water from one of the capture sites. Six Panhandle Crayfish with carapace lengths between 25–30 mm were collected from inundated areas on Eglin AFB. We housed crayfish individually, overnight, in small plastic containers.

We arranged 12, 10-gal (~38 L) glass aquaria in a 4 × 3 array in the same field where the large scale experiment took place. Tanks were randomly assigned one of four treatment combinations, which were replicated three times. We manipulated the amount of vegetation (high or low) and the presence of a single crayfish. We omitted the 'no vegetation' level for logistical reasons (insufficient number of tadpoles) and because it is unlikely that Ornate Chorus Frogs would use habitat with no herbaceous vegetation. We used the same type of artificial vegetation for this experiment, but vegetation was cut into smaller pieces so that it fit into the smaller tanks. The 'high vegetation' treatments received 80% vegetation coverage, and the 'low vegetation' treatments received 40% vegetation coverage.

We filled the 10-gal aquaria to a depth of 15 cm (18.7 L) with a 40/60 mixture of filtered pond water and dechlorinated tap water. Each aquarium had 2 cm of sand in the bottom and 1.5 g of ground rabbit chow to promote algal growth. We covered all the aquaria with a large tent, which had mesh sides to allow sunlight to reach the aquaria. On 23 March 2014, we added six Ornate Chorus Frog tadpoles (Gosner stage 26–30) to each aquarium from a combined sample of all tadpoles that were collected (approximately one tadpole per 3 L). All tadpoles were measured (SVL and TL) prior to being added to aquaria. Presence of a single Panhandle Crayfish was randomly assigned to each tank according to the predator treatment.

We sampled tadpoles in each aquarium twice a week for 4 wk. Artificial vegetation and crayfish were removed prior to sampling to reduce the chances of influencing the predation rate. Tadpole SVL, TL, and instances of tail injury were measured once a week, and the number of surviving tadpoles in each aquarium was recorded twice a week. We also conducted 50% water changes using dechlorinated tap water once a week while the study animals were removed from the aquaria. There was no crayfish mortality in this experiment. On 20 April 2014, all surviving tadpoles were euthanized in a buffered solution of tricaine methane sulfonate (MS-222).

Statistical Analysis.—We used linear mixed-effects models to analyze the effects of vegetation and crayfish on tadpole survival and SVL. We fit two models for each experiment (one for survival and one for SVL). We used SVL instead of TL because the tail injury inflicted by crayfish caused TL means to vary substantially from week to week. Linear mixed-effects models allowed us to include data from mesocosms that had data from the beginning of the experiment but had no measurements later in the experiment because there were no surviving tadpoles. We included the week of measurement, presence of a predator, vegetation level, and all two-way interactions as fixed effects. The individual tub was included as a random effect to account for differences between mesocosms and the repeated measures of experimental units. All models were fitted with random intercepts only. Model likelihoods were calculated using restricted maximum likelihood (REML), and Wald tests were used to calculate *P*-values for the fixed effects.

We performed contrasts on significant two-way interactions using *Z*-tests on the calculated least squared means. For interactions involving time, we did not examine differences between weeks as we expected measurements to change over time. We did test for differences between different levels of vegetation and predator within the same week. We adjusted *P*-values for contrasts using the Holm-Bonferroni correction (Holm, 1979). We adjusted the *P*-values for each mixed-model separately because models were generated using different datasets. We used an analysis of variance (ANOVA) to examine whether the vegetation treatments affected the percentage of surviving tadpoles with tail injury at the end of Experiment 1 (week 10 data) and during the first 3 wk of Experiment 2. We performed post hoc multiple comparisons (Tukey's honest significant difference [HSD]) on the means at different vegetation levels. All analyses were performed in R (R Development Core Team, 2014). Mixed-effects models were fit using the 'nlme' package (Pinheiro et al., 2014), and least squared means and contrasts were calculated using the 'lsmeans' package (Lenth, 2014).

RESULTS

Experiment 1.—Mean survival of Southern Leopard Frogs was 74% lower in treatments containing crayfish than in those without (Fig. 1A). Over time, there was a significant effect of crayfish presence on tadpole survival ($F_{9,234} = 51.1$, $P < 0.001$). The number of surviving tadpoles in the predator treatments (averaged across vegetation levels) was lower than the number in the nonpredator treatments by week 3 ($Z = 3.6$, $P = 0.001$), and this effect continued through the end of the experiment ($P < 0.001$ for weeks 4–10). There was no interaction between vegetation and crayfish presence on tadpole survival ($F_{2,24} = 0.4$, $P = 0.71$) and no effect of vegetation over time on survival ($F_{2,24} = 0.6$, $P = 0.88$); however, the high vegetation treatments had approximately two more surviving tadpoles from weeks 5–10 than did the other treatments, but these differences were not significant.

Over the course of the experiment, crayfish presence had a significant effect on leopard frog tadpole SVL ($F_{9,229} = 12.3$, $P < 0.001$). Surviving tadpoles in the crayfish treatments were 6.9% larger than tadpoles in nonpredator treatments by week 7 ($Z = 3.3$, $P = 0.032$; Fig. 1B). This trend continued through the end of the experiment, and by week 10, tadpoles in predator treatments were 13.0% larger than tadpoles in nonpredator treatments. Over time, the amount of vegetation also had an effect on tadpole SVL ($F_{18,229} = 3.3$, $P < 0.001$). Tadpoles in both the high and low vegetation treatments tended to be larger than tadpoles in the no vegetation treatment. Tadpoles in the low vegetation treatment were the largest and were significantly larger than tadpoles from the no vegetation treatment during 5 of the last 6 wk (Fig. 1C). Finally, there was no significant interaction between vegetation and predator effect on tadpole SVL ($F_{2,24} = 0.4$, $P = 0.67$).

Tail injury was observed in all 15 mesocosms with a crayfish (only three instances of tail injury occurred in noncrayfish mesocosms, likely caused by other tadpoles [Petranka and Thomas, 1995] or possibly during the capture process). By week 10, there was a significant difference between the percentage of surviving tadpoles with tail injury in the different vegetation treatments ($F_{2,10} = 6.8$, $P = 0.013$). The high vegetation treatment had a significantly lower percentage of tail injury compared to the no vegetation treatment (Tukey HSD, $P = 0.014$; Fig. 2); however, this trend was variable over weeks 6–10 of the experiment.
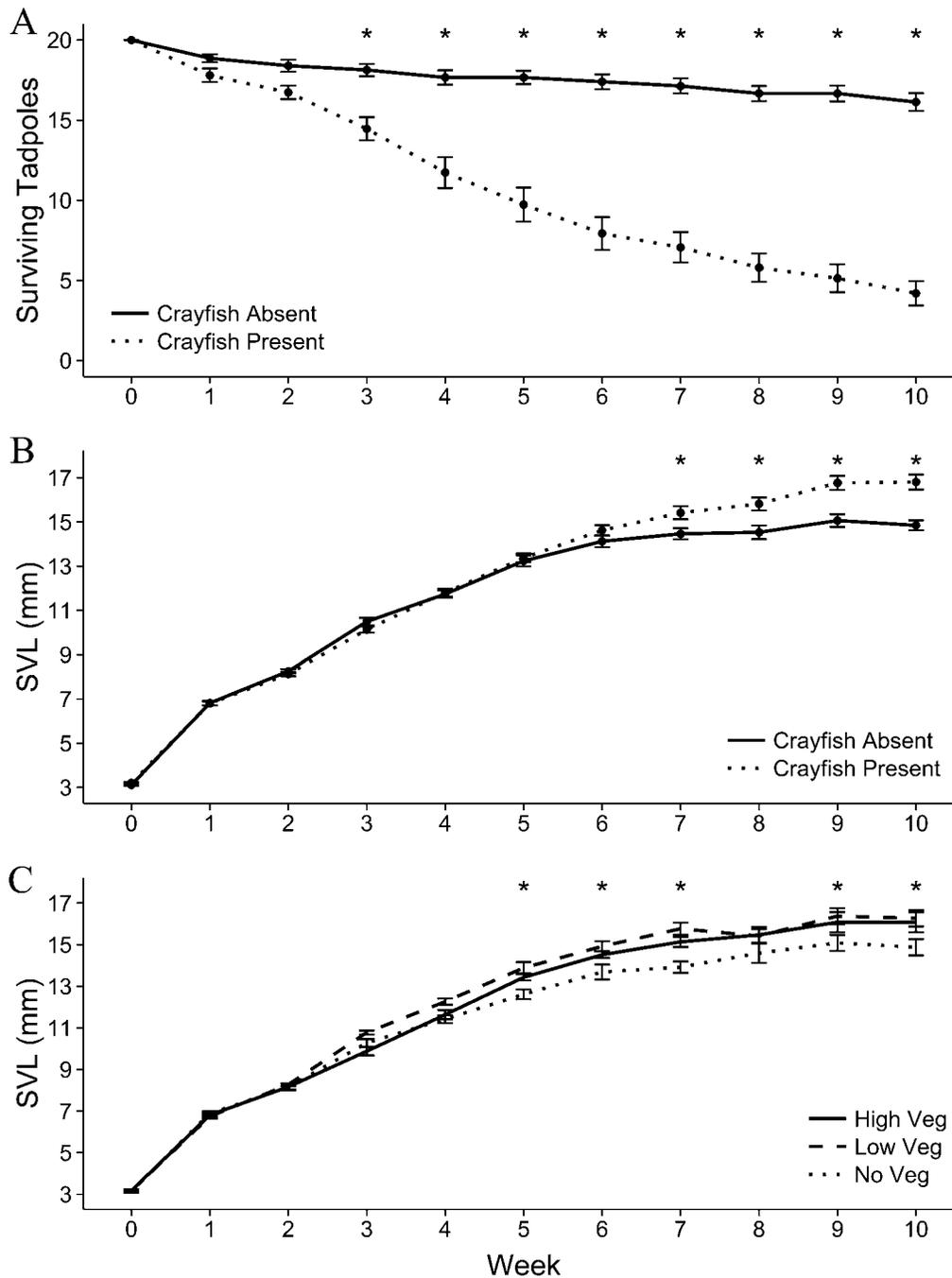
FIG. 1. Mean number of surviving Southern Leopard Frog (*Lithobates sphenocephalus*) tadpoles (A) and mean tadpole SVL (B,C) over time in a mesocosm experiment with six treatments: high vegetation (68% coverage) with and without a predator, low vegetation (34% coverage) with and without a predator, and no vegetation with and without a predator. A single Panhandle Crayfish (*Procambarus evermanni*) was present in the predator treatments. Plots show tadpole survival and SVL calculated across vegetation (A,B) and predator treatment groups (C), as there were no significant interactions between vegetation and predator. Asterisks represent weeks when significant differences in survival or SVL were identified. For panel C, these differences occurred only between the low vegetation and no vegetation treatments. Error bars represent standard error.

Experiment 2.—Ornate Chorus Frog tadpole survival was significantly affected by the presence of crayfish over time ($F_{7,63} = 6.5$, $P < 0.001$). This effect was evident throughout the experiment, and by week 4, 66% of aquaria with a crayfish had no surviving tadpoles. On average, there were 4.3 more surviving tadpoles in the nonpredator aquaria by week 4 ($Z = 7.6$, $P < 0.001$; Fig. 3). Tadpole survival was not significantly affected by the amount of vegetation present in the tanks ($F_{7,63} = 0.3$, $P = 0.59$). There were no initial differences in tadpole SVL between tanks ($F_{11,60} = 1.013$, $P = 0.45$). Furthermore,

neither crayfish nor vegetation had an effect on *P. ornata* SVL ($F_{3,22} = 0.7$, $P = 0.42$; $F_{3,22} = 0.1$, $P = 0.81$, respectively), and there was no interaction between vegetation and crayfish presence on tadpole survival ($F_{1,8} = 0.5$, $P = 0.48$) or *P. ornata* SVL ($F_{1,8} = 0.5$, $P = 0.50$). We also observed significantly more tail injury from weeks 1–3 in the predator treatments when compared to the nonpredator treatments (all $P < 0.02$; we did not test for differences in week 4 because the majority of predator tanks had no surviving tadpoles); however, there were no significant differences in the percentage of tadpoles
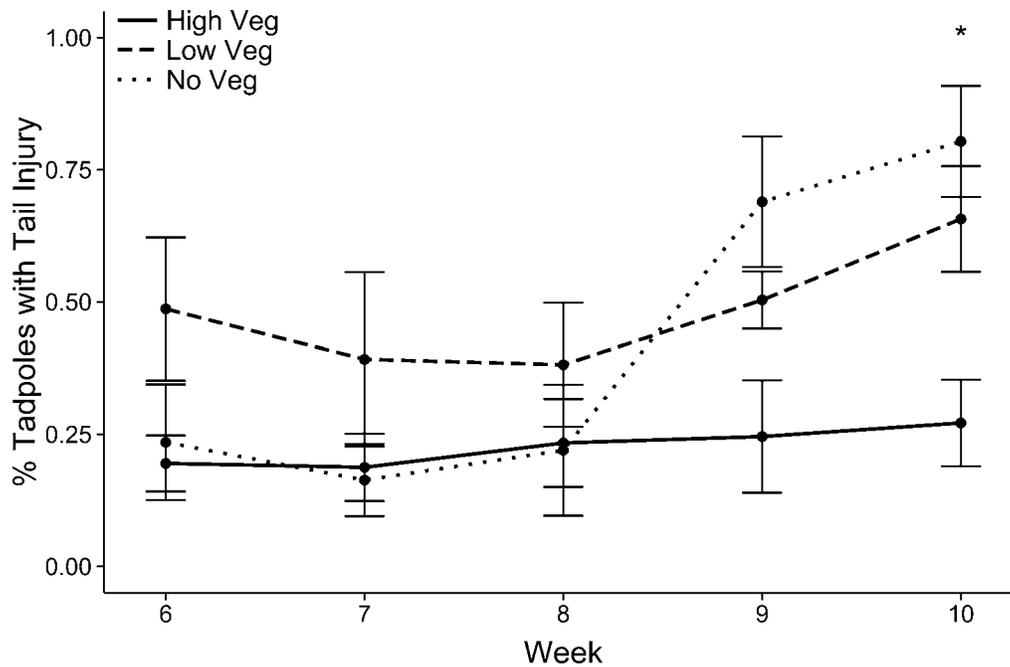
FIG. 2. Frequency of tail injury to Southern Leopard Frog (*Lithobates sphenocephalus*) tadpoles in mesocosms containing a single Panhandle Crayfish (*Procambarus evermanni*). Mesocosms with a crayfish had three different amounts of herbaceous vegetation coverage: high (68% coverage), low (34% coverage), and no vegetation. By week 10, a significantly higher percentage of tadpoles with tail injury occurred in the no vegetation treatment than in the high vegetation treatment. Error bars represent standard error.

with tail damage between the vegetation treatments ($P > 0.05$ for all 3 wk).

DISCUSSION

Overall, the effects of crayfish predation on larval anurans in ephemeral wetlands are poorly studied compared to the effects

of other common predators. Previous studies have indicated that crayfish can exert strong predation pressure on larval anurans in a variety of habitats, especially if the species is invasive (Figiel and Semlitsch, 1991; Gherardi et al., 2001; Cruz et al., 2006; Davis et al., 2012). In both experiments, we observed a rapid decline in tadpole survival when a crayfish was present. The effect of predation was evident in all three vegetation
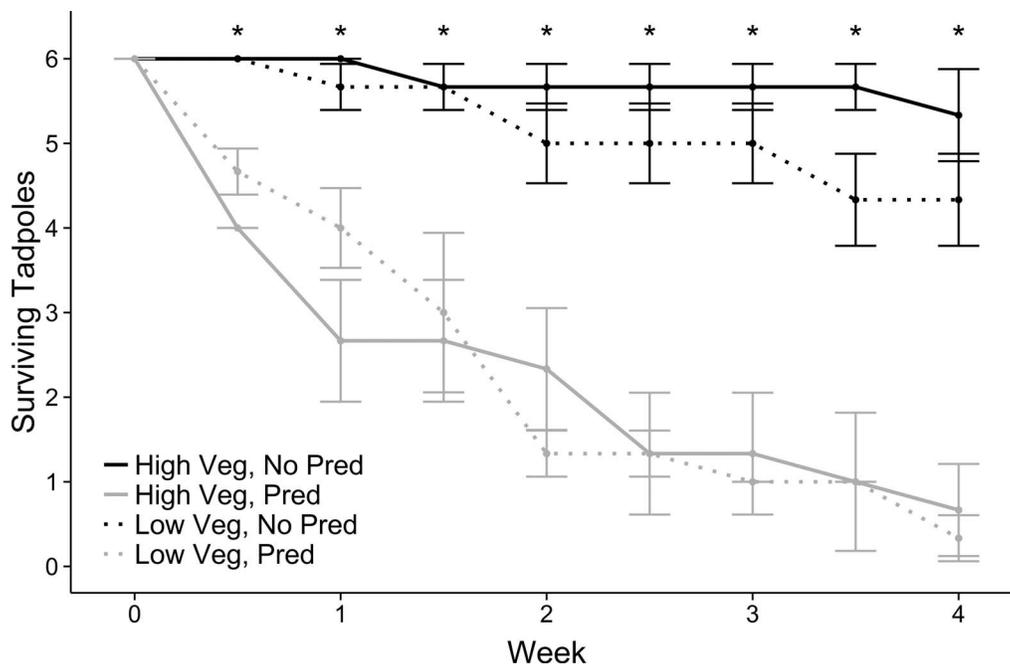

FIG. 3. Mean number of surviving Ornate Chorus Frog (*Pseudacris ornata*) tadpoles in four treatments including high vegetation (80% coverage) with and without a predator and low vegetation (40% coverage) with and without a predator. A single Panhandle Crayfish (*Procambarus evermani*) was present in the predator treatments. Asterisks represent weeks when there were significantly more tadpoles alive in nonpredator treatments compared to predator treatments. There were no significant effects of vegetation level on tadpole survival. Error bars represent standard error.

treatments, indicating that crayfish can be effective predators even in environments with a high level of vegetation structure. Contrary to our expectations, we did not detect an interaction effect between crayfish presence and vegetation on tadpole survival in either experiment, but there was a tendency for leopard frog tadpoles to survive at a slightly higher rate (~10%) in the high vegetation treatment. Figiel and Semlitsch (1991) also found that crayfish predation was not affected by the presence of structure in the environment. Furthermore, in certain situations, crayfish may actually become more successful predators by using vertical structure to reach the water's surface where tadpoles can congregate when a predator is present (Davis et al., 2012). We did not observe crayfish exhibiting this behavior during our experiment, but Chandler (pers. obs.) observed *P. evermanni* climbing on vegetation near the water's surface in natural wetlands. Overall, increasing habitat complexity appears to have little effect on the ability of crayfish to capture prey items, and some crayfish may even prefer vegetated habitats as a means to reduce their own predation risk (Jordan et al., 1996).

In addition to the rapid decline in tadpole survival, we also observed a high percentage of tail injury in both experiments. By the end of Experiment 1, significantly more leopard frog tadpoles in the no vegetation treatment had tail injury than did tadpoles in the high vegetation treatment. This, plus the slightly higher survival in treatments with high vegetation, suggests that predator–prey encounters may have been less frequent when higher amounts of vegetation were present (Babbit and Tanner, 1998; Nunes et al., 2010). To our knowledge, this is the first study to experimentally demonstrate that crayfish frequently cause nonlethal tail injury in larval anurans; however, crayfish presence has been shown to increase tail injury rates in natural wetlands (Nunes et al., 2010). Tail injury in larval anurans reduces swimming velocity and travel distances, which increases an injured tadpole's susceptibility to future predation attempts by crayfish (Figiel and Semlitsch, 1991) and other predators (Semlitsch, 1990).

Despite the negative impacts of crayfish on overall tadpole survival, leopard frog tadpoles grew larger when a crayfish was present. This is likely because of reduced intraspecific competition, which has been shown to increase tadpole growth rates when predators are present (Morin, 1983, 1987; Babbit and Tanner, 1998). We also observed a general trend of increasing leopard frog tadpole size when vegetation was present, although this relationship was less consistent, possibly because of random bias associated with measuring only 10 tadpoles each week. Even though both increases in tadpole size were small, they suggest that more resources were available to the surviving individuals in predator treatments (because of reduced competition) and when herbaceous vegetation was present (possibly because of increased surface area for algal growth). This is reinforced by the larger size of tadpoles from treatments with a predator and high vegetation than in tadpoles from other predator treatments. The lower percentage of tail injury in the high vegetation treatment also could have allowed these tadpoles to grow faster by spending less energy regenerating their tails. Increases in growth rate when accompanied by increases in development rate can provide important ecological advantages, especially in ephemeral wetlands where metamorphosing faster decreases the potential for mortality from drying events (Skelly, 1997).

In both experiments, we failed to detect any interactions between crayfish presence and the amount of vegetation. This was somewhat expected for leopard frogs because they are a generalist species that can breed in a variety of wetland types ranging from heavily vegetated wetlands to unvegetated borrow pits. Leopard frogs may be poorly suited to taking advantage of potential refugia offered by aquatic vegetation. On the contrary, we expected interaction effects for Ornate Chorus Frogs because this species breeds almost exclusively in wetlands dominated by herbaceous vegetation. In this case, our sample size was perhaps too small to detect any differences that may have existed, given the complete mortality in most tanks with crayfish by week 4. Furthermore, starting the experiment with larger tadpoles (because of an inability to locate *P. ornata* egg masses) may have limited the effects on growth that could be observed. Growth rates also slowed during the second half of both experiments, and tadpoles in both experiments likely were food-limited. Wilbur and Fauth (1990) indicated that leopard frog tadpoles can become crowded in mesocosm experiments at around one tadpole per 2 L, which is similar to the initial densities in our second experiment.

Aquatic vegetation and habitat complexity can have differing effects on predator–prey interactions depending on the type of predator involved in the interaction (Figiel and Semlitsch, 1991; Lefcort and Eiger, 1993; Davis et al., 2012). Crayfish generally employ a sit-and-wait strategy that allows them to effectively capture prey in diverse environments (Gherardi et al., 2001). Our results demonstrated that crayfish are equally effective predators regardless of the amount of herbaceous vegetation present in a wetland. In ephemeral wetlands, the ability of crayfish to persist through dry periods by burrowing to reach the water table allows them to rapidly recolonize wetlands after they fill, which allows them to effectively exploit prey in newly filled wetlands. Further, we demonstrated that encounters between crayfish and tadpoles often result in nonlethal tail injury, which may increase susceptibility to future predation events (Semlitsch, 1990; Figiel and Semlitsch, 1991).

We did not find an effect of reduced herbaceous vegetation cover on tadpole growth or survival in the presence of a predatory crayfish. Herbaceous vegetation tended to increase growth rates, but this effect was weaker than expected, and using artificial vegetation eliminated any potential benefits from increased DO or primary production. These two effects are likely important for anuran larvae in natural wetlands. Increased growth rates are important in ephemeral wetland systems because rapid growth may allow tadpoles to develop faster and shorten time to metamorphosis, allowing them to leave wetlands before they dry. Further, metamorphosing at a larger size may increase fitness by allowing earlier reproduction, higher survival (Smith, 1987), larger adult body size, or a combination of these, all of which are tied to higher reproductive output in anurans (Howard, 1978). Finally, even though crayfish appear to be efficient predators regardless of vegetation structure, decreased herbaceous vegetation cover through loss of natural fire regimes could still negatively affect amphibians by reducing suitable breeding habitat, reducing the amount of food available for anuran larvae, and altering wetland hydrology (Bishop and Haas 2005; Gorman et al., 2009; Gorman et al., 2013).

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