



RESEARCH ARTICLE

Refining the activity level-predation risk paradigm in larval anuran communities

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Abstract

The activity level-predation risk paradigm of community assembly is based on observable trade-offs between activity level and predation risk. Many species that live in ephemeral habitats are relatively more active, grow faster, and metamorphose sooner than those in more permanent habitats, thus enabling them to survive by escaping drying ponds. Species with high activity levels are shown to be superior competitors in temporary ponds, but are at greater risk of predation by visually cued predators. We take a comprehensive approach to testing if the activity-predation paradigm drives community assembly of a four-species guild of larval anurans through field surveys and a series of laboratory experiments quantifying their activity level, anti-predatory responses, swim performance, and escape behavior. Activity level was a good predictor of susceptibility to predation and habitat association for most species in our study, but not all species fit the pattern. Secondary anti-predator mechanisms contributed to differences in susceptibility to predation. Some species were more capable of avoiding predation through swim performance and escape behavior, thus allowing them to occupy a greater range of the water permanency continuum than was predicted by activity level alone. Because performance traits are deeply rooted, evolutionary history plays a major role in determining tadpole performance and life-history traits. Whole-organism performance traits (e.g., swim performance, escape behavior) have not generally been considered in the classic activity-predation paradigm. Our results show that accounting for individual and species-level performance reveals the understudied, yet important role of species-specific performance traits in disentangling the mechanisms driving community assembly.

Keywords Community assembly · Whole-organism performance · Predator–prey interactions · Hydroperiod gradients · Anti-predator behavior

Introduction

Understanding of how ecological communities are assembled in freshwater habitats has been advanced through two major, parallel, lines of research. The activity-predation paradigm relies on knowledge of how tradeoffs between the

activity level of organisms and its relation to risk of predation influences the ability of species to persist in a community (Skelly 1995). In parallel, the hydroperiod-predation paradigm explains community assembly in terms of abiotic and biotic drivers of community membership (Wellborn et al. 1996; Skelly 1997). Species membership in communities is correlated with gradients of water permanency (abiotic driver) because of increasing risk of predation (biotic driver) in more permanent water. On this ecological stage, organisms' activity levels strongly influence interspecific competition and susceptibility to predation along the hydroperiod gradient (Anholt and Werner 1995; Skelly 1995, 1997; Wellborn et al. 1996; Stoks and McPeck 2003; Richter-Boix et al. 2007; Gleason and Rooney 2017; Lent and Babbitt 2020). Constraints posed by drying aquatic habitats are an important cause of mortality for many organisms that inhabit freshwater systems (Smith 1983; Banks and Beebe 1988; Chandler et al. 2016a, b) and have profound effects

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on the structure and function of ecological communities. Amphibious vertebrates that develop relatively slowly with long larval stages are constrained from using ponds that dry quickly, whereas completely aquatic forms, like most fish, are constrained from sites that dry with any frequency over longer time scales (Wellborn et al. 1996). However, some vertebrates, in particular amphibians, possess life-history traits that allow them to thrive in ephemeral aquatic environments (Werner and Anholt 1993).

In freshwater environments, a gradient of predator richness is typically correlated with water permanency (Werner and McPeck 1994; Werner et al. 2007). Woodward (1983), for example, found more predator species and more individual aquatic predators per cubic meter in permanent ponds than in temporary ponds. Moreover, experiments demonstrate that predators in these systems affect the distribution of prey species locally and across landscapes (Wilbur 1972; Morin 1981; Dayton and Fitzgerald 2001; Pintar and Reseratis 2017).

Tadpoles of many anuran species that live in ephemeral habitats are relatively more active to procure resources, grow faster, and metamorphose sooner, thus enabling them to complete their life cycle in drying ponds (Lawler 1989; Skelly 1992; Pujol-Buxó et al. 2016; Schalk 2016; Schiwitz et al. 2020). However, species with high activity levels that have high fitness in temporary ponds (Ludwig and Rowe 1990), are at greater risk of predation from visually cued predators that are more common with increasing hydroperiod (Woodward 1983; Lawler 1989; Richards and Bull 1990; Skelly 1994, 1995; Smith and Van Buskirk 1995; Dayton and Fitzgerald 2011). Some larval anurans exhibit phenotypic plasticity across heterogeneous environmental gradients, which also influences site-specific competition and predation. Phenotypic responses include changes to morphology (e.g., deeper tail fins) or behavior, such as reduced activity (Schalk 2016; Ramamonjisoa et al. 2018a, b, 2019). However, reduction of activity level is costly because it reduces resource acquisition (i.e., feeding) and consequently slows growth and development (Richter-Boix et al. 2007; Schiwitz et al. 2020). The constraints of hydroperiod are relaxed in species adapted to more permanent ponds. These species can rely on reduced activity to avoid predation because the cost of a slower growth rate is mitigated by reduction in detection by predators and longer time spent in the larval stage (Richter-Boix et al. 2007; Pujol-Buxó et al. 2016).

Herein, we take a comprehensive approach to testing the central hypothesis of the predation-hydroperiod paradigm, that activity and predation tradeoffs drive community assembly of a winter-breeding guild of four anuran species. By determining breeding site associations for a guild of species, we test the prediction of habitat segregation among species according to the hydroperiod gradient. The hypothesis predicts that species in ephemeral habitats should have higher

activity levels and be more susceptible to predation than their counterpart species that occupy more permanent water sites. We test this by quantifying measures of whole-organism performance in controlled laboratory trials, variables of tadpole swim performance and success at evading predators (escape performance). This approach allows us to account for individual and species-level performance when identifying mechanisms that explain anuran community composition. Our findings show the importance of including traits related to performance that enhances our understanding of how the predation-hydroperiod paradigm and activity-predation tradeoffs work to assemble aquatic communities.

Methods

Study system description

We collected field data on the larvae of four winter-breeding anuran species that commonly occur in second-growth loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) dominated forests in eastern Texas: Spring peeper (*Pseudacris crucifer*: Hylidae), Cajun chorus frog (*Pseudacris fouquettei*: Hylidae), southern leopard frog (*Rana sphenoccephala*: Ranidae), and Hurter's spadefoot (*Scaphiopus hurterii*: Scaphiopodidae). *Anax junius* (Odonata: Ashmeidae) larvae, the focal predator in this study, are sit-and-wait predators (Brockelman 1969; Skelly and Werner 1990) that generally require movement to detect prey and elicit an attack (Oakley and Palka 1967; Kanou and Shimozawa 1983).

Breeding site associations

All native anurans that occur in eastern Texas lay their eggs in an aquatic environment where they hatch into tadpoles and live as larvae until metamorphosis (Altig and McDiarmid 2015; Powell et al. 2016). This allowed us to effectively document the community composition of multiple locations for the presence of tadpoles. We surveyed 75 aquatic sites in Houston, Nacogdoches, and San Augustine Counties in eastern Texas for evidence of anuran breeding from 15 January 2001 through 15 March 2001. At smaller sites with little or no vegetation structure, we were able to completely sample the anuran community composition of the site in one sweep of a net, but at larger, deeper sites we spent up to 30 min sampling (up to 50 net sweeps) the littoral zone (Skelly and Richardson 2010). Once tadpoles were captured, they were identified to species and released.

We estimated pond length, width, depth and soil type for each site, and estimated length of time the pond would hold water to develop basic categories of breeding site use by winter breeding anurans in eastern Texas. These categories are intended for reference and to add context to existing

distributions of anuran populations. This is in contrast to the approach of measuring the hydroperiod of a wetland at a particular point in time that would reflect dependence on exogenous factors, such as frequency and volume of rain and exposure to evaporation, that are independent of pond attributes.

Tadpole experiments

We conducted independent movement trials that included a range of tadpole sizes and developmental stages (Gosner 1960) for each of the four tadpole species. Egg masses and tadpoles were collected within Houston, Nacogdoches, and San Augustine Counties in eastern Texas and maintained in the lab under identical conditions until used in experiments. Tadpoles were kept in dechlorinated, aged tap water and fed tropical fish food flakes (48% crude protein). One ration was roughly equivalent to 10% of a tadpole's body weight (Alford and Harris 1988). The tadpoles were kept under fluorescent lights on a photoperiod that matched actual daylight hours.

Tadpole movement

For the movement trials, seventy-five 3-L plastic tubs ($19 \times 19 \times 33.5$ cm) were filled with 2 L of dechlorinated tap water at room temperature (21 °C). Four conspecific tadpoles were placed into each of the 75 tubs and were allowed to acclimate for 30 min. There was a range of tadpole sizes among tubs, but equal-sized tadpoles within tubs. All tadpoles were fed 1 h prior to trials to standardize hunger levels, but no food was provided during trials. After acclimatization, each tub was sampled by a single observer closing their eyes and upon opening them, counting the number of tadpoles moving in each tub the instant the tub was first viewed (Skelly 1995). Each tub was observed every 30 min for a total of five observations per tub. All trials took place between 0800 and 1430 h. Immediately following the trials, we measured the tadpoles and determined developmental stage (Gosner 1960) for all individuals. Using the mean proportion of tadpoles moving per tub as the response variable, our data indicated that *S. hurterii* tadpoles increased in activity as they grew and developed, while the other species in the experiment showed no interactions between activity and growth (see Saenz 2004). The differences in slopes between the species meant that our data did not meet the assumptions for ANCOVA with all of the species, so *S. hurterii* was excluded from species comparison analysis in the movement experiment. Analysis of covariance was used to determine the effects of size/age on the proportion moving for the remaining three species. The slopes of the covariates were not significantly different from zero ($P > 0.05$), therefore the model reduced to a one-way analysis of variance.

Differences in species proportion moving were determined by pairwise differences in least squares means with a Tukey adjustment ($\alpha \leq 0.05$).

Susceptibility to predation

Multiple species predation trials

We placed one tadpole of each of the four species and an *A. junius* naiad in a 3-L tub filled with dechlorinated water (21 °C). Tadpoles used in the experiment ranged in size from 20 to 30 mm in total length; however, tadpoles in a given tub did not differ by more than 2 mm total length. While the sizes of the tadpoles used in this experiment did not differ in size across species, developmental stages did differ. All of the *R. sphenoccephala* tadpoles used in the experiment were Gosner stage 26 but the three other species ranged from stage 28–37. *Anax junius* larvae varied greatly in size (30–60 mm total length) and developmental stage (third through fifth instar), but all sizes of naiads used in our experiment could have easily dispatched the small tadpoles chosen for the trials. All *A. junius* larvae were randomly selected for each trial. The four tadpoles were placed into the tub and allowed to acclimate for 30 min before introducing the naiad. The naiad was gently released into the tub to avoid startling the tadpoles and the dragonfly naiad. Disturbing the tadpoles could alter their behavior, which in turn could affect their susceptibility to predation, and disturbance to the naiad could affect its motivation to feed.

The experiment lasted until one tadpole in a given tub was captured and eaten by the dragonfly naiad ($n = 129$ replicates). Naiads and uneaten tadpoles were not reused in other trials. The captured species was assigned a value of one and the other three species were assigned a value of zero. We used a logistic regression model with species as a categorical predictor, to model the probability of being eaten first to compare the susceptibility of the four species while in the presence of each other.

Relationship between activity levels (stimulus) and susceptibility to predation

We calculated cumulative total movement for all four species in the movement experiment, which we predicted would equal the total amount of stimulus that the tadpoles provide to potential predators. We then calculated the proportion of the total stimulus (proportion moving) contributed by each species. We predicted the proportion of the stimulus (movement) should reflect the relative susceptibility of each species to predation in the multiple species predation trials. We tested the null hypothesis that the proportion of stimulus (tadpole movement) contributed by each species would be similar to the proportion of tadpoles eaten first in the

multiple species predation trials (Chi-square analysis for specified proportions $\alpha \leq 0.05$).

Single species escape performance

We tested the relative abilities of the four tadpole species to escape predation. We did this by placing four tadpoles of a single species and a randomly selected *A. junius* naiad in a 3-L tub filled with dechlorinated water (21 °C). In each tub, we visually counted the total number of predation attempts by the naiad in pursuit of a tadpole until a tadpole was captured in that tub or until 30 min had passed. Dragonfly naiads in the family Ashmeidae extend their spiny labium in a quick strike manner to ensnare a prey item (Pritchard 1965). Recording of a predation attempt started when a naiad extended its labium in an attempt to capture a tadpole; however, the attempt was not complete until the naiad became motionless and had abandoned pursuit of the tadpole. Therefore, a single attempt could have included several strikes with the labium in a single pursuit, but a chase was not counted if a strike was not made with the labium. Trials where no successful predation event was recorded were not included in the analyses.

We determined the number of dragonfly larvae attacks made prior to a successful predation event by visual observation. The experiment was repeated for each of the four species; *R. sphenocéphala* ($n=30$ replicates), *P. crucifer* ($n=29$ replicates), *P. fouquettei* ($n=33$ replicates) and *S. hurterii* ($n=33$ replicates). We used a one-way ANOVA general linear model with a Poisson distribution ($\alpha \leq 0.05$) to compare the mean number of attacks made by naiads to capture a tadpole of each of the four anuran species. Tadpoles used in this experiment ranged in size from 23 to 27 mm in total length, but mean tadpole size was similar among species.

Escape performance

Individual tadpoles were placed in approximately 10 L of water in a 100 cm \times 40 cm glass arena and allowed to acclimate for 1 min. We probed the proximal end of the tail of each tadpole with a sharp dissecting probe to simulate an attack. Responses were recorded using a digital camcorder placed 2 m above the enclosure. Each tadpole was filmed from the time of the simulated predation attempt until the tadpole stopped moving. We excluded trials when the tadpole moved into the glass edge of the arena as it interrupted their escape path. For each trial ($n=30$ replicates per species) we calculated sprint speed, net and total distance traveled, time spent during escape move, and complexity of escape trajectories.

We calculated sprint speed (m/s) by measuring distance traveled by each individual tadpole during the first 0.2 s immediately after a simulated attack. We used one-way

ANOVA general linear model with a Poisson distribution, followed by a Tukey's multiple range test ($\alpha \leq 0.05$) to test the hypothesis that sprint speeds did not differ among species. Length of the escape moves was calculated three different ways. First, the length of time a tadpole moved after a simulated attack was measured to the nearest 0.01 s. Then total distance traveled was measured to the nearest 0.01 mm for the entire escape move. Finally, the net escape distance (the straight-line distance from the point where the tadpole started its escape move to the point where it stopped) was measured to the nearest 0.01 mm. All trials started when the tadpole was first prodded and ended when the tadpole came to rest. We used one-way ANOVA general linear model with a Poisson distribution, followed by Tukey's multiple range tests ($\alpha \leq 0.05$) to test the hypothesis that the length of evasive movements (length of time moving, total escape distance, net escape distance) did not differ among species.

Escape patterns were analyzed by projecting movements onto a grid with 5 mm \times 5 mm cells, and converting the paths into a series of x, y coordinates. Coordinates were recorded every time the path crossed a grid line or turned. We estimated the complexity of each escape path using the fractal dimension (D) calculated by the basic dividers method (Dicke and Burrough 1988). We used the mean value by calculating D numerous times (1000 bootstrap replications) based on a randomly selected starting point (Nams 1996). Values range from 1 for a straight path to 2 for a plane-filling path. We used a one-way ANOVA followed by a Tukey's multiple range test ($\alpha \leq 0.05$) to test the hypothesis that the complexity of escape maneuvers did not differ among species.

Results

Breeding site associations

We classified 75 surveyed sites according to three major hydroperiod types used by the four winter-breeding species. Species used different parts of the hydroperiod gradient, however, no tadpoles of the four species were collected from permanent water sites. The first and the rarest type of site was a single "extremely short" duration site. The site was large, 600 m², but was on well-drained soil and did not hold water for more than a few days except for instances of flood-level rain events. The next type was the "short duration" site. This was the most common type of site comprising 66 of the 75 total sites. The short duration sites were small, extremely abundant, and very unpredictable. Many were tree tip-overs, road ruts, or roadside ditches as small as 2 m². These would fill with a single rain event and could appear rapidly by some random event such as a tree fall. Clay-rich soils allowed them to hold

water for several weeks to months. The final type was the “seasonal site.” The eight seasonal sites were large, ranging from 500 m² to 2 ha in surface area, located on poorly drained soils, and held water for at least 6 months. Often these sites required several rain events to collect a sufficient amount of water for successful anuran breeding.

Scaphiopus hurterii tadpoles were only observed in the single extremely short duration breeding site and did not co-occur with any other species of tadpoles (Table 1). *Pseudacris crucifer* tadpoles were observed only at the eight seasonal sites (Table 1). *Pseudacris crucifer* tadpoles co-occurred with *P. fouquettei* tadpoles in two of the seasonal sites and co-occurred in all 8 seasonal sites with *R. sphenoccephala* tadpoles. *Pseudacris fouquettei* was found in 39 sites, 37 of which were short duration sites and 2 seasonal sites. They co-occurred in two seasonal sites with *P. crucifer* and *R. sphenoccephala*. In the short duration sites, *P. fouquettei* co-occurred with *R. sphenoccephala* in 19 of 37 sites. We found *R. sphenoccephala* tadpoles at 48 sites (Table 1). This species overlapped with 100% of the sites used by *P. crucifer* and more than 50% of the sites used by *P. fouquettei*.

Tadpole movement

As predicted by species segregation along the hydroperiod gradient, and although they were not included in the model, *S. hurterii* tadpoles moved, on average, more than three times as much as either *P. fouquettei* or *R. sphenoccephala* (Fig. 1). *Pseudacris crucifer* moved less than 5 percent of the time during the experiment, significantly less than *P. fouquettei* and *R. sphenoccephala* ($F_{222} = 21.85$, $P < 0.001$). *Pseudacris fouquettei* used sites intermediate in permanency relative to *P. crucifer* and *S. hurterii*, reflecting the same pattern as their intermediate activity levels. However, *R. sphenoccephala* exhibited intermediate movement, but also occurred in sites near both ends of the hydroperiod gradient continuum.

Table 1 Percent of ponds by hydroperiod occupied by each species

Hydroperiod	Number of ponds	Percent of ponds			
		<i>Scaphiopus hurterii</i>	<i>Pseudacris fouquettei</i>	<i>Rana sphenoccephala</i>	<i>Pseudacris crucifer</i>
Days	1	100	0	0	0
Weeks to months	66	0	56	60	0
Seasonal	8	0	25	100	100

A total of 75 breeding sites were surveyed in Houston, Nacogdoches, and San Augustine Counties from 15 January through 15 March 2001

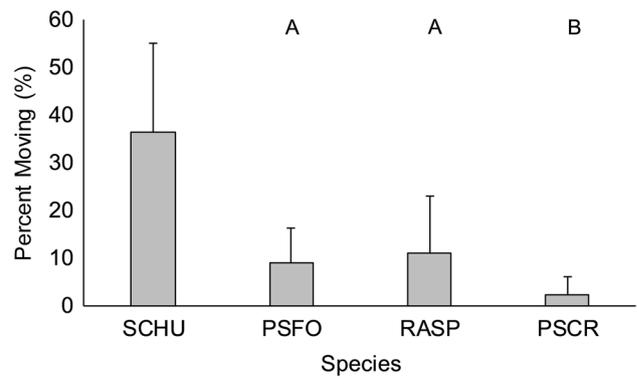


Fig. 1 Activity rates (\pm SE) of each anuran species in motion during movement trials. Letters above bars indicate significantly different subgroups ($P < 0.05$) according to Tukey’s post hoc tests. SCHU=*Scaphiopus hurterii*; PSFO=*Pseudacris fouquettei*; RASP=*Rana sphenoccephala*; PSCR=*Pseudacris crucifer*. *Scaphiopus hurterii* was not included in the statistical analysis because of violations of test assumptions

Susceptibility to predation

Multiple species predation trials

As predicted, and in concordance with the high activity levels of this species, the probability of a dragonfly naiad capturing and eating a *S. hurterii* tadpole first was greater than for the other three species (Wald $\chi^2 = 133.3$, $P < 0.001$). Independent contrasts showed the odds of being eaten first were greater for *P. fouquettei* tadpoles (intermediate activity levels) than *P. crucifer* (lowest activity levels) or *R. sphenoccephala* (intermediate activity levels) tadpoles. However, the odds of being eaten first were similar for *P. crucifer* and *R. sphenoccephala* tadpoles (Fig. 2).

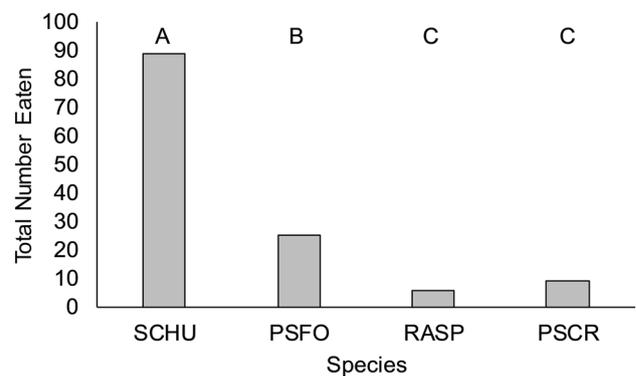


Fig. 2 Mean number of individuals (\pm SE) of each anuran species captured and eaten first by a dragonfly naiad during 129 trials. Letters over the bars indicate significantly different odds of being eaten first ($P < 0.05$). Species codes are listed in the Fig. 1 caption

Relationship between activity levels (stimulus) and susceptibility to predation

The proportion of movement contributed by each species was not a good predictor of predation risk ($\chi^2 = 18.1$, $P < 0.001$). However, upon closer inspection, it was apparent *R. sphenoccephala* showed the unique combination of intermediate activity levels and low susceptibility to predation (Fig. 3a). When *R. sphenoccephala* data were omitted, the results ($\chi^2 = 1.4$, $P = 0.496$) indicated that movement was indeed a good predictor of susceptibility to predation (Fig. 3b).

Single species escape performance

Tadpoles showed marked differences in their ability to escape a predator's attack from *Anax junius* naiads ($F_{3,121} = 121.08$, $P < 0.001$). Dragonfly naiads averaged 4.25 attacks before successfully capturing a *R. sphenoccephala* tadpole. Dragonfly naiads were most efficient at capturing *S. hurterii* tadpoles, with over one half of all attempts resulting in a successful predation event. The ability to escape

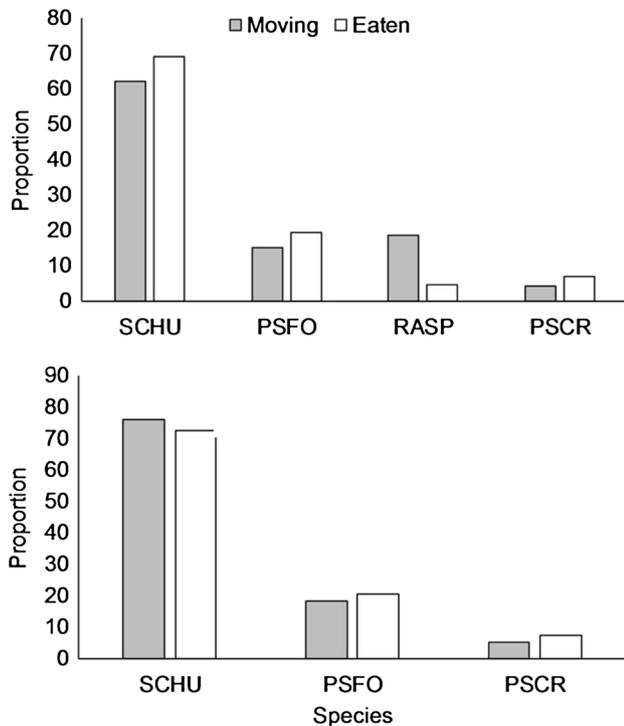


Fig. 3 **a** Percent of total movement contributed by each anuran species during movement trials compared to the percent of total tadpoles eaten first in the multiple species predation experiment. All species included. **b** Percent of total movement contributed by each species during movement trials compared to the percent of total tadpoles eaten first in the multiple species predation experiment. *Rana sphenoccephala* excluded. Species codes are listed in the Fig. 1 caption

predation was intermediate for *P. crucifer* and *P. fouquettei* tadpoles (Fig. 4).

Escape performance

After a simulated attack, species differed in escape speed ($F_{4,116} = 18.1$, $P < 0.001$). *Rana sphenoccephala*, *P. fouquettei*, and *P. crucifer* tadpoles did not differ from each other in their escape speed, but all three tadpoles exhibited greater escape speed than *S. hurterii* (Fig. 5). The duration of escape moves differed significantly among the species ($F_{4,103} = 6.39$, $P < 0.001$). *Scaphiopus hurterii* tadpoles moved significantly longer after the simulated predation attempts than the other three species. *Rana sphenoccephala*, *P. crucifer* and *P. fouquettei* tadpoles did not differ in the length of time spent moving after a simulated attack (Fig. 6a).

Total distance traveled from the point of the simulated attack also differed significantly among the species ($F_{4,103} = 5.08$, $P = 0.002$). *Pseudacris fouquettei* and *S.*

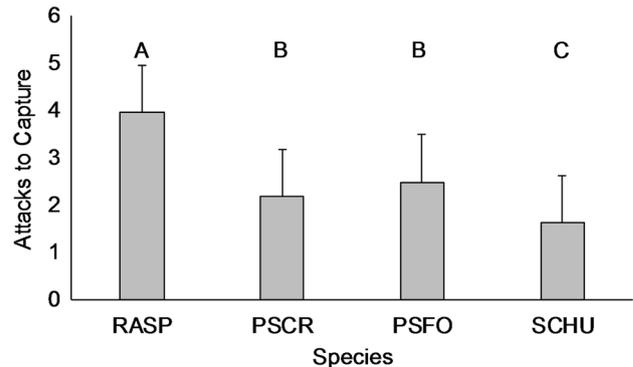


Fig. 4 Mean number (\pm SE) of individual attacks by a dragonfly naiad per successful capture of a tadpole. Different letters over the bars represent significantly different subgroups based on Tukey's post hoc tests ($P < 0.05$). Species codes are listed in the Fig. 1 caption

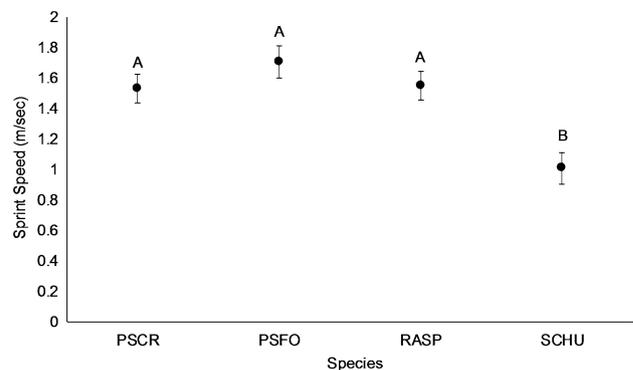


Fig. 5 Mean sprint speed (m/s \pm SE) of each tadpole species during the first 0.2 s of their escape move. Letters over the bars represent significantly different subsets in sprint speed according to Tukey's post hoc tests. Species codes are listed in the Fig. 1 caption

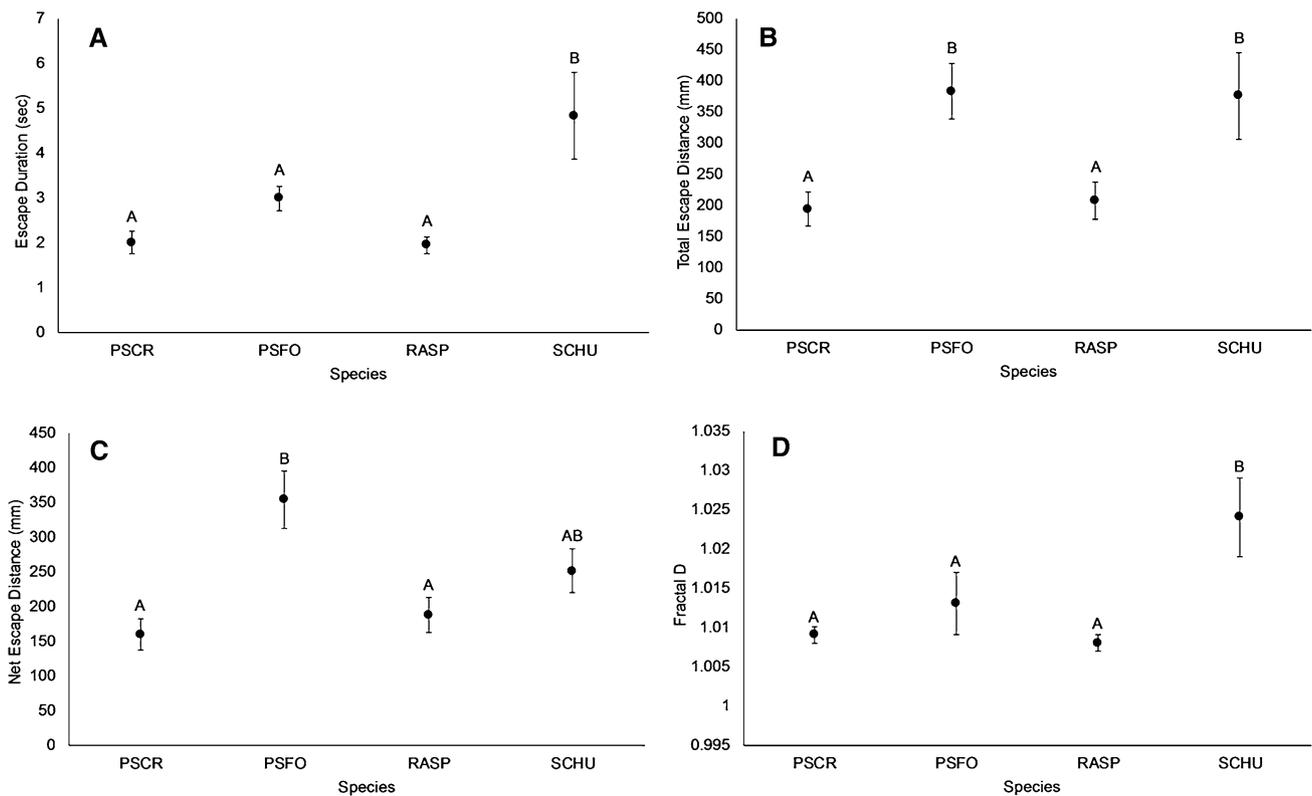


Fig. 6 **a** Mean duration in seconds (\pm SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets identified by Tukey's post hoc tests. **b** Mean total distance in millimeters (\pm SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets in the total distance of escape moves identified by Tukey's tests. **c** Mean net distance in millimeters (\pm SE) of the escape

move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets in the net distance of escape moves identified by Tukey's tests. **d** Mean fractal dimension (D) values (\pm SE) of the escape move by each tadpole of each species during the escape behavior experiment. Letters over the bars represent significantly different subsets of mean D identified by Tukey's tests. Species codes are listed in the Fig. 1 caption

hurterii tadpoles did not differ from each other in distance moved and moved significantly farther after being attacked compared to the other two species. *Pseudacris crucifer* and *R. sphenoccephala* tadpoles moved shorter distances and did not differ from each other (Fig. 6b).

The net escape distance from the point of the simulated attack to the point where the tadpole stopped moving differed significantly among species ($F_{4,103} = 7.90$, $P < 0.001$). Results for straight-line differences were similar to the results from the total escape distance comparisons. *Pseudacris fouquettei* ended its escape move farther from the point of the simulated attack than *R. sphenoccephala* or *P. crucifer* but did not differ from *S. hurterii*. *Pseudacris crucifer*, *R. sphenoccephala*, and *S. hurterii* tadpoles did not differ from each other in net distances traveled in their escape paths (Fig. 6c).

Path complexity during escape moves varied markedly among the species ($F_{4,103} = 4.94$, $P = 0.003$). *Scaphiopus hurterii* took significantly more tortuous paths than the other three species of tadpoles. *Pseudacris crucifer*, *P. fouquettei*,

and *R. sphenoccephala* did not differ significantly in the tortuosity of their escape paths (Fig. 6d).

Discussion

The idea that the distribution of populations across the hydroperiod continuum is limited by tolerances to pond drying and predator-prey interactions is a commonly accepted paradigm in freshwater community assembly (Heyer et al. 1975; Werner and McPeck 1994; Smith and Van Buskirk 1995; Dayton and Fitzgerald 2001; Schiwitz et al. 2020; Tavares-Junior et al. 2020). Evidence from this study suggests that these paradigms are applicable to the winter breeding anurans in eastern Texas, however, there are some notable inconsistencies in this guild that were revealed by measures of activity, swim performance, and escape performance.

In the field, the species differentially used portions of the hydroperiod gradient with some overlap in pond

use. This was not unexpected since Skelly (1996) found a high frequency of co-occurrence between *P. crucifer* and *P. triseriata* in southeastern Michigan. However, the large variation in their relative abundances over a range of pond types suggests these two species differed in their ability to cope with pond drying and predators (Skelly 1996). The association between ephemeral breeding sites and *S. hurterii* has been known for decades (Bragg 1944, 1967; Hansen 1958; Palis 2005). Several other studies also demonstrated segregation in tadpole species along the hydroperiod gradient, and pond drying and predation were identified as the major mechanisms controlling community assembly (Heyer et al. 1975; Werner and McPeck 1994; Skelly 1995; Smith and Van Buskirk 1995; Pujol-Buxó et al. 2016; Kloskowski et al. 2020).

Activity rates of tadpoles have been correlated to occupancy of different portions of the hydroperiod continuum, with increasing activity levels corresponding to decreasing water permanency (Morin 1983; Woodward 1983; Bridges 2002; Werner et al. 2007; Schiwitz et al. 2020). Higher activity levels may reflect selection for positive benefits of higher growth rates (Lent and Babbitt 2020), greater competitive ability, and faster development leading to a decreased susceptibility to mortality due to pond drying (Skelly and Werner 1990; Werner 1991, 1992; Skelly 1995; Touchon et al. 2015). Activity levels among the species in our study followed the expected pattern, with more ephemerally associated species moving a greater proportion of the time than more permanently associated species.

Rana sphenoccephala tadpoles inhabited a wide range of habitats with regard to water permanency. They had higher activity levels than *P. crucifer*, with whom they overlapped in pond use in more permanent sites and similar activity levels to *P. fouquettei* tadpoles with which they overlapped in site use in more ephemeral ponds. It is possible that pond drying may be a stronger constraint than the risk of predation because a dry pond means certain death while the presence of predators does not. Therefore, *R. sphenoccephala* tadpoles must conform to ephemeral pond activity levels by moving more so that they can more quickly acquire energy for rapid development.

Several studies have described the trade-offs between activity levels and susceptibility to predation, in which high activity allows existence in ephemeral ponds with few predators while low activity allows coexistence with predators in permanent ponds (Woodward 1983; Skelly 1996; Bridges 2002). Encounter rates with predators are likely to increase with increased activity and play a major role in a species' susceptibility to predators (Abrams 1991; Werner and Anholt 1993; Pacheco et al. 2019; Zlotnik et al. 2018; Start 2020). The means by which prey might be detected are either visual (McPeck 1990; Espanha et al.

2016) or via mechanosensory stimulation (Kanou and Shimozawa 1983; Richards and Bull 1990).

Activity rates of anurans in our study did not predict relative susceptibility to predation to the extent we expected. In particular, *Rana sphenoccephala* tadpoles did not fit the expected pattern because they exhibited greater secondary antipredator abilities (i.e., ability to escape predation post-attack) than the other species.

Rana sphenoccephala tadpoles have activity levels similar to *P. fouquettei* that are high enough to allow rapid growth and development sufficient for successful metamorphosis in more ephemeral sites. However, *R. sphenoccephala* tadpoles have low susceptibility to predation by *A. junius* naiads, similar to *P. crucifer*, which allows them to exist in more permanent sites. We suggest the anti-predator mechanisms that allow *R. sphenoccephala* and *P. crucifer* tadpoles to coexist with predators in the more permanent sites differ. *Pseudacris crucifer* tadpoles seem to rely on primary antipredator mechanisms to escape predation (e.g., crypsis; Huffard 2006). Their activity levels are low compared to the other species in this guild; therefore, they should have fewer encounters with predators (Schiwitz et al. 2020). However, their ability to escape predation subsequent to an attack is not better than *P. fouquettei* tadpoles that inhabit more ephemeral sites. Secondary antipredator abilities, by contrast, likely allow *R. sphenoccephala* to exist in the more permanent sites even though they have high activity rates compared to *P. crucifer* (Huffard 2006; Schiwitz et al. 2020). Higher activity in *R. sphenoccephala* should increase encounters with predators, but they are not more susceptible to predation due to their greater ability to escape an attack. It has been suggested that ephemeral site use is likely derived in *R. sphenoccephala*, and it is intriguing to speculate that escape behavior is possibly due to ancestral adaptations to permanent sites (Saenz 2004).

In addition to activity levels, differential abilities to escape predation attempts are known to be important factors determining distributional differences in some anurans (Werner and McPeck 1994; Touchon and Vonesh 2016). Caldwell et al. (1980) conducted escape behavior experiments with *Hyla gratiosa* and found that upon being prodded tadpoles moved away quickly then became immobile shortly thereafter. They concluded it would be advantageous to a tadpole to escape quickly then stop when pursued by an *Anax* predator because they hunt visually and might not be able to relocate their prey. *Rana sphenoccephala* tadpoles seemed to employ the same strategy in this study. This “run and freeze” strategy may be quite prevalent and effective in amphibians (Matich and Schalk 2019).

We were able to control size differences in our experiments, however, *R. sphenoccephala* attain much greater size than the other species in our study and several researchers have suggested that risk of predation to tadpoles decreases as size increases (Caldwell et al. 1980; Smith 1983; Travis

et al. 1985; Cronin and Travis 1986; Werner and McPeck 1994; Gazzola et al. 2017; Ramamonjisoa and Mori 2019). Caldwell et al. (1980) found the tadpoles most vulnerable to predators were the smallest individuals (less than 30 mm total length). Pritchard (1965) demonstrated that the dragonfly, *Aeshna interrupta*, would not attack a disc that was greater than 20 mm² which is greatly exceeded by *R. sphenoccephala*. Had the complete range of sizes of *R. sphenoccephala* tadpoles been used in this study, or had we standardized trials by tadpole developmental stage, the likely outcome would have been an even greater disparity in the abilities of the tadpoles to escape predation. Larger *R. sphenoccephala* tadpoles would undoubtedly have been stronger and faster making them even less vulnerable to predation (Dayton et al. 2005; Johnson et al. 2015).

Rana sphenoccephala is part of a clade of anurans associated primarily with permanent breeding sites (Saenz 2004; Hillis and Wilcox 2005). These sites are known to have a greater variety and density of predators, and the increased diversity of predators may require a more diversified system of tadpole defenses (Woodward 1983). The large size and greater escape ability are likely two consequences of phylogeny, meaning that most species in this clade are large and likely possess a diversity of defenses. We suggest *R. sphenoccephala* may be a recent member of the ephemeral pond breeding community and secondary antipredator mechanisms the species possesses are plesiomorphic traits. Given their phylogenetic history (Hillis and Wilcox 2005), it seems plausible that *R. sphenoccephala* possess secondary antipredator abilities that are more developed compared to other members of the winter breeding guild.

The other three species in this study belong to taxonomic groups that are associated primarily with ephemeral breeding sites that tend to have fewer predators (Saenz 2004). Their predator defenses tend to be simpler than that of *R. sphenoccephala* where primary antipredator mechanisms accurately explain the observed patterns of habitat association and predator vulnerability. While habitat associations most certainly play a role in determining functional relationships among species, they alone are not adequate to make predictions about membership in ecological communities. This study demonstrated through rigorous testing of the predation-hydroperiod paradigm the probable mechanisms responsible for structuring the winter-breeding community of anurans in eastern Texas. In addition to the complex interplay among both primary and secondary antipredator behaviors and susceptibility to predation, it is likely that evolutionary history also plays a major role in determining tadpole performance and life-history traits.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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