

Activity Level-Predation Risk Tradeoff in a Tadpole Guild: Implications for Community Organization Along the Hydroperiod Gradient

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ABSTRACT.—Increasing activity levels permit greater food intake for use towards growth and reproduction, consequently increasing predation risk via increased detection. Larval anurans are models to examine activity level-predation risk tradeoffs, as they occupy a variety of lentic habitats that impose constraints on the distribution and abundance of species. Ephemeral ponds have a low abundance and diversity of predators and as a result tadpole species tend to have high foraging rates for rapid development. Permanent ponds generally possess a greater diversity and abundance of predators and tadpoles inhabiting these locations tend to have low activity rates or chemical defenses to minimize predation risk. The objective of this research was to examine how interspecific variation in activity level and response to predation risk, corresponds to the distributions of tadpole species along the hydroperiod gradient. Furthermore, we examined the intraspecific variation in activity level among the species. We conducted a series of laboratory experiments in which we quantified baseline activity patterns and the change in activity after the addition of a predator or exposure to alarm cues, for 12 species of larval anurans native to East Texas. Species that maintained a high activity level generally occupied ephemeral ponds and species that maintained low activity levels generally occupied permanent ponds. Only one species (*Gastrophryne carolinensis*) decreased their activity level in the presence of predator cues or conspecific alarm cues. These results highlight this tradeoff can have consequences on the life histories of multiple species, providing insight into how it affects the organization of ecological communities.

INTRODUCTION

Ecological communities are organized along multiple abiotic (*e.g.*, precipitation, temperature) and biotic (*e.g.*, predation, competition) gradients that vary in strength across spatial and temporal scales (Cummins, 1975; Vannote *et al.*, 1980; McDonnell and Pickett, 1990; Ricklefs and Schluter, 1993; Mittelbach and McGill, 2012). Community organization in response to environmental gradients is widespread across multiple ecosystems and taxa, such as bacteria assembled along a salinity gradient (Shen *et al.*, 2018), early successional plant species distributed along a soil moisture gradient (Pickett and Bazzaz, 1978), and predation structuring desert rodent communities (Kotler *et al.*, 1994). Lentic aquatic habitats, in particular, have served as model systems to examine these patterns of community organization in response to environmental gradients (Wellborn *et al.*, 1996; Van Buskirk, 2002; Urban, 2004; Werner *et al.*, 2007; Schalk *et al.*, 2017).

Lentic aquatic habitats are arrayed along a gradient of permanency ranging from ephemeral ponds that last for only brief periods to permanent habitats that persist for millennia (Wellborn *et al.*, 1996). The mechanisms that structure species' distribution and

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the ecological communities of these lentic habitats vary in accordance with pond permanency (Skelly, 1997; Tarr *et al.*, 2005; Hoverman *et al.*, 2011). Larval anurans are an excellent model to explore this tradeoff as they occupy a multitude of habitats arrayed along a hydroperiod gradient (Wellborn *et al.*, 1996; Relyea and Werner, 2000). In ephemeral ponds the greatest source of mortality for species is pond drying that leads to tadpole desiccation. Larval anurans must maintain a high growth rate to develop rapidly in an environment that poses a high desiccation risk (Skelly, 1996). The demand of a high growth rate is achieved by maintaining a high activity level to maximize energy intake (Wellborn *et al.*, 1996). Compared to permanent ponds, temporary ponds have a lower abundance and diversity of predators (Heyer *et al.*, 1975; Tonn and Magnuson, 1982; Turner and Montgomery, 2009), allowing species to maintain high foraging rates for rapid development with minimal risk of interactions with predators (Skelly, 1996; Dayton and Fitzgerald, 2001; Smith *et al.*, 2004). Species found in permanent ponds face a lower risk of dessication but usually maintain a low activity rate and slower rate of development, due to a higher risk of detection by predators (Skelly, 1994). However, some species develop defense strategies in the form of chemical defenses, phenotypic plasticity (*e.g.* tail shape, color, and swim performance) and escape behavior that reduces their susceptibility to predation (Saenz, 2004; Hall, 2010; Adams *et al.*, 2011; Johnson *et al.*, 2015). For example some species in permanent ponds, such as the tadpoles of American bullfrogs (*Lithobates catesbeianus*), develop defenses in the form of noxious chemicals that are costly in terms of energy but allow individuals to co-exist with predators while maintaining a high activity level in the presence of predatory fish (Kats *et al.*, 1988; Adams *et al.*, 2011; Bókony *et al.*, 2016).

Ecological and developmental factors influence a species' behavior, and these behavioral responses can shape species interaction strengths that impact survivorship and distributions across the landscape (Werner, 1992; Chandrasegaran *et al.*, 2018; Gazzola *et al.*, 2018). These behavioral responses are influenced by several abiotic and biotic factors in the environment that change along the hydroperiod gradient (Werner and McPeck, 1994), including pond duration and predators (Heyer *et al.*, 1975). Furthermore, closely related species may evolve under different selective forces and consequently could display different adaptive traits to local environmental conditions (Richardson, 2001). For example Striped Chorus Frogs (*Pseudacris triseriata*) in Michigan were never found in permanent ponds and exhibited higher survival in ephemeral ponds compared to Spring Peepers (*P. crucifer*), which were more abundant in permanent ponds (Skelly, 1996). Other examples of general ecological patterns conforming to this paradigm include Couch's Spadefoot tadpoles (*Scaphiopus couchii*) in desert ephemeral pools (Dayton and Fitzgerald, 2001) and Wood Frogs (*Lithobates sylvaticus*) in temporary ponds of Michigan (Relyea and Werner, 2000), with both species exhibiting high activity levels in habitats with a high abundance of invertebrate predators. It is important to highlight these species-specific responses across habitats and ecosystems as they can help explain the differences in species composition along the hydroperiod gradient in each region, yet exhibit similar ecological patterns.

Some amphibian species are widely distributed across the United States and subsequently span multiple ecological communities. Within each community the spatiotemporal composition of competitors, predators, as well as available breeding habitats, vary producing context-dependent responses of certain behaviors, such as activity level. In this study we quantified the activity level of a larval anuran community in East Texas to understand how species-specific activity rates might correlate to the larval amphibian community structure across pond habitats. In addition we quantified activity level with an increasing risk of predation to understand how species respond to predatory threats. We

hypothesized species will differ in activity level based on pond association type, and individual species will decrease activity level with increasing predation risk, dependent on their predatory defenses.

METHODS

From April 2000 to July 2002, we periodically collected anuran egg masses and tadpoles that represented a wide range of body sizes and Gosner stages (GS range: 25–42) from ponds located in Houston, Nacogdoches, and San Augustine Counties in eastern Texas. We conducted behavioral trials on 12 species of larval anurans that represented five families: Ranidae (Bronze Frog [*Lithobates clamitans*], American Bullfrog [*L. catesbeianus*], Southern Leopard Frog [*L. sphenoccephalus*]); Hylidae (Spring Peeper [*P. crucifer*], Cajun Chorus Frog [*P. fouquettei*], Green Treefrog [*Hyla cinerea*], Gray Treefrog [*H. versicolor*], Blanchard's Cricket Frog [*Acris blanchardi*]); Microhylidae (Eastern Narrow-mouthed Toad [*Gastrophryne carolinensis*]); Bufonidae (Gulf Coast Toad [*Incilius nebulifer*], Woodhouse's Toad [*Anaxyrus woodhousii*]); and Scaphiopodidae (Hurter's Spadefoot [*Scaphiopus hurterii*]). Prior to their use in the experiments, we housed tadpoles at densities no greater than 10 individuals per liter of water in 3-l plastic tubs (19 × 19 × 33.5 cm) filled with dechlorinated aged tap water at a consistent room temperature (21 °C). We fed tadpoles tropical fish food flakes (48% crude protein) daily, where one ration was roughly equivalent to 10% of a tadpole's body weight. Tadpoles were maintained under fluorescent lights on a photoperiod that matched daylight hours.

Our activity experiment had three treatments, that averaged 64 replicates for each species (range: 15–75 replicates) totaling 2298 trials. The three treatments consisted of a predator-free treatment (*i.e.*, control) and two different predator treatments where tadpoles were exposed to different cues that corresponded to an increasing predation threat (*sensu* Schalk, 2016). Larval dragonflies (Family Libellulidae) were used as the predators in the experiment. Libellulids are predators occurring throughout ephemeral and permanent east Texas ponds (D. Saenz, pers. obs.) and are documented predators of larval amphibians (Babbitt and Tanner, 1998; Touchon and Vonesh, 2016). All experiments were conducted by placing tadpoles in 3-l plastic tubs (19 × 19 × 33.5 cm) filled with 2 L of dechlorinated aged tap water. In the nonlethal predator treatment, a predator was placed in a mesh cage (4.4 cm × 3.8 cm × 3.8 cm, mesh size = 2 mm) preventing direct access between the larval dragonfly and tadpoles but allowed chemical cues from the predator to be exchanged in the water. The mesh cage was present in all treatments to standardize effects the cage may pose on tadpole behavior. The lethal predator treatment consisted of exposing tadpoles to multiple cues, being the predator chemical cues plus an alarm cue from a consumed conspecific, with no dragonfly present. The cues were collected from a separate tub that contained a predator fed with a conspecific tadpole. Once a dragonfly larva began consuming a conspecific tadpole, we immediately collected 30 ml of water from that tub to introduce into each of the tubs containing the tadpoles.

Four conspecific tadpoles were placed into each of the tubs, aligned side by side in groups of five, and were allowed to acclimate for 30 min. There were a range of sizes among tubs, but equal sized tadpoles were placed within tubs. We did not feed tadpoles during the trials. However, we fed all tadpoles 1 h prior to trials to standardize hunger levels. After tadpoles were acclimatized, an observer quantified tadpole activity level in each tub by standing approximately 3 m away with their eyes closed and, upon opening them, counting the number of tadpoles moving (*i.e.*, tail movement) in each tub the instant the tub was first viewed (Skelly, 1995). Each tub was observed every 30 min for a total of five replicates. The

TABLE 1.—Larval period, pond type association, and defenses of the 12 species of tadpoles used in this study. Tadpoles were classified in being associated with ephemeral (E) or permanent (P) ponds. The presence and type of defenses included the presence of chemical defenses (C), escape behavior (E), and phenotypically plastic defenses such as changes in tadpole shape (P-S), color (P-C), and/or swim performance (P-P). Those species that lack defenses are designated N/A

Species	Species code	Average/range/ median length of larval period	Pond type association	Defense	Reference
<i>Acris blanchardi</i>	ACBL	70 d	P	P-S, P-C	Conant and Collins, 1998; Hall, 2010
<i>Incilius nebulifer</i>	INNE	20 d	E	C	Garrett and Barker, 1987; Adams <i>et al.</i> , 2011
<i>Anaxyrus woodhousii</i>	ANWO	35 d	P	C	Wright and Wright, 1949; Adams <i>et al.</i> , 2011
<i>Gastrophryne carolinensis</i>	GACA	23 d	E	N/A	Pechmann, 1994
<i>Hyla cinerea</i>	HYCI	55 d	P	P-S, P-C	Garrett and Barker, 1987; Saenz, pers. obs.
<i>Hyla versicolor</i>	HYVE	35 d	E	P-S, P-C	Ritke <i>et al.</i> , 1990
<i>Pseudacris crucifer</i>	PSCR	90 d	E	N/A	Garrett and Barker, 1987
<i>Pseudacris fouquettei</i>	PSFO	48-80 d	E	N/A	Livezey, 1952
<i>Lithobates catesbeianus</i>	LICA	365 d	P	C	Graves and Anderson, 1987; Adams <i>et al.</i> , 2011
<i>Lithobates sphenoccephalus</i>	LISP	67 d	E	E	Wright and Wright, 1949; Saenz, 2004
<i>Lithobates clamitans</i>	LICL	90 d	P	C, P-S, P-P	Conant and Collins, 1998, Johnson <i>et al.</i> , 2015
<i>Scaphiopus huerterii</i>	SCHU	14 d	E	N/A	Garrett and Barker, 1987

average proportion of tadpoles moving in each tub was used as our response variable in our analyses.

We compared intraspecific variation in activity level by comparing the proportion of tadpoles for each species moving in the control, nonlethal, and lethal treatments. To compare differences in baseline activity level (*i.e.*, control) across each species as well as species-specific responses to an increasing predation threat, we used a generalized linear model (GLM) with a log link function. Because a large number of the observations contained instances in which no tadpoles were moving, we used a zero inflated distribution for 11 of the 12 species. Because *Scaphiopus huerterii* was the only species that was always observed moving, we used a zero inflated negative binomial distribution for our analysis.

RESULTS

Development periods and known predator defenses of the species in our study are presented in Table 1. Tadpoles in this assemblage have developmental periods that span from 14 to 365 d and contain species known to occur in habitats ranging from ephemeral ponds (n = seven species) to permanent ponds (n = five species). Eight of the 12 species of tadpole in this assemblage are known to possess predator defenses, four of which are known to possess multiple defenses. The remaining four species are not known to have any antipredator defenses.

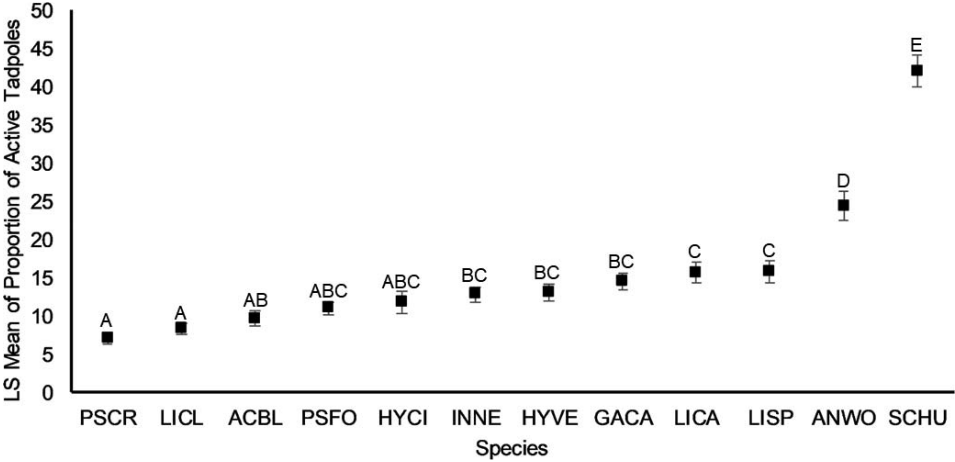


FIG. 1.—Percent mean and standard error of baseline tadpole activity for each species in the control treatment (*i.e.*, in the absence of predator chemical cues). Species that share a letter are not significantly different from one another in their activity level, ($P \leq 0.05$). Species codes are listed in Table 1

Significant differences in the proportion of active tadpoles were observed across species (Figs. 1, 2; Table 2), and we observed a general trend that ephemeral pond species had a higher activity level than species that occupy permanent ponds. In the control treatment, we found *Pseudacris crucifer* tadpoles were the least active, while *Scaphiopus hurterii* tadpoles were the most active (Figs. 1, 2; Table 2). Even within families we observed differences in baseline activity levels. For example within Hylidae, *P. crucifer* had significantly lower activity levels compared to *H. versicolor* (Figs. 1, 2; Table 2). Within Ranidae, *L. clamitans* exhibited much lower activity levels compared to both *L. catesbeianus* and *L. sphenoccephalus* (Figs. 1, 2; Table 2). Within Bufonidae, *A. woodhousii* had a significantly higher activity level than *I. nebulifer* (Figs. 1, 2; Table 2).

Comparing intraspecific responses, 11 species exhibited no significant differences in activity levels with an increasing threat of predation (Table 2). Only one species, *Gastrophryne carolinensis*, exhibited significant differences in activity level and decreased their activity in the nonlethal treatment (Table 2). However, their activity did not decrease further in the lethal treatment (Table 2).

DISCUSSION

Tadpole activity level varied greatly among the 12 tadpole species that occupy different portions of the hydroperiod gradient. Generally, we observed a lower activity level in those species that utilize more permanent ponds and a higher activity level in those species that utilize more ephemeral ponds. Even within families, species spanned a range of activity levels with discernable patterns. These results support our hypothesis species that exhibit low activity levels are predicted to be more associated with permanent ponds and those that maintained a high activity level, despite the increasing threat of predation, are predicted to be associated with ephemeral ponds. Skelly (1994) suggested larval anurans generally decrease their activity level with an increase in pond permanency. Our results fit these findings, as we found significant differences in activity level in species arrayed along a

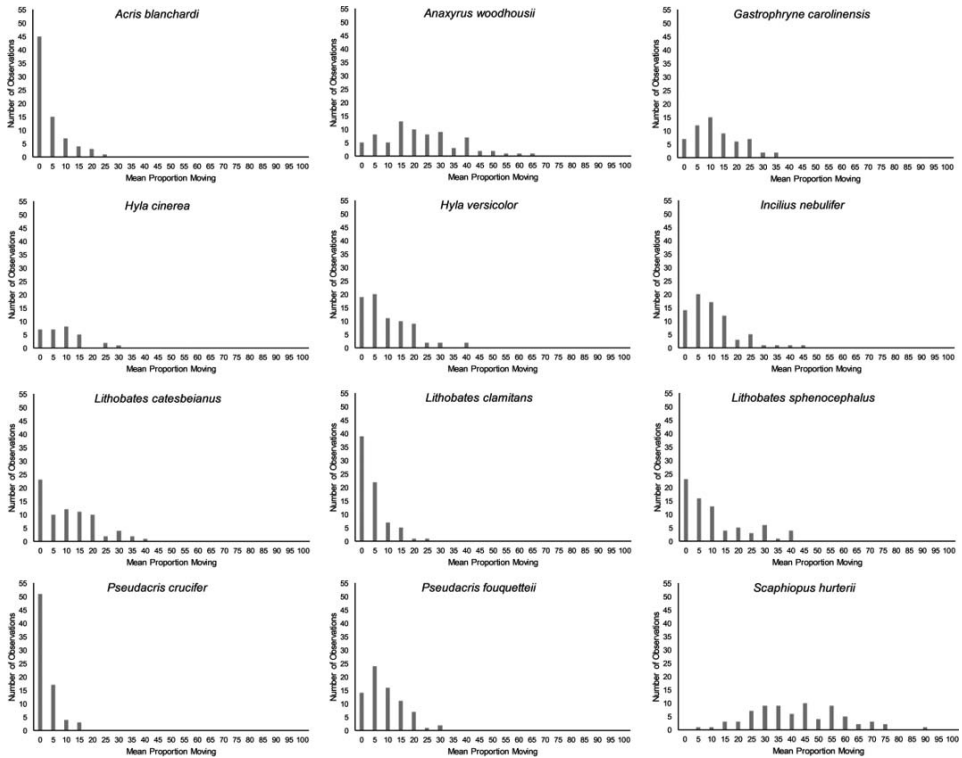


FIG. 2.—Frequency histograms of the proportion of active tadpoles for each species observed across the control treatment (*i.e.*, in the absence of predator chemical cues)

gradient with increasing pond permanency. Interestingly, we found *L. catebeianus*, found in permanent ponds, generally maintained a high activity level even with an increased predation threat. This species is unpalatable to fish predators, due to production of noxious chemicals, but is palatable to dragonfly predators, despite the presence of noxious chemicals; however, size could serve as an antipredator strategy as they become less vulnerable to predation as size increases (Adams *et al.*, 2011). Production of noxious chemicals is costly in terms of energy, but enables individuals to maintain a high activity level despite the threat of predation (Kats *et al.*, 1988; Adams *et al.*, 2011). This is advantageous as it allows species in these systems to exploit resources at a higher rate than species that maintain low activity levels as their primary predatory avoidance tactic.

Pseudacris crucifer, a permanent pond species, exhibited the lowest activity levels across all species. This low activity level could reduce the detection by predators, minimizing predation risk to improve survival (Carfagno *et al.*, 2011; Gordon *et al.*, 2016). *Scaphiopus huerterii* exhibited the highest activity level across all species and did not respond to an increasing predation threat. *Scaphiopus huerterii* tadpoles can occupy ponds with the shortest hydroperiod (Bragg, 1944) and must consume resources to develop rapidly in a dramatically changing environment. Activity for *S. huerterii* parallel those of *S. couchii*, a species that also occupies ephemeral ponds and does not exhibit a change in activity level despite the threat of predation (Dayton and Fitzgerald, 2011). Our results suggest the cost of predation risk

TABLE 2.—The mean and SD of active tadpoles for each species across the control, lethal, and nonlethal treatments and the number of replicates per species per treatment (n). Species codes are listed in Table 1

Species	Control			Lethal			Nonlethal		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
ACBL	75	3.9	6.0	45	3.1	5.6	45	3.3	5.0
ANWO	75	22.8	14.9	75	17.7	16.8	75	16.1	13.2
GACA*	60	12.8	9.2	15	7.0	5.6	15	6.3	4.8
HYCI	30	9.0	7.9	15	9.0	8.1	30	8.7	6.8
HYVE	75	9.7	9.4	60	9.8	8.1	60	9.0	9.0
INNE	75	10.5	9.6	75	10.3	9.2	75	7.5	7.6
LICA	75	10.9	10.4	75	10.4	11.2	75	9.1	11.2
LICL	75	4.0	5.5	60	2.9	4.8	72	5.8	6.8
LISP	75	10.9	11.9	75	8.8	10.7	75	13.3	10.5
PSCR	75	2.3	3.9	69	2.3	3.9	69	3.8	4.7
PSFO	75	8.9	7.3	75	7.4	6.9	75	9.2	8.2
SCHU	75	41.9	16.9	75	41.8	17.6	75	40.1	16.4

* Asterisk signifies a significant difference across treatments

could be lower compared to that imposed by pond drying and these species have adapted to this stronger source of mortality. This high activity level, combined with a low predation risk, enables species to consume resources to meet these developmental constraints imposed by pond permanency. These species may be unable to adapt to changing environments as a consequence of these adaptations, restricting their occupancy to these ephemeral sites.

Only one species exhibited significantly different responses in their activity level in response to an increasing threat of predation. We found *G. carolinensis*, occupying ephemeral ponds (Pechmann, 1994), significantly decreased their activity level with the introduction of a predatory alarm cue. The results parallel those observed with *Gastrophryne olivacea*, as predation and competition for limited resources were large factors contributing to their distribution patterns (Dayton and Fitzgerald, 2001). However, *G. carolinensis* exhibited an intermediate activity drop despite their occupancy in more ephemeral ponds. The results could suggest the cost of predation risk may be similar to that imposed by pond drying, where species have adapted to these different sources of mortality. Furthermore, compared to the other rasping tadpole species in this assemblage, *G. carolinensis* has an alternative foraging strategy (*i.e.*, suspension feeding). Suspension feeding could provide flexibility in foraging behavior as an individual may not need to forage widely for food, which in turn allows activity levels to be adjusted under the threat of predation (Altig *et al.*, 2007; Montaña *et al.*, 2019).

Predation risk depends on multiple factors, including the frequency of encounter rate between predator and prey, body size asymmetries, and effectiveness of prey defenses against a predator (Jobe *et al.*, 2019; Schalk and Cove, 2018). While we used a single predator (dragonfly larvae) to quantify shifts in activity level in members of this tadpole assemblage, these species may exhibit different responses in the presence of different predators (*e.g.*, fish). Exploring species-specific responses to a broad diversity of predators (*sensu* Adams *et al.*, 2011) may provide further insights as to the strengths of the predator-prey relationships for each species of anuran larvae. Activity level and shifts in activity are primary defense mechanisms to reduce predation risk; however, the species within this tadpole guild exhibit

a suite of alternative defenses that enable them to co-exist with predators. Many species (*e.g.*, within Bufonidae and Ranidae) also possess chemical defenses (Adams *et al.*, 2011), likely enabling those species to maintain high activity levels in the presence of predators. *Lithobates clamitans* exhibit significant phenotypic differences in size and morphology in response to the top predator in east Texas ponds (*e.g.*, being more streamline when co-occurring with fish), which may enable tadpoles to escape predation after detection (Johnson *et al.*, 2015). *Acris blanchardi* and *Hyla* spp. also exhibit differences in shape and coloration depending on the top predator in east Texas ponds (Hall, 2010; D. Saenz, pers. obs.). Differences in tail shape and morphology are an effective means to lure predator strikes away from the tadpole's head and towards the tail, increasing their ability to escape and subsequently increasing survivorship (Caldwell, 1982; Van Buskirk *et al.*, 2003). Finally, certain escape strategies are more effective against specific predators. For example *L. sphenoccephalus* tadpoles in east Texas can escape invertebrate predators with greater success than other species in winter breeding guilds due to a suite of performance and behavior traits that are utilized when attacked (Saenz, 2004).

The constraints that activity levels impose on life history traits of species can serve as a predictor of their distribution across the landscape (Skelly, 1996). Our results support an association between activity levels and pond ephemerality and parallels other studies that test this model (Skelly, 1994; Griffiths *et al.*, 1998). Predation also serves as an important factor in determining community structure across the landscape (Heyer *et al.*, 1975; Skelly, 1997; Schalk, 2016). The community of East Texas larval anurans exhibited a range of behavioral responses in activity level to predation risk along the hydroperiod gradient, and provides insights to the underlying mechanisms that scale up to affect their community organization.

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LITERATURE CITED

- ADAMS, C. K., D. SAENZ, AND R. N. CONNER. 2011. Palatability of twelve species of anuran larvae in eastern Texas. *Am. Midl. Nat.*, **166**:1:211–224.
- ALTIG, R., M. R. WHILES, AND C. L. TAYLOR. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshwater Biol.*, **52**:2:386–395.
- BABBITT, K. J. AND G. W. TANNER. 1998. Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia*, **114**:2:258–262.
- BÓKONY, V., Á. M. MÓRICZ, Z. TÓTH, Z. GÁL, A. KURALI, Z. MIKÓ, K. PÁSZTOR, M. SZEDERKÉNYI, Z. TÓTH, J. UJSZEGI, B. ÜVEGES, D. KRÜZSELYI, R. J. CAPON, H. HOI, AND A. HETTYEY. 2016. Variation in chemical defense among natural populations of common toad, *Bufo bufo*, tadpoles: the role of environmental factors. *J. Chem. Ecol.*, **42**:4:329–338.
- BRAGG, A. N. 1944. Breeding habits, eggs, and tadpoles of *Scaphiopus huerterii*. *Copeia*, **1944**:4:230–241.
- CALDWELL, J. P. 1982. Disruptive selection: a tail color polymorphism in *Acris* tadpoles in response to differential predation. *Can. J. Zool.*, **60**:11:2818–2827.
- CARFAGNO, G. L., J. M. CARITHERS, L. J. MYCOFF, AND R. M. LEHTINEN. 2011. How the cricket frog lost its spot: the inducible defense hypothesis. *Herpetologica*, **67**:4:386–396.
- CHANDRASEGARAN, K., R. K. SAMYUKTHA, S. QUADER, AND S. A. JULIANO. 2018. Playing it safe? Behavioural responses of mosquito larvae encountering a fish predator. *Ethol. Ecol. Evol.*, **30**:1:70–87.

- CUMMINS, K. W. 1975. Ecology of running waters; theory and practice. Sandusky River Basin Symposium, Tiffin, Ohio, U.S.A.
- DAYTON, G. H. AND L. A. FITZGERALD. 2001. Competition, predation, and the distributions of four desert anurans. *Oecologia*, **129.3**:430–435.
- AND L. A. FITZGERALD. 2011. The advantage of no defense: predation enhances cohort survival in a desert amphibian. *Aquat. Ecol.*, **45.3**:325–333.
- GAZZOLA, A., A. BALESTRIERI, J. MARTÍN, AND D. PELLITTERI-ROSA. 2018. Is it worth the risk? Food deprivation effects on tadpole anti-predatory responses. *Evol. Biol.*, **45.1**:67–74.
- GORDON, A. M., M. B. YOUNGQUIST, AND M. D. BOONE. 2016. The effects of pond drying and predation on Blanchard's cricket frogs (*Acris blanchardi*). *Copeia*, **104.2**, 482–486.
- GRIFFITHS, R. A., L. SCHLEY, P. E. SHARP, J. L. DENNIS, AND A. ROMAN. 1998. Behavioural responses of Mallorcan midwife toad tadpoles to natural and unnatural snake predators. *Anim. Behav.*, **55.1**:207–214.
- HALL, T. L. 2010. Predator induced defense mechanisms of larval Blanchard's cricketfrogs (*Acris blanchardii*), and their post-metamorphic effects. Ms. Thesis, Stephen F. Austin State University.
- HEYER, W. R., R. W. MCDIARMID, AND D. L. WEIGMANN. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica*, **7**:100–111.
- HOVERMAN, J. T., C. J. DAVIS, E. E. WERNER, D. K. SKELLY, R. A. RELYEA, AND K. L. YUREWICZ. 2011. Environmental gradients and the structure of freshwater snail communities. *Ecography*, **34.6**:1049–1058.
- JOBÉ, K. L., C. G., MONTAÑA, AND C. M. SCHALK. 2019. Emergent patterns between salamander prey and their predators. *Food Webs*, e00128.
- JOHNSON, J. B., D. SAENZ, C. K. ADAMS, AND T. J. HIBBITTS. 2015. Naturally occurring variation in tadpole morphology and performance linked to predator regime. *Ecol. Evol.*, **5.15**:2991–3002.
- KATS, L. B., J. W. PETRANKA, AND A. SIH. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. *Ecology*, **69.6**:1865–1870.
- KOTLER, B. P., J. S. BROWN, AND W. A. MITCHELL. 1994. The role of predation in shaping the behavior, morphology and community organization of desert rodents. *Aust. J. Zool.*, **42.4**:449–466.
- MCDONNELL, M. J. AND S. T. A. PICKETT. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology*, **71.4**:1232–1237.
- MITTELBACH, G. G. AND B. J. MCGILL. 2012. Community ecology, 1st ed. Oxford University Press, UK. 408p.
- MONTAÑA, C. G., S. SILVA, D. HAGYARI, J. WAGER, L. TIEGS, C. SADEGHIAN, T. A. SCHRIEVER, AND C. M. SCHALK. 2019. Revisiting 'What do tadpoles really eat?': A ten-year perspective. *Freshwater Biol.*, **64**:2269–2282.
- PECHMANN, J. H. K. 1994. Population regulation in complex life cycles: aquatic and terrestrial density-dependence in pond-breeding amphibians. Ph.D. Thesis, Duke University, Durham, North Carolina.
- PICKETT, S. T. A. AND F. A. BAZZAZ. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology*, **59.6**:1248–1255.
- RELYEA, R. A. AND E. E. WERNER. 2000. Morphological plasticity in four larval anurans distributed along an environmental gradient. *Copeia*, **2000.1**:178–190.
- RICHARDSON, J. M. 2001. A comparative study of activity levels in larval anurans and response to the presence of different predators. *Behav. Ecol.*, **12.1**:51–58.
- RICKLEFS, R. E. AND D. SCHLUTER. 1993. Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, U.S.A. 416p.
- SAENZ, D. 2004. Ecological correlates of anuran breeding activity and community structure. Ph.D. Dissertation, Texas A&M University, College Station. 177p.
- SCHALK, C. M. 2016. Predator-induced phenotypic plasticity in an arid-adapted tropical tadpole. *Austral. Ecol.*, **41.4**:415–422.
- , C. G. MONTAÑA, K. O. WINEMILLER, AND L. A. FITZGERALD. 2017. Trophic plasticity, environmental gradients and food-web structure of tropical pond communities. *Freshwater Biol.*, **62.3**:519–529.
- AND M. V. COVE. 2018. Squamates as prey: predator diversity patterns and predator-prey size relationships. *Food Webs*, **17**:e00103.

- SHEN, D., K. JÜRGENS, AND S. BEIER. 2018. Experimental insights into the importance of ecologically dissimilar bacteria to community assembly along a salinity gradient. *Environ. Microbiol.*, **20.3**:1170–1184.
- SKELLY, D. K. 1994. Activity level and the susceptibility of anuran larvae to predation. *Anim. Behav.*, **47**:465–468.
- . 1995. A behavioral trade-off and its consequences for the distribution of *Pseudacris* treefrog larvae. *Ecology*, **76.1**:150–164.
- . 1996. Pond drying, predators, and the distribution of *Pseudacris* tadpoles. *Copeia*, 599–605.
- . 1997. Tadpole communities: pond permanence and predation are powerful forces shaping the structure of tadpole communities. *Am. Sci.*, **85.1**:36–45.
- SMITH, G. R., H. A. DINGFELDER, AND D. A. VAALA. 2004. Asymmetric competition between *Rana clamitans* and *Hyla versicolor* tadpoles. *Oikos*, **105.3**:626–632.
- TARR, T. L., M. J. BABER, AND K. J. BABBITT. 2005. Macroinvertebrate community structure across a wetland hydroperiod gradient in southern New Hampshire, U.S.A. *Wetl. Ecol. Manag.*, **13.3**:321–334.
- TONN, W. M. AND J. J. MAGNUSON. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology*, **63.4**:1149–1166.
- TOUCHON, J. C. AND J. R. VONESH. 2016. Variation in abundance and efficacy of tadpole predators in a Neotropical pond community. *J. Herpetol.*, **50.1**:113–119.
- TURNER, A. M. AND S. L. MONTGOMERY. 2009. Hydroperiod, predators and the distribution of physid snails across the freshwater habitat gradient. *Freshwater Biol.*, **54.6**:1189–1201.
- URBAN, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology*, **85.11**:2971–2978.
- VAN BUSKIRK, J. 2002. A comparative test of the adaptive plasticity hypothesis: relationships between habitat and phenotype in anuran larvae. *Am. Nat.*, **160.1**:87–102.
- , ANDERWALD, S. LÜPOLD, L. REINHARDT, AND H. SCHULER. 2003. The lure effect, tadpole tail shape, and the target of dragonfly strikes. *J. Herpetol.*, **37.2**:420–425.
- WERNER, E. E. 1992. Individual behavior and higher-order species interactions. *Am. Nat.*, **140**:S5–S32.
- , AND M. A. McPEEK. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology*, **75.5**:1368–1382.
- , D. K. SKELLY, R. A. RELVEA, AND K. L. YUREWICZ. 2007. Amphibian species richness across environmental gradients. *Oikos*, **116.10**:1697–1712.
- WELLBORN, G. A., D. K. SKELLY, AND E. E. WERNER. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annu. Rev. Ecol. Syst.*, **27.1**:337–363.