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Variation in Abundance and Efficacy of Tadpole Predators in a Neotropical Pond Community

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ABSTRACT.—Variation in predation risk plays an important role in shaping prey behavior, morphology, life history, population dynamics, and community structure in freshwater systems. Anuran larvae are important prey in freshwater communities and spatiotemporal variation in risk can arise from changes in the number and identity of predators; however, our understanding of variation in abundance, identity, and foraging rates for natural predator assemblages in tropical pond communities is limited. We surveyed ponds near Gamboa, Panama in 2004 and 2010 to estimate variation in predator communities of tadpoles over space and time. We also conducted short-term predation trials with the 10 most common predators using hatchling tadpoles of two widespread Neotropical frog species, Red-Eyed Treefrogs (*Agalychnis callidryas*) and Pantless Treefrogs (*Dendropsophus ebraccatus*). Predator abundance varied nearly threefold across ponds within a single year and as much as 19-fold within a pond across years. Dominant taxa also varied, with backswimmers (Notonectidae), poeciliid fish, or libellulid dragonfly naiads being the most common depending upon pond and year. Predation trials revealed that prey-specific predation rates differed among predator taxa. Some presumed predators did not consume hatchlings, whereas others consumed >90% of prey. The smaller *D. ebraccatus* hatchlings generally experienced higher predation rates; however, large invertebrate predators like aeshnid dragonfly naiads, giant water bugs, and fishing spiders consumed more *A. callidryas*. These results suggest that strong but variable larval-stage risk may be an important selective factor shaping tadpole communities and phenotypes in Neotropical ponds.

RESUMEN.—Variación en el riesgo de depredación tiene una función importante sobre el comportamiento, morfología, historia de vida, dinámicas de poblaciones y la estructura de comunidades en sistemas acuáticos. Las larvas de ranas, renacuajos, son presas importantes en las comunidades acuáticas y la variación espacio-temporal en el riesgo puede deberse a cambios en el número y la identidad de los depredadores. Sin embargo, nuestra comprensión de la variación en la abundancia, la identidad, y las tasas de forrajeo de los depredadores de las comunidades de estanques tropicales es limitado. Encuestamos a cerca de los estanques de Gamboa, Panamá, en 2004 y 2010 para estimar la variación en las comunidades de depredadores de renacuajos en el espacio y el tiempo. También realizamos pruebas de depredación a corta plazo con los 10 depredadores más comunes utilizando los renacuajos de dos especies de ranas neotropicales con amplios rangos, ranas arborícolas de ojos rojos (*Agalychnis callidryas*) y sin pantalones (*Dendropsophus ebraccatus*). La abundancia de los depredadores varió casi tres veces a través de estanques dentro de un solo año y tanto como 19 veces en un estanque a través de años. Las especies dominantes también variaron, con Notonecta, peces poeciliidos y náyades siendo el más común, dependiendo de la charca y año. Las pruebas de depredación revelaron que la depredación de cada especie de presa diferían entre los taxones depredadores. Algunos depredadores presuntos no consumieron renacuajos, mientras que otros consumieron >90% de las presas. El renacuajo más pequeño, *D. ebraccatus*, generalmente sufrió tasas de depredación mas altas, pero los depredadores mas grandes, como las ninfas de libélulas de la familia Aeshnidae, Belostoma y arañas de pesca, consumieron más *A. callidryas*. Estos resultados sugieren que el riesgo fuerte pero variable durante la etapa de renacuajo puede ser un factor selectivo importante para la formación de comunidades de renacuajos y fenotipos en estanques neotropicales.

Predators consume prey, but not all predators are equivalent and variation in predation risk can be extremely important for prey community dynamics (Paine, 1966, 1969; Janzen, 1970). Communities are often stabilized by top-down forces of predators and removing predators can disrupt lower trophic levels (Paine, 1966; Connell, 1975; Pace et al., 1999; Heithaus et al., 2008). Furthermore, when not directly consumed, prey often respond to perceived predation risk by altering their behavior or morphology and these responses can carry costs as large or larger than their consumptive effect (Creel and Christianson, 2008). Because most predators exist at a lower density than the prey they consume, they generally are not homogeneously distributed in the environment. Such heterogeneity leads to variation in predation risk across both space and time, which in turn leads to observable differences in producer and consumer

communities (e.g., Menge et al., 1994; Estes and Duggins, 1995) and has caused the evolution of flexible phenotypes in many prey species (Pigliucci, 2001; West-Eberhard, 2003; DeWitt and Scheiner, 2004).

Crucial to understanding predator-prey dynamics is an appreciation of the basic diversity of the predator community. Tadpoles are model organisms for understanding predator-prey dynamics and are commonly used as prey subjects in studies of aquatic communities. Predators of tadpoles include fish, cannibalistic tadpoles, and a multitude of invertebrates such as spiders, shrimp, true bugs, and various aquatic insect larvae (Heyer et al., 1975; Duellman and Trueb, 1986; Benard, 2004; Wells, 2007). In nature, the density and identity of invertebrate predators can be highly stochastic, such that predator communities may vary both spatially and temporally (Brodie and Formanowicz, 1983; Werner and McPeck, 1994; Van Buskirk, 2005). This variation in predator density, coupled with the fact that not all predators are equivalent, can lead to highly variable risk to prey. Alternatively, if predators share functional roles in

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TABLE 1. Locations of ponds near Gamboa, Panama.

Pond	Latitude	Longitude
Ocelot	9°6'8.62"N	79°40'56.96"W
Bridge	9°6'50.26"N	79°41'48.13"W
Quarry	9°7'22.71"N	79°41'36.37"W
Railroad	9°7'19.65"N	79°43'21.73"W
Pipeline	9°8'35"N	79°43'34"W

the food web, risk to prey may be relatively stable despite unique predator communities across habitats (Amarasekare, 2008).

We were interested in understanding spatiotemporal predation risk for hatchlings of two widely distributed and abundant Neotropical anurans—Red-Eyed Treefrogs (*Agalychnis callidryas*) and Pantless Treefrogs (*Dendropsophus ebraccatus*). In comparison with the abundance of research in temperate lentic systems (Sih et al., 1985), surprisingly little is known about the diversity of predator–prey systems in tropical ponds (but see Heyer et al., 1975; Gascon, 1991, 1995; Azevedo-Ramos et al., 1999). Furthermore, biotic interactions such as those between predators and their prey are hypothesized to be stronger and more important in tropical systems because of climatic stability allowing greater degrees of coevolution and specialization (reviewed in Schemske et al., 2009). We quantified the density of *A. callidryas* and *D. ebraccatus* tadpoles and their putative vertebrate and invertebrate predators in five ponds near Gamboa, Panama. We conducted short-term predation trials exposing hatchlings of each tadpole species to each putative predator to quantify species-specific risk. We resurveyed three of these ponds 6 yr later to estimate consistency of predator communities.

MATERIALS AND METHODS

Study System.—*Agalychnis callidryas* and *Dendropsophus ebraccatus* represent two of the most abundant and common pond-breeding amphibian species in the Neotropics (Duellman, 2001). Both species occur in low- to mid-elevation tropical forest from southern Mexico to Colombia and northern Ecuador. They commonly co-occur in ponds throughout the range and both species reproduce by laying eggs on leaves above permanent and semi-permanent ponds (Duellman, 2001), although *D. ebraccatus* will lay eggs directly in the water in unshaded habitats (Touchon and Warkentin, 2008a). *Agalychnis callidryas* eggs require 6–7 d to hatch if undisturbed, but can hatch up to 30% sooner if attacked by predators or pathogens (Warkentin, 1995, 2000; Warkentin et al., 2001), whereas *D. ebraccatus* eggs hatch after 3–3.5 d and also can hatch early if attacked by predators (Touchon et al., 2011). At hatching, *D. ebraccatus* are approximately 5.5 mm total length, whereas *A. callidryas* are 10.5–12 mm total length (Warkentin, 1999b; Touchon and Warkentin, 2010).

Although *A. callidryas* and *D. ebraccatus* are the most abundant species at the ponds we studied, other anurans can include *Dendropsophus microcephalus*, *Dendropsophus phlebodes*, *Engystomops pustulosus*, *Hypsiboas rosenbergi*, *Scinax ruber*, and *Scinax boulengeri*. Although these species do occur in ponds, they are more commonly found in highly ephemeral water bodies. Very rarely *Leptodactylus (pentadactylus) savagei*, *Chiasmocleis panamensis*, and *Trachycephalus venulosus* can be found calling at these ponds. None of these species is known to be

TABLE 2. Total length (mean \pm SD) of all species used in predation trials.

Species	Predator/prey	Total length (mm)
<i>Agalychnis callidryas</i>	Prey	12.40 \pm 0.93
<i>Dendropsophus ebraccatus</i>	Prey	6.07 \pm 0.40
<i>Astyanax ruberrimus</i>	Predator	33.78 \pm 10.75
Aeshnidae naiad	Predator	30.14 \pm 6.52
Large water bug	Predator	35.82 \pm 5.59
Diving beetle larvae	Predator	17.14 \pm 0.76
Notonectidae	Predator	7.87 \pm 0.62
<i>Gambusia nicaraguensis</i>	Predator	32.21 \pm 8.62
Shrimp	Predator	39.01 \pm 5.28
Small water bug	Predator	11.66 \pm 3.31
Fishing spider	Predator	15.03 \pm 2.54
Libellulidae naiad	Predator	17.73 \pm 4.45

predatory except *L. savagei*, whose tadpoles are extremely rare to encounter.

Pond Sampling.—Between 22 and 27 November 2004, we sampled five ponds near the Smithsonian Tropical Research Institute (STRI) field station in Gamboa, Panama (Table 1). All ponds are located within 6.6 km of each other (mean \pm SD distance between ponds: 3.47 \pm 1.63 km). These ponds represent shallow flooded forest that fills and dries multiple times throughout the wet season (Pipeline), relatively deep permanent ponds (Railroad, Ocelot, and Quarry), and a shallow seasonal pond that fills at the start of the wet season and generally holds water until the dry season (Bridge). All ponds are surrounded by vegetation on all sides. We used standardized sweep sampling using a dip net with surface area of 430 cm² and a sweep distance of approximately 1 m for sweep volumes of ca. 0.043 m³. We conducted 12–18 sweeps per pond. These sweeps provided periodic snapshots of the continuous, seasonal variation that exists within predator–prey communities. We recorded the numbers of two focal tadpole species (*A. callidryas* and *D. ebraccatus*) and all putative invertebrate and vertebrate predators in each pond. We identified invertebrate predators to family and morphospecies (Oliver and Beattie, 1996; Pik et al., 1999), and vertebrate predators to species. We resampled three of these ponds (Bridge, Ocelot, and Quarry) in November of 2010 using the same methods, but with a larger dip net (2,030 cm² surface area for sweeps of approximately 0.203 m³).

Tadpoles were identified on the basis of morphology and color pattern, as they are not similar to tadpoles of any other species in the study area. *Agalychnis callidryas* is the only phyllomedusid frog in the area and their tadpoles are larger than any other treefrog species except *H. rosenbergi*, whose tadpoles have characteristic black spots (Duellman, 2001). Similarly, *D. ebraccatus* tadpoles are easily distinguishable from *D. microcephalus* and *D. phlebodes* tadpoles on the basis of tail shape and coloration (Duellman, 2001).

Predation Trials.—Between 6 June and 1 July 2004, we conducted short-term predation trials in an open-air laboratory in Gamboa using an array of putative tadpole predators commonly found in our study ponds (Table 2). Predation trials consisted of 10 one-day posthatching tadpoles of either *A. callidryas* or *D. ebraccatus* and 1 predator per trial. *Agalychnis callidryas* eggs were stimulated to hatch 5 d postoviposition and *D. ebraccatus* eggs were allowed to hatch naturally on the third day postoviposition. We allowed hatchlings to age 1 d before trials to reduce any increased vulnerability because of early hatching in *A. callidryas* (Warkentin, 1995, 1999b). Predation trials were conducted in 6-L round bowls filled with aged tap water

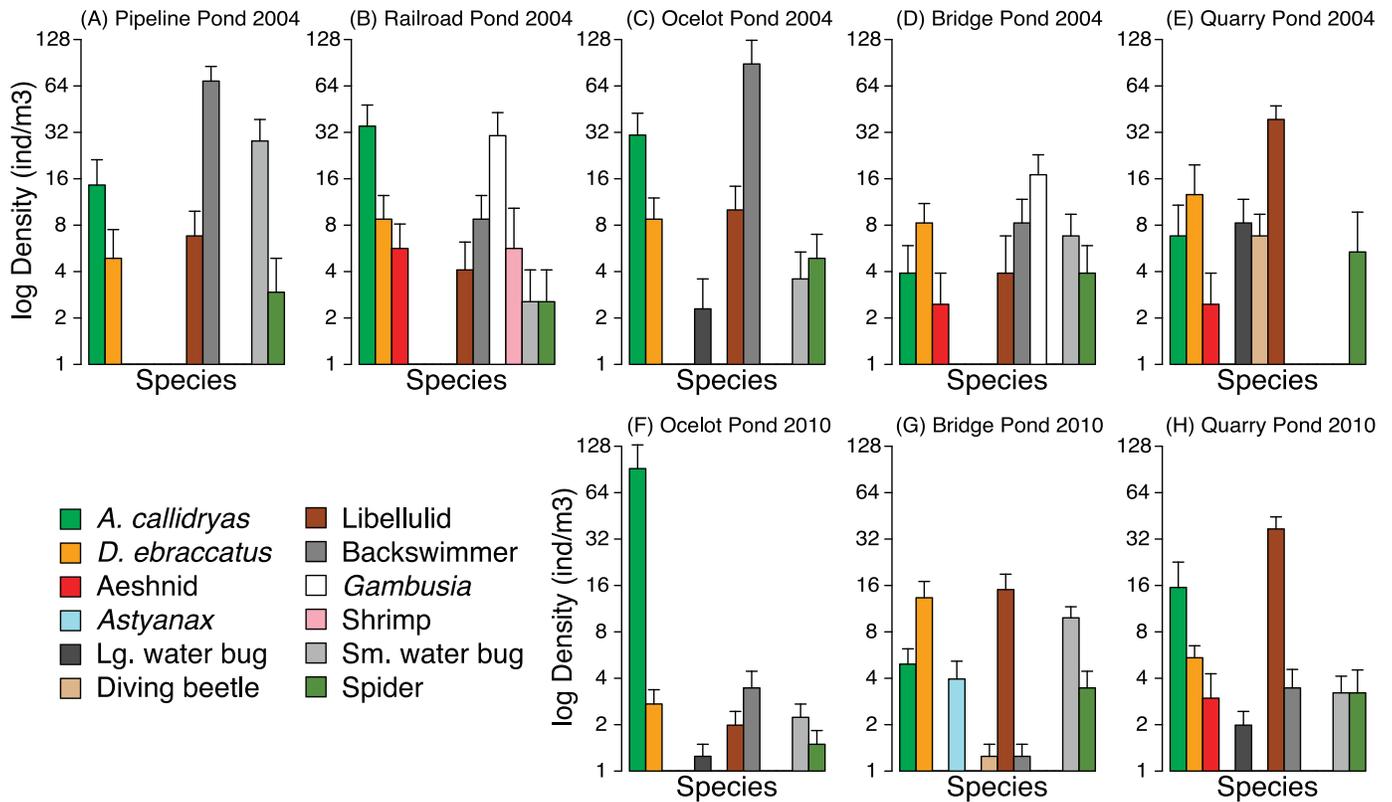


FIG. 1. Densities of *Agalychnis callidryas* and *Dendropsophus ebraccatus* tadpoles and 10 vertebrate and invertebrate predators in five ponds near Gamboa, Panama. All ponds were originally sampled in 2004 and three of the ponds were resampled in 2010.

and covered with mesh to prevent colonization by other animals. We placed a stick in each bowl for predators to use as a perch, if needed. Trials were conducted on four shelves in a fully randomized design. We conducted eight to nine trials for each predator-prey combination, except for diving beetle larvae, for which we only conducted four trials per tadpole species. We photographed all predators and tadpoles at the start of each experiment, including a ruler for scale. We then used ImageJ (Rasband, 2012) to record the sizes of all animals used (Table 2). Trials were conducted in three temporal blocks, each lasting 24 h, at which point the predator was removed and the number of surviving tadpoles recorded. All predators were represented in all blocks except for large water bugs and diving beetle larvae, which were present in two of the three blocks.

Statistical Analyses.—All analyses were conducted in R v2.15.1 (R Core Development Team, 2014). We used the package “vegan” (Oksanen et al., 2012) to conduct several analyses comparing pond communities across space and time. To estimate β diversity, we calculated Bray–Curtis and Jaccard dissimilarity matrices between pond communities, where the former accounts for variation in abundance of species and the latter accounts for only presence/absence of species (Anderson et al., 2011). Species abundances from sweeps were standardized before calculating Bray–Curtis dissimilarity. We used nonmetric multidimensional scaling to visualize dissimilarity matrices. We included all eight sampled communities, the five ponds sampled in 2004 and the three ponds resampled in 2010. This allowed us to assess similarity of ponds spatially and temporally. If pond communities were stable over time, we would expect the resampled ponds to cluster together. We also conducted a Mantel test to test if pond community similarity in 2004 was related to physical distance between ponds.

Predation trials were analyzed with generalized linear mixed models (GLMM) with underlying binomial error structure and logit link function using the lme4 package (Bates et al., 2013). In all models, the response variable was the number of surviving tadpoles of the initial number after 24 h (10). For the initial model, fixed effects were the predator and tadpole species and random effects were the temporal and spatial blocks of the experiment. Data were not substantially overdispersed ($\Phi = 1.8$). After a significant predator-by-tadpole interaction in the overall model (see Results), we conducted analyses for each predator species, testing if predation was greater on *D. ebraccatus* or *A. callidryas*. In all GLMM, significance of fixed effects was assessed using likelihood ratio tests of increasingly simplified nested models. For all statistical tests, $\alpha = 0.05$.

RESULTS

Pond Communities.—We documented the presence of both focal species of tadpoles in all ponds in both survey years, but the presence and abundance of predators were highly variable. We identified eight morphospecies of invertebrate predators and two species of vertebrate predators. The composition of predator communities varied across both the relatively small geographic area in our study and across the 6 yr between sampling periods (Fig. 1), ranging from as few as four predator taxa in Pipeline Pond in 2004 to as many as seven predator taxa in Railroad Pond in 2004. Predators included two morphospecies of water bug, one large and one small (Belostomatidae), two morphospecies of dragonfly naiads (in the families Aeshnidae and Libellulidae), backswimmers (Notonectidae), diving water beetle larvae (Dytiscidae), fishing spiders (*Thaumasia* sp.), freshwater shrimp

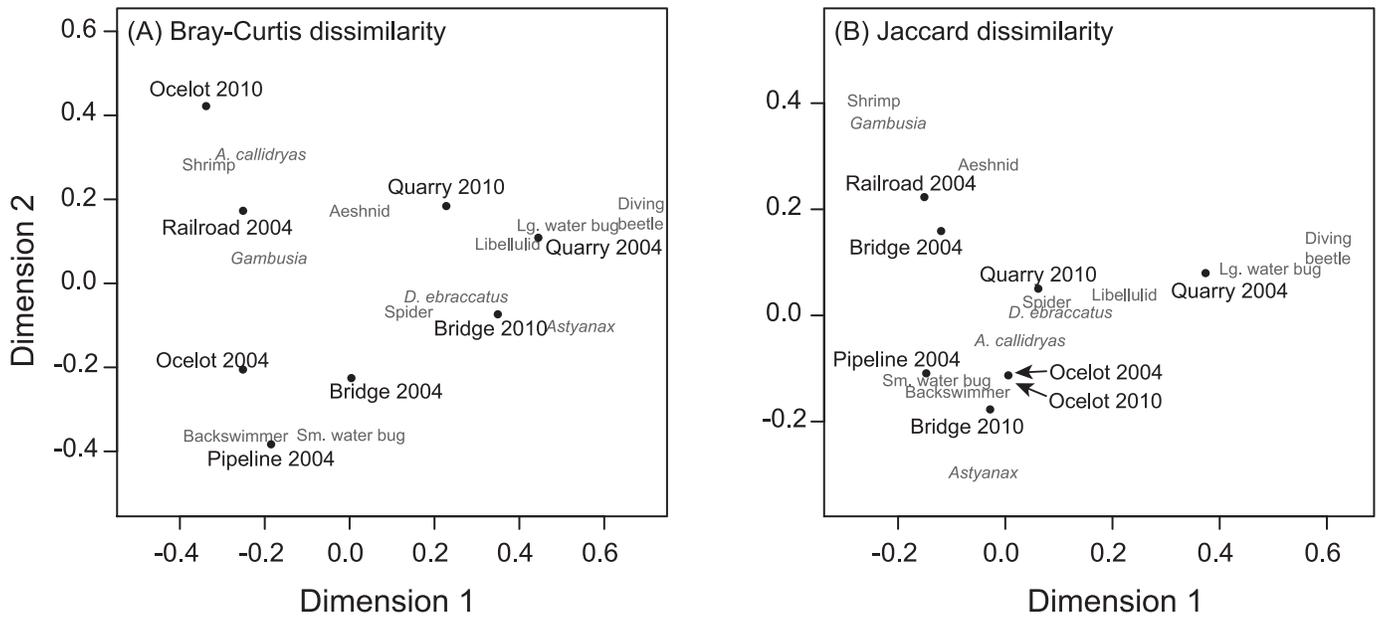


FIG. 2. Nonmetric multidimensional scaling (NMDS) plots of five ponds in Gamboa, Panama. NMDS plots were based on (A) Bray-Curtis dissimilarity, which takes into account abundance data, and (B) Jaccard dissimilarity, which only considers presence/absence data. Note that the x and y scales differ in the two plots. Loadings of ponds are shown in black and of individual species in gray.

(Palaemonidae), and two species of fish, *Gambusia nicaraguensis* (Poeciliidae) and *Astyanax ruberrimus* (Characidae). The primary dragonfly naiads in each family were *Anax amazili* (Aeshnidae) and *Pantala flavescens* (Libellulidae), although other species in each family were present. The two sizes of water bugs were clearly different species, as we found males of both sizes carrying eggs. We also found and conducted predation trials with water boatmen (Corixidae), water scorpions (Nepidae), and damselfly larvae (Zygoptera), but they did not consume tadpoles of either species and so are not considered tadpole predators in this community.

Excluding instances where we found no individuals of a given predator morphospecies, the abundance of predaceous invertebrates varied 60-fold across ponds in 2004 and 147-fold across ponds in 2010, from only 0.25 water bugs or diving beetle larvae m^{-3} in Ocelot and Bridge ponds in 2010 to as many as 88 backswimmers m^{-3} in Ocelot Pond in 2004 (Fig. 1). Across all ponds, the most common predators were libellulid dragonfly naiads (range: 1.0–38.0 individuals m^{-3}) and fishing spiders (range: 0.5–4.4 individuals m^{-3}), which occurred in all ponds in all years. Only Quarry Pond in 2004 lacked backswimmers. Shrimp and *Astyanax* were the least common predators, each occurring in only one pond in 1 yr, followed by the diving water beetle larvae, which were found twice (Fig. 1).

Tadpole densities were variable across ponds and years, with densities of *A. callidryas* and *D. ebraccatus* varying 31-fold and 7-fold, respectively. Both species of tadpoles were found in all ponds in both years, but *A. callidryas* tadpoles were often more abundant than those of *D. ebraccatus* (Fig. 1). Bridge Pond was the only pond with consistently higher densities of *D. ebraccatus*, although they were also more abundant at Quarry Pond in 2004.

In general, aquatic communities (both predators and prey) in the same ponds over time were as dissimilar to one another as they were to other ponds in the same year (Fig. 2). For example, the aquatic communities in Bridge Pond in 2004 and 2010 were as different from each other as Bridge Pond was from Ocelot or Pipeline ponds in 2004 (Fig. 2a). Additionally, considering

species abundances or simply presence/absence did not markedly change how ponds clustered in multivariate space. The main exception to this was Ocelot Pond in 2004 and 2010, where Bray-Curtis distance demonstrated that the abundance of species was very different over time (Fig. 2a), whereas Jaccard distance demonstrated that the species present in the pond in each year were identical (Fig. 2b). Additionally, pond community composition in 2004 was not related to distance between ponds (Mantel test: $r = -0.59$, $P = 0.97$).

Predation Trials.—The efficacy of different predators feeding on *A. callidryas* or *D. ebraccatus* hatchlings varied substantially, as demonstrated by a significant predator-by-prey species interaction (Fig. 3; predator: $\chi^2 = 305.3$, $P < 0.00001$; prey: $\chi^2 = 13.1$, $P = 0.0003$; predator \times prey: $\chi^2 = 159.8$, $P < 0.00001$). Aeshnid dragonfly naiads, large water bugs, and spiders all had higher feeding efficacy on *A. callidryas* hatchlings (Fig. 3; aeshnid and large water bug: $P < 0.00001$; spider: $P = 0.04$). On the contrary, backswimmers, both fish species, shrimp, and diving beetle larvae all consumed significantly more *D. ebraccatus* hatchlings (Fig. 3; backswimmer: $P = 0.001$; *Astyanax*: $P = 0.001$; *Gambusia*, shrimp, beetle larvae: all $P < 0.00001$). Libellulid naiads and the small morphospecies of water bug did not differ in the proportion of each tadpole species they consumed, although small water bugs were relatively poor predators, whereas libellulids consumed 50–60% of available tadpoles.

DISCUSSION

Predators play an extremely important role in shaping communities at lower trophic levels because they change prey survival, growth, behavior, and competition (Paine, 1966; Pace et al., 1999; Eklov and Werner, 2000; Gurevitch et al., 2000; McCoy et al., 2011). Here, we have used a series of field surveys to document how Neotropical freshwater predator communities vary across space and time and used short-term laboratory experiments to estimate how those communities may affect the survival of hatchlings of two Neotropical anurans.

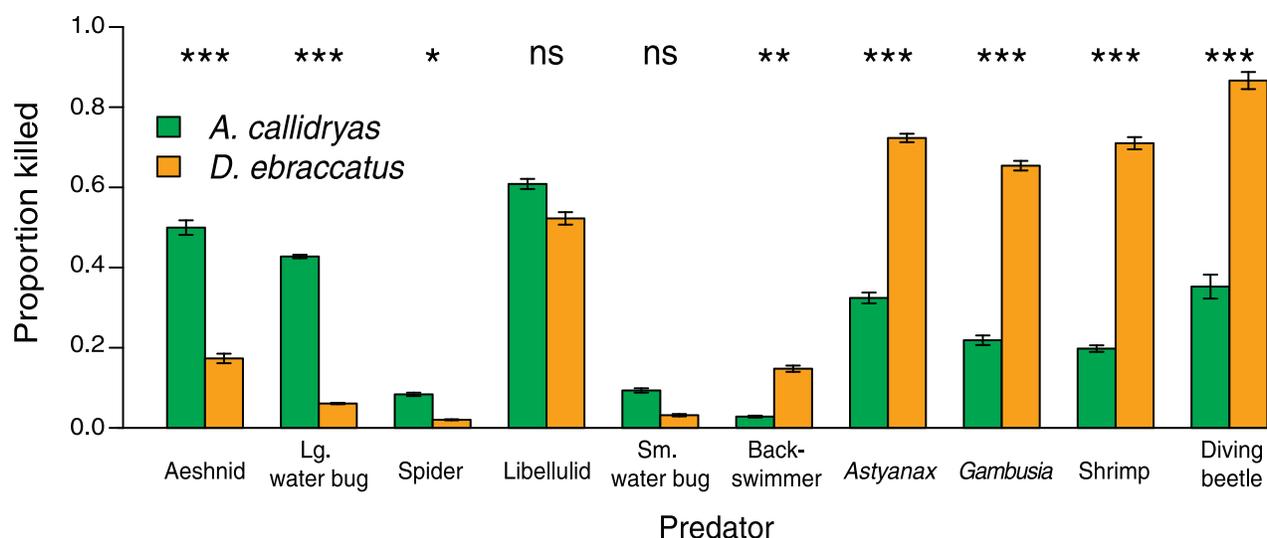


FIG. 3. Proportion of either *Agalychnis callidryas* or *Dendropsophus ebraccatus* tadpoles that were eaten in 24-h predation trials with 1 of 10 different predators. Bars are mean \pm SE. Symbols above bars indicate if there was a difference in predation on the two tadpole species: $P > 0.05$ (NS), $P < 0.05$ (*), $P < 0.01$ (**), or $P < 0.001$ (***).

We found that predator communities varied considerably across a relatively small spatial area and across years (Figs. 1, 2). For example, Bridge and Quarry ponds are only 1.06 km from one another, yet had strikingly different predator communities (Fig. 1). In 2004, Bridge Pond contained high densities of small water bugs and *Gambusia*, whereas Quarry Pond contained primarily large water bugs and diving beetle larvae. Both ponds contained libellulid dragonfly naiads, but the density at Quarry Pond was eight times greater than at Bridge Pond. Furthermore, Bridge Pond in 2004 was vastly different from 2010, having lost two predators (aeshnid dragonfly naiads and *Gambusia*) and gained two others (*Astyanax* and diving beetle larvae). In fact, the aquatic community of Bridge Pond was as different over time as it was from other communities over space (Fig. 2a). The ponds we sampled differed in many characteristics including, but not limited to, the presence of emergent vegetation, depth, likelihood of inundation from nearby streams or rivers, hydroperiod, amount of canopy shade, proximity to other ponds, and proximity to roads or other sources of pollution. These factors may influence the spatial variation we detected, but do not explain the tremendous temporal variation we found.

Fish were found in two of five ponds during 2004 and one in 2010. More important, the presence of fish did not exclude either tadpole species from ponds (Fig. 1). Fish often are considered to be the most important predator of aquatic invertebrate larvae (Eriksson, 1979; Wellborn et al., 1996; Tate and Hershey, 2003) and amphibian larvae (Semlitsch and Gibbons, 1988; Hecnar and M'Closkey, 1997), although not all tadpole species are susceptible to fish predation (Kats et al., 1988; Werner and McPeck, 1994). Despite being among the strongest predators of *D. ebraccatus* tadpoles in the lab, fish did not dramatically reduce *D. ebraccatus* density in nature (Figs. 1, 3). Like many anuran larvae (Benard, 2004), *D. ebraccatus* tadpoles will alter their phenotype when exposed to chemical cues of fish, developing a more streamlined and clear tail, which may help them coexist with fish (Touchon and Warkentin, 2008b). This streamlined tail morphology may increase swimming speed and therefore enhance escape from actively pursuing predators such as *Gambusia* or *Astyanax* fish (Van Buskirk and McCollum, 2000; Wilson et al., 2005).

Neither species of fish was a particularly strong predator on *Agalychnis callidryas* hatchlings, which was surprising, as *A. callidryas* are not known to be distasteful or toxic (Wassersug, 1971). Furthermore, Wojdak et al. (2014) found that *Gambusia* were very strong predators of *A. callidryas* in large mesocosms over the course of 4 wk; however, our predation trials used only a single fish, and the predatory efficacy of *Gambusia* likely increases in groups (Wojdak et al., 2014). When *A. callidryas* are subjected to *Gambusia* predation, they develop a larger tail muscle and fin, the opposite response of *D. ebraccatus* (Touchon and Wojdak, 2014). That fish and tadpoles coexist in natural ponds implies that some other mechanism is at play in nature. For example, the structural complexity of underwater vegetation in ponds may provide refugia for tadpoles, helping reduce predation (Sredl and Collins, 1992; Babbitt and Jordan, 1996; Kopp et al., 2006).

Our predation trials revealed that *D. ebraccatus* hatchlings are more susceptible to predation and to a greater array of predators than the larger *A. callidryas* hatchlings (Fig. 3). At hatching, *D. ebraccatus* are approximately half the size of *A. callidryas* (Warkentin, 1995; Touchon and Warkentin, 2010, 2011), which may be the principal cause of this difference. At hatching, both species are relatively inactive (J. C. Touchon, unpubl. data; Warkentin, 1999a) and so behavioral variation after hatching probably does not explain the difference in survival. Five of the 10 predators in our study consumed *D. ebraccatus* to a greater degree than *A. callidryas*; however, four of these predators (*Astyanax*, *Gambusia*, shrimp, and diving beetle larvae) were among the most patchily distributed predators in our surveys, and no more than two ever co-occurred (Fig. 1). Intraguild predation is known to occur between other members of this predator community (e.g., water bugs eating libellulid naiads; Wojdak et al., 2014) and fish predation likely prevents diving beetle larvae from being more common (Eriksson, 1979; Tate and Hershey, 2003). Only 3 of the 10 predators consumed *Agalychnis callidryas* hatchlings more than *D. ebraccatus*. The greatest overall predator was libellulid dragonfly naiads, which consumed 50–60% of both tadpole species, as opposed to aeshnid dragonfly naiads or fish, as has been commonly found

in temperate studies (Werner and McPeck, 1994; Eklov and Werner, 2000; Relyea, 2001).

Our effort here is to provide an initial understanding of the dynamism present in a Neotropical freshwater community over space and time. Much research has shown, however, that the combined effects of predators often cannot be predicted from their individual effects, leading to enhanced or reduced risk in the presence of multiple predators (Sih et al., 1998; McCoy et al., 2012). Given the diversity of predators in our aquatic communities, the potential for nonlinear intraguild interactions is high. For example, both water bugs and fishing spiders are predators of metamorphosing *A. callidryas* (Touchon et al., 2013); however, water bugs also prey on spiders (Touchon et al., 2015), thereby reducing the density of the second predator and most likely reducing overall predation risk as *A. callidryas* transitions out of the aquatic environment. Fish are likely predators of aquatic invertebrate larvae (Eriksson, 1979; Werner and McPeck, 1994; Tate and Hershey, 2003). Even within taxonomic groups, there are likely predatory interactions (e.g., between dragonfly naiad instars; Wissinger, 1988). Predation by *P. flavescens*, the most common libellulid in this system, decreases markedly as both tadpole species grow (Touchon and Warkentin, 2010; McCoy et al., 2011). Because many of the predators here are larvae as well, their efficacy also is likely to change through their own ontogeny (e.g., dragonflies; Corbet, 1999). Therefore, in the actual pond environment where multiple predators are competing and preying on one another, the realized risk to tadpole prey is certainly less than the additive individual effects we measured here.

Tropical pond environments, like the tropics in general, are more diverse than their temperate counterparts (e.g., Gascon, 1991; Van Buskirk, 2005) and the importance and strength of biotic interactions are likely stronger and more important to community dynamics in the tropics (Schemske et al., 2009). Furthermore, although most studies of aquatic predation pressure on tadpoles have focused on only one or two primary predators, we attempted to quantify the predation capacity of the entire potential community of predators. This provides a first step in understanding how risk varies across environments for Neotropical anurans. The number of major tadpole predators identified here provides a daunting array of potential interactions and future work will need to tease these apart to fully understand predator-prey dynamics in tropical environments.

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