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Oviposition Site Selection in Three Glass Frog Species

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Oviposition site selection is critical for the reproductive success of oviparous organisms. We investigated oviposition site selection in three species of glass frogs—*Espadarana prosoblepon, Hyalinobatrachium valerioi,* and *Teratohyla spinosa*—in northeastern Costa Rica. We conducted nocturnal visual encounter surveys to estimate glass frog egg mass abundance and characterize oviposition site features in streams of three different habitats (pasture, secondary forest, and mature forest). Our results show differential oviposition site selection among all three species depending on vegetation and stream features. *Hyalinobatrachium valerioi* and *T. spinosa,* which oviposit almost exclusively on the underside of leaves, selected smooth leaves, while *E. prosoblepon*, which oviposits on the upper side of leaves or in moss, used moss eight times more than expected on the basis of availability. *Hyalinobatrachium valerioi* was found on larger leaves than *T. spinosa* and *E. prosoblepon. Teratohyla spinosa* and *E. prosoblepon* both oviposited most frequently above slow-moving water, while *H. valerioi* oviposited most frequently above fast-moving water. *Espadarana prosoblepon* was the only species affected by habitat type and had higher abundances of egg masses in mature forest than in secondary forest and pasture. Our results suggest that microhabitat plays a larger role in oviposition site selection than larger habitat classification. We propose that appropriate riparian microhabitat is a critical factor in sustaining glass frog populations in modified habitats and highlight the importance of preserving riparian corridors in altered landscapes.

La selección del sitio de ovipostura es fundamental para el éxito reproductivo de los organismos ovíparos. Investigamos la selección de los sitios de ovipostura en tres especies de ranas de cristal—*Hyalinobatrachium valerioi, Espadarana prosoblepon*, y *Teratohyla spinosa*—en el noreste de Costa Rica. Realizamos muestreos nocturnos visuales para estimar la abundancia de posturas de ranas de cristal y determinamos las características de los sitios de ovipostura en quebradas de tres hábitats diferentes (potrero, bosque secundario, y bosque maduro). Nuestros resultados indican una diferencia en selección de los sitios de ovipostura entre las tres especies basada en características de la vegetación y de las quebradas. *Hyalinobatrachium valerioi* y *T. spinosa*, que depositan los huevos casi exclusivamente en la parte inferior de las hojas, utilizaron hojas lisas mientras *E. prosoblepon*, que deposita los huevos en la parte superior de las hojas o en musgo, utilizó el musgo ocho veces más de lo esperado. *Hyalinobatrachium valerioi* utilizó hojas más grandes que *T. spinosa* y *E. prosoblepon*. Ambos *T. spinosa* y *E. prosblepon* depositaron los huevos mayormente sobre aguas lentas mientras *H. valerioi* depositó los huevos mayormente sobre aguas rápidas. *Espadarana prosoblepon* fue la única especie influida por el tipo de hábitat y se encontró una abundancia más alta de posturas en los bosques maduros que los bosques secundarios y los potreros. Nuestros resultados sugieren que el microhábitat es más importante en la selección de los sitios de ovipostura para estas ranas que la clasificación de macrohábitat. Proponemos que el microhábitat apropiado es clave para sostener las poblaciones de ranas de cristal en hábitats modificados y destacamos la importancia de preservar los corredores ribereños en paisajes alterados.

THE selection of a favorable oviposition site is critical for the reproductive success of oviparous organisms (Resetarits, 1996). With many amphibian populations in rapid decline because of habitat loss and degradation (Sodhi et al., 2008), it is important to understand how species use and select habitat so that we may better implement conservation efforts and restoration practices. However, little is known about oviposition site selection in most amphibians (see review by Buxton and Sperry, 2017 [13 anuran species studied]; review by Silva and Giaretta, 2008 [24 species studied]; Rojas-Morales and Escobar-Lasso, 2013).

Amphibian eggs and larvae generally develop in discrete habitats. Therefore, the oviposition site selected by adults directly affects reproductive success. In the tropics, high humidity levels and relatively constant temperatures have allowed many species to adopt semi-terrestrial reproductive modes and lay their eggs out of water (Crump, 1974; Duellman, 1992). While escaping aquatic egg predation, terrestrial eggs remain highly vulnerable to desiccation, terrestrial predators, fungi, and parasitization (Bokermann, 1957; Duellman and Trueb, 1986; Gomez-Mestre and Warkentin, 2007; Wells, 2007; Vockenhuber et al., 2008). Relatively constant temperatures and long rainy seasons found in the tropics also permit some species to have extended reproductive periods and a diverse array of aquatic habitats to choose from, which will vary in levels of food resources, predators, and other risk factors (Murphy, 2003).

Site-specific differences in offspring survival are likely to drive the ability to recognize and select a favorable site for oviposition. Oviposition site selection is generally the product of female choice (Bernardo, 1996), but the reasons behind that choice are not always clear and vary both among and within taxa (Refsnider and Janzen, 2010). Offspring survival may be maximized by selecting sites that are

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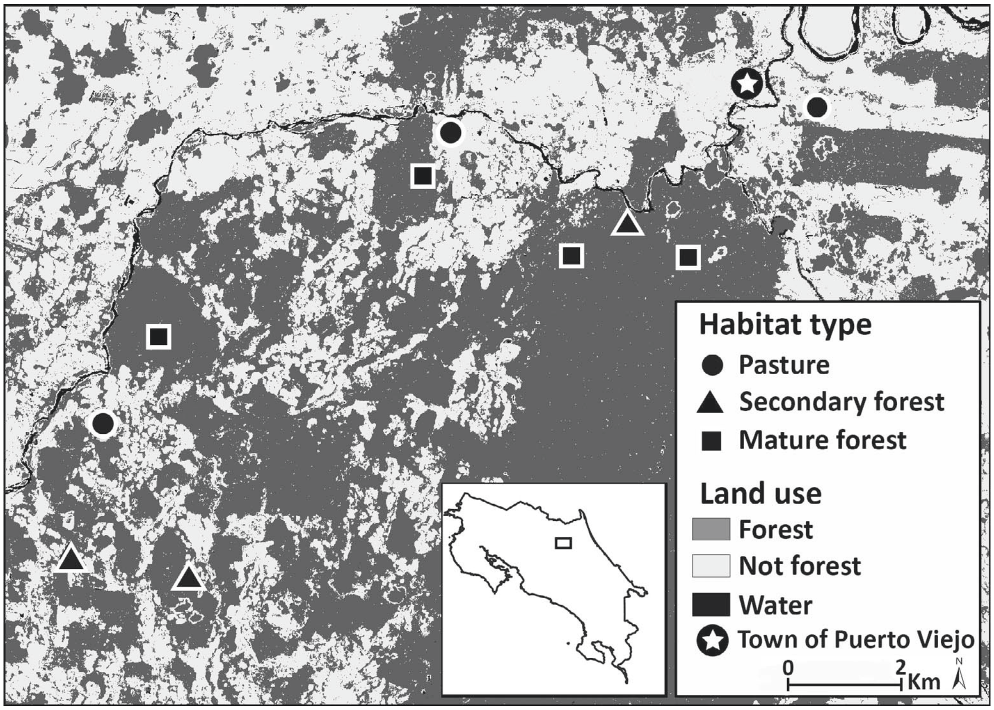

Fig. 1. Map of the survey sites in Sarapiquí, northeastern Costa Rica.

inconspicuous to predators (Delia et al., 2010), have low desiccation risk (Jacobson, 1985; Touchon and Warkentin, 2008), low intraspecific competition (Crump, 1991; Dillon and Fiaño, 2000), or are most appropriate for egg attachment (Refsnider and Janzen, 2010). However, oviposition site selection may also be associated with calling sites that improve male detectability (Greer and Wells, 1980).

Glass frogs (Centrolenidae) are a family of Neotropical frog that have a semi-terrestrial reproductive mode (Savage, 2002; Kubicki, 2007). They are associated with riparian habitats and typically oviposit eggs on leaves or rocks overhanging streams. Hatched larvae drop in the water where they finish developing (Jacobson, 1985; Guayasamin et al., 2006; Wells, 2007). Although there is scarce information on the reproductive biology of many members of the family Centrolenidae, diverse patterns of calling and oviposition site selection have been shown in some species (McDiarmid and Adler, 1974; Greer and Wells, 1980; Jacobson, 1985; Vockenhuber et al., 2008; Lehtinen and Georgiadis, 2012; Cabanzo-Olarte et al., 2013; Vargas-Salinas et al., 2014; Basto-Riascos et al., 2017).

We investigated oviposition site selection in three species of glass frogs that show a diverse range of reproductive behavior across a variety of habitats in northeastern Costa Rica. We tested for oviposition site selection of macrohabitat (pasture, secondary, and mature forest) and vegetative and stream microhabitat characteristics and whether oviposition site selection differs among three species that occur syntopically, *Espadarana prosoblepon, Hyalinobatrachium valerioi,* and *Teratohyla spinosa*.

MATERIALS AND METHODS

Study species.—We collected data on three species of glass frog: *Espadarana prosoblepon, Hyalinobatrachium valerioi,* and *Teratohyla spinosa*. These species of glass frog are fairly common in the study region but exhibit patchy distributions in the landscape (Thompson, 2018). The species vary in individual body size (snout–vent length [SVL]), egg mass qualities, territoriality, and parental care (Kubicki, 2007). *Espadarana prosoblepon* is the species with the largest body size, followed by *H. valerioi* and then *T. spinosa,* which has a smaller body size than the other two species. In accordance with size, the two larger species lay larger clutches than the smallest. All eggs are laid in a single layer of jelly. The eggs of *H. valerioi* and *T. spinosa* are yellowish-green and laid on the underside of leaves, while those of *E. prosoblepon* are darkly pigmented and laid on the upper side of leaves (or on moss). Dark pigment may help shield eggs from the sun, but egg coloration may also be differentially cryptic when observed from above or below (Savage, 2002). *Espadarana prosoblepon* and *H. valerioi* exhibit considerably greater territoriality than *T. spinosa,* but only *H. valerioi* exhibits parental care in the form of 24-hour egg-guarding (Vockenhuber et al., 2008).

Study sites.—We surveyed streams in a total of ten randomly selected sites in pastures, secondary forests regenerating from pastures, and mature forests (no or minimal history of disturbance). All sites were located in the tropical lowland wet forest life zone in the district of Sarapiquí, northeastern Costa Rica (Fig. 1; Holdridge, 1971).

Visual encounter surveys.—Our study combines data from two survey periods: 1) data collected from October 2014 to December 2016 as part of a community-level study consisting of six surveys per site, conducted year-round (one survey each in the rainy season, dry season, and transition from rainy to dry season each, for two years) and 2) data collected June–July 2017 (rainy season) consisting of three additional surveys per site focused on glass frogs. We surveyed the same sites and transects in the two surveys periods, with the exception of one mature forest site (a new site was selected for surveys in 2017 because of access issues; Fig. 1). To survey for egg masses and adults, we conducted nocturnal visual encounter surveys (Crump and Scott, 1994) in three 50 × 2 m transects at each site along streams for approximately 25 minutes of search time for a total of 165 nocturnal transect surveys. Number of observers during surveys ranged from 1–3 people. The start coordinates of the first transect were chosen using a random number generator and subsequent transects were kept at least 50 m apart when total stream length allowed it. For each egg mass encountered, we recorded oviposition site data (vegetation and stream features) and identified egg mass to species. The egg masses of the different species were sufficiently different to allow for easy field identification (Kubicki, 2007). Vegetation features included plant family (and identified to species when possible), leaf area (calculated using ImageJ [Schneider et al., 2012]), leaf surface type (glabrous [free from hair, hereinafter called smooth], hairy, or with spores), position of egg mass on leaf (upper or underside) or if it was laid in moss, and height above stream. Stream features included water velocity (slow, medium, fast) and substrate type (boulder, mud, rock, sand) directly below the egg mass. Stream velocity was visually assessed as slow, medium, or fast, an absolute value not relative to the site. Attempts were made to use a float to quantify flow rate, but stream complexity made estimations inaccurate. Using a current meter, only available to us for a short period during the study, we corroborated that our visual categorizations were consistent and estimated that flow of medium and slow streams was approximately 50 and 5% of the fast streams.

Habitat availability.—To estimate microhabitat selection, we compared samples of habitat use with availability (Johnson, 1980; Beyer et al., 2010). We used a line-intersect method to record frequency of available vegetation and stream features (outlined in the previous section). For each of two randomly selected transects from all pasture sites, all secondary forest sites, and three of the mature forest sites, we randomly selected a side of the stream and recorded the features of the plant that touched the meter tape at 2-meter intervals. To record stream substrate, we also used 2-meter intervals while stream velocity was estimated across 10-meter intervals.

Analysis.—To determine whether habitat type (pasture, secondary forest, mature forest) had an effect on the abundance of egg masses of each species, we used generalized linear mixed model with a Poisson distribution and log link function. We used habitat type as a fixed factor, treated site as a random intercept to account for non-independence of multiple transects within a site, and used log(person hours of search time) as an offset. To determine microhabitat selection, we compared habitat use with habitat availability using Manly selection ratios (Manly et al., 2002). For Manly selection ratio analyses, we categorized leaf area by size in bins of 0–100 cm^2, 101–300 cm^2, 301–600 cm^2, and >600 cm^2. We used linear mixed models with species as a fixed factor and site treated as a random intercept to compare the height and leaf size used by each species. To normalize the data, we log-transformed leaf area. To calculate average number of eggs per clutch, we only used egg clutches within approximately four days of oviposition (Gosner stage 17) to reduce the risk of biasing counts with predation events or partial hatching of clutches. We determined days since oviposition as defined by Vockenhuber et al. (2009). For analyses, we used packages lme4 (Bates et al., 2015), lmerTest (Kuznetsova et al., 2016), and adehabitatHS (Calenge, 2006) in R version 3.31 (R Core Team, 2017).

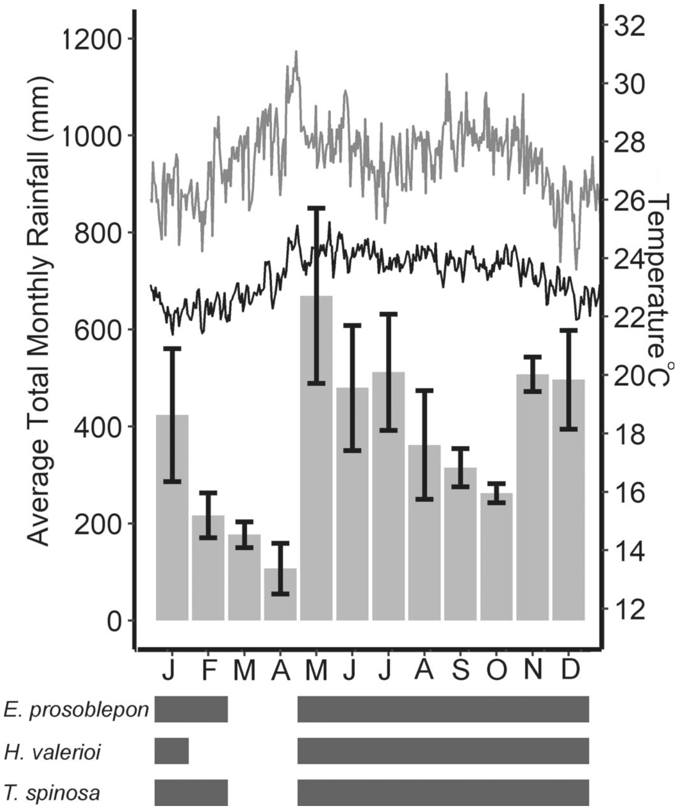

Fig. 2. Breeding phenology of three focal glass frog species at sites surveyed in Sarapiquí, Costa Rica, October 2014 to July 2017. Horizontal gray bars below the x-axis indicate months for which eggs masses were observed in study sites for each species. The bar graph indicates average total monthly rainfall ±1SD, and the line graph indicates average daily air temperature (gray line) and average nightly air temperature (black line) at La Selva Biological Station during the study period.

RESULTS

During our nocturnal visual encounter surveys, we identified 295 egg masses (72 for *E. prosoblepon,* 95 for *H. valerioi*, and 128 for *T. spinosa*). Average number of eggs per clutch ±1SD was 26±7 ($n = 4$) for *E. prosoblepon,* 41±9 ($n = 15$) for *H. valerioi*, and 21±4 ($n = 34$) for *T. spinosa*. Average SVL of adult frogs observed ±1SD was 24.1±2.1 ($n = 20$) for *E. prosoblepon*, 22.7±1.5 ($n = 39$) for *H. valerioi*, and 19.1±1.5 ($n = 77$) for *T. spinosa* (data pooled across sex). We observed egg masses of all three species throughout the rainy season, May through December, with sparse observations throughout the dry season, January through April (Fig. 2).

Habitat selection.—There was a higher abundance of egg masses from *E. prosoblepon* in mature forests than in secondary forests ($\beta = 1.88$, $z = –3.32$, $P = 0.001$) and pastures ($\beta = –3.71$, $z = –2.67$, $P = 0.008$; Fig. 3; Supplementary Table A; see Data Accessibility). There was a suggestive trend of lower abundance of egg masses of *T. spinosa* in pastures than in mature ($\beta = –1.65$, $z = –1.94$, $P = 0.05$) and secondary forests ($\beta = 1.77$, $z = 1.99$, $P = 0.05$), although the trend was not statistically significant. We found no relationship between abundance of egg masses and habitat type for *H. valerioi* (Fig. 3; Supplementary Table A; see Data Accessibility).

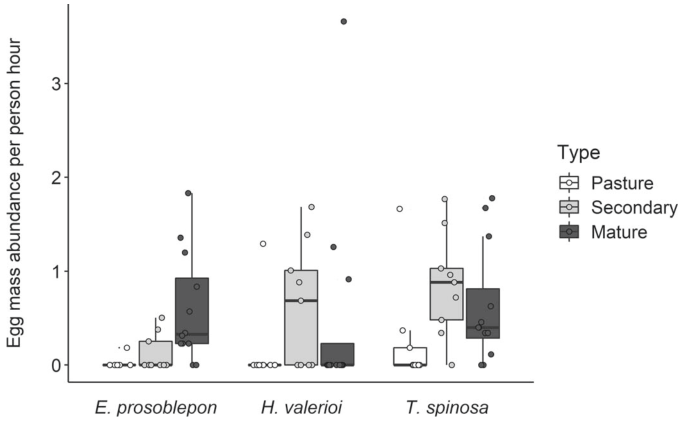

Fig. 3. Relative abundance of egg masses in pasture, secondary forest, and mature forest sites for *Espadarana prosoblepon*, *Hyalinobatrachium valerioi*, and *Teratohyla spinosa*. Boxplots indicate the median, interquartile range (IQR), and 1.5*IQR, and dots are values for individual transects. *Espadarana prosoblepon* had a significantly higher abundance of egg masses in mature forest than in secondary forest ($P = 0.008$) or pastures ($P = 0.001$), and *T. spinosa* had a lower but not statistically significant abundance ($P = 0.05$) of egg masses in pasture than mature forests and secondary forests.

Microhabitat selection.—The three species selected for different vegetation features. Both *H. valerioi* and *T. spinosa* preferred smooth leaves (Table 1; *H. valerioi* 20% more than expected, $P < 0.0001$; *T. spinosa* 15% more than expected, $P = 0.005$). *Espadarana prosoblepon* did not show preference for any leaf type or leaf size but had a clear preference for moss (over eight times more than expected on the basis of availability, $P < 0.0001$). All egg masses from *H. valerioi* and 96% of egg masses from *T. spinosa* were observed on the underside of leaves, and of the egg masses of *E. prosoblopon* that were observed on non-bryophytes, 92% were observed on the upper side of the leaf. *Hyalinobatrachium valerioi* selected large leaves for oviposition (over 300 cm^2; $P < 0.0001$), while *T. spinosa* selected leaves sized between 100–300 cm^2 ($P < 0.0001$; Table 1, Fig. 4). Among species, *Hyalinobatrachium valerioi* selected larger leaves, followed by *T. spinosa* and then *E. prosoblepon* (Fig. 4A; *H. valerioi–T. spinosa*: $\beta = -1.02$, $t = -2.92$, $P = 0.007$; *E. prosoblepon–T. spinosa*: $\beta = 1.03$, $t = 2.68$, $P = 0.01$; *H. valerioi–E. prosoblepon*: $\beta = -2.05$, $t = 4.72$, $P < 0.001$). Furthermore, egg masses from *H. valerioi* and *E. prosoblepon* were found higher in the vegetation than *T. spinosa*, although *T. spinosa* was only significantly lower than *H. valerioi* (Fig. 4B; *H. valerioi–T. spinosa*: $\beta = -84.52$, $t = 9.35$, $P = 0.003$; *E. prosoblepon–T. spinosa*: $\beta = -47.74$, $t = -1.94$, $P = 0.06$; *H. valerioi–E. prosoblepon*: $\beta = -36.78$, $t = -1.24$, $P = 0.22$).

We sampled a total of 56 plant families during our habitat surveys. In terms of availability, the most abundant family sampled was Araceae (representing 14% of total families sampled) followed by Melastomataceae (9%), Poaceae (8%), Fabaceae (7%), and Piperaceae (7%; Supplemental Figure A and Table B; see Data Accessibility). Poaceae dominated pasture sites but was rare in secondary and mature forest sites. Glass frog egg masses were found on only 29 different families, approximately half of the families recorded during habitat surveys. Furthermore, egg masses of different species were found on different families (Supplemental Figure A and Table B; see Data Accessibility). Clutches of *E. prosoblepon* were found on 16 different families, especially on Piperaceae (14%), Rubiaceae (11%), and on division Bryophyta (36%). Clutches of *H. valerioi* were found on 17 different families, especially on Araceae (14%), Rubiaceae (14%), and Cyclanthaceae (11%), and *T. spinosa* used 21 different families, especially on Araceae (27%) and Piperaceae (16%).

Both *E. prosoblepon* and *T. spinosa* oviposited directly over slow-flowing water more often than expected based on availability, while *H. valerioi* oviposited over fast-flowing water (Table 1). *Espadarana prosoblepon* avoided rocky substrates (Table 1).

DISCUSSION

Our results of a non-random pattern of oviposition site use in relation to habitat and microhabitat characteristics provide evidence of oviposition site selection by glass frogs *H. valerioi, E. prosoblepon,* and *T. spinosa*. We found differential selection among the three glass frog species dependent on vegetation and stream features.

Habitat selection

There was a higher abundance of egg masses from *E. prosoblepon* in mature forest than in secondary forest or pasture. We found no significant difference in abundance of egg masses of *H. valerioi* and *T. spinosa* among macrohabitat types. While no egg masses of any glass frog species were found in two of our three pasture sites, the third pasture site had abundances of egg masses comparable to sites in secondary and mature forests (for species *H. valerioi* and *T. spinosa*). The variation in presence of egg masses in pasture sites is unlikely a cause of dispersal distance effects at our field sites because all pastures we sampled were adjacent to old growth forest patches. The most striking difference among pasture sites with and without egg masses was vegetation composition. The stream banks in pastures with no egg masses were highly composed of grasses and scattered remnant trees and had little overhanging vegetation other than the tall canopy cover of remnant trees (i.e., little mid-canopy vegetation structure). A similar pattern was found in the Osa Peninsula, Costa Rica where adult glass frogs and egg masses were found in streams in the two of three pasture sites surveyed with more heterogeneity in vegetation structure (Thompson, 2018). Our results are also consistent with a demographic study on *E. prosoblepon* that suggested availability of overhanging vegetation used for reproductive activities may limit the population size of this species (McCaffery and Lips, 2013). The large variability in egg mass abundance among sites that was not explained by habitat type suggests microhabitat along stream banks is more meaningful than habitat type in predicting abundance of glass frog egg masses. Our results add further evidence on the importance of remnant vegetation for species diversity and persistence (Becker et al., 2007; Lorion and Kennedy, 2009; Robinson et al., 2013; Thompson et al., 2018) and support the importance of enforcing legislation protecting riparian buffer zones. However, we also caution the interpretation of our results because substantial forest cover and forest connectivity still exist at the landscape scale in the Sarapiquí region. It remains to be tested if riparian forest corridors in a landscape dominated by matrix with few forest remnants can be effective in sustaining populations of glass frogs in altered habitat.

Table 1. Manly selection ratio results for vegetation and stream oviposition site features. *Khi2L*: log-likelihood chi-square statistic. For tests with overall significant results, significant positive (+) or negative (–) associations from bivariate tests with Bonferroni corrections are shown.

	E. prosoblepon			*H. valerioi*			*T. spinosa*		
	Khi2L	df	*P*	*Khi2L*	df	*P*	*Khi2L*	df	*P*
Stream									
Substrate	13.8	3	0.003	2.613	3	0.546	0.420	3	0.936
		Rock(–)							
Velocity	15.4	2	<0.001	10.9	2	0.004	9.05	2	0.011
		Slow(+), Fast(–)			Fast(+)			Slow(+)	
Vegetation									
Leaf area	4.42	3	0.220	87.6	3	<0.001	25.1	3	<0.001
					>300 cm^2(+)			100–300 cm^2(+)	
Leaf type	4.40	2	0.111	17.0	2	<0.001	10.6	2	0.005
					Smooth(+), Hairy(–)			Smooth(+)	

Microhabitat selection

We show that *E. prosoblepon, H. valerioi,* and *T. spinosa* select different oviposition sites on the basis of microhabitat features such as leaf size, substrate, height, and stream characteristics.

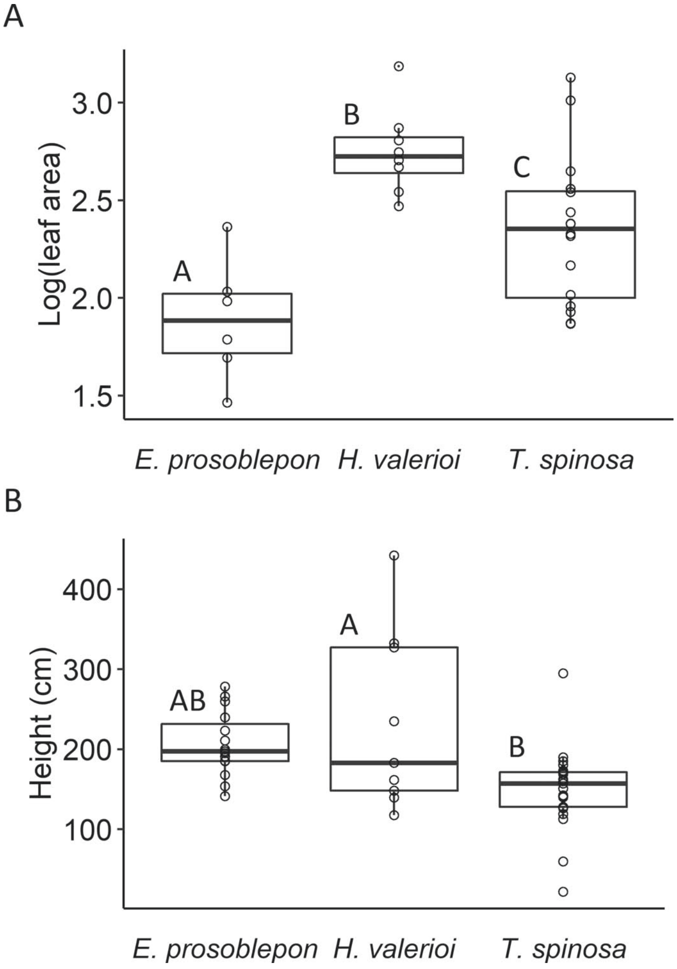

Fig. 4. Box plots of (A) log (leaf area) cm^2 and (B) leaf height (cm) of oviposition sites for *Espadarana prosoblepon*, *Hyalinobatrachium valerioi*, and *Teratohyla spinosa*. Boxplots indicate the median, interquartile range (IQR), and 1.5*IQR, and dots are values for individual transects. For (A) log (leaf area) cm^2, letters show significant differences (A–B, $P <$ 0.001; A–C, $P = 0.01$; B–C, $P = 0.007$), and for (B), letters show significant (A–B, $P = 0.003$) or near significant differences (AB–B, $P = 0.06$).

Leaf size.—*Hyalinobatrachium valerioi* preferred larger leaves than both *E. prosoblepon* and *T. spinosa*. The preference, consistent with an earlier study (Vockenhuber et al., 2008), may be a direct result of parental care behavior. *Hyalinobatrachium valerioi* is often found guarding multiple clutches at once and may benefit from a larger surface area for oviposition, but intraspecies variation in leaf size used does not seem to correlate with number of clutches obtained (Vockenhuber et al., 2008). *Teratohyla spinosa* may select smaller leaves than *H. valerioi* because of its small clutch size, but it still avoided leaves smaller than 100 cm^2. Because larger leaves offer better sound propagation (Wells and Schwartz, 1982), lower leaf-size limits could be imposed by decreased male detectability to females, while upper leaf-size may be determined by clutch-size space requirements and interspecific competition. Future studies focused on other characteristics of vegetation structure and choice experiments will help tease out nuances in site selection behavior.

Substrate.—We found that glass frog species more frequently oviposit on some plant families than others. However, the most striking association was between egg masses of *E. prosoblebon* and moss. We found egg masses of *E. prosoblepon* on moss eight times more often than would be expected at random on the basis of availability, in consensus with Basto-Riascos et al. (2017) who reported that 93.1% ($n = 21$) of egg masses from *E. prosoblepon* were found in fronds of *Selaginella geniculata* (a spike moss which can have very similar growth forms to true mosses). Jacobson (1985) found that egg masses of *E. prosoblepon* laid in moss had higher survival rates than those laid on leaves, which suggests that this species selects moss to increase hatching success. Basto-Riascos et al. (2017) suggested that this selection is driven by female choice because they often observed that amplexus started on leaves of other plant families (e.g., Araceae, Costaceae) but was then redirected towards *Selaginella geniculata* by females. The moss likely provides a moist environment that reduces desiccation risk or decreases detection by predators. This raises the question of why other species do not use moss more often. *Espadarana prosoblepon* may exclude other species from these sites, or its egg masses may be especially vulnerable to desiccation. Some species in the genus *Hyalinobatrachium* may decrease desiccation by exhibiting parental care in the form of ventral brooding according to some studies (Hayes, 1991; Vockenhuber et al., 2009; Valencia-Aguilar et al., 2012), although not others (Jacobson, 1985). Furthermore, while not quantified, egg masses of *T. spinosa* appear to have more jelly than the other species, which could confer protection against desiccation.

Height.—Egg masses of *Teratohyla spinosa* were found on leaves lower in height than those of clutches of *H. valerioi* and tended to be lower than those of *E. prosoblepon*. High sites have been shown to correlate with increased mating success within the species *H. fleischmanni* (Greer and Wells, 1980), which is likely a result of its effect on sound propagation. *Hyalinobatrachium fleischmanni* tends to call from the underside of leaves, and sound pressure levels are highest on the side of the leaf where males are calling (Wells and Schwartz, 1982). Therefore, for species that call from the underside of leaves, increased height allows better detectability from below. As a consequence of their egg guarding behavior, males of *H. valerioi* are mostly obligated to call from the underside of leaves where the eggs are laid, which may put them at a disadvantage in lower vegetation. On the other hand, *E. prosoblepon* and *T. spinosa* tend to call from the tops of leaves and do not guard their egg masses. While calling site and oviposition site may be closely related in most species, they are necessarily overlapping in those that engage in parental care, like *H. valerioi*. The obligatory relationship may result in less flexible behavior, enhanced selectivity, or different oviposition and calling-site selection criteria in species with parental care, but no studies have investigated the relationship conclusively.

Stream characteristics.—Two species, *E. prosoblepon* and *T. spinosa*, selected slow-flowing water, while the egg masses of *H. valerioi* were almost twice as likely to be found over fast-flowing water. While our measurements of stream characteristics were somewhat limited, our results coupled with findings of past experimental choice studies that revealed that anurans use cues to time oviposition with respect to future water presence (Crump, 1991; Rudolf and Rödel, 2005) suggest that cues indicative of aquatic habitat quality for tadpole development are important for oviposition site selection. We structured our data collection to record water velocity close to the day of oviposition (but not at the exact time oviposition took place) and did not rigorously consider mean and variation of velocity of a stream across the long term. More precise timing (i.e., at exact time of oviposition), long-term monitoring of stream characteristics at oviposition sites, and experimental choice experiments to sort out the relative importance of cues at time of oviposition and long-term stream characteristics in oviposition site selection will be critical. Additionally, studies focused on the larval biology of these species, such as swimming ability, habitat use, thermal limits, and predator avoidance across the full spectrum of stream features available across the geographic ranges of these species are required for a robust determination of what stream features are likely to affect their persistence.

Conclusions and conservation implications

Little is known about the reproductive behavior, habitat selection, and the extent of habitat partitioning within syntopic glass frog species (Vockenhuber et al., 2009; Dautel et al., 2011). We hypothesize that species-dependent differences in our study may be the result of biological and life history differences in oviposition site requirements or competition (Buxton and Sperry, 2017). Previous studies of oviposition site selection in glass frogs have largely consisted of focused observations on a section of a single stream (e.g., Greer and Wells, 1980; Jacobson, 1985; Vockenhuber et al., 2008, 2009; Cabanzo-Olarte et al., 2013; Mangold et al., 2015). These focused studies have contributed valuable information to the understanding of the natural history of glass frogs; however, we stress the importance of replicating research efforts across different study sites and regions to understand fully macrohabitat and microhabitat selection.

Increased rates of deforestation coupled with the effects of climate change have been identified as significant threats to amphibian communities in the tropics (Beebee and Griffiths, 2005; Sodhi et al., 2008; Newbold et al., 2015). The effectiveness of conservation efforts relies on a thorough understanding of the spatial distribution and habitat use of species of concern. Oviposition site selection can drive the spatial distribution of a species and determine its ecological impact. Therefore, by understanding the factors affecting oviposition site selection, we can better predict the distribution and abundance of a species and how these may change as land use and climate change alter the landscape. Our findings contribute to the understanding of the ecology and habitat use of glass frogs and have demonstrated the potential for these riparian species to persist in altered landscapes so long as the appropriate microhabitat is preserved.

DATA ACCESSIBILITY

Supplemental information is available at https://www.copeiajournal.org/ce-19-243.

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