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Shelter from the sand: microhabitat selection by the bromelicolous tree frog *Scinax cuspidatus* (Anura, Hylidae) in a Brazilian restinga

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Abstract. Habitat selection is one of the main factors influencing life-history evolution in animals, and is especially relevant for amphibians that must avoid desiccation. In environments such as the Brazilian *restinga*, where freshwater is scarce, bromeliads can provide suitable microhabitats and be an important determinant of amphibian diversity. Here, we used multiple logistic regression to investigate microhabitat selection by the bromelicolous tree frog *Scinax cuspidatus* in a *restinga* in the Brazilian southeastern coast in the state of Rio de Janeiro. Bromeliad use by *S. cuspidatus* was mainly influenced by pH and volume of stored water, while temperature of the water, potential prey abundance, number of leaves, height, and radius of the plant had little influence. There was no relationship between body size of *S. cuspidatus* and bromeliad size. Our results provide further evidence that microhabitat selection in the region is closely linked to some bromeliads characteristics such as water volume and pH, and highlight the important role of bromeliads as fundamental freshwater sources for amphibians in the *restinga*.

Key words: amphibian, diet, habitat selection, pH, *Scinax ruber* group.

Introduction

The fact that individuals discriminate between available habitats and only occupy a non-random set of them is a widely accepted concept in ecology, usually referred to as habitat selection (Morris 2003). Early ecological theory suggests that habitat selection patterns are primarily affected by inter- and intraspecific competition (Rosenzweig 1981), and more recent studies have focused on individuals' interactions with their surrounding environment (Fieberg et al. 2010, Piper 2011). Furthermore, organisms can be severely impacted by the physiological consequences of habitat selection, especially ectotherms (Huey 1991). From the standpoint of the individual, habitat selection is known to affect predation risk (Morey 1990) and may also influence reproductive success (Martin 1998). As a consequence, specific decisions regarding the use of a particular microhabitat will depend on the trade-off between its advantages (e.g., shelter; less competition) and its potential impacts on reproductive success and survival (Mysterud & Ims 1998).

Specific microhabitats such as tree holes, soil, and vegetation can buffer extreme local conditions and provide important shelters from physiological stressors (Scheffers et al. 2014). Considering that amphibians must avoid desiccation (Seebacher & Alford 2002), microhabitat selection should play an important role in their life-history evolution (Lehtinen et al. 2004). In certain environments where freshwater is scarce, bromeliads phytotelmata can provide a desirable microhabitat for a variety of vertebrates (Neill 1951). In addition, these plants can store rainwater in their tanks for long periods (Zotz & Thomas 1999), which provides a stable environment where several micro- and macro-invertebrates live (Frank 1983, Kitching 2001). For this reason, they are particularly important microhabitats for animals living in the coastal *restinga* of Brazil, an area characterized by high temperatures, high air evaporative potential, and great salt spray exposure (Franco et al. 1984). The *restinga* is a lowland forest with sandy soils belonging to the Atlantic Forest biome (Oliveira-Filho & Fontes 2000), where several terrestrial species of bromeliads occur (Cogliatti-Carvalho et al. 2008).

Bromeliads are an important factor driving amphibian diversity in *restinga* habitats (Silva et al. 2011, Pontes et al. 2013). While some adult frogs use them only as shelter (bromelicolous species), others exhibit a closer relationship throughout their life cycle, reproducing and feeding inside the plant (bromeligenous; Peixoto 1995). Previous studies have found that the occurrence of amphibians in bromeliads is associated with the number of individual bromeliads (Bastazini et al. 2007), the size of the plant and the characteristics of the stored water (Oliveira & Navas 2004), and whether the plant was exposed to direct sunlight (Bastazini et al. 2007, Silva et al. 2011).

Scinax cuspidatus (Lutz, 1925) is a bromelicolous tree frog species (Teixeira et al. 2002) that occurs in several *restinga* areas in southeastern and northeastern Brazil (Alves & Silva 2002, Frost 2014) in the states of Espírito Santo, Rio de Janeiro, and Alagoas (Frost 2014). Tadpole development occurs in seasonal water ponds during the rainy season in February, while adults are found using bromeliads as daytime shelter (Teixeira et al. 2002). Females lay about 280 eggs that develop into greenish-brown or yellowish-brown colored tadpoles covered with dark brown spots (Alves & Silva 2002).

Considering the stressful environmental conditions in *restinga* areas of Southeastern Brazil, we were interested in microhabitat selection by *S. cuspidatus*. Specifically, we wanted to determine the biotic and physio-chemical characteristics of bromeliads that are important predictors of microhabitat use by this species.

Materials and Methods

Our study site was in a coastal *restinga* area in Macaé, Rio de Janeiro, Brazil (22º18'09"S, 41º41'54"W, 10 m a.s.l., DATUM=SRTM3). We randomly collected 20 individuals of the terrestrial bromeliad *Neoregelia cruenta* over two hours (1100–1300) on 22 September 2006, in a 50.5 m^2 area, choosing plants at least 30 m apart. We recorded water temperature (Incoterm thermometer), maximum height above ground (i.e., from soil to top of the plant) and maximum radius to the nearest centimeter of each bromeliad. We also recorded whether the plant was in direct sunlight or not; those not under the canopy or shaded by adjacent bromeliads were considered to be in direct sunlight. Bromeliads were carefully removed from the soil to avoid the loss of the water stored in the tank, placed in plastic bags, and subsequently taken to the laboratory for screening.

For each bromeliad, we measured water volume (1 mL precision), pH (pH meter Digimed), and salinity (LabComp salinometer), and counted the number of leaves. The water was sieved (mesh diameter 0.125 mm) and aquatic and cursorial invertebrates were fixed in 70% ethanol. When found, individuals of *Scinax cuspidatus* were euthanized with lidocaine ointment, then fixed in 10% formalin and preserved in 70% ethanol. All specimens (n = 10) were deposited at the 'Coleção Herpetológica da Universidade de Brasília' (CHUNB 48298-48307).

We measured the snout-vent length (SVL) of all *S. cuspidatus* using Mitutoyo® calipers (0.01 mm precision), and determined sex by direct observation of gonads. Stomach and intestines of the animals were removed, and diet items identified to the lowest taxonomic group possible (class, order, or family). In addition to providing a preliminary account of the species diet, the aim of investigating diet was to determine which invertebrate groups should be considered potential prey of *S. cuspidatus*. This measure was adopted to avoid biased estimates of potential prey abundance. We calculated potential prey abundance as the total number of invertebrates found in each bromeliad, considering only those invertebrates from groups previously identified as being in the diet of *S. cuspidatus*. Invertebrates were identified under a stereomicroscope (Olympus TL3 10x).

We constructed a global model with the incidence of *S. cuspidatus* (binary response variable) in bromeliads modeled by plant characteristics, water chemistry, and potential prey abundance (predictor variables) (Quinn & Keough 2002). Then, we calculated all other possible models, i.e., all possible subsets of the global logistic regression model. Because of their refined prediction power and unbiased estimates when employing random sampling, logistic regression models are particularly appropriate for modeling habitat use (Keating & Cherry 2004). Those models were entered in a model selection procedure followed by a model averaging, which uses the average of the regression scores and Akaike Information Criterion (AIC) to estimate the best model (Burnham & Anderson 2002). While collinearity between predictors will not influence the logistic regression (Quinn & Keough 2002), it can inflate the error estimations and produce unreliable results (Tabachnick & Fidell 1996). To check for collinearity, we calculated the Variance Inflation Factors (VIF) but none had values higher than five (Table 1).

Table 1. Variance Inflation Factors (VIF) of bromeliad variables that were included in the logistic regression.

Bromeliad variables	VIF
Radius	4.39
Height	3.17
Water temperature	2.15
Water volume	2.24
Water pH	3.27
Water salinity	1.88
Number of leaves	2.65
Prey abundance	2.77

To test whether bromeliad selection was related to frog body size, we performed a multiple regression of SVL against the height and radius of the bromeliads. All statistical analyses were carried out in R v3.0.1 (R Core Team 2013), using the packages *boot* (Canty & Ripley 2014) and *MuMIn* (Bartón 2013).

Results

We found 8 adult male and 2 adult female *Scinax cuspidatus*, with no more than one individual per plant. Frog diets consisted primarily of arthropods, either body parts or whole animals of the following groups: Araneae, Diptera (Chironomidae), Hymenoptera (Formicidae), Ostracoda, Coleoptera (Carabidae), and Odonata, of which Carabidae, Odonata, and Formicidae were the most common. All prey groups were found inhabiting bromeliads, except for Araneae and Formicidae. A small number of Acari, Collembola, and Hemiptera were also found in the plants, but because these were not represented in the diet, they were excluded from estimates of potential prey abundance.

A model that included only pH and volume of water stored in the bromeliads was the best model selected (Table 2), and pH and volume of water exhibited the highest relative importance in the model, respectively (Table 3). All *S. cuspidatus* were found in bromeliads exposed to direct sunlight, and salinity was constant among plants; therefore, these two variables were not included in the logistic regression and model selection analyses. Moreover, temperature seems to be a good surrogate for sunlight exposure, and pH for the effect of vegetation structure (see Discussion). Being so, not using sunlight exposure in the regression avoids any unwarranted multicollinearity problem.

Specimens of *S. cuspidatus* were found both in the rosette center and in the leaf axils of bromeliads. The mean SVL of collected individuals was 22.4 ± 4 mm (15.8–26.4 mm). There was no relationship between body size of *S. cuspidatus* and the height and radius of bromeliads ($R^2 = 0.2965$, $F_{2,7} = 1.475$, $P = 0.292$), indicating that *S. cuspidatus* probably did not select bromeliads based on relative plant size.

Discussion

This study provided evidence that microhabitat selection by *S. cuspidatus* was primarily influenced by water pH, followed by water volume of bromeliads. Water temperature, potential prey abundance, number of leaves, height and radius of the bromeliad had little influence on microhabitat selection.

The effect of pH on amphibian egg development and tadpole survival is well recognized, both in laboratory experiments and in the field (Freda & Dunson 1986, Barth & Wilson 2010). However, the effect of water pH on the distribution and habitat use by adults is less understood (Hecnar & M'Closkey 1996). Previous work has investigated how pH affects reproductive site quality (Pierce 1985, Hecnar & M'Closkey 1996), and pH may show indirect effects on adult distribution by affecting the invertebrate community and changing resource availability (Horne & Dunson 1995), but it seems not to affect adult selection of breeding sites in a broad spatial scale (Provete et al. 2014). However, *S. cuspidatus* does not reproduce in bromeliads, and resource (prey) availability was not significant. Considering that the degree to which amphibians respond to pH varies among species (Pierce 1985), further research is needed to investigate a possible relationship between pH and adult physiological condition in this species.

Because pH is expressed in a decimal logarithmic base, small pH differences between occupied and non-occupied bromeliads (Table 4) can actually represent large differences in ionic activity. Similar results regarding pH differences between occupied and non-occupied bromeliads were found in a study on microhabitat selection of bromelicolous Neotropical salamanders of the genus *Bolitoglossa* (Ruano-Fajardo et al. 2014). Our results suggest that *S. cuspidatus* prefer bromeliads with higher pH. Indeed, higher pH was also associated with the presence of the bromeligenous tree frog *Scinax perpusillus* (Oliveira & Navas 2004). Under experimental conditions, the presence of the salamander *Desmognathus ochrophaeus* increased the pH of the solution in which they were maintained (Woodley et al. 2014). Considering the correlative nature of our study variables, distinguishing between microhabitat selection by *S. cuspidatus* or pH increases caused by the presence of the frogs (possibly via excretion) is not possible and would require controlled lab experiments.

Desiccation avoidance is one of the main issues driving amphibian microhabitat selection (Seebacher & Alford 2002). Due to the sandy soil and open vegetation, the evaporation rate in the *restinga* is very high (Franco et al. 1984), making freshwater a relatively limited resource. For bromelicolous species like *S. cuspidatus*, sheltering in phytotelmata during the day provides the means to overcome this issue, and is probably the reason water volume was important in microhabitat selection.

Table 2. Most supported models (ΔAIC < 4) for habitat selection by *Scinax cuspidatus*.

Models	Deviance	AICc	ΔAIC	Weight
pH + Volume	21.7	29.4	0.0000	0.1370
pH	24.6	29.4	0.0552	0.1330
(Null)	27.5	29.7	0.3710	0.1140
Prey abundance + pH + Volume	19.5	30.6	1.1800	0.0760
pH + Temperature + Volume	20.4	31.4	2.0700	0.0487
pH + Temperature	23.8	31.5	2.0900	0.0481
Volume	26.8	31.5	2.1000	0.0479
Temperature	27.1	31.8	2.4100	0.0411
Radius + pH	24.4	32.1	2.7200	0.0351
Prey abundance	27.5	32.2	2.7800	0.0340
Number of leaves + pH	24.5	32.2	2.7900	0.0339
Radius	27.5	32.2	2.8100	0.0336
Height	27.5	32.2	2.8100	0.0335
Number of leaves	27.5	32.2	2.8500	0.0329
Height + pH	24.5	32.3	2.8700	0.0325
Prey abundance + pH	24.6	32.3	2.9300	0.0317
Number of leaves + pH + Volume	21.3	32.4	2.9900	0.0307
Height + pH + Volume	21.3	32.4	3.0100	0.0304
Radius + pH + Volume	21.6	32.7	3.3200	0.0260

Table 3. Logistic regression averaged model parameters of the analysis of habitat selection by *Scinax cuspidatus*.

Variable	Coefficient	Standard error	Standardized coefficient	Relative variable importance
Intercept	1.930	5.870	–	–
pH	-0.015	0.707	-0.002	0.66
Water Volume	-0.003	0.004	-0.131	0.40
Prey abundance	0.002	0.005	0.027	0.14
Water Temperature	-0.041	0.093	-0.018	0.14
Number of leaves	0.001	0.008	0.001	0.10
Height	-0.001	0.006	-0.003	0.10
Radius	-0.002	0.008	-0.004	0.09

Table 4. Descriptive statistics of bromeliad variables (*Neoregelia cruenta*) in relation to the incidence of *Scinax cuspidatus*.

Variables	Present	Absent
pH	5.28 ± 0.50	5.12 ± 0.78
Volume (ml)	240.56 ± 99.57	315.68 ± 255.69
Prey abundance	43.88 ± 40.91	37.63 ± 64.46
Temperature (°C)	25.83 ± 1.34	26.32 ± 1.94
Number of leaves	22.00 ± 7.73	22.27 ± 10.48
Height (cm)	39.17 ± 10.91	38.18 ± 11.85
Radius (cm)	26.20 ± 7.18	27.00 ± 10.42

All *S. cuspidatus* were found in plants exposed to direct sunlight, which has been reported for several other hylids occurring in *restinga* habitats (Silva et al. 2011). The physio-chemical characteristics of the water stored in the bromeliads can be influenced by its exposure to sunlight (Guimarães-Souza et al. 2006). These authors reported a significant pH decrease in the water accumulated by *N. cruenta* when exposed to the sun compared to plants in the shade, probably because of the higher organic matter input from the surrounding vegetation in the latter case. As such, the selection of plants by *S. cuspidatus* exposed to direct sunlight might be due to altered physio-chemical characteristics of the water, such as pH, and not selection for sunlight exposure *per se*.

Different variables have been previously reported to influence the selection of a particular bromeliad by frogs, including shape and size of the plant, number of leaves, and volume of stored water (Mesquita et al. 2004, Oliveira & Navas 2004, Silva et al. 2011, Pontes et al. 2013). Selection based on bromeliad size occurs in larger species like *Aparasphenodon brunoi*, in which body size was positively correlated with size of the bromeliad (Mesquita et al. 2004). We did not observe the same pattern for *S. cuspidatus*, as their SVL was not correlated with bromeliad size. However, unlike the large *A. brunoi,* which always occupy the rosette center of the bromeliad (Mesquita et al. 2004), small-sized *S. cuspidatus* can easily find shelter in the leaf axils of the bromeliad. Therefore, the size of the plant is probably not an important variable for microhabitat selection, but we acknowledge that our sample size of *S. cuspidatus* was low.

It is worth noting that no bromeliads contained more than one *S. cuspidatus*. Species of the *Scinax perpusillus* group actively inspect bromeliads before reproducing (Alves-Silva & Silva 2009), and detailed behavior studies could shed light on the possibility that *S. cuspidatus* might inspect plants and choose those without other individuals. Previous studies found that around 40% of bromeliads were occupied by anurans (Silva et al. 2011, Pontes et al. 2013). Even though no other species were recorded during our survey, we found *S. cuspidatus* individuals in 50% of the bromeliads, which indicates a similarly high usage of bromeliads by amphibians and highlights the importance of these plants to amphibians (Silva et al. 2011).

Because life-history evolution is connected to habitat use (Morris 2003), microhabitat selection will be linked to extinction risk in certain amphibian species (Becker et al. 2007). The reasons for the decline of many amphibian populations is not yet completely understood, but physiological traits might be playing an important role in these declines (Stuart et al. 2004). Despite being listed as "Least Concern" in the IUCN red list, habitat loss and bromeliad collection might represent potential threats for *S. cuspidatus* (Van Sluys & Rocha 2004). Less than 0.47% of the area originally covered by *restinga* in the Atlantic Forest remains intact (Ribeiro et al. 2009). In relation to the whole Atlantic Forest biome, around 12% remains intact and of that only 9% is under legal protection (Ribeiro et al. 2009). *Restinga* habitats are still under extreme degradation pressure and most of the remaining patches are not under legal protection (Rocha et al. 2007). In addition, several bromeliad species are frequently extracted from the wild for commercial use (Versieux & Wendt 2007). Therefore, the conservation status of several amphibian species and other animals associated with bromeliads in this area may drastically change in the near future. Thus, we believe that investigating ecophysiological processes that influence the distribution of these organisms in the *restinga*, and understanding details of microhabitat use and selection can be important to inform conservation strategies for this and other bromelicolous species.

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+ Appendix I – one page (one table)

Appendix I. Bromeliad (*Neoregelia cruenta*) data in relation to the incidence of *Scinax cuspidatus*.

Bromeliad	*Scinax cuspidatus*	Radius (cm)	Height (cm)	Water temperature (°C)	Water volume (ml)	pH	Number of leaves	Prey abundance
1	Yes	20	33	24	340	4.84	24	60
2	No	44.5	65	25.5	440	3.81	44	0
3	Yes	24.3	33	25	270	6.42	23	110
4	Yes	23	33.5	26.5	260	5.42	18	0
5	No	32	42	24	745	4.25	29	0
6	No	40	34	27	640	4.78	26	152
7	Yes	22	30	27	400	4.75	39	75
8	No	13	48	31	235	6.45	13	44
9	No	22.5	34	26	280	5.59	28	0
10	Yes	32	42	25	175	5.46	17	0
11	No	28	39	27	85	5.55	13	10
12	Yes	35	60.5	27	250	5.15	13	9
13	No	14	18	27.5	2.5	–	15	0
14	Yes	27	35	24.5	200	5.47	24	63
15	Yes	37	54	25.5	50	4.97	15	5
16	Yes	15.5	31.5	28	220	5.08	25	73
17	No	18	33	27	165	5.19	17	0
18	Yes	21.9	30.1	27	350	–	38	71
19	No	27	33.5	24.5	305	4.95	21	32
20	No	36.5	43	25	575	5.49	31	176