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Bromeliad Selection by *Phyllodytes luteolus* (Anura, Hylidae): The Influence of Plant Structure and Water Quality Factors

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ABSTRACT.—**Bromeliads are used by many frog species because of their capacity to accumulate rainwater. The bromeligenous frog, *Phyllodytes luteolus* (Yellow Heart-Tongued Frog), uses bromeliads for its entire life cycle including shelter, foraging, and reproduction. We evaluated the effect of plant morphometrics and the properties of water accumulated in bromeliads on the selection of these plants by *P. luteolus*. We sampled 103 bromeliads of which 41 were unoccupied and 62 were occupied by *P. luteolus*. Results suggest that bromeliad occupation by *P. luteolus* is nonrandom. We found that occupied plants were shorter in height, had a greater number of leaves, and had lower water conductivity than did unoccupied plants. Males were more likely to occupy plants with more leaves than were females. Plant selection may be related to the reproductive success of *P. luteolus* because frogs using plants with more leaves and lower conductivity may experience reductions in competition for space, predator encounters, and desiccation. Considering that illegal bromeliad harvesting threatens many bromeligenous frogs, improved understanding of bromeliad selection may determine which bromeliad species should be targeted for conservation to ensure the population viability of frogs.**

RESUMO.—**Bromélias são usadas por muitas espécies de anuros, devido à sua capacidade de acumular água da chuva. O anuro bromelígena *Phyllodytes luteolus*, usa bromélias para todo o seu ciclo de vida, incluindo abrigo, forrageamento e reprodução. Avaliamos o efeito da morfometria e as propriedades da água acumulada em bromélias na seleção dessas plantas por *P. luteolus*. Foram amostradas 103 bromélias, das quais 41 estavam desocupadas e 62 foram ocupadas por *P. luteolus*. Os resultados sugerem que a ocupação de bromélia por *P. luteolus* não é aleatória. Descobrimos que as plantas ocupadas eram menores, tinham um maior número de folhas, e tiveram menor condutividade da água que as plantas desocupadas. Os machos tendem a ocupar plantas com mais folhas do que as fêmeas. A seleção de bromélias pode estar relacionada com o sucesso reprodutivo de *P. luteolus*; por exemplo, os anuros que utilizam plantas com mais folhas e menor condutividade podem experimentar uma redução da concorrência por espaço, encontro predador, dessecação, porque mais axilas com água estarão disponíveis, resultando em um maior sucesso reprodutivo. Considerando-se que o extrativismo ilegal de bromélias ameaça muitos anuros bromelígenas, a melhor compreensão da seleção bromélia pode determinar as espécies de bromélias que devem ser priorizadas para a conservação a fim de assegurar a viabilidade da população de anuros.**

Habitat selection by frogs implies that some characteristics of reproductive sites that increase reproductive success may be preferred (Von May et al., 2009). Selection can be influenced by biotic factors such as the presence of predators and competitors as well as by abiotic factors such as desiccation risk (Fincke, 1992; Sih, 1994; Stav et al., 1999; Kiflawi et al., 2003a,b). These same factors can influence the selection of different sites for oviposition and vocalization, by females and males, respectively (Lea, 2000; Von May et al., 2009; Ferreira et al., 2012). In addition, abiotic factors such as temperature, water volume, and pH may limit oviposition and larval development (Duellman and Trueb, 1994; Von May et al., 2009).

Frogs inhabiting Brazil's Atlantic Forest have a great diversity of reproductive and foraging modes (Haddad and Prado, 2005; Haddad et al., 2013). Some frog species use water accumulated in bromeliads for breeding, foraging, and shelter (Peixoto, 1995). The use of bromeliads as a resource is possible because some bromeliads species accumulate water between the leaves, forming a viable microenvironment (Schneider and Teixeira, 2001; Armbruster et al., 2002; Silva et al., 2011). The selection of breeding habitat is likely critical to ensure the survival of tadpoles and maintain stability of bromeligenous populations (Schulte et al., 2011). We know little, however, about which characteristics of bromeliads make them good breeding habitat for most tropical bromeligenous frog species (Oliveira and Rocha, 1997; Armbruster et al., 2002; Oliveira and Navas, 2004; Ferreira et al., 2012).

Variation in bromeliad morphology and structural complexity can result in variation of the volume, quality, and stability of stored water (Frank, 1983; Zotz and Thomas, 1999). Bromeligenous frogs that choose bromeliads in which to breed likely make their choice on the morphology of the plant, specifically its ability to hold water (Zotz and Thomas, 1999; Cogliatti-Carvalho et al., 2010; Pontes et al., 2013) as well as on the physical–chemical factors of the accumulated water (Schulte et al., 2011). In addition, different sexes may choose different bromeliad characteristics for different activities: males for attracting females who, after amplexus, can visit other plants for ovoposition.

The bromeligenous Yellow Heart-Tongued Frog, *Phyllodytes luteolus* (Wied-Neuwied, 1824) has a wide distribution along the eastern coast of Brazil (Frost, 2013). This species is found mostly in a sandy coastal plain called a "restinga," an ecosystem of the Atlantic Forest known for its variety of bromeliads (Fontoura et al., 1991; Araújo, 1992; Cogliatti-Carvalho et al., 2001). However, this species does not occupy all bromeliads, suggesting selection for certain breeding sites (Ferreira et al., 2012). Males call near water to attract females, which usually lay one to three eggs per axil in several bromeliads (Bokermann, 1966; Weygoldt, 1981). Although some studies describe occupancy and selection of *P.*

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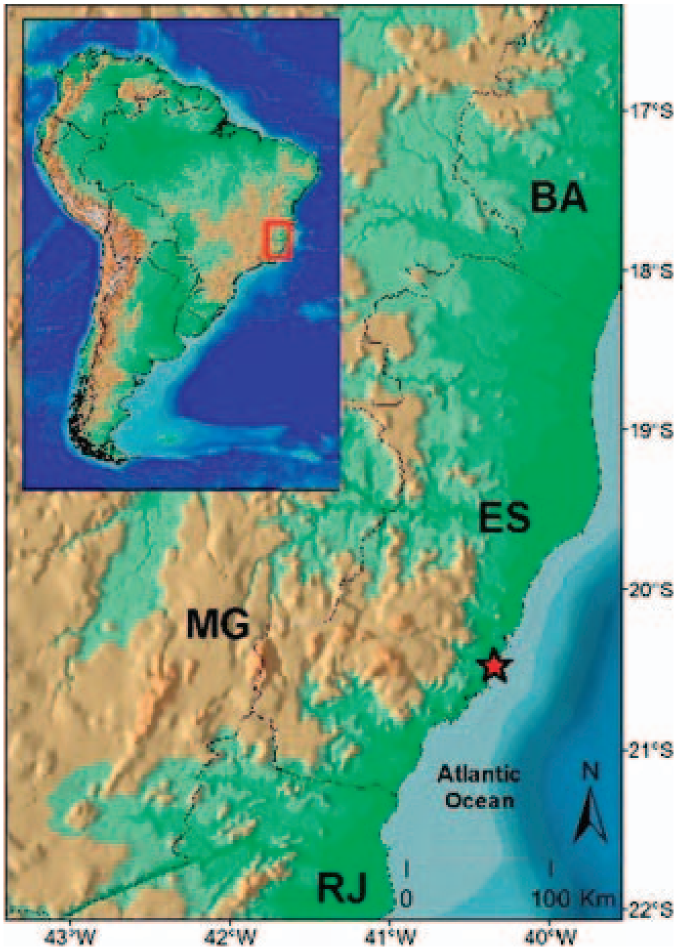

FIG. 1. Location of the Parque Estadual Paulo César Vinha (PEPCV), Guarapari, state of Espírito Santo, southeastern Brazil. States: Bahia (BA), Espírito Santo (ES), Minas Gerais (MG), and Rio de Janeiro (RJ).

luteolus in other localities (Eterovick, 1999; Schneider and Teixeira, 2001; Ferreira et al., 2012), few data exist that describe how structural complexity of the plant and physical–chemical factors of the water influence selection by male and female frogs.

The goal of this study was to investigate bromeliad selection by *P. luteolus* to determine if this selection differed by sex. To accomplish this goal, we determined the presence and absence of frogs in bromeliads and measured several structural variables and water quality variables of bromeliads in a restinga ecosystem. More specifically, because the selection of this microenvironment by bromeligenous frogs is likely to depend on factors related to structural complexity of the bromeliad (plant height, plant diameter, cup height, cup diameter, number of leaves, and axils) and water quality (volume, pH, temperature, saturated oxygen, dissolved oxygen, and solids in suspension), we investigated these particular factors (Oliveira and Navas, 2004).

Finally, the collection and trade of bromeliads in the restinga has become an important conservation issue for bromeligenous frogs (Salles and Silva-Soares, 2010). A related goal of this study is to highlight the importance of protecting bromeliads to promote the conservation of bromeligenous frogs.

MATERIALS AND METHODS

Study Sites.—We conducted fieldwork in a restinga ecosystem in the Parque Estadual Paulo César Vinha reserve (PEPCV; 20°33′–20°38′S and 40°23′–40°26′W, datum WGS 84), located in the Municipality of Guarapari, State of Espírito Santo, southeastern Brazil (Fig. 1). This ecosystem is greatly influenced by the ocean and is highly limited by the availability of fresh water. Therefore, rainwater accumulated in bromeliads is one of the few sources of fresh water available to bromeligenous frogs (Schneider and Teixeira, 2001; Teixeira et al., 2002). The climate is classified as Am Köppen (Köppen, 1948), with a mean temperature of 25°C and 80% relative humidity (Fabris, 1995; Clima Tempo Meteorologia, 2013).

We selected two areas in PEPCV, which are 1,100 m apart, where we sampled soil bromeliads. One area is a rocky outcrop (RO) and the other is a nonflooded open shrub formation on sandy soil (OF). The RO is 0.12 ha and 8 m above sea level (m a.s.l. [Barcelos et al., 2011]), near brackish temporary water bodies, and close to the ocean approximately 145 m away. This site lacks forest cover and experiences intense solar radiation. The OF is 8.5 ha and 6 m a.s.l. and is approximately 600 m from the ocean (Barcelos et al., 2011). Cactaceae and soil Bromeliaceae are the main vegetation at both sites. Bromeliads at the study site occur only in the soil, and other water-containing plants are either absent (on RO) or do not support bromeliad-breeding frogs, possibly because of their small size and inability to hold water. Therefore, we focused our surveys on soil-dwelling bromeliads in two survey areas. Dominant bromeliad species used by frogs at the sites include *Aechmea blanchetiana* (Baker) L. B. Smith (1955), *Aechmea nudicaulis* (L.) Griseb, 1864, in RO and OF, *Vriesea neoglutinosa* Mez, in OF, and *Quesnelia quesneliana* (Brongn.) L. B. Sm., in RO. In both sites, bromeliads form clumped distributions near shrubs.

Data Collection.—We conducted nocturnal samplings using both visual and audio detection to locate frogs (Heyer et al., 1994). Sampling occurred for 2–8 days per month from January to April 2013 in each of the two sites. To survey in each site, we examined each soil bromeliad we encountered to determine if it was occupied. If it was occupied, we hand-captured the frog, identified it to species, and recorded its sex (Izecksohn and Carvalho-e-Silva, 2010; Haddad et al., 2013). After identification, we released frogs into their original bromeliad. Males were identified by vocalization and presence of vocal sacs; females were identified by the absence of vocal sacs and the presence of eggs or tadpoles in bromeliads. To conduct physical–chemical and morphological comparisons, we standardized the number of bromeliads sampled (i.e., 30 bromeliads occupied by male, 30 occupied by female, and 30 unoccupied). The plants were identified based on their inflorescence morphology (Nara and Webber, 2002; Proença and Sajo, 2004; Machado and Semir, 2006; Braga, 2008).

We used a water multiparameter device (Model 85/100, YSI, Inc., Yellow Springs, Ohio, USA) to measure dissolved oxygen (O_2), saturated dissolved O_2, salinity, conductivity, and temperature, and an EcoSense pH 100 meter (YSI Serial No. JC03893) to measure pH in the central axil. For each bromeliad, we calculated the volume of phytotelmata (cm^3) using the formula:

$$\text{Volume} = \pi * \text{radius of the central axil}^2 * \text{height of the cup.}$$

Immediately after evaluating an occupied bromeliad, we repeated the same measurements in the nearest unoccupied bromeliad of the same species. To assess the structural architecture of each bromeliad, we measured plant height (from the root base to the tip of the longest leaf), plant diameter (distance between the two longest leaves), cup height (from the root base to the water surface level), cup diameter (diameter of

TABLE 1. Mean values (±SE) of characteristics of bromeliads selected by adults of *P. luteolus* in the Parque Estadual Paulo César Vinha, state of Espírito Santo, Brazil.

	Bromeliad species	
Plant characteristics	*A. nudicaulis*	*A. blanchetiana*
Plant height (cm)*	66.06 (2.77)	54.00 (1.83)
Plant diameter (cm)*	22.01 (1.07)	36.08 (2.01)
Cup height (cm)*	27.40 (1.14)	19.53 (1.13)
Cup diameter (cm)*	5.63 (0.19)	7.11 (0.38)
Number of leaves*	3.16 (0.17)	10.92 (0.33)
Hydrogenic potential (pH)	4.20 (0.10)	4.29 (0.09)
Saturated oxygen (%)*	31.46 (0.62)	10.29 (2.73)
Water temperature (°C)*	26.47 (0.20)	24.19 (0.19)
Conductivity (μi/cm^3)	63.81 (7.97)	45.71 (8.26)
Dissolved oxygen (mg/L)*	1 (0.23)	3.07 (0.56)

* Significant differences between the two species ($P < 0.05$).

the central axil, a measure of water storage capacity), number of leaves, and number of axils (space between leaves that store rainwater).

Data Analysis.—We used correlation analysis to test for the presence of collinearity in the morphometric parameters of the plant- and water-quality variables (Hair et al., 2005; Zar, 2010). Data with high collinearity ($r > 0.75$) were excluded from the analyses; number of axils was correlated with number of leaves, water volume was correlated with height and diameter of cup, and water salinity was correlated with conductivity. We checked the normality of data with the Shapiro–Wilk test. Only pH had a normal distribution. The other variables were log-transformed as a final attempt to meet assumptions of normality.

We applied a Student's *t*-test with normal data, or a Mann–Whitney *U*-test with nonnormal data, to evaluate differences in morphometrics and water quality between the two plant species most often used by frogs (*A. nudicaulis* and *A. blanchetiana*). For *V. neoglutinosa*, this was not possible because of the low number of samples ($n = 4$).

We used a one-way analysis of variance to examine the effects of bromeliad occupancy (0 or 1) and sex differences on pH, plant height, saturated O_2, and water temperature and a Kruskal–Wallis (KW) to examine their differences on conductivity, plant diameter, cup height, cup diameter, number of leaves, number of axils, water volume, salinity, and dissolved O_2. If differences were detected in the overall model, we used a Fisher's least significant difference (LSD) post hoc test to further evaluate differences. We analyzed data using R, v. 3.1.1 (R Development Core Team, 2014) and Statistica v.7 (Statsoft, Inc., Tulsa, Oklahoma, USA). For all statistical tests we established $\alpha = 0.05$.

RESULTS

We visually inspected 931 bromeliads of which 489 were *A. nudicaulis*, 354 were *A. blanchetiana*, 65 were *V. neoglutinosa*, and 23 were *Q. quesneliana*. *Vriesea neoglutinosa* had only four juveniles of *P. luteolus* and *Q. quesneliana* had no frogs, so they were excluded from further analysis. We sampled 62 bromeliads occupied by *P. luteolus*, which was more-often found in *A. blanchetiana* ($n = 36$; 54.6%) followed by *A. nudicaulis* ($n = 26$; 39.4%).

Bromeliad species differed in almost all parameters evaluated. *Aechmea blanchetiana* had wider and more leaves, a lower concentration of O_2 (dissolved and saturated), and lower temperatures than did *A. nudicaulis* (Table 1); however, these species did not differ in conductivity or pH (Table 1).

TABLE 2. Mean values (±SE) measured in bromeliads with males and females of *P. luteolus* and in unoccupied plants in the Parque Estadual Paulo César Vinha, state of Espírito Santo, Brazil.

	Occupied plants		
Variables	Males	Females	Unoccupied plants
Plant height (cm)*	58.50 (2.88)^a	54.54 (2.87)^a	65.17 (2.90)^b
Plant diameter (cm)	32.01 (2.63)	30.85 (2.05)	25.32 (1.80)
Cup height (cm)	21.15 (2.08)	21.80 (1.22)	24.08 (1.42)
Cup diameter (cm)	6.85 (0.54)	5.99 (0.36)	5.91 (0,25)
Number of leaves*	10.51 (1.20)^a	6.87 (0.73)^b	5.73 (0.62)^b
Hydrogenic potential	4.26 (0.14)	4.32 (0.11)	4.17 (0.12)
Saturated oxygen (%)	21.67 (3.33)	21.70 (2.64)	18.92 (2.97)
Water temperature (°C)	25.20 (0.33)	25.26 (0.28)	25.56 (0.31)
Conductivity (μi/cm^3)*	36.69 (10.14)^a	47.93 (8.70)^{a,c}	70.32 (9.97)^{b,c}
Dissolved oxygen (mg/L)	1.71 (0.26)	2.48 (0.81)	1.82 (0.36)

* $P < 0.05$.

^{a,b,c} Superscripts indicate similarity in the posteriori test of Fisher's LSD.

Of 931 bromeliads, we chose a random sample of 103 plants of *A. blanchetiana* and *A. nudicaulis*. This extracted value resulted in similar proportions of occupation for males, females, and unoccupied plants. Of these plants, 62 contained individuals of *P. luteolus* (29 males and 33 females) and 41 were unoccupied. Frogs were more likely to be found in bromeliads shorter in height, with lower water conductivity and fewer leaves (Table 2). Bromeliads occupied by males were similar to those occupied by females in height, diameter, cup height, cup diameter, O_2 (dissolved and saturated), conductivity, water temperature, and pH; however, males occupied plants with more leaves than did females (Table 2).

DISCUSSION

Selection of bromeliads by *P. luteolus* was not random, and characteristics of these plants appeared to influence occupation by frogs. Our study suggests that *P. luteolus* select plants based on specific architectural characteristics and physical–chemical characteristics of the water. *Phyllodytes luteolus* may use different characteristics of bromeliads to assess their suitability for reproduction purposes, similar to other anurans and salamanders (Pontes et al., 2013; Ruano-Fajardo et al., 2014). We found that bromeliad species had different morphological and physical–chemical characteristics that may be selected by frogs and differently between males and females.

In general, we found that *P. luteolus* occupied smaller plants with more leaves and water with lower conductivity than unoccupied plants. This would lead *P. luteolus* to have a greater occupancy rate in *A. blanchetiana*, which tend to have more of these characteristics. Smaller bromeliads can facilitate the movement of adults between leaves (Alves-Silva and Silva, 2009) for competition (escape or territory defense), oviposition, predation, and foraging and can allow rapid access to accumulated water with less energetic cost. A greater number of leaves may be correlated with water storage capacity

(Schneider and Teixeira, 2001; Cogliatti-Carvalho et al., 2010; Pontes et al., 2013), reducing the chances of desiccation of tadpoles. In addition, a greater number of leaves may reduce competition, facilitate escape from predators, and increase prey and satellite behavior (Lea, 2000; Cogliatti-Carvalho et al., 2010; Ferreira et al., 2012). Conductivity is closely related to organic matter accumulation (Silva et al., 2011) and salinity (Gervásio et al., 2000). Conductivity was the only physical–chemical parameter that negatively affected plant selection in our study site. Frogs may be avoiding highly conductive water in bromeliads because it can result in water loss and dehydration and, thus, potentially affect survival (McNab, 2002); or the presence of amphibians may change the chemistry of the bromeliad tank water (Ruano-Fajardo et al., 2014). This has been observed in others studies. For example, excretion by the bromelicolous Bathroom's frog Treefrog, *Scinax hayii* (Barbour, 1909) increases nitrogen in the resident water (Romero et al., 2010), and Common Coqui frogs, *Eleutherodactylus coqui*, increase nitrogen and phosphorous in throughfall (Sin et al., 2008). We could not separate the effect of frogs on water chemistry and their selection for particular water characteristics in this study.

The choice of bromeliad by males does not imply that females will use the same plant (Alves-Silva and Silva, 2009). We found differences in bromeliad selection between the sexes only for bromeliad complexity (i.e., number of leaves). Females seemed to select less-complex plants (mean of number of leaves = 6.9), directing their selection toward *A. nudicaulis*. Schneider and Teixeira (2001) found a similar result for restinga in the northern part of the state of Espírito Santo, where this bromeliad species showed the highest number of eggs and tadpoles and, therefore, was considered the main site of spawning by *P. luteolus*. Although less complex, *A. nudicaulis* leaves are organized in a single, wider, central tube resulting in a deep axil with a capacity to accumulate a higher volume of water (Schneider and Teixeira, 2001). Often, larger volumes are associated with more nutrients that favor the growth of tadpoles and are less likely to dry out and cause tadpole mortality (Lehtinen, 2004; Von May et al., 2009). Bromeliad selection by females should have a positive effect on larval development and survival. We found males in bromeliads with more leaves (mean of number of leaves = 10.5), which would favor *A. blanchetiana*. This agrees with Schneider and Teixeira (2001), who found a greater number of frogs in this bromeliad species. Males may select more-complex plants because competition may be reduced for calling sites, courtship, and fewer predator encounters, and there may be an increase in prey availability in these plants (Srivastava and Lawton, 1998; Pröhl and Hödl, 1999; Srivastava, 2006; Ferreira et al., 2012).

Plants that were unoccupied by *P. luteolus* in our study area had greater height, higher conductivity, and fewer leaves in relation to the occupied ones. *Phyllodytes luteolus* avoided bromeliads higher off the ground, which also was observed by Schneider and Teixeira (2001). In addition to the increased difficulty of occupying bromeliads higher off the forest floor, these plants may be occupied by other larger species of frogs that coexist with *P. luteolus* such as *Aparasphenodon brunoi* (Casque-Headed Frog), *Rhinella crucifer* (Striped Toad), and *Scinax alter* (Coast's Tree Frog). Even though these species do not use bromeliads for breeding, they can compete with other frogs for space and similar prey within bromeliads (see Teixeira et al., 2002; Ferreira et al., 2012).

While habitat loss is a major threat to all frog species in restinga ecosystems, bromeliad collection is another increasingly important cause of vulnerability for bromeligenous frogs, with a twofold impact: Collection of bromeliad species can increase the endangerment of these frogs, and the collection (and movement) of bromeliads can lead to the introduction of bromeligenous frogs elsewhere (Izecksohn and Carvalho-e-Silva, 2010; Salles and Silva-Soares, 2010). In addition, changes in the number of bromeliads available may result in changes in the proportion of males and females, populational inviability, and local extinctions in bromeligenous populations. As we improve our understanding of the ecology of bromeligenous frogs and gain a better appreciation of the types of bromeliads that these frogs select, we can improve conservation efforts for these frog species by protecting plants with specific characteristics (e.g., more structural complexity and greater storage capacity of water) to maintain the viability of these frog populations.

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