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# Where to call tonight? Selection of breeding sites by *Phyllodytes luteolus* (Anura: Hylidae), Brazil

**ILHÉUS - BAHIA**
**2023**

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Dissertação apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Mestre em Ecologia e Conservação da Biodiversidade.

Área de concentração: Ecologia e conservação de comunidades.

Orientador: Prof. Mirco Solé

Coorientador: Profª. Daniela Talora

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# SUMÁRIO

# Onde vocalizar essa noite? Seleção de habitat reprodutivos por *Phyllodytes luteolus* (Anura: Hylidae), Brasil


## RESUMO

Diversos traços do micro-habitat podem impactar significativamente o desenvolvimento embrionário e a sobrevivência dos anfíbios anuros. Fitotelmata, são pequenas cavidades com água encontradas em plantas, e desempenham um papel importante como micro-habitats para a reprodução de anuros em ecossistemas de florestas tropicais, contribuindo para sua sobrevivência. Determinados atributos morfológicos são comumente selecionados com base em exigências ecológicas, como a reprodução. Anuros bromelígenos, exemplificados pelas espécies do gênero *Phyllodytes*, endêmicas da Mata Atlântica, completam todo o seu ciclo de vida dentro de bromélias. Apesar dos esforços de pesquisas anteriores, há uma lacuna no conhecimento sobre a reprodução dessas espécies, o que apresenta amplas oportunidades para investigações adicionais na área. Assim, o presente estudo teve como objetivo identificar quais características das bromélias são selecionadas como locais de vocalização pelos machos e quais delas contribuem para o sucesso reprodutivo de *Phyllodytes luteolus* na região. Nossos esforços amostrais se concentraram em bromélias encontradas em uma área periurbana chamada Acuípe, situada em um ambiente de restinga no sul da Bahia, Brasil. Oito variáveis preditivas foram escolhidas para caracterizar a estrutura do micro-habitat utilizado tanto pelos machos quanto pelos girinos. Nossos resultados demonstraram que quatro características morfológicas (volume de água do copo central e da axila, o diâmetro da axila e número de folhas) das bromélias são traços importantes para a reprodução de *P. luteolus* na área de estudo. Nosso estudo gerou dados que podem auxiliar para uma melhor compreensão da história natural de *P. luteolus*, especialmente considerando a limitada pesquisa conduzida nesse campo específico.



Palavras-chave: História Natural; Ecologia; Anuros; Mata Atlântica; Bahia.

# Where to call tonight? Selection of breeding sites by *Phyllodytes luteolus* (Anura: Hylidae), Brazil


## ABSTRACT

Several micro-habitat traits can significantly impact the embryonic development and survival of anuran amphibians. Phytotelmata, small water-filled cavities found in plants, play a crucial role as micro-habitats for anuran reproduction in tropical forest ecosystems, contributing to their survival. Certain morphological attributes are commonly selected based on ecological requirements, such as reproduction. Bromeligenous anurans, exemplified by species of the genus *Phyllodytes*, endemic to the Atlantic Forest, complete their entire life cycle within bromeliads. Despite previous research efforts, there is a gap in knowledge about the reproduction of these species, presenting ample opportunities for additional investigations in the field. Thus, the present study aimed to identify which bromeliad characteristics are selected as vocalization sites by males and which ones contribute to the reproductive success of *Phyllodytes luteolus* in the region. Our sampling efforts focused on bromeliads found in a peri-urban area called Acuípe, situated in a restinga environment in southern Bahia, Brazil. Eight predictive variables were chosen to characterize the micro-habitat structure used by both males and tadpoles. Our results demonstrated that four morphological characteristics (volume of water in the central cup and leaf axil, axil diameter, and number of leaves) of bromeliads are important traits for the reproduction of *P. luteolus* in the study area. Our study generated data that can contribute to a better understanding of the natural history of *P. luteolus*, especially considering the limited research conducted in this specific field.



Keywords: Natural History; Ecology; Anurans; Atlantic Forest; Bahia.

# Where to call tonight? Selection of breeding sites by *Phyllodytes luteolus* (Anura: Hylidae), Brazil

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Several micro-habitat traits can significantly impact the embryonic development and survival of anuran amphibians. Phytotelmata, small water-filled cavities found in plants, play a crucial role as micro-habitats for anuran reproduction in tropical forest ecosystems, contributing to their survival. Certain morphological attributes are commonly selected based on ecological requirements, such as reproduction. Bromeligenous anurans, exemplified by species of the genus *Phyllodytes*, endemic to the Atlantic Forest, complete their entire life cycle within bromeliads. Despite previous research efforts, there is a gap in knowledge about the reproduction of these species, presenting ample opportunities for additional investigations in the field. Thus, the present study aimed to identify which bromeliad characteristics are selected as vocalization sites by males and which ones contribute to the reproductive success of *Phyllodytes luteolus* in the region. Our sampling efforts focused on bromeliads found in a peri-urban area called Acuípe, situated in a restinga environment in southern Bahia, Brazil. Eight predictive variables were chosen to characterize the micro-habitat structure used by both males and tadpoles. Our results demonstrated that four morphological characteristics (volume of water in the central cup and leaf axil, axil diameter, and number of leaves) of bromeliads are important traits for the reproduction of *P. luteolus* in the study area. Our study generated data that can contribute to a better understanding of the natural history of *P. luteolus*, especially considering the limited research conducted in this specific field.

Keywords: Natural History; Ecology; Anurans; Atlantic Forest; Bahia.

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## *Introduction*

The process of habitat selection plays a key role in shaping the distribution patterns of organisms and is often mediated by behavioral mechanisms (Bonatti, 2006). Anuran amphibians, for instance, exhibit a diverse range of microenvironmental preferences to maintain favorable physiological conditions (Duellman & Trueb, 1994; Toledo et al., 2021). These preferences include seeking shelter under rocks, leaf litter, inside tree holes and within axial leaves (phytotelmata) of *Araceae* and *Bromeliaceae* plants (Rudolf & Rödel, 2005). Such microhabitats offer more stable temperature and moisture conditions compared to exposed sites (Wells, 2007). Numerous microhabitat traits (i.e vegetation structure, water volume or depth) can significantly impact the embryonic development and survival of anuran amphibians (Schulte & Lötters, 2013; Rojas, 2014; Pettitt et al., 2018). Phytotelmata, which are small water-filled cavities found in plants, serve as important microhabitats for anuran reproduction (Duellman & Trueb, 1994). These microhabitats play a crucial role in tropical forest ecosystems contributing to their survival (Richardson, 1999), where in some environments, such as in restingas, they are the only available water source. When anurans complete their entire life cycle within bromeliads they can be functionally categorized as bromeligenous or bromeligen species (Peixoto, 1995). Bromeliad morphological attributes are commonly selected by anurans based on a range of ecological requirements, including food availability, predator avoidance, and competition reduction (Poelman et al., 2013; Ruano-Fajardo, 2016).

Many aspects of frog species that breed in phytotelmata remain poorly understood, with several new species and novel reproductive modes having been described only recently (e.g., Ferreira et al., 2015; Vörös et al., 2017; Marciano-Jr et al., 2017; Folly et al., 2018; Orrico et al., 2018; Malagoli et al., 2021). However, we already know that the ecological specialization exhibited by these species renders them particularly vulnerable to environmental disturbances, once there are limited to a specific microhabitat to survive (Papp & Papp, 2000; Dos Anjos et al., 2021). Therefore, offspring development and survival potentially depend on which microhabitat features parents select for oviposition and tadpole rearing, selection should favor parents that incorporate information about local environmental factors into selecting habitats that promote offspring development and survival (Pettitt et al., 2018). Among the bromeligenous species, the genus *Phyllodytes* (Wagler, 1830) encompasses

15 endemic species found within the Atlantic Forest domain (Frost, 2021). It is noteworthy that a significant portion of these species lack sufficient data regarding their conservation status and population dynamics, resulting in a classification as Data Deficient (DD) by the International Union for Conservation of Nature (IUCN, 2023). Despite previous research efforts that have explored the reproductive biology of these species, a gap in knowledge remains, presenting ample opportunities for further investigations in this field.

*Phyllodytes luteolus* was originally described by Wied-Neuwied in 1821 and is distributed along the coastal region of eastern Brazil, ranging from Paraíba to northern Rio de Janeiro, northeastern Minas Gerais, and southern Bahia (Frost, 2021). However, it is important to highlight that there is one record of the species in Rio de Janeiro (Salles & Silva-Soares, 2010) corresponding to an introduced population, likely resulting from imported and planted bromeliads used in landscaping. Given that the trade of certain bromeliad species takes place freely, the anthropogenic pressure on the plant may be greater than if it were illicit. Blotto et al. (2021) indicated the presence of other species within the *P. luteolus* group, based on its phylogenetic results. However, integrative analyses need to be conducted to confirm the presence of these additional species. Males and females tend to inhabit bromeliads with different complexities (e.g., number of leaves, with more complex bromeliads having a higher number of leaves). Thus, the selection of habitats by this species is possibly related to the reproductive preferences of each individual (Mageski et al., 2016). Mageski and colleagues (2016) observed that males and females tend to occur in bromeliads with different complexities (e.g., number of leaves). Thus, this selection is possibly related to the reproductive preferences of each sex. Also, it it's know that in the deposition micro-habitat, females lay one to three eggs per leaf axil, utilizing multiple bromeliads, with intervals of a few days (Bokermann 1966; Weygoldt 1981). Eterovick (1999) also states that male site selection for vocalization may involve preference for certain sustainable characteristics conducive to offspring development. However, the knowledge regarding this behavior and the preferred environmental conditions by individuals in the choice of microhabitat is still scare.

Therefore, the present study aims to achieve the following objectives: (1) Identify which characteristics of bromeliads are selected as vocalization sites by adult males of *P. luteolus* in a region in southern Ilhéus, Bahia. Our hypothesis is that males of the species have a preference for vocalizing in bromeliads that offer a greater availability of resources, maximizing their reproductive fitness. This includes more complex and robust bromeliads that can provide a greater number of sites for vocalization and tadpole development (Mageski et al., 2016; Ruano-Fajardo, 2016). We expect to find males calling in bromeliads with a greater number of refuges (available axils) and suitable microenvironmental conditions (water volume available in the bromeliad) for the survival of their future offspring. And also (2) investigate which characteristics of bromeliads contribute to the reproductive success of the species in the sampled region. Our hypothesis is that pairs with the ability to recognize bromeliads that are more suitable for offspring development follow a pattern of selection in choosing oviposition sites. This preference is driven by the fact that only certain microhabitats, such as those with a high water storage capacity, can support successful tadpole development (Krebs, 2001; Bonatti, 2006). Consequently, we anticipate finding evidence of tadpole presence, serving as an indicator of the species' reproductive success, predominantly in bromeliads exhibiting similar morphological characteristics. These specific microhabitat features hold greater importance for optimal offspring development.

## *Material and Methods*

### *Study Site*

The research site encompasses a peri-urban area called Acuípe, situated in restinga environment between the municipalities of Ilhéus and Una, in the state of Bahia, Brazil and it is located close to the BA-001 highway. The focal species of our investigation was *Aechmea blanchetiana* (Baker) L. B. Smith (1955), which exhibits a clustered distribution pattern, wherein several individuals are found in proximity. These clusters occur naturally in the study area, although they are occasionally cultivated as ornamental plants in proximity to coastal structures. We examined bromeliads (Figure 1) that already had been previously identified (15° 05 '10.8"S 38° 59' 55.1"W) and utilized in other studies (Salinas et al., 2018; Abreu et al., 2023), and bromeliads that was newly discovered by our research team (15° 05' 09.5"S 38° 59 '55.1"W). Within these groups, we examined every living bromeliad situated on the ground. However, not all bromeliads were found to be alive, but all living ones were evaluated. The Yellow

Heart-Tongued Frog, referred to as *P. luteolus*, is commonly found in the region and has been the subject of analysis in prior investigations conducted within the same locale (Salinas et al., 2018; Abreu et al., 2023).

**Figura. 1** Groups of bromeliads **s**elected to investigate the selection of breeding sites by *P. luteolus*.

### *Sampling*

Eight predictive variables were selected to characterize the micro-habitat structure, encompassing cup diameter (CD) and water volume (CV), number of axils with water (NAX), number of leaves (NL) and leaf length (LL), leaf width (LW), axil diameter (AD) and water volume at the location of individuals (AV) (Table 1 and 2). The following measurement instruments were employed: a measuring tape with a length of 1.5 meters to assess LL and LW, a study compass to measure CD and AD, and a PVC tube with a diameter of 10 mm for water extraction from bromeliads, subsequently measured using a 250 ml measuring cup to determine AV and CV.

Sampling occurred for 5 days per month from December 2022 to February 2023 between 20:00h and 23:30h, based on previously personal observations on the calling period of individuals in the region. Each micro-habitat was individualized and distinguished by employing distinct color tapes corresponding to the type of occupancy: male adults and/or tadpoles. Adult male frogs were detected through acoustic surveillance and had their sites measured. Subsequently, the bromeliads inhabited by any male were assessed, and without delay, identical measurements of the predicted variables were conducted in this individual and on the adjacent bromeliads (ranging from 1 to 3 bromeliads). Since *P. luteolus* was the only bromeligenous species find in the sampling area, we used visual detection techniques in order to determine the presence of tadpoles, with emphasis on identifying a distinct light reflecting structure located on their snouts (Figure 2). The sampling approach employed for the assessment of bromeliads with tadpoles was consistent with the method used for measurements of bromeliads with presence/absence of calling males.

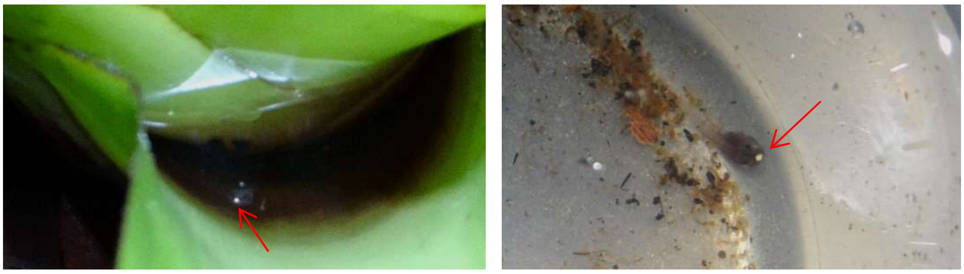


**Figure 2.** Tadpoles of *P. luteolus* in the sample area. The red arrows indicate the presence of light reflecting structure located on their snouts.

**Table 1.** Descriptive statistics of environmental variables in bromeliads with (n=37) and without (n=59) males of *Phyllodytes luteolus* in vocal activity.

| | Presence of vocalization | | | | Absence of vocalization | | | |
|---|---|---|---|---|---|---|---|---|
| **Variables** | **N** | **Mean** | **DP** | **Range** | **N** | **Mean** | **DP** | **Range** |
| CV | 37 | 168.7 | 67.2 | (45.0-310.0) | 59 | 109.2 | 69.3 | (0.0-310.0) |
| AV | 37 | 166.7 | 76.2 | (10-370.0) | 59 | 103.5 | 82.9 | (0.0-367.0) |
| AD | 37 | 3.95 | 1.21 | (1.60-6.5) | 59 | 4.34 | 1.29 | (1.2-8.0) |
| CD | 37 | 4.78 | 0.95 | (2.2-6.4) | 59 | 4.35 | 1.28 | (1.9-7.4) |
| NL | 37 | 18.81 | 4.19 | (10.0-28.0) | 59 | 15.54 | 4.56 | (6.0-26.0) |
| NAX | 37 | 12.65 | 3.33 | (5.0-20.0) | 59 | 11.08 | 3.83 | (4.0-19.0) |
| LL | 37 | 66.43 | 15.5 | (31.5-104.0) | 59 | 65.69 | 17.0 | (24.50-100.0) |
| LW | 37 | 10.76 | 1.40 | (7.0-13.50) | 59 | 9.85 | 1.68 | (5.30-13.10) |

CV = Cup volume (ml); CD = Cup diameter (cm); AV = Axil volume (ml); AD = Axil diameter (cm); NL = Number of leaves; LW = Leave width (cm); LL = Leave length (cm); NAX = Number of axils with water.

**Table 2**. Descriptive statistics of environmental variables in bromeliads with and without tadpoles of *Phyllodytes luteolus*.

| | Presence of tadpoles | | | | Absence of tadpoles | | | |
|---|---|---|---|---|---|---|---|---|
| **Variables** | **N** | **Mean** | **DP** | **Range** | **N** | **Mean** | **DP** | **Range** |
| CV | 51 | 182.0 | 71.6 | (50.0-380.0) | 61 | 106.2 | 68.1 | (5.0-290.0) |
| AV | 51 | 188.2 | 97.1 | (0.5-455.0) | 61 | 105.5 | 73.2 | (0.0-260.0) |
| AD | 51 | 3.89 | 1.38 | (2.60-6.80) | 61 | 4.15 | 0.93 | (1.20-5.90) |
| CD | 51 | 4.89 | 0.95 | (2.60-6.80) | 61 | 3.96 | 1.21 | (1.90-6.80) |
| NL | 51 | 19.94 | 3.92 | (11.0-30.0) | 61 | 15.59 | 4.66 | (6.0-24.0) |
| NAX | 51 | 13.67 | 3.45 | (4.0-20.0) | 61 | 10.85 | 4.12 | (4.0-19.0) |
| LL | 51 | 63.36 | 16.2 | (26.0-104.0) | 61 | 61.91 | 15.0 | (29.0-87.50) |
| LW | 51 | 10.92 | 1.63 | (7.0-14.50) | 61 | 9.40 | 1.62 | (5.30-11.70) |

CV = Cup volume (ml); CD = Cup diameter (cm); AV = Axil volume (ml); AD = Axil diameter (cm); NL = Number of leaves; LW = Leave width (cm); LL = Leave length (cm); NAX = Number of axils with water.

### *Data Analysis*

The Spearman correlation coefficient was utilized to examine the relationship between the eight predictor variables that characterized the structure of bromeliads. Predictor variables exhibiting high correlation coefficients ($r < 0.7$) were excluded from the analysis (see Figure 3) due to the potential collinearity among variables, which could compromise the reliability of parameter estimation in the subsequent analyses (Zuur et al., 2009). None of the eight variables showed high correlation coefficients. Thus, the variables were subjected to a generalized linear model (GLM) using the "glm" function from the "stats" package (R Core Team, 2021). This analysis aimed to assess the morphological characteristics of bromeliads that significantly influence the selection of breeding sites by *P. luteolus*. Given that the predictor variables were measured in different units, we performed data standardization using the "*scale*" function prior to modeling (R Core Team, 2021). This standardization process ensured that all variables were on a comparable scale, allowing for more reliable model interpretation and parameter estimation.

The bromeliads chosen by males as vocalization sites were assessed using a binary variable indicating the presence (1) or absence (0) of vocalization within each bromeliad. We also used presence (1) or absence (0) of tadpoles as a binary variable like a proxy to evaluate the reproductive success of the species in the area. The primary objective of these samplings was to examine the variations between micro-habitats that play a crucial role in the species' reproduction and those bromeliads that were not selected by adults. To construct the models in this investigation, we employed a Binomial distribution, considering the nature of the response variable. To explore the relationship between predictor variables and breeding sites, we generated models encompassing all possible combinations of these predictors using the *'dredge'* function from the *'MuMIn'* package (Bartom K, 2020). These models were then ranked based on the Akaike Information Criterion (*AICc*). Models exhibiting a $\Delta AICc < 2$ were deemed the most parsimonious (Burnham & Anderson, 2002), furthermore these selected models were further analyzed to identify the predictor variables associated with breeding site selection.

Finally, we employed a Generalized Linear Model (GLM) exclusively incorporating the predictor variables deemed most influential according to the selected models. This GLM allowed us to assess the influence of these variables on the breeding behavior of the Yellow Heart-Tongued Frog.

## *Results*

A total of 149 bromeliads were sampled in the selected clusters. Among them, the sites with male vocalization (n = 37) were fewer compared to bromeliads with tadpole presence (n = 51), while the number of unoccupied bromeliads was higher (n = 61). The sites of vocalization and the bromeliads that facilitated successful reproduction of the species showed variations in relation to the associated microhabitats (see Figure 3). However, we obtained three common characteristics (cup and axil water volume, and axil diameter) among the breeding sites, as indicated by our models.

### *Vocalization site*

We sampled 96 bromeliads to detect the presence/absence of vocalizing males. Where 37 bromeliads were found to be used as vocalization sites, while 59 bromeliads did not contain vocalizing males. Within the best models, according to the lowest AICc, some predicted variables showed influence over vocalization sites selection (Table 3). The first two models (weight: *0.303* and *0.252*, respectively) included CV, AV, AD and

LW as characteristics that may influence on the vocalization sites by males of *P. luteolus*.

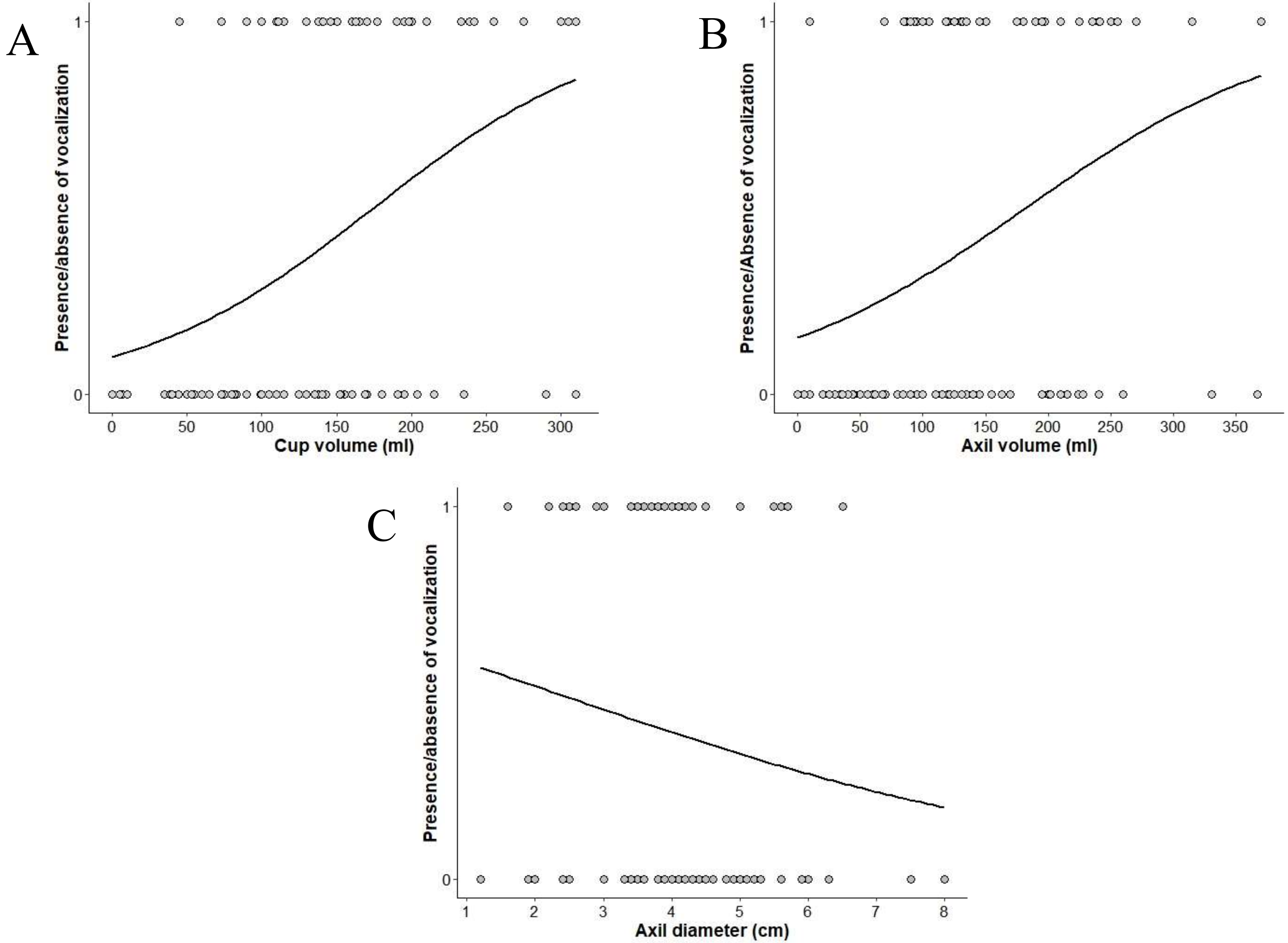
**Table 3.** Six models with the highest rankings among the 128 models that explore the relationship between predictor variables and calling sites. Second order Akaike information criterion values (AICc), AICc weights (Weights), AICc differences (Delta), log-likehood (loglik) and degrees of freedom (df). The best model is the one with the lowest AICc, the highest LogLik and weight (AICc: 107.5).

| Model | df | LogLik | AICc | Delta | Weight |
|---|---|---|---|---|---|
| CV + AV + AD | 4 | -49.549 | 107.5 | 0 | 0.303 |
| CV + AD + AV + LW | 5 | -48.619 | 107.9 | 0.37 | 0.252 |
| CV + AV + AD + NAX | 5 | -49.002 | 108.7 | 1.13 | 0.172 |
| CV + AD + AV + LW + NAX | 6 | -47.939 | 108.8 | 1.29 | 0.16 |
| CV + AV + AD + CD | 5 | -49.427 | 109.5 | 1.98 | 0.112 |

CV = Cup volume; CD = Cup diameter; AV = Axil volume; AD = Axil diameter; NL = Number of leaves; LW = Leave width; NAX = Number of axils with water.

The variables with the greatest relative importance were CV (*w = 0.855*), AV (*w = 0.772*), AD (*w = - 0.664*), while LW showed little lower relative importance (*w = 0.433*). When analyzing the predictor variables with the highest relative importance in the selection of vocalization sites, we can observe that the characteristics of AD (*p = 0.01810*), CV (*p = 0.00278*) and AV (*p = 0.00434*) are involved in determining the specific location for attracting the female. We observed *P. luteolus* males vocalizing in bromeliads with a similar pattern of available water volume and axils that were not formed by leaves too far apart from each other (*2.5 – 4.5 cm*) (Figure 4). The selected bromeliads were concentrated in the range of median volume compared to the unoccupied bromeliads. Given that we also found males vocalizing in the central cup, it was expected that the variation in cup volume (*110 – 250ml*) and axil volume (*80 – 255ml*) would be similar.

**Figure 4.** Relationship between calling sites by males of *Phyllodytes luteolus* and the bromeliad traits with greatest relative importance. A. Cup volume, B. Axil volume, C. Axil diameter.



### *Tadpoles presence*

To investigate which bromeliads facilitated tadpole development during the sampling period, 112 bromeliads were assessed for the presence or absence of tadpoles. Among them, 51 bromeliads contained tadpoles in their leaf axils or central cup, while 61 bromeliads were characterized by the absence of tadpoles. None of the tadpoles was quantify for abundance analysis. The best models for this goal, ranked by the lowest *AICc*, indicated predicted variables that may influence over breeding sites selection (Table 4). The first two models (weight: *0.291* and *0.205*, respectively) included CV, AV, AD, NL and NAX as characteristics that may influence the development of P. *luteolus* tadpoles.

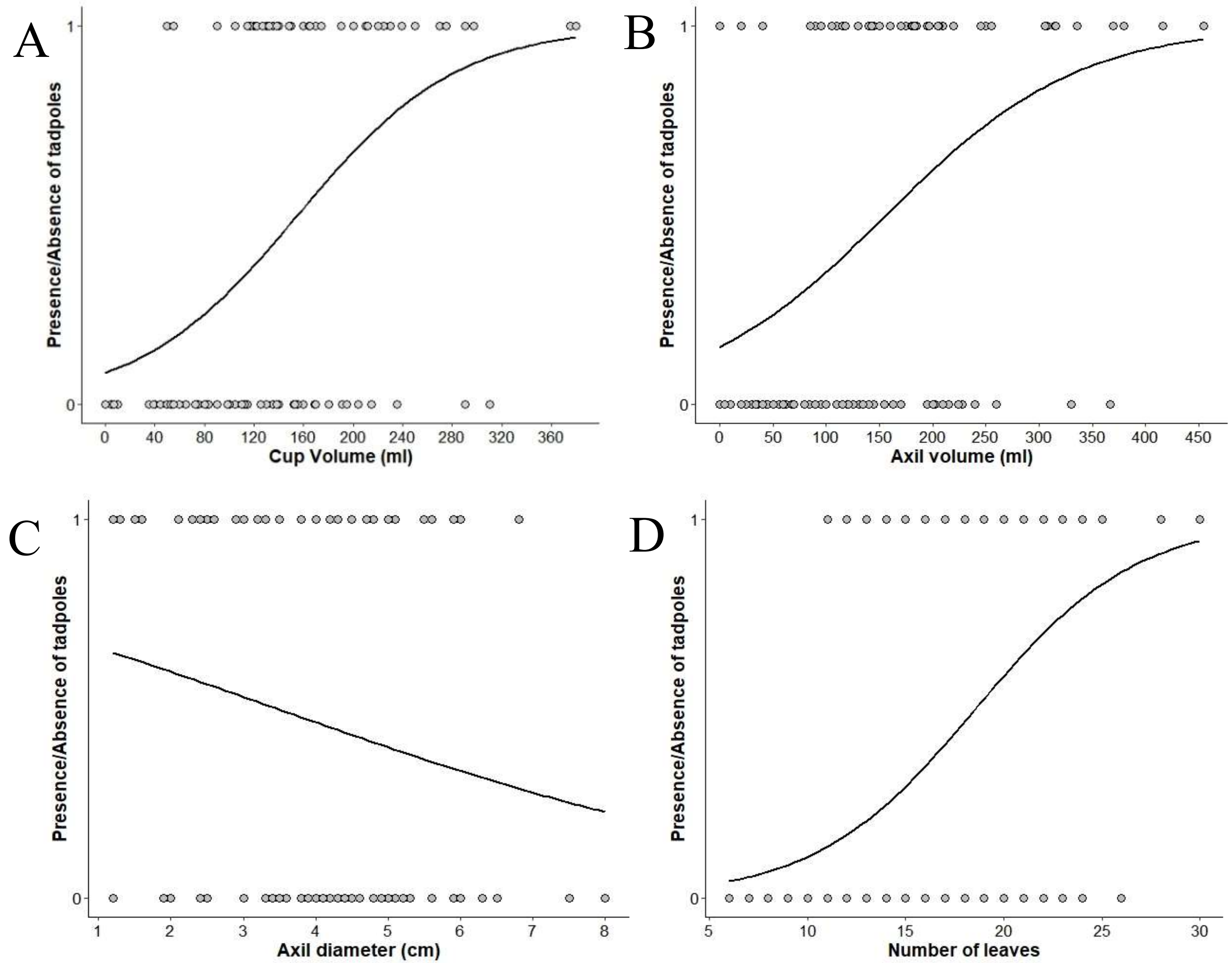
**Table 4.** Six models with the highest rankings among the 256 models that explore the relationship between predictor variables and breeding sites. Second order Akaike information criterion values (AICc), AICc weights (Weights), AICc differences (Delta), log-likehood (loglik) and degrees of freedom (df). The best model is the one with the lowest AICc, the highest LogLik and weight (AICc: 107.4)

| Model | df | LogLik | AICc | Delta | Weight |
|---|---|---|---|---|---|
| AD + LN + CV + AV | 5 | -48.422 | 107.4 | 0 | 0.291 |
| AD + LN + NAX + CV + AV | 6 | -47.655 | 108.1 | 0.70 | 0.205 |
| AD + CD + LN + CV + AV | 6 | -47.992 | 108.8 | 1.38 | 0.146 |
| AD + LN + LW + CV + AV | 6 | -48.118 | 109.0 | 1.63 | 0.129 |
| AD + LN + LL + CV + AV | 6 | -48.180 | 109.2 | 1.75 | 0.121 |
| AD + CD + LN + NAX + CV + AV | 7 | -47.155 | 109.4 | 1.98 | 0.108 |

CV = Cup volume; CD = Cup diameter; AV = Axil volume; AD = Axil diameter; LN = Number of leaves; LW = Leave width; NAX = Number of axils with water.

When examining the relationship between the most important variables indicated by the best model and the presence of tadpoles, we can also observe a pattern in the water volume of the selected microhabitats for egg deposition. However, unlike the vocalization sites, there is a difference in the volumes of the central cup (*110 – 300ml*) and the leaf axil (*80 – 260ml*). Thus, we can observe that even though adults deposit eggs in bromeliads with a large water-holding capacity and a large number of leaves (*n = 11 – 25*), they still tend to choose locations with a medium water volume within this micro-habitat.

**Figure 5.** Relationship between tadpoles of *P. luteolus* and the bromeliads traits with greatest relative importance. **A.** Cup volume, **B.** Axil volume, **C.** Axil diameter, and **D.** Number of Leaves



These bromeliads also have a wide variation in the diameter of the leaf axil (*1.2 - 6 cm*). However, among these values, axils with a smaller diameter were more frequently selected. This may support the notion that the complexity of the microhabitat, as indicated by the variable of NL ($p = 0.00355$) may have a relative importance in the survival of *P. luteolus* tadpoles in the region (Figure 5). Furthermore, the characteristics of the sites where these tadpoles were found, were described by the variables AD ($p = 0.00213$), CV ($p = 0.00354$) and AV ($p = 0.0064$), exhibit a pattern of selection by adults with higher reproductive success in this population.

## *Discussion*

Our findings provide evidence that reproductive site selection by *P. luotelus* is indeed non-random, and males have the ability to recognize the tanks offering them a better condition for reproduction, once some vocalization sites and sites with tadpoles showed similarity within some variables. Both chosen bromeliads for vocalization and those harboring tadpoles exhibit a consistent morphological pattern. They tend to occur in bromeliads with medium size, with traits of high water storage capacity and that presents axils within a specific size. Moreover, it is noteworthy that unoccupied bromeliads also exhibit a discernible pattern of unselected characteristics. This may indicate that despite the availability of unoccupied microhabitats, which could avoid intraspecific competition, these animals do not select such locations for breeding purposes.

### *Vocalization site*

According to our findings, male *P. luteolus* individuals prioritize selecting their vocalization sites based on the characteristics that are associated with favorable oviposition sites, perhaps because these animals court and reproduce in the same location and need to choose sites that attract their mates (Duellman & Trueb, 1994; Silva & Giaretta, 2008; Malagoli et al., 2021). According to Silva and Giaretta (2008), the selection of oviposition sites is primarily carried out by females (e.g., *Dryophytes femoralis, Buergeria japonica*), but in some species as *Edalorhina perezi, Lithobates catesbeianus, Phrynobatrachus guineensis* and seen in *Boana faber* (Martins et al., 1998), males also participate in the process by choosing vocalization sites with favorable conditions for oviposition. We believe that the same may occur with the sampled individuals since the majority of amplexi and spawnings (personal observation) were in the same axil where males were observed vocalizing. Eterovick (1999) indicated that males of *P. luteolus* may select bromeliads as vocalization sites based on preferences for microenvironmental characteristics that are favorable for offspring development. Males in the sampled region exhibited a greater interest in the volume of water and vocalization site's structure (AD and LW). The preference for vocalization sites exhibiting intermediate volume levels (CV and AV) may be attributed to a reduction in competitive interactions (Lantyer-Silva et al., 2018), and for mate success once the evaporation of the temporary water body inside the bromeliad results in reproductive failure, once their eggs and tadpoles need water to develop. For the majority of anuran species, the modulation of Evaporative Water Loss (EWL) is predominantly linked to the utilization of moist microenvironments (Andrade & Abe, 1997). Our study also corroborates that individuals of *P. luteolus* do not tend to select bromeliads with cup or axils water volumes less than 100 ml (Teixeira et al., 1997). Very large and water-filled tanks could reduce the male's ability to avoid predation or call to mating females (Lantyer-Silva et al., 2018). This result suggests that males possess the cognition to recognize bromeliads with morphological characteristics that do not allow for excessive water accumulation.

These facts can also be related to the chosen values of the axil diameter and leaf width by these phytotelmata species. Furthermore, it was noted that specimens of *P. luteolus* exhibit tactile exploration behavior on the foliage found at vocalization sites (personal observation), a behavior that could potentially support the relative significance of axil diameter as a critical microhabitat characteristic in site selection, as suggested by our analysis. Therefore, we believe that further studies should be conducted to confirm the influence of this vocalization site characteristic on its selection. In contrast to previous studies (Eterovik, 1999; Teixeira et al., 1997; Ferreira et al., 2012; Mageski et al., 2016), we add by observation that these animals also engage in amplexus in the central cup of the selected habitat. This behavior can potentially be explained by the similarity in water volume between the cup and the axils of the bromeliad. These findings suggest that these animals have the potential to initiate reproductive activities not only in the axils of bromeliads, where their presence is predominantly documented, but also within the central cup of these plants. Similar to the study conducted by Schneider and Teixeira (2001), which reported a significant number of eggs from *P. luteolus* in the bromeliad species *Aechmea nudicaulis*, a bromeliad characterized by possessing only the central tube. Therefore, it would be interesting to explore why they are more frequently observed in the axils than in the central up of bromeliads.

***Tadpoles presence***

Our models indicate that the reproductive success of the sampled species tends to be linked to specific characteristics selected by adults in the region. Several microhabitat features impact the development and survival of anuran embryos and tadpoles and, therefore, should influence decisions by parents about suitable oviposition sites and tadpole rearing sites (Rojas, 2014; Pettitt et al., 2018). Bromeliads with the presence of tadpoles represent sites of greater complexity (Mageski et al., 2016) and with a high water storage capacity. However, when examining the quantities of water-filled bromeliads that play a role in the reproductive success of the species within the area, it becomes evident that locations with intermediate volumes were more frequently seen to be positive for the development of eggs. But is important to emphasize that the water volume during tadpole sampling is not necessarily the same as that selected by the breeding pair during spawning. Therefore, tadpoles were more frequently observed in bromeliads with lower volumes, probably because natural selection tends to favor parents that consider information concerning local environmental factors when selecting habitats that enhance the development and survival of their offspring (Pettitt et al., 2018).

The large variation in the estimated volumes among these reproductive sites could be related to the greater number of water-filled axils in these microhabitats, when the spawning occurs and the climatic conditions. We believe that heavy rains can facilitate the movement of tadpoles from higher to lower axils, where this translocation may be associated with the spacing between leaves that form the oviposition site (personal observation). This could also explain the large variation found in the diameter of axils with tadpoles. Nonetheless, even with axils of different sizes, it is worth noting that tadpoles were predominantly observed in more closed axils. This may be related to their body size, where specific diameters can provide refuge for these animals against predators, allowing them to survive. However, there are no studies on the maximum size of *P. luteolus* tadpoles, therefore, further research should be conducted to confirm this hypothesis. The greater number of bromeliads with tadpoles and the similarities between these sites can also be explained by the behavior of one single female using more than one microhabitat with intervals of a few days between the depositions (Bokermann, 1966; Weygoldt, 1981). We have also observed that within a single axil, tadpoles of different sizes may coexist, suggesting a potential site fidelity by males or intraspecific competition among them, once this species is already recognized for tending to have territorial behavior (Eterovick, 1999; Salles & Silva-Soares, 2010; Ferreira et al., 2012). The fact that tadpoles can potentially feed on eggs of their own species (Weygoldt, 1981; Santos et al., 2019), as already registered *Phyllodytes amadoi* (Vörös et al. 2022), can also explain the coexistence of these individuals.

Furthermore, we do not observe the behavior of females leading males for another axil (personal observation), this could corroborate to an important participation of males in the choice of oviposition sites and the presence of different stages of tadpoles within the same axil. Once that species that have males being a part of these process tend to be less selective in the presence of conspecific tadpoles (Silva & Giaretta, 2008). Therefore, to accurately identify and understand the pattern of tadpoles with different sizes in the same axil or central cup, we believe that conducting population monitoring studies is crucial. The similarity between the water-filled volume of some vocalization sites and bromeliads with tadpoles could also support the notion that this characteristic is intentionally selected and recognized by adults as crucial for the survival of the offspring, as indicated by our models.

### *Impacts for conservation*

According to the IUCN (2023), anuran amphibians are the most threatened group of terrestrial vertebrates in the global fauna. One of the primary causes for the decline of these animals' populations are loss of habitat and fragmentation (Toledo et al., 2021). The correlation between amphibian physiology and their habitats is not only significant for their biology but also for their conservation, as these relationships can have a deep impact on ecological interactions (Rowley & Alford, 2010; Goméz-Hoyos et al., 2018). Variation in habitat heterogeneity influences the composition of species assemblages (Ricklefs, 1977), and dissimilar forest matrices present both biotic and abiotic resources that may determine the occurrence of a particular species (Melo & Waechter, 2018). To bromeligenous anurans, breeding microhabitat is an essential and limited resource due to high competition for space and risk of predation (Crump, 1974). In contrast, if this microhabitat is affected by environmental change, those specialists might be more prone to extinction (Tonini et al., 2020). When we look at the natural history of species specialized in depositing eggs and tadpoles in bromeliad tanks, it is known that they rarely use other resources (Ferreira et al., 2019). This suggests high specificity for microhabitat selection, and once that phytotelm-breeding frogs might have distinct physiological requirements compared to closely related species breeding in ponds and streams, this can affect how they respond to global climate change (Tonini et al., 2020).

Demonstrating that individuals of *P. luteolus* have a preference for specific bromeliads emphasizes the need for conservation actions that maintain the integrity of the ecosystems where both taxa occur. This is particularly important because one of the criteria set by the IUCN (2012) for the Red List of endangered species is that if any taxon is obligatorily dependent on another taxon to complete all or part of its life cycle, biologically appropriate values should be applied to the host taxon. Without knowledge of the ecology and reproductive biology of *P. luteolus*, there is not enough information to identify the causes of a potential decline in populations (Papp & Papp, 2000). Amphibians are fundamental components of trophic networks in various ecosystems, being preyed upon by a wide range of vertebrates and invertebrates and forming the basic diet of many species (e.g., snakes and birds), thus the loss of a species can result in environmental imbalance within its respective habitat (Toledo et al., 2021). Another example that can be applied to highlight the ecological importance of the species is that their tadpoles are capable of preying on mosquito larvae, making them potential biocontrollers of disease vectors such as dengue, Zika, and chikungunya (Salinas et al., 2018). Therefore, we conclude that the information generated by the present study can help identify which bromeliads are essential as reproductive sites to *P. luteolus* in the southern region of Bahia state, aiding in the conservation and monitoring of the species and its microhabitats. In addition, we acknowledge that our study has contributed valuable data to the understanding of *P. luteolus* natural history, particularly considering the limited research conducted in this specific field.

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### *Declaration of interest statement*

No potential conflict of interest was reported by the authors.

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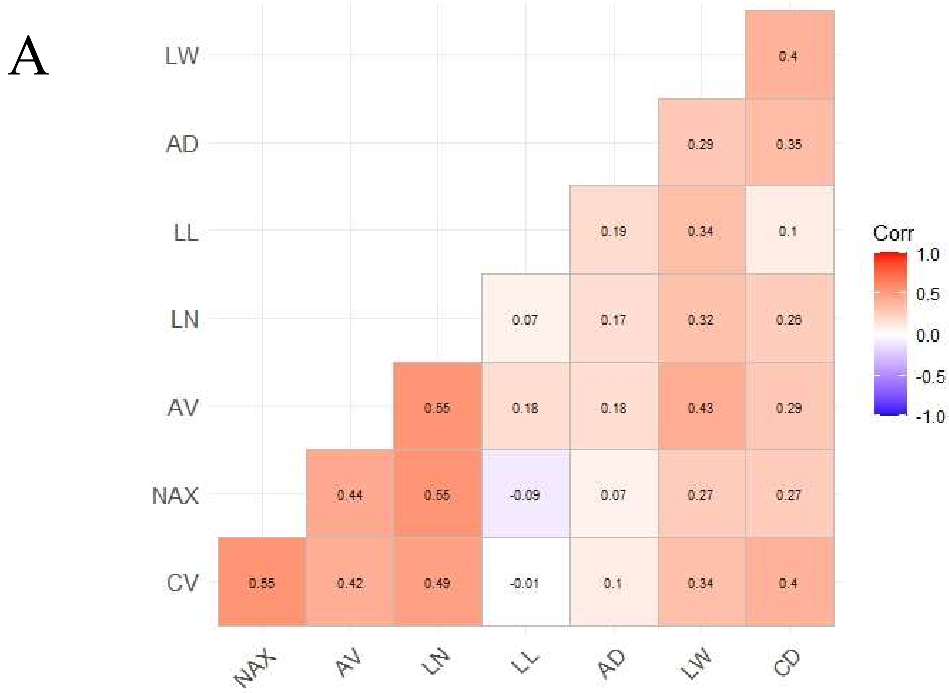
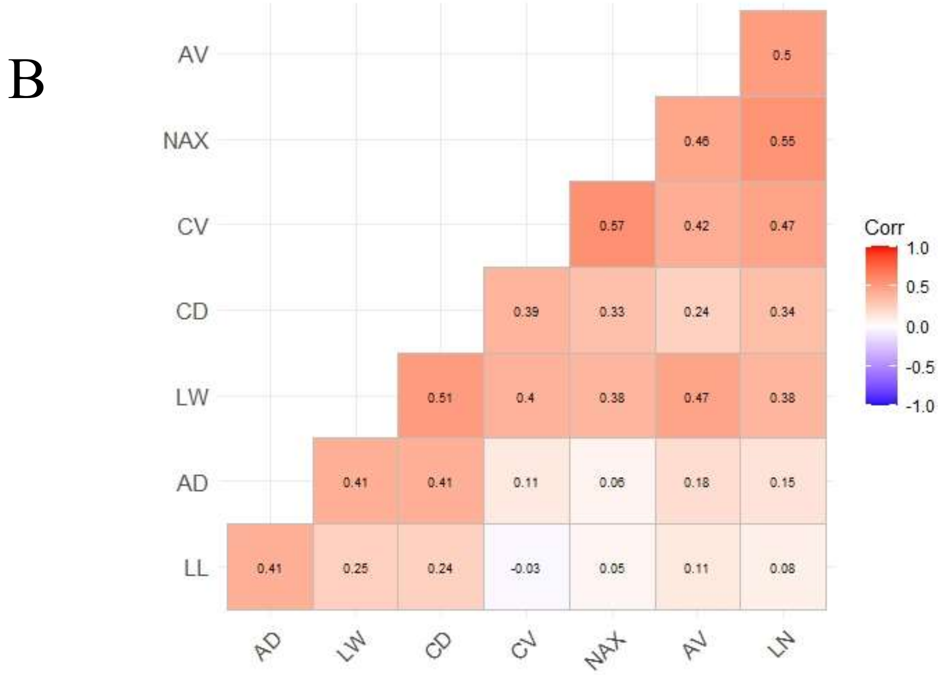
Figure. 3. Spearman correlations between variables with non-normal distribution.

**A**: Vocalization sites




**B**: Breeding sites.




CV = Cup volume; CD = Cup diameter; AV = Axil volume; AD = Axil diameter; NL = Number of leaves; LW = Leave width; NAX = Number of axils with water.