Habitat preferences in tree frogs and linkage to reproductive strategies

Daisy van de Biezen[1]

[1]Alliance for a Sustainable Amazon (ASA), Las Piedras, Madre de Dios, Peru
Corresponding emails: Daisy_1605@hotmail.nl & info@sustainableamazon.org

Abstract

Amphibians are among the terrestrial vertebrates with the most diverse reproductive strategies. The diversification of these strategies has allowed many species to occupy a wide variety of different habitats. Particularly in anurans, where evolution has led to different degrees of water dependence in reproduction. However, basic knowledge is lacking on habitat use and linkages to reproduction (strategies). Especially in tree frogs since they are an understudied group due to their arboreal nature. Reproduction, however, is a crucial process for species survival and therefore a basic understanding of habitat use in tree frogs is needed for effective conservation efforts. To study possible linkages between habitat use and reproductive strategies, the species richness and abundance between a palm swamp habitat with wetlands and an adjacent stream was compared to a terra firme forest in which these elements were absent. Most species and individuals were found in the palm swamp habitat in comparison to the terra firme forest. It was calculated that this difference was significant, indicating a preference for the palm swamp habitat. The two most abundant species in the palm swamp habitat were found to have aquatic and semi-terrestrial reproductive strategies, whereas the most abundant species in the terra firme forest habitat has a terrestrial reproductive strategy. Although this study gives an insight into a possible habitat use and reproduction linkage, the data is insufficient to fully understand how these aspects are linked. It is therefore important that more studies are conducted in the dry and wet season, especially during the reproductive peak.

Introduction

The diversification of reproductive strategies is a significant theme within animal evolution (Touchon & Warkentin, 2015). Particularly in vertebrate history, in which the transition from water to land was a major evolutionary event. The transition, however, has imposed challenges to morphological and physiological mechanisms, leading to changes in fundamental biological processes such as reproduction (Kardong, 2008; Finn et al., 2014). The diversification of reproductive strategies has allowed species to occupy a wide variety of specific habitats (Bertoluci & Rodrigues, 2002).

Anurans (frogs) have among the most diverse reproductive strategies of terrestrial vertebrates (Haddad & Sawaya, 2000; Haddad & Prado, 2005). Although anurans and other amphibians retain an ancestral dependence on water (Salthe & Duelmann, 1973; Wells, 2007), great diversity in reproductive strategies more independent of aquatic environments have developed through evolution. These evolutionary strategies are only possible in moist and humid environments, such as tropical rainforests (Salthe & Duellman, 1973, Müller et al., 2013). In these regions in particular, anurans have a profound variation in reproductive modes (Haddad & Prado, 2005; Wells, 2007). There are currently 41 modes known globally (Iskandar et al., 2014; Crump, 2015; Kusrini et al., 2015). This great variety is a result of an array of complex life-history traits including oviposition site, larval development, parental care, and egg characteristics (Salthe, 1969; Salthe & Duelmann, 1973). The reproductive modes are not limited to water, but rather range from fully aquatic to terrestrial and arboreal modes (Haddad & Prado, 2005; Crump, 2015; Portik & Blackburn, 2016). Reproductive modes more independent of water are mainly driven by selective pressures such as aquatic predation or terrestrial vacant niches (Magnusson & Hero, 1991; Touchon & Worley, 2015).

However, little is known about the ecology of anuran communities in tropical rainforests. Especially in terms of their assemblages (Duellman & Trueb 1986). Although many anuran species are well-studied, knowledge is lacking on the pattern of habitat use by tropical tree frogs. Understanding their habitat use is an important step in recognizing how this may be linked to reproduction (strategies). Knowledge on the patterns of habitat use is crucial in understanding what elements tree frogs need in their environment for successful reproduction, which is an essential process in species survival (Soulé, 1986). This is especially true for tree frogs since tree frogs occupy aquatic, terrestrial, and arboreal habitats (Salthe & Duelmann, 1973; Hödl, 1990; Rodríquez & Duellman, 1994). Many species rely on waterbodies by laying their eggs on leaves above ponds or streams (Rodríquez & Duellman, 1994; Zumbado-Ulato et al., 2021), creating foam nests on the water surface or laying their eggs on land and carrying tadpoles to water for further development (Hödl, 1990). Most females of species within the *Hemiphractidae* subfamily, for example, have modified pouches on their backs to raise their tadpoles (Zumbado-Ulato et al., 2021). However, there are species that reproduce in phytotelma (small water-filled cavities) in the canopy like bromeliads and palms in which non-feeding tadpoles develop in water basins created by leaf axils (Hödl, 1990). Some mate in trees or create large terrestrial nests in which non-feeding tadpoles develop. As a result, tree frog species that have terrestrial reproductive strategies that result in non-feeding tadpoles, may not be as dependent on nearby (standing) waterbodies. This would indicate that the habitat use of these species may differ from the species with aquatic reproductive strategies.

In order to determine whether a variety of reproductive strategies in tree frogs leads to a difference in habitat use, I compared tree frog species richness and abundance in a palm swamp habitat containing wetlands and a stream to an upland rainforest habitat in Madre de Dios, Peru. The purpose of this study was to get a broad idea of whether the variation in reproductive strategies can lead to a decreased dependence on waterbodies in some tree frog species, resulting in the occupation of habitats further away from water bodies. For this, I compared species richness and abundance of tree frogs in the terra firme forest and palm swamp habitats and investigated if differences in habitat use are linked to their reproductive strategies. I predicted that the terra firme forest habitat would have the lowest species richness, but would accommodate tree frogs with terrestrial reproductive strategies that are non(less)-dependent on standing water bodies. The abundance of species with terrestrial reproductive strategies may therefore be higher in this habitat in comparison to the palm swamp habitat. I also predicted that the palm swamp habitat would have the highest species richness caused by many tree frogs having aquatic reproductive strategies dependent on standing water bodies (Hödl, 1990; Rodríquez & Duellman, 1994; Zumbado-Ulato et al., 2021). It is therefore likely that the abundance of tree frogs with aquatic reproductive strategies may be higher in the palm swamp habitat.

This study provides a better understanding of a possible linkage between habitat use and reproductive strategies. Reproduction is crucial for species survival (Soulé, 1986) and therefore provides information that can be used in more effective conservation efforts.

Methodology

The study was conducted between 25 April and 05 June 2022 at the Finca Las Piedras Biological Station, which is the field site of the Alliance for a Sustainable Amazon, approximately an hour north along the Interoceanic Highway from Puerto Maldonado, Madre de Dios, Peru [S 12°13.570'; W 069°06.850']. The site is an estimated 54 hectares and is home to a variety of different habitats such as 'terra firme' rainforest and Mauritia palm swamps (aguajales). Terra firme forests are upland forests which are never subject to seasonal flooding (Pitman et al, 1999). At Finca Las Piedras, the terra firme forest is a relatively undisturbed natural habitat mainly dominated by the Brazil nut tree (*Bertholletia excelsa*) and other tropical hardwood species. The palm swamp habitat, referred to as aguajal in Peru, is a peatland swamp mainly dominated by aguaje palms (*Mauritia flexuosa*) (Householder et al., 2012). Data collection occurred at the onset of the southern Amazonian dry season.

Study group

For this project, the focus lies on species richness and abundance of tree frogs within the *Hylidae* and *Phyllomedusidae* families. These are the two main tree frog families present at the Finca Las Piedras property based on the current species list.

Sampling methods

For this study, two methods were included to determine the species richness and abundance of tree frogs in the two habitats: time and distance constrained visual encounter surveys (VES) and tree-based PVC pipes. Tree frogs, as well as various other herpetofauna species, are nocturnal and therefore night VES's are commonly used to survey and monitor amphibians (Doan 2003; Donnelly et al. 2005). Tree frogs, however, are arboreal and therefore require more specialized methods since they are challenging subjects to survey in situ (Corn, 1994). Ground survey methods like pitfalls, for example, are ineffective since tree frogs can easily escape from them (Corn, 1994; Myers et al., 2007). A specialized method for tree frog surveying are tree-based PVC pipes. The tubes mimic tree holes that tree frogs use during the day as a safe place to hide and rest before coming out at night (Boughton et al., 2000). These artificial refuges for tree frogs were included to function as an efficient sampling method in addition to the VES's (Myers et al., 2007; McRath-Blaser et al., 2021).

Visual encounter surveys

I established two ca. 500 m transects; one was located in the palm swamp habitat following wetlands and an adjacent stream, and the other extended through the terra firme forest. Both habitats are present within the same continuous forest area at the field site but ca. 400 m apart. The major difference between the two transects is the absence of a stream and adjacent wetlands in the terra firme forest habitat. The VES's were conducted along the two transects using a headlamp. Each transect followed existing trails present within each habitat. Both transects were sampled five consecutive nights a week (after 7:00 pm). During the VES's I systematically searched tree trunks, leaves, and branches within 2 m on either side of the trail and up to 3 m in height (e.g. Von May et al., 2010 & Kurz et al., 2014). This survey box was chosen due to time constraints and practicality since tree frogs higher up in vegetation are very challenging to see, photograph, and identify. Each transect was sampled by walking at a medium pace and all tree frogs encountered within a time constraint of 60 minutes per transect (photographing excluded) were photographed and later identified at the field station.

Tree-based PVC pipes

The PVC artificial refuges consisted of 50 cm long tubes with a ca. 3-4 cm inside diameter. Drainage holes were placed 15 cms from the bottom and tapered rubber was used to plug the bottom of the tubes. This created a water reservoir that allowed for increased humidity in the tubes and prevented tubes from overflowing during rainfall (Boughton et al., 2000; Meyers et al., 2007; McRath-Blaser et al., 2021). A total of 25 tubes were used per habitat and were evenly distributed through each habitat following the established transects. Each tube was attached to a tree using 20 m intervals along the transects. All tubes were labeled with a number to be able to register where the individuals and/or species were found. All tubes were checked twice a week in the morning (after 7:00 am) using a light. If a frog was found, plastic bags were used to drain the tubes, and frogs were carefully shaken into the plastic bags to prevent them from escaping (McRath-Blaser et al., 2021). They were then transferred into a clear container for photo identification.

Categorization of reproductive strategies

The species found in each habitat were categorized based on their reproductive strategies: aquatic, semiterrestrial, and terrestrial. This categorization was used for the habitat-reproductive strategy analysis to create a general view of the habitat use of the species in relation to their reproductive strategies. All reproductive strategies were determined as follows (Crump, 1974):

- Aquatic: eggs on the water surface or submerged, tadpoles develop in water;
- Semi-terrestrial: eggs deposited out of the water, tadpoles develop in water (i.e. eggs on vegetation);
- Terrestrial: eggs and development of tadpoles independent of standing water (i.e. waterfilled cavities);
- Mix: a combination of strategies listed above.

Data collection and analysis

Each time an individual was encountered along the VES-transects, the species scientific name, number of individuals, habitat type, sampling method, and date were recorded. The same data were recorded during the tube surveys. However, the pipe number in which an individual was found was added to the tube survey data. All data were used to analyze the species richness and abundance between the palm swamp habitat and the terra firme forest habitat. To do this, I calculated and compare d the abundance between habitats looking at the mean encounter rates of individuals per day for both the palm swamp habitat and the terra firme forest habitat. All individuals encountered were identified to species level. For proper identification, multiple photos were taken from each individual including the eyes, ventral pattern, dorsal pattern, lateral pattern, and hind legs. Every individual was then released at the capture site.

Since the data was not normally distributed, a Mann-Whitney U test was used to determine whether the difference between the mean encounter rates was statistically significant. This comparison provided an insight in the habitat preference of the tree frogs found at Finca Las Piedras. This test could not be applied for the comparison of species richness between habitats because not enough species were collected to conduct this test . Instead, a descriptive analysis was conducted in which I looked at the number of species per habitat and the most abundant species that were found. I then looked into the reproductive strategies of these species specifically (aquatic, semi-terrestrial, terrestrial or mix) to find a linkage between the habitat in which they are found.

I also compared all reproductive strategies found per habitat, calculating the proportion of all individuals found per each reproductive category. In addition, I compared the reproductive strategies per habitat showing the number of species per each reproductive category. The data on the reproductive strategies were analyzed descriptively. Some tree frog species, however, are understudied. Information on their reproductive strategies may be insufficient. These reproductive strategies will therefore be excluded from the data analysis. During data analysis, only the data of the VES-transects were used since only one species of tree frog was found using the artificial PVC pipes.

Table 1: All VES-encountered species and the number of individuals found in the terra firme forest (TFF) and the palm swamp (PS) habitat.

Species	Habitat	No. of individuals
Boana cinerascens	TFF	0
	PS	1
Boana geographica	TFF	0
	PS	9
Boana lanciformis	TFF	0
	PS	1
Boana punctata	TFF	0
	PS	1
Dendropsophus parviceps	TFF	0
	PS	14
Dendropsophus schubarti	TFF	2
	PS	0
Dendropsophus leali	TFF	2
	PS	0
Osteocephalus castaneicola	TFF	11
	PS	4
Osteocephalus buckleyi	TFF	2
	PS	7
Osteocephalus taurinus	TFF	0
	PS	17
Phyllomedusa vaillantii	TFF	2
	PS	9
Scinax garbei	TFF	2
	PS	2
Scinax ictericus	TFF	0
	PS	3
Hylidae sp. (juveniles)	TFF	1
	PS	5

Results

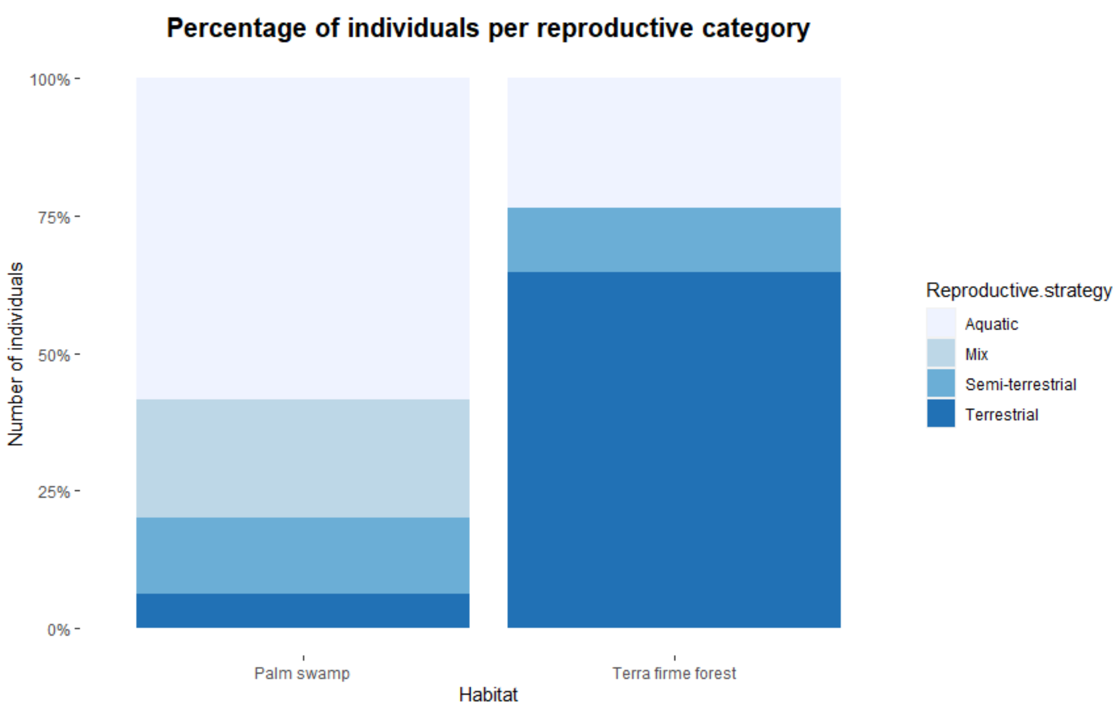
Visual encounter survey

A total of 95 individuals were encountered across 30 VES-survey nights. Of the 95 total individuals, 65 (68,4%) were found in the palm swamp habitat, and 30 (31,6%) individuals were found in the terra firme forest habitat. A total of 13 unique species of tree frogs were encountered, 12 (92,3%), of which were found in the palm swamp habitat and 5 (38,5%) of which were found in the terra firme forest habitat [table 1]. There were significantly more individual tree frogs found in the palm swamp habitat in comparison to the terra firme forest habitat (Mann-Whitney U test, P=0.0001452). Of all species found, only one was absent in the palm swamp habitat: *Dendropsophus leali.*

During 12 days of tube-surveys, only 1 tree frog was found in the tubes. This individual unfortunately escaped and could not be identified.

Reproductive strategies

Species with terrestrial, semi-terrestrial, and aquatic strategies were encountered in both the terra firme forest and the palm swamp habitat [see figure 1]. However, one species was found having both aquatic and terrestrial reproductive strategies (*Dendropsophus parviceps*). This mix of strategies was only found in the palm swamp habitat. Most species encountered in both habitats were found to have aquatic reproductive strategies (n=2 terra firme forest; n=7 palm swamp), whereas only one species in the terrestrial and semi-terrestrial categories were found.



Artificial PVC pipe refuges

Figure 1: The number of species encountered per reproductive category, showing that double the amount of species were found in the palm swamp habitat in comparison to the terra firme forest. Most species have aquatic reproductive strategies.

However, the abundance of the species in each category [see figure 2] shows that most individuals found in the terra firme forest habitat have a terrestrial reproductive strategy (n=11; 64,7%), whereas very few individuals were found having terrestrial strategies in the palm swamp habitat (n=4; 6,2%). All individuals with a terrestrial reproductive strategy were found to be of the same species [figure 1]: Osteocephalus castaneicola, highlighting a clear preference for the drier terra firme forest habitat. In the palm swamp habitat, most individuals were found to have aquatic reproductive strategies (n=38; 58,5%) in comparison to the terra firme forest habitat (n=4; 21,5%). The most abundant species in this habitat were Osteocephalus taurinus (n=17) and Dendropsophus parviceps (n=14). Osteocephalus taurinus was commonly found along the stream, whereas Dendropsophus parviceps was commonly found in the wetland area. Both of these species were absent in the terra firme forest, showing a clear preference for the palm swamp habitat. Low abundance was found in all other species encountered.

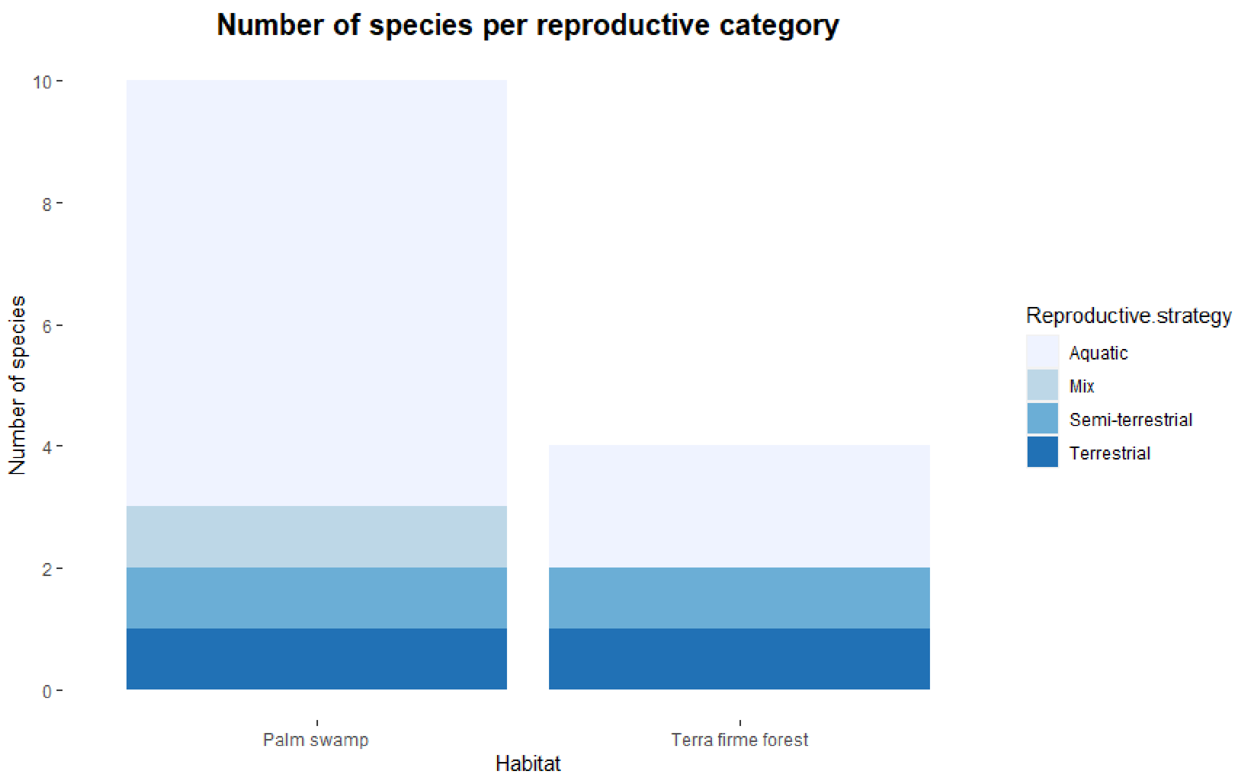


Figure 2: The proportion of individuals per reproductive category, showing that a big proportion of all individuals found in the terra firme forest habitat have a terrestrial reproductive strategy, whereas very few individuals have terrestrial reproductive strategies in the palm swamp habitat.

Discussion

Abundance and species richness

Most species and individuals were found in the palm swamp habitat (n=65; n=12), twice as much in comparison to the terra firme forest (n=30; n=5), supporting the hypothesis of this study. A significant difference was found between the mean encounter rates of the individuals per habitat (Mann-Whitney U test, P=0.0001452). The encountered individuals seemed especially abundant in the palm swamp wetlands. Palms serve as an important habitat for a wide variety of species (Kahn & De Granville, 1992). Aguajes, the dominant species in Finca Las Piedras' palm swamps, are a preferred breeding site for many species of frogs, including tree frogs (Huber & Febres, 2000).

Reproductive strategies and commonly found species

Generally speaking, most reproductive strategies found in the palm swamp habitat are aquatic while some are semi-terrestrial. Tree frogs with these reproductive strategies need larger standing water bodies for reproduction, which the palm swamp habitat provides. Most individuals found in the terra firme forest have terrestrial reproductive strategies, meaning the species utilize waterfilled cavities for reproduction (Crump, 1974; Hödl, 1990). These are also results supporting the stated hypothesis.

Osteocephalus taurinus and *Dendropsophus parviceps* were the most abundant species in the palm swamp habitat. *O. taurinus* was only found along the present stream and *D. parviceps* was most abundant in the wetlands with very few individuals found along the stream. *O. taurinus* has an aquatic reproductive strategy, meaning they lay their eggs in water. *D. parviceps*, however, have both aquatic and terrestrial egg-laying. This variation in reproductive strategies could help the species' persistence during periods of less-predictable rain (Touchon & Warkentin, 2008). This could be beneficial within wetlands and swamps since these dry out easily during the dry season.

The most abundant species found in the terra firme forest habitat, however, was *Osteocephalus castaneicola*. The only species found with a terrestrial reproductive strategy in this habitat. The dominant tree species in the terra firme forest habitat at Finca Las Piedras is the Brazil nut tree. Adult *O. castaneicola* have been found to use waterfilled Brazil nut fruit capsules (castañas) as a breeding location in which tadpoles were found. The fruit capsules provide protection and stable water conditions because the water remains in the capsules much longer in comparison to temporary puddles on the forest floor (Caldwell, 1993). Looking into the most abundant species and their reproductive strategies, it seems to show a linkage to their habitat use.

Unexpected findings

One species was found in the terra firme forest having a semi-terrestrial reproductive strategy: *Phyllomedusa vaillantii*. This species, as well as several other *Phyllomedusidae* species, deposit eggs on leaves above lentic water bodies (Silva e Silva et al., 2020). There are various explanations as to why this species was found in the absence of water. One of which is that the distance (400m) between the two transects may not have been great enough, though knowledge is lacking on the travel and migration distance of tree frogs in between habitats. However, many amphibians move to drier habitats for non-breeding activities (Wake, 1982). This phenomenon could explain why semi-terrestrial and aquatic species were sporadically found in the terra firme forest. Unfortunately, there is insufficient information on the species found in the terra firme forest having aquatic reproductive strategies: *Scinax garbei* and *Osteocephalus buckleyi*. However, it is likely that the same interpretations could apply to these two species.

Another finding was that some species were only found once during data collection. Tropical frogs have many different reproductive phenologies. Some species breed year-round (Berry, 1964; Inger, 1969), whereas others only breed during the wet season (Heyer, 1973; Aichinger, 1987; Gascon, 1991). However, most species have their reproduction peak in the rainy season (Salthe & Duellman, 1973). Since this study was conducted at the onset of the dry season, it could have led to a lower abundance in those species found.

Arboreal nature and tube effectiveness

Tree frogs are a challenging group to survey due to their arboreal nature (Corn, 1994). The majority of the frog species have a reproduction peak during the rainy season, of which some only come down at ground level during their reproduction (i.e. *D. parviceps*). During the dry season, some tree frogs move higher up in the canopy. The artificial tubes used to survey the frogs were placed at eye level. The tubes might have been too close to the ground for these species to occupy the tubes, hence leading to no frog encounters in them. Not only their arboreal nature but also seasonality plays a role in the habitat use of tree frogs. The tubes were placed at the start of the dry season. However, during the rainy season, leaf axils, branches, and tree holes fill up with water, acting as a hideaway or breeding spot for frogs (Boughton et al., 2000). This seasonal aspect may have led to these natural cavities to still be sufficiently filled with water, creating the humid environments the tree frogs need (Boughton et al., 2000; Meyers et al., 2007; McRath-Blaser et al., 2021). This could have resulted in the very low capture rate in the tubes

The way forward

Based on the results of this study, there appears to be some linkage between reproductive strategy and habitat use. However, there are other aspects that seem to determine the use of habitat such as distance from water sources, seasonality, and species ecology in general. These aspects are likely to have had an effect on the results of this study. Unfortunately, knowledge is lacking on many tree frog species in terms of both species-specific habitat use and reproductive strategies. This study alone, conducted during the transition from the wet season to the dry season, did not provide sufficient data to draw hard conclusions on habitat usage and linkage to reproductive strategies. For this reason, it is important that similar studies are conducted in both the peak of the wet and dry season for a better understanding of habitat usage of frogs and the linkage to reproductive strategies. Data from the wet and dry seasons could have different results in terms of abundance and species richness in the two different habitats. The more data there is, the better researchers are able to understand species ecology. It is especially important to conduct research in the peak of the reproductive season since this provides valuable information of habitat use during reproduction. This is essentially a crucial step towards understanding the linkage between habitat use in relation to reproductive strategies and one step closer towards a better understanding of how to effectively protect and conserve tree frogs in the Amazon.

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