**An Acad Bras Cienc (2020) 92(1): e20190458 DOI 10.1590/0001-3765202020190458**
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

BIOLOGICAL SCIENCES

# Seasonal and habitat structure of an anuran assemblage in a semideciduous forest area in Southeast Brazil

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**Abstract:** In this study, we evaluated the reproductive activity and the temporal and spatial distributions of anuran assemblages in three environments within a semideciduous forest in Southeast Brazil, located at Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil. The field activities were carried out during three consecutive days, monthly throughout the rainy seasons of 2013–2014 and 2014–2015. We recorded 28 anurans species, distributed in eight families. We observed the spatial-temporal distribution of some species, and their associated reproductive behaviors through exploration of vocalizations at different sites. The spatial and temporal distribution of the species seems to adapt to abiotic and biotic factors of their environment.

**Key words:** Anuran community, community ecology, environmental heterogeneity, niche breadth, vocalization sites.

## INTRODUCTION

Information about anuran habitat use and reproductive ecology allows us to interpret the relationships between these animals and abiotic and biotic factors (Eterovick & Sazima 2004). In several vertebrate groups (e.g. birds, anurans, mammals), it has been shown that the coexistence of populations in the same area is facilitated by ecological differences (e.g. habitats, microhabitats, seasonality), due in part to interspecific behavioral interactions, involving the social organization and spatial and temporal distribution of the species in the communities (Cardoso et al. 1989, Cardoso & Haddad 1992, Menin et al. 2005, Vogel et al. 2011, van Beest et al. 2014, Costa et al. 2016, Cloyed & Eason 2017, Schirmer et al. 2019). Currently, the most functional concept of an ecological community is defined as a group of organisms that coexist in a determined habitat and also interact with one another and the surrounding environment (Begon et al. 1990). The structure of adult amphibian assemblages has been studied based on habitat and microhabitat (Eterovick & Sazima 2000, Rojas-Ahumada et al. 2012), and in terms of reproductive periods (Aichinger 1987, Sabbag & Zina 2011). Intuitively, due to morphological variability associated with certain clades of amphibians (e.g. arboreal, aquatic), we assume that phylogenetic relationships have a significant effect on the structure of amphibian communities.

Amphibians exhibit different strategies for occupying their environment. The occupation by species differs mainly related to vegetation structure (for species in the forest and open areas), as well as the duration of water bodies

(temporary or permanent) (Díaz-Paniagua 1990, Rossa-Feres & Jim 2001, Bertoluci & Rodrigues 2002). However, several characteristics of the habitat such as food availability, hydroperiod, availability of oviposition sites, rainfall, and refuges determine the patterns of organization of anuran assemblages (Lillywhite et al. 1973, Crump 1974, Toft 1985, Pulliam 1989, Barbault 1991, Arzabe 1999, Skelly et al. 1999, Eterovick & Sazima 2000, Eterovick & Fernandes 2001, Prado et al. 2005, Richter-Boix et al. 2006).

The relationship between environmental heterogeneity and species diversity can be explained by habitat heterogeneity (Simpson 1949, MacArthur & MacArthur 1961, MacArthur & Wilson 1967). Studies about amphibians have demonstrated that complex and heterogeneous environments promote more microhabitats and ways of exploiting environmental resources, and thus, allow for a larger group of species to co-occur (Pianka 1969, Duellman & Trueb 1986, Cardoso et al. 1989, Pombal Junior. 1997, Brandão & Araújo 1998, Bernarde & Kokubum 1999, Conte & Machado 2005, Vasconcelos & Rossa-Feres 2005). In anurans communities, species coexistence may result in a differential use of habitats for vocalization, reproduction and larval developmental activities (Duellman & Trueb 1986, Bernarde & Anjos 1999, Bastos 2007, Purrenhage & Boone 2009). Other influential factores include the presence of bromeliads (Schineider & Teixeira 2001, Bastazini et al. 2007), soil and moisture (Bernarde & Anjos 1999, Toledo et al. 2003, Bastazini et al. 2007), leaf litter, fallen logs, and temporary pools (Bernardo & Anjos 1999, Toledo et al. 2003, Bastazini et al. 2007). Some species show plasticity in the use of spatial resources (Santos et al. 2008) and variation in the availability of these resources can affect the number of species, reproductive modes, and the activity period of anurans (Duellman & Trueb 1986, Kopp et al. 2010).

Another intrinsic trait structuring an anuran community should consider phylogeny as an explanatory variable, which may reveal how related assemblages occupy different environments, and also understand why certain assemblages are similar or different (Losos 1996). Studies about the structure of assemblages are still mainly descriptive (Wells 2007) and those that consider the effect of phylogeny are scarce, especially for amphibians (Eterovick & Fernandes 2001, Eterovick et al. 2010).

Most of the studies focusing on Neotropical anuran assemblages were carried out in the Amazon basin (e.g. Crump 1974, Aichinger 1987, Neckel-Oliveira et al. 2000) and in the Atlantic Forest, Southeastern Brazil (e.g. Haddad & Sazima, 1992, Bertoluci 1998, Bertoluci & Rodrigues 2002). Their findings show that most species reproduce during the rainy season, and a strong association between abundance and species richness with rainfall and temperature (Eterovick & Sazima 2000, Toledo et al. 2003, Santos et al. 2008, Kopp et al. 2010, Hartel et al. 2011, Maffei et al. 2011). According to Santos et al. (2009), the species composition of anurans in semideciduous forest areas is more similar to those recorded in areas of Cerrado, Pantanal and even Pampa than with the communities of the ombrophilic areas of the Atlantic Forest. It is expected that studies of anuran communities in semideciduous forest will demonstrate several levels of reproductive segregation among species in the same community. The species may range from complete spatial and/or temporal sharing, to total overlapping of these factors (e.g. Bernarde & Kokubum 1999, Rossa-Feres & Jim 2001).

The general objective of this study was to describe the spatial-temporal distributions of anurans in a semideciduous forest area, located in the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil. More specifically,

we first described the reproductive period and activity of the species during two rainy seasons, as well as their spatial distribution considering reproductive site characteristics. We also tested the hypothesis that phylogenetic distances, reproductive mode, and reproductive period explain differences in reproductive site characteristics of anurans.

## MATERIALS AND METHODS

### Study area

The study was carried out in the Municipality of Barão de Monte Alto (21°14'42"S, 42°14'16"W, WGS84), State of Minas Gerais. The climate of the region is classified as Aw (*sensu* Köppen 1918), with a dry season that coincides with winter, and the maximum observed precipitation for the driest month of this season is less than 60 mm (Kottek et al. 2006). The local vegetation is characterized as Seasonal semi-deciduous Forest of lowlands between 132 and 700 m elevation (Veloso et al. 1991). Mean annual rainfall is about 1.287 mm and the mean annual temperature is 22.6°C. We monitored three habitats: a temporary stream and marsh (Area A) in a forested area, a temporary marsh and pond (Area B), and a marsh and permanent pond (Area C) (Figure 1; Table I).

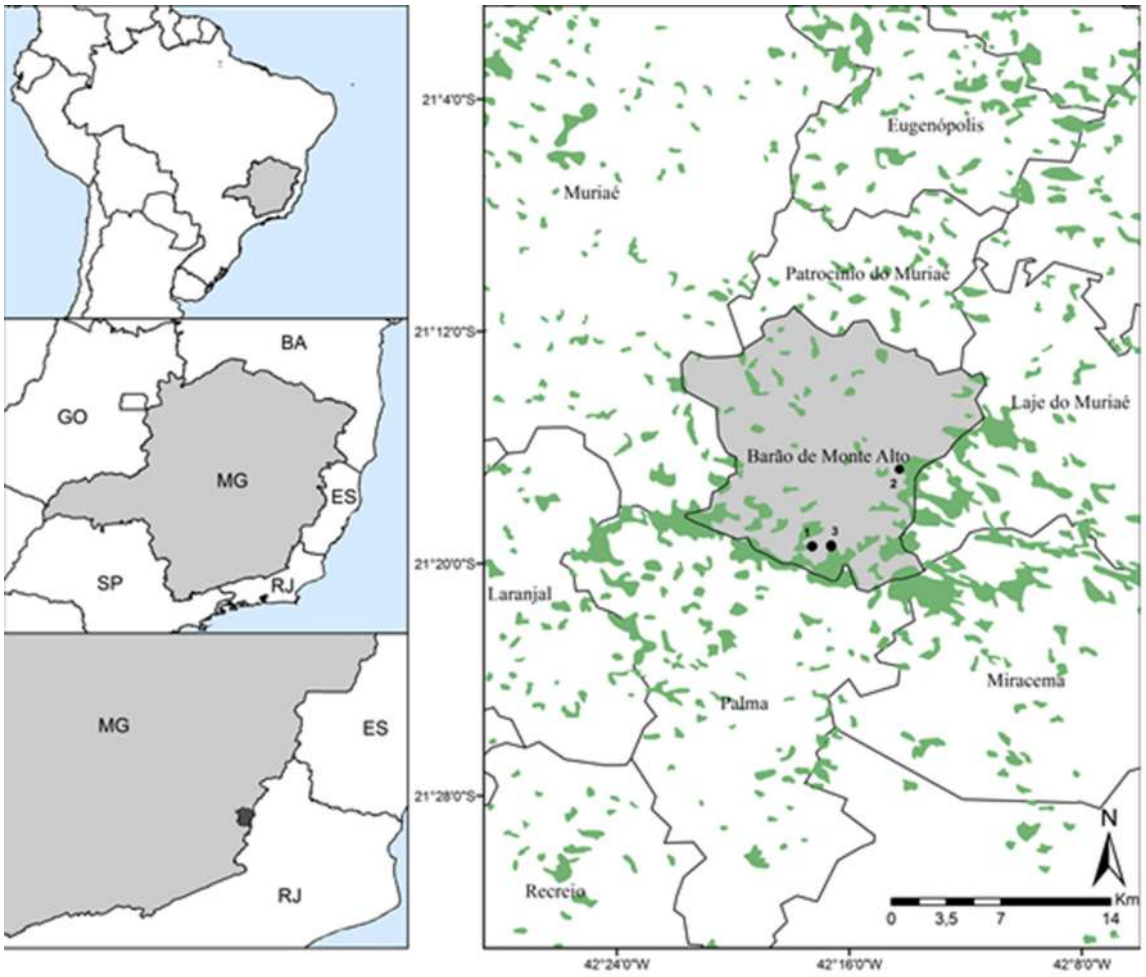


**Figure 1. Location of the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil. Points: (1) Area A, (2) Area B and (3) Area C.**

**Table I. Environments monitored during rainy seasons 2013–2014 and 2014–2015 (October to March, respectively) in the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil.**

| Environment | | Coordinates | Elevation (m) | Description |
|---|---|---|---|---|
| 1 | Area A | 21° 32' 39" S<br>42° 27' 55" W | 390 m | 50m permanent marsh in a secondary forest area surrounded by trees and bushes on the banks and permanent anthropogenic pond with approximately 1.100m$^2$ of water surface, with secondary forest fragment and pasture on the banks. |
| 2 | Area B | 21° 27' 59" S<br>42° 23'50" W | 560 m | 200m a temporary stream within semideciduous forest with sandy/rocky bed and riparian forest preserved. |
| 3 | Area C | 21° 32'42" S<br>42° 29' 00" W | 360 m | 150m$^2$ temporary marsh surrounded by pastures and 4.000m$^2$ permanent pond stretch with secondary forest fragment and pasture on the banks. |

## Fieldwork

Field studies about temporal and spatial distributions of anurans were carried out during three consecutive days, monthly throughout the rainy seasons of 2013–2014 and 2014–2015 (October to March), monitoring one area per night. We performed the fieldwork between 18:00 h and 23:30 h, with a total of 88 observation hours, and a sampling effort of 196h/person. The same person counted and carried out the measurements with the individuals. Monthly climatic data of mean temperature and accumulated rainfall were obtained from the Automatic Weather Station of Muriaé, located approximately 19 km in a straight line from the study area. At the beginning of each collection, we also measured air and water temperature of each environment with a Digital Thermometer Western with Clock for Internal and External Environments (Internal Temperature: -10°C to +50°C, External Temperature: -50°C to +70°C, Accuracy: ±1°C, Clock Accuracy: ±1 minute/month).

We performed active searches for anurans in the field, registering species found, along with data on microhabitat that they used as calling sites. We established seven possible calling site microhabitats: exposed roots, rock, leaf litter, cattail leaf, ground, partially submerged, and grass, for use in the descriptive part and to acquire the spatial measurements of the species. From the data obtained from these seven microhabitats, we defined four other types of microhabitats (height above water and distance from water, microhabitat (separated into fifteen new categories): ground, rock; ground and rock; ground, rock and root; ground and partially submerged; root; leaf litter; ground and grass; partially submerged; leaf litter and grass; leaf litter and cattail; partially submerged and grass; grass; grass and cattail; cattail; and extract (separated into 2 categories): herbaceous or arboreal) to test the hypotheses. For species that were actively calling during the same night and in the same habitat, we estimated the number of calling males and assigned them to the following abundance classes: (1) 1–2; (2) 3–10; (3) 11–50 and (4) more than 50 calling individuals. We recorded the calls with the Sony IC Recorder to help with species identification and deposited the sound files in the Fonoteca Mapinguari da Universidade Federal de Mato Grosso do Sul. An estimated number of calling individuals is widely used for anurans (Heyer et al. 1994) and assessed as efficient, provided that

estimates are always done by the same observer (Shirose et al. 1997).

Based on calling activity periods during the months of monitoring, we defined five different reproductive patterns (adapted from Canelas & Bertoluci 2007): (1) species that call in the beginning of the rainy season; (2) species that call in the middle of the rainy season; (3) species that call at the end of the rainy season; (4) species that call throughout the entire rainy season; (5) species that call only in the beginning and end of the rainy season. The vertical and horizontal distribution of species was studied by characterizing the calling sites, and measuring the height and distance (through a tape measure) that animals were located in the microenvironment in relation to the nearest body of water. We also noted age and reproductive data, such as young individuals, ovigerous females, froglets, couples in amplexus, and tadpoles.

All voucher specimens were collected with a license from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio n° 40744–1 e 40744–2), and were housed in the herpetological collection of the Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV).

### Statistical analysis

We used four characteristics to describe the reproductive sites of species: height and distance from water; microhabitat, and extract. We organized each individual based on reproductive site characteristics using Non-metric Multidimensional Scaling (NMDS) (Manly 1994), combining the two rainy periods (October to March, 2013-14 and 2014-15). Thus, we defined the response variable as the axis of the NMDS in one dimension, which recovered 92% of the variance of the original distances ($r^2$ = 0.929). We used the phylogenetic tree based on Pyron & Wiens (2011) and reduced the tree to only one species per genus that was included in our sampling, using the function drop.tip () and created a matrix of phylogenetic distances among each genus. From this distance, we ordered genera based on phylogenetic relatedness reproductive modes following Haddad et al. (2013) and reproductive period determined during this study. Due to correlations among some of these explanatory variables, we applied a Variation Partitioning method (Borcard et al. 1992) using partial regression, which results in percentages of variation explained only by each explanatory variable and shared by them. The variation partitioning results were represented in a Venn diagram. We also verified the relationship between rainfall and number of species in calling sites using a linear regression with a Poisson distribution.

The significance level used to explain the spatial organization of the composition of species in the habitats was $P < 0.05$. For this, the data were analyzed using the statistical software R version 3.1.3. (R Core Team 2015), using the "cluster" package (Maechler et al. 2015) to create the Gower distance matrix among the species based on the environmental measurements: we used the "ape" package (Paradis et al. 2004) to create the phylogenetic distance matrices among genera, and finally the "vegan" package (Oksanen et al. 2015) to create the NMDS and variation partitioning.

## RESULTS

In the three monitored habitats in the study area, we found 28 species of anurans belonging to the families Bufonidae (1), Brachycephalidae (1), Craugastoridae (1), Cycloramphydae (1), Hylidae (15), Microhylidae (1), Leptodactylidae (6), Odontophrynidae (1), and Ranidae (1). Area

B showed the greatest richness with 21 species present, of these, 11 are hylids. Areas A and C, however, showed a richness of 20 species each, but in Area A there were 14 hylids and in Area C only 11 (Table II). Table III (a, b and c) shows the results of the spatial-temporal distribution of species found over the six months of sampling of the rainy season (2013–14 and 2014–15).

In the months of February and March, we found the fewest number of species (14) with calling activity, and in December we registered the highest number of calling species (20). Only three species did not fit into the established reproductive patterns due to absence of calling observations (*Adenomera marmorata*), or because it had incipient vocalization activity (*Elachistocleis cesarii* and *Scinax fuscovarius*).

With environmental occupation, we found six species (22%) using just one single type of microhabitat as a calling site, whereas 10 (37%) species used two and/or three microhabitats, and only one species (3.7%) used four microhabitats (*Pithecopus rohdei*). The grass microhabitat was utilized most (21 species: 77%), whereas rock microhabitat was utilized least (one species: *Thoropa miliaris*). Of the seven microhabitats defined in this study, Area A was the only one that contained all of the different types of calling sites (Table IIIa).

Of the registered species, five (17.8%) occurred exclusively in Area A: *Dendropsophus pseudomeridianus*, *Elachistocleis cesarii*, *Adenomera marmorata*, *Proceratophrys boiei*, and *Leptodactylus catesbeianus*. On the other hand, Area B had only three (10.7%) exclusive species: *Ischnocnema* sp., *Leptodactylus labyrinthicus*, and *Leptodactylus spixi*. Only *Ischnocnema* sp. occurred exclusively in Area C (Table II).

In both rainy seasons sampled, the reproductive activity of the species, characterized by the presence of calling males, was not associated with the highest rainfall, ($Z$=0.775, $P$=0.438) (Figure 2). Considering the overall analysis (sum of the periods 2013–14 and 2014–15) the peaks of abundance of calling males, with more than 50 individuals vocalizing, were recorded at the beginning (October 2013) and end (March 2015) of the rainy season (Tables IIIa, b and c).

Through regressions of all these explanatory variables with species scores, only reproductive modes (0.02%), genus (0.06%), and reproductive period (0.16%) were significant. However, there was no significant interaction among these three variables, but reproductive mode and genus shared 0.08% of the variables (Figure 3). We also removed from the phylogenetic tree of Pyron (Pyron & Wiens 2011) only the families and genera included in the sample design, we defined the scores and based on this tree, we made a patristic distance matrix between each family and gender. From this distance we order families and genera based on phylogenetic proximity. The influence of historical factors was significant, the phylogeny explained part of the variation in the use of micro-habitat by the species, being basically related to the basal separation between Hylidae and other terrestrial families.

**Table II. List of anurans species and habitats where they occur in the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil: Area A, Area B and Area C. RM – Reproductive Modes (According to Haddad & Prado 2005). (-) – No species.**

| Taxa | Environments | | | RM |
|---|---|---|---|---|
| | Area A | Area B | Area C | |
| **Bufonidae** | | | | |
| *Rhinella ornata* (Spix 1824) | X | X | X | 1 |
| **Brachycephalidae** | | | | |
| *Ischnocnema* sp. | - | - | X | 23 |
| **Craugastoridae** | | | | |
| *Haddadus binotatus* (Spix 1824) | X | X | X | 23 |
| **Cycloramphidae** | | | | |
| *Thoropa miliaris* (Spix 1824) | X | X | X | 19 |
| **Hylidae** | | | | |
| *Dendropsophus bipunctatus* (Spix 1824) | X | - | - | 1 |
| *Dendropsophus branneri* (Cochran 1948) | X | X | X | 1 |
| *Dendropsophus decipiens* (Lutz 1925) | X | - | X | 24 |
| *Dendropsophus elegans* (Wied-Neuwied 1824) | X | X | X | 1 |
| *Dendropsophus minutus* (Peters 1872) | X | X | X | 1 |
| *Dendropsophus pseudomeridianus* (Cruz, Caramaschi & Dias 2000) | - | X | - | 1 |
| *Boana albomarginata* (Spix 1824) | X | - | X | 1 |
| *Boana albopunctata* (Spix 1824) | X | X | X | 1 |
| *Boana faber* (Wied-Neuwied 1821) | X | X | X | 4 |
| *Boana pardalis* (Spix 1824) | X | X | X | 4 |
| *Boana polytaenia* (Cope 1870 “1869”) | X | X | X | 1 |
| *Boana semilineata* (Spix 1824) | X | X | X | 1 |
| *Scinax crospedospilus* (Lutz 1925) | X | - | X | 1 |
| *Scinax fuscovarius* (Lutz 1925) | X | X | - | 1 |
| **Microhylidae** | | | | |
| *Elachistocleis cesarii* (Schneider 1799) | - | X | - | 1 |
| **Leptodactylidae** | | | | |
| *Adenomera marmorata* Steindachner 1867 | - | X | - | 32 |
| *Leptodactylus fuscus* (Schneider 1799) | X | - | X | 30 |
| *Leptodactylus labyrinthicus* (Spix 1824) | - | - | X | 11 |
| *Leptodactylus latrans* (Steffen 1815) | X | X | X | 11 |
| *Leptodactylus spixi* Heyer 1983 | - | X | X | 30 |
| *Physalaemus cuvieri* Fitzinger 1826 | X | X | X | 11 |
| **Odontophrynidae** | | | | |
| *Proceratophrys boiei* (Wied-Neuwied 1825) | - | X | - | 2 |

**Table II.** Continuation

| Taxa | Environments | | | RM |
|---|---|---|---|---|
| | Area A | Area B | Area C | |
| **Phyllomedusidae** | | | | |
| *Pithecopus rohdei* (Mertens 1926) | X | X | - | 24 |
| **Ranidae** | | | | |
| *Lithobates catesbeianus* (Shaw 1802) | - | X | - | - |
| **Total** | 20 | 21 | 20 | |

**Table III.** Areas in the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil. Male classes in vocalization activity: - 1-2; - 3-10; - 11-50 and - over 50. S: Found only individuals that were not vocalizing; Ov: ovate; Ju: juvenile; Fg: froglet. AE (Arboreal Extract): H: herbaceous; Sh: shrubby. MV (Microenvionment Vocalization): Lt: litter; Gn: ground; Gr: grass; C: cattail; Ro: rock; Rt: root, PS: partially submerged. Months of the rainy season (2013–14 and 2014–15).

| (a) Species | Oct | Nov | Dec | Jan | Feb | Mar | AE | MV |
|---|---|---|---|---|---|---|---|---|
| *D. bipunctatus* | | | | | | | Sh, H | C, Gr |
| *D. branneri* | | | Ju | | | | H | Gr, C |
| *D. decipiens* | S | | | | | | H | Gr, C |
| *D. elegans* | | | Ju | | S, Ju | | H | C, Gr |
| *D. minutus* | | | | | | | H | Gr, C |
| *B. albomarginata* | | | | | | | Sh, H | Gr, C |
| *B. albopunctata* | | | | | S | | H | Gr, C |
| *H. binotatus* | | | | | | | H | Gn |
| *B. faber* | | | | Ju | | | H | Gr, PS |
| *B. pardalis* | | | | | | | H | C, Gr |
| *B. polytaenia* | | | | | | | H | Gr, C |
| *B. semilineata* | | | S, Ju | Ju | | Fg, Ju | H | C, Gr |
| *L. fuscus* | | | | | | | H | Gn |
| *L. latrans* | S, Ju | S, Ju | S | S, Ju | S | S, Ju | H | Gn, Gr |
| *P. curvieri* | | | | | | | H | PS |
| *P. rohdei* | | Ju | | | | | H | Gn, Gr |
| **(a) Species** | **Oct** | **Nov** | **Dec** | **Jan** | **Feb** | **Mar** | **AE** | **MV** |
| *R. ornata* | | | | | | | H | Gn |
| *S. crospedospilus* | | | | | | | Sh, H | Gr |
| *S. fuscovarius* | | | | | | | H | Gr |
| *T. miliaris* | | | | S | | | H | Gn |
| **N° species vocalizing** | 11 | 12 | 10 | 10 | 07 | 10 | | |
| **N° species registered** | 13 | 13 | 11 | 11 | 09 | 11 | | |

**Table III. Continuation**

| (b) Species | Oct | Nov | Dec | Jan | Feb | Mar | AE | MV |
|---|---|---|---|---|---|---|---|---|
| *A. marmorata* | | | | S | | | H | Lt |
| *D. branneri* | | | | | | | H | C, Gr |
| *D. elegans* | | | | | | | H | C, Gr |
| *D. minutus* | | | | | | | H | C, Gr |
| *D. pseudomeridianus* | | | | | | | H | Gr |
| *E. cesarii* | | | | | | | H | Gn |
| *B. albopunctata* | | | Ju | | | | H | C, Gr |
| *H. binotatus* | | | | S | | | H | Gn |
| *B. faber* | | | S | | | | Sh, H | PS, Gr |
| *B. pardalis* | | | | Ju | | | H | C, Gn, Gr |
| *B. polytaenia* | | | S, Ju | | | | H | C, Gr |
| *B. semilineata* | Fg | S, Fg | | | Fg | Fg | H | C, Gn, Gr |
| *L. latrans* | S | | S | Ju | S | | H | Gn, Gr, PS |
| *P. boiei* | S | S | | S, Ju, Fg | | S | H | Rt, Gn, Lt |
| *P. cuvieri* | | | J, Fg | | | | H | PS |
| *P. rohdei* | | | S | | | | H | Lt, C, Gn, Gr |
| *R. ornata* | S | | | | S | | H | Gn, Gr |
| *S. fuscovarius* | S | S | | | S | | Sh, H | C, Gn, Gr |
| *T. miliaris* | S | S | | S | | S | H | Rt, Ro, Gn |
| **N° species vocalizing** | 10 | 11 | 12 | 10 | 10 | 10 | | |
| **N° species registered** | 12 | 12 | 15 | 12 | 13 | 10 | | |
| | | | | | | | | |
| **(c) Species** | **Oct** | **Nov** | **Dec** | **Jan** | **Feb** | **Mar** | **AE** | **MV** |
| *D. branneri* | | | | Ju | | | H | C, Gr |
| *D. decipiens* | Ov | | | | | | H | Gr |
| *D. elegans* | Ov | Ju, Ov | Ju, Ov | | Fg | Ju, O Fg | H | C, Gr |
| *D. minutus* | | | | Ov | Ju, Ov, Fg | | H | C, Gr |
| **(c) Species** | **Oct** | **Nov** | **Dec** | **Jan** | **Feb** | **Mar** | **AE** | **MV** |
| *B. albomarginata* | | | | | | | Sh, H | Gr, C |
| *B. albopunctata* | | | | | | | H | Gr, C |
| *H. binotatus* | S | | S | S | | | H | Gn |
| *B. faber* | | | | | | | H | PS, Gr, Gn |
| *B. pardalis* | | Fg | | | | | H | Gr |
| *B. polytaenia* | | | | | | | H | C |
| *B. semilineata* | Ju, Fg | | Fg | Ju, Fg | | | H | Gr |

**Table III.** Continuation

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Ischnocnema* sp. | | | | | | | Sh | Gr |
| *L. fuscus* | | | Ju | S | | | H | Gn, Gr |
| *L. labyrinthicus* | | | | | | | H | PS, Gn, Gr |
| *L. latrans* | S | | Ju | S | S | S | H | Gn, Gr, PS |
| *L. spixi* | | | | | | | H | Gn |
| *P. cuvieri* | | | | | S | S | H | Gn, PS, Gr |
| *R. ornata* | | | | | | | H | Gn |
| *S. crospedospilus* | S | | | | S | S | Sh, H | Gn, Gr, C |
| *T. miliaris* | S | | | | | | H | Gn |
| **N° species vocalizing** | 11 | 12 | 13 | 13 | 10 | 08 | | |
| **N° species registered** | 13 | 12 | 14 | 13 | 13 | 10 | | |

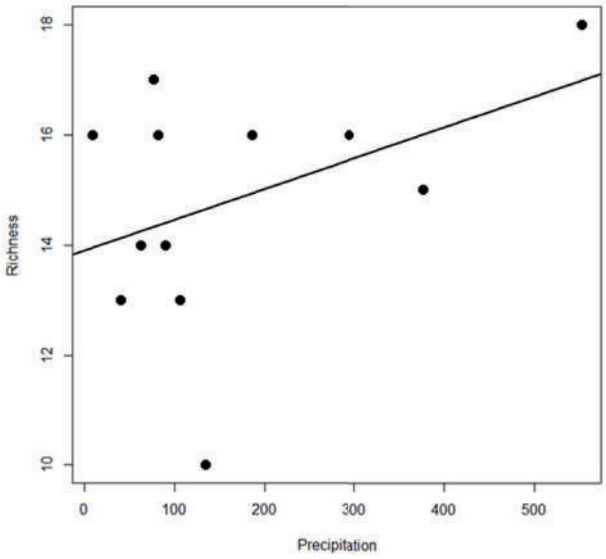


**Figure 2.** Linear regression comparing the richness of anurans in breeding activity with rainfall in the rainy season (October to March) between 2013–14 and 2014–15. Black dots (each point represents one month of study).

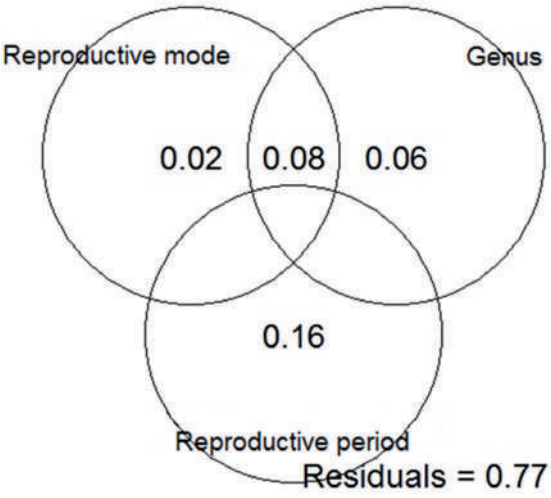


**Figure 3.** Venn diagram representing the percentages of each significant explanatory variable and the correlation between them based on the spatial organization of species composition in habitats in the Municipality of Barão de Monte Alto, State of Minas Gerais, Brazil.

## DISCUSSION

We found 28 species of anurans, distributed in 14 genera and 10 families: Bufonidae (1), Brachycephalidae (1), Craugastoridae (1), Cycloramphydae (1), Hylidae (14), Microhylidae (1), Leptodactylidae (6), Odontophrynidae (1), Phyllomedusidae (1) and Ranidae (1) (Table II). The assemblage of anurans studied is predominated by Hylids (*sensu* Pyron & Wiens 2011), the same pattern was found in various studies in the neotropical region (e.g. Gottsberger & Gruber 2004, Abrunhosa et al. 2006, Juncá 2006, Canelas & Bertoluci 2007, Moreira et al. 2007, Santana et al. 2010, Pereira et al. 2016). The sampled localities do not have a strong seasonality of climatic variables (precipitation, temperature) due to the small amplitude of thermal variation during the study months. This may explain why the reproductive season of the species is not concentrated during the two rainy seasons. Some variables were more important than others and among the most important, habitat heterogeneity, reproductive period, reproductive mode, and phylogenetic distance had a greater influence on the species, as was observed in the overlap in the vocalization period of several species in the same environment. Because most of the variables are synchronized, the interactions of these external factors are often more important than a single environmental factor. The analyzed variables are discussed below.

In tropical regions rainfall seems to be the principal factor regulating the reproductive activities of anurans (Heyer 1973), because it determines the availability and duration of reproductive sites (Gottsberger & Gruber 2004). In this study, the linear regression showed there was no relationship between the presence of actively calling species and temperature (Figure 2). The study site showed a small range of thermal variation during the study months (23 to 26.5° C), which may explain why temperature had no apparent effect on the reproductive activity on anurans. However, this is not commonly found in studies of amphibian communities, which generally show correlations between reproductive activity and environmental temperature (e.g. Vasconcelos & Rossa-Feres 2005, Conte & Rossa-Feres 2006). Other studies have shown that the reproductive activity of only a few species within an assemblage is influenced by temperature, and also depends on their reproductive mode (Gottsberger & Gruber 2004, Moreira et al. 2007).

Area C can be considered the most heterogeneous, as it is located in a transition from pasture and secondary forest. The positive association between richness of anurans and habitat heterogeneity is compatible with various studies that relate richness of different animal groups with area and habitat heterogeneity (Ricklefs & Lovette 1999, Vallan 2000, Báldi 2008, Silva et al. 2011, Souza et al. 2014, Araújo et al. 2018). The most accepted explanation for this association (Tews et al. 2004) is the habitat heterogeneity hypothesis (Simpson 1949). It assumes that more structurally complex environments hold more niches and have various forms of environmental resource exploitation, thus increasing species diversity (Campos & Vaz-Silva 2010).

However, this hypothesis does not conform exactly to the results of this research, because the vertical stratification, one component of environmental heterogeneity, promoted greater hylid richness, thus allowing more species to co-exist given there was greater resource availability (Colli et al. 2002, Nogueira et al. 2009). On one hand, this explains the higher number of hylids (14) in Area A, but does not explain why Area C, which is also located in a forested area, does not have an equally rich

hylid fauna. Maybe the higher richness of hylids in Area A could be best explained by the intermediate disturbance hypothesis (Connell 1978). Area A is the environment that suffered the greatest and most frequent anthropogenic interference; it was used for logging *Eucalyptus* plantations and raising cattle. With a moderate level of disturbance, the assemblage comprises a mosaic of habitats, favoring the occurrence of high species diversity (Huston 1994, Pianka 1994, Ricklefs 2003). Changes in plant community and soil can also be instrumental in structuring the assemblage of anurans (Bastazini et al. 2007).

Temporal differences in reproductive seasons can be an important factor in the reproductive isolation of species that share the same habitat (Bertoluci & Rodrigues 2002). We observed overlap in calling periods of many species in the same habitat (Tables IIIa, b and c). This overlap is possible because species exploit different microhabitats, which is an important factor for reproductive isolation (Cardoso et al. 1989, Pombal Junior 1997, Toledo et al. 2003), and reduces the occurrence of interspecific territorial disputes. This is the case for *Boana albopunctata* and *B. faber*, which call during the same period, but almost always occupy different microhabitats. However, *Dendropsophus branneri*, *D. elegans,* and *D. minutus* co-occur in all of the habitats and have overlapping calling periods. Nevertheless, *Dendropsophus elegans* was found calling in higher strata and sometimes in large sized trees, whereas *D. branneri* and *D. minutus* shared shrubs of aquatic vegetation. In cases of temporal and spatial overlap, reproductive isolation can occur due to acoustic divergence (Pombal Junior 1997, Bernarde & Machado 2001, Toledo et al. 2003). Eterovick (2003) pointed out the call behavioral flexibility and interactions with physical and biotic variables as one of the determining factors of reproductive patterns in anurans.

Of the species that were not possible to establish a temporal calling pattern, such as *Thoropa miliaris*, it is possible that they have an explosive reproductive pattern, and their calling nights may have not coincided with our collection nights in the field (Toledo et al. 2003). This may be the case for *Elachistocleis cesarii* and *Proceratophrys boiei,* which also have explosive patterns of reproduction (Bertoluci 1998, Canelas & Bertoluci 2007).

The phylogenetic signal related to the use of microhabitat of species reflects old evolutionary relationships, which are related to the separation between terrestrial and arboreal species during the Cretaceous period, approximately 100 million years ago (Duellman & Trueb 1986, Igawa et al. 2008, Báez et al. 2009). Within each of these clades, other factors are related to the use of micro-habitat among the species involved, such as selective pressures of the past causing recent niche displacement or evolutionary divergence (Zimmerman & Simberloff 1996, Eterovick et al. 2010). Although relatively small, the phylogenetic signal is fundamental in explaining the evaluated niche variation. Because, traits exhibited by species may be influenced to various degrees by their phylogenetic history, as well as contemporary selective pressures. Species in a given clade may show high similarity for traits with strong phylogenetic signal, whereas labile traits may differ even in closely related species that have diversified into different ecological niches (Richardson 2001).

In most habitats, the abiotic structure of the environment determines the community and influences the distributions and interactions of animal species (Bell et al. 1991, Tews et al. 2004). When we evaluated which variables best explain the anuran species composition among the areas, we observed that part of the explanation for reproductive mode or for genus was due

to the correlation between the two (0.08). On the scale of this study, the reproductive modes are probably phylogenetically conserved. The presence of a phylogenetic signal indicates that phylogeny represents a fraction of the variation in the use of habitat for each species. It represents an important vertical segregation in forming patterns of diversity and local distribution of anurans. However, according to our results the factor that best explained the differences in individual habitats was the reproductive period (0.16) (Figure 3). Because the species may differ in their annual reproductive periods (Wells 1977), daily periods of calling activity, acoustic parameters of their advertisement calls, and time sharing of resources are important mechanisms of reproductive isolation (Wells 1977). A phylogenetically pooled community contains species that are, on average, more related than expected by chance (Webb 2000, Webb et al. 2002). The results of this study demonstrate that the occupation of breeding sites does not occur randomly, but occurs through the selection of preferred habitats for individual species. The habitat level can be related to phylogenetic niche conservation, which is maintained during the process of Atlantic Forest occupation by the group studied.

**Acknowledgments**

We would like to thank everyone who helped us during the fieldwork. All residents of Barão de Monte Alto. EAP thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support and the Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio for collecting license.

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**How to cite**

PEREIRA EA, NEVES MO, SUGAI JLMM, FEIO RN & SANTANA DJ. 2020. Seasonal and habitat structure of an anuran assemblage. An Acad Bras Cienc 92: e20190458. DOI 10.1590/0001-3765202020190458.

*Manuscript received on May 10, 2019;*
*accepted for publication on August 15, 2019*

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## Authors Contributions

Elvis Almeida Pereira conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft. Matheus de Oliveira Neves performed the experiments, authored or reviewed drafts of the paper, approved the final draft. José Luíz Massao Moreira Sugai analyzed the data and approved the final draft. Diego José Santana conceived and designed the experiments, performed the experiments, analyzed the data, contributed analysis tools, authored or reviewed drafts of the paper, approved the final draft. Renato Neves Feio authored or reviewed drafts of the paper, approved the final draft.

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