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ECOLOGY, BEHAVIOR AND TAXONOMY OF ANURANS
FROM BRAZIL'S ATLANTIC FOREST

by

Rodrigo Barbosa Ferreira

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Ecology, Behavior and Taxonomy of Anurans from Brazil's Atlantic Forest

by

Rodrigo Barbosa Ferreira, Doctor of Philosophy

Utah State University, 2015

Major Professor: Dr. Karen H. Beard
Department: Wildland Resources

The Atlantic Forest extends mainly along the Atlantic coast of Brazil, but today the native habitat is reduced to 14.5% of its historical range. This biome is among the fifth most important biodiversity hotspots in the world due to the high richness and endemism and also high degree of human-induced habitat modification. Understanding the response of species with differing life-history traits to habitat modification such as forest edges and matrix types helps predict species occurrence across changing landscapes. Previous studies have used amphibians as a biological indicator of habitat quality due to their physiological and morphological constraints. Amphibians are also an excellent taxon model to study antipredator behavior due to their variety of defensive postures, vocalizations, skin secretions and aposematic colors. Brazil has currently 1026 recognized amphibian species, of which 60 species were described in the past five years, mostly from the Atlantic Forest biome. New species are increasingly described with the increase in sampling effort at microhabitats from remote areas. My study aimed to understand frog response to habitat modification and their antipredator behaviors, and also to describe a new frog species. First, I demonstrated that the breeding guild was the most important variable explaining frog response to edge effects and matrix types. Leaf-litter and bromeliad breeders decreased in richness and abundance from the forest interior toward the matrix habitats. Water-body breeders increased in richness toward the matrix and remained relatively stable in abundance across distances. Second, I created a database comprising 224 records of frog antipredator behavior, of which 102 (45%) were collected during our fieldwork, 116 (52%) were compiled from the literature, and six (3%) were reported by colleagues. The 224 records represented 165 species, and included 16 families of anurans. Lastly, I described the first bromeliad-dwelling species among the 96 species of the genus *Dendropsophus*. The new species was diagnosed by its small size, framed dorsal color pattern, medium-sized vocal sac, and short membrane in the fifth toe. Phylogenetic analysis based on molecular data indicated this new species should not be assigned to any of the currently recognized species groups of *Dendropsophus.*

(145 pages)

PUBLIC ABSTRACT

Ecology, Behavior and Taxonomy of Anurans from Brazil's Atlantic Forest

Rodrigo B. Ferreira

Anura is a diverse group with more than 7382 species described, which represents 88% of the species belonging to the Class Amphibia. Anurans are among the first organisms to be affected by environmental stressors, so when they show decline in the wild, it is a warning to other species, including humans. It is alarming that one-third of the world's anurans are facing extinction. Following the same trend, a substantive portion of the 988 recognized species of the Atlantic Forest have suffered population declines and local extinctions, attributed primarily to habitat changes.

Despite the unique life history characteristics that make amphibians valuable as an indicator taxon and the expectation that they might respond strongly to habitat changes because of their physiological needs and tolerances, few studies have examined edge effects and matrix use in anurans of the Atlantic Forest. Habitat modification urges scientists to study and understand frog response to these potential threats and also gather data on their ecology and taxonomy.

Ecology of most species has been neglected; for example, no extensive compilation of antipredator behavior has been published for Atlantic Forest frogs. Habitat modification is especially problematic considering that some species can disappear even before being formally described. New species are increasingly described with the increase in sampling effort in remote areas and microhabitats, such as in the pitcher plants of Bromeliaceae from the mountainous region. In this dissertation, I sought to overcome the poor knowledge on anuran response to habitat changes and showed that breeding guild determines anuran response to edge effects and matrix use. Furthermore, I present a database comprising 224 records, of which 102 (45%) were collected during my fieldwork, 116 (52%) were compiled from the literature, and six (3%) were reported by colleagues. The 224 records represent 165 species, and include 16 families of anurans.

During my fieldwork, I found five undescribed species of anurans and herein I present a description of the first bromeliad-dwelling species of the genus *Dendropsophus*. My results provide: i) essential information for conservationists elaborating more reliable management initiatives to protect anuran species from different breeding guilds, ii) an extensive database of antipredator behavior of anurans that could be used to understand interesting ecological and evolutionary questions, and iii) a description of a new anuran species including its phylogenetic relationship, vocalization, ecology and conservation status.

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Rodrigo B. Ferreira

PREFACE

The format of the Introduction, Chapter 3, and Conclusion of this dissertation follow that of the professional Journal of Ecology with the necessary adaptations required by the School of Graduate Studies at Utah State University. Chapter 2 has been submitted to Biological Conservation. Chapter 4 has been submitted to the journal PlosOne.

CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Anura

Anura is a diverse group with more than 7382 species described which represents 88% of the species belonging to the Class Amphibia (AmphibiaWeb 2015). The living amphibians have a very long evolutionary history, with many of the modern families having been well established for at least 50 to 100 million years (Duellman and Trueb 1994). This group of vertebrates inhabits nearly every available habitat on earth except for open oceans, distant oceanic islands, and the Arctic and Antartic (Frost 2014). Anurans live in varied habitats such as rainforests, rivers and streams, deserts and alpine environments. Some amphibians live entirely in water, others entirely on the land (Crump 2015). Some live in freshwater swamps, ponds, lakes, rivers, and streams, environments where water is nearly always available. Some species have also direct development and are independent of a water body, relying only upon humid habitats for reproduction (Crump 2015).

Anurans are among the first organisms to be affected by environmental stressors, so when they show decline in the wild, it is a warning to other species, including humans. It is alarming that one-third of the anurans are facing extinction (IUCN 2014). This would be the largest mass extinction since the disappearance of the dinossaurs (AmphibiaWeb 2015). About 122 species are believed to have become extinct since 1980 (Wells 2007).

Atlantic Forest

The Atlantic Forest is a region of tropical and subtropical forests, which extends along the Atlantic coast of Brazil, and inland as far as Paraguay and the Misiones Province of Argentina. Originally this biome extended for 1,300,000 km^2 along the Atlantic coast, but today the native habitat is reduced to approximately 14% of its historical range (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais 2013). Brazil’s Atlantic Forest is recognized worldwide recognized for harboring one of the highest biodiversities in the world (Brooks et al. 2006). This enormous biodiversity results in part from the wide range of latitude it covers, its variations in altitude, its diverse climatic regimes as well as the geological and climatic history of the whole region (Haddad et al. 2013).

Today the Atlantic Forest is a highly threatened biodiversity hotspot, being considered one of the top ten most important for conservation and is considered a World Biosphere Reserve (Morellato and Haddad 2000). This biome is threatened because of severe habitat destruction, changing the landscape configuration from immense forests to mostly small fragments less than 50 ha and isolated from each other by a matrix of human settlements, pastures, plantations, and roads (Tabarelli et al. 2005). The human-induced deforestation causes in the Atlantic Forest a very distinct configuration, where forests occur mostly on steeper slopes and hilltops. This pattern of deforestation makes this biome an ideal place to investigate the response of species life-history traits to habitat change such as edge effects and matrix-habitat types, which likely have direct implications for conservation planning.

The Atlantic Forest has faced three types of habitat changes termed: ‘habitat loss’, ‘habitat fragmentation’, and ‘habitat-split’. ‘Habitat loss’ occurs due to the destruction of native habitats and currently is mostly conducted by local farmers intending to amplify their agricultural area. ‘Habitat fragmentation’ is defined as the process whereby habitat loss results in the division of large, continuous habitats into smaller, isolated habitat fragments (Ranta et al. 1998). Generally, forest fragments are the result of the logistic difficulties involved in deforesting steep hilltops. A common resulting landscape scenario is the disconnection between upland forest fragments from the water bodies in the valleys, which has recently been referred to as ‘habitat-split’ in reference to amphibians that need both upland forest and water body habitats to complete their life cycle (Becker et al. 2007, 2010).

It is mostly assumed that these habitat changes have had negative consequences for living organisms in this biome although little scientific research has been conducted in the Atlantic Forest. Among the three landscape alteration types, ‘habitat loss’ is considered the most devastating to biodiversity (Fig. 1). Habitat loss and fragmentation adversely affect species persistence mainly through reduction in native habitat, increase in isolation among remnant patches, and the creation of edge effects (Murcia 1995, Fahrig 2003). In general, habitat fragmentation increases the likelihood of stochastic extinction in fragments; an effect that is rarely offset by migrants due to increased patch isolation (Hanski, 1998). The areas deforested across the Atlantic Forest are mostly replaced by non-native habitats, termed matrix habitat.

Matrix habitat and edge effects

The landscape changes across the Atlantic Forest have confined most species to small, isolated patches of habitats considering the inability of these species to use the new matrix habitats (Barlow et al. 2007). While historically, island biogeography theory has been used to understand patch occupancy, particularly, area and isolation (Macarthur and Wilson 1967), in a recent review Prugh et al. (2008) found that isolation and area are relatively poor predictors of patch occupancy, and that the type of land cover separating habitat patches (or matrix habitat) strongly affects species presence in fragmented landscapes. It is now recognized that the majority of species on Earth depend on how the matrix is managed (Franklin and Lindenmayer 2009). Surprised with the delay in recognizing the importance of matrix habitat, Franklin and Lindenmayer (2009) asked why it took so long for academic conservation biologists to accept the importance of matrix. It was likely a result of the fact that ecologists were very interested in testing the island biogeography theory that did not focus at all on matrix habitat.

The importance of matrix habitat is not limited to its potential to promote species movements, but also to provide suitable habitat and resources for native biota (Ewers and Didham 2006). It is hypothesized that matrix habitats can be of particular importance for native species when they present low structural contrast with the primary habitat. For example, in tropical landscapes, although second-growth forests are not surrogates for primary forest, they can provide suitable habitat for a component of local assemblages (Barlow et al. 2007). Considering the rapid pace of deforestation, it is important to establish the conservation value of these matrix-habitat types for biodiversity conservation (Gardner et al. 2007).

In addition to understanding the use of matrix habitats, another consequence of habitat loss and fragmentation are the abiotic and biotic changes that occur in the remaining habitats as a result of this juxtaposition (i.e., edge effects) (Gascon et al. 1999). The formation of boundaries between different patch qualities creates edge effects. Edges alter many aspects of the structure, microclimate, dynamics, and species composition of fragmented ecosystems (Laurance 2008). Understanding how community structure changes near edges is key to understanding the effects of fragmentation (Ries and Sisk 2004). By determining the degree of penetration into the remaining undisturbed habitat of changes in microclimatic variables and the response of fauna and flora to these changes, it is possible to estimate more realistically the impact of fragmentation at the landscape level.

While it is well recognized that abiotic factors may change in the remaining habitat due to edges and create conditions that are not favorable to interior habitat organisms, this is not the only change due to edges that are expected to influence organisms' responses. Responses to edges might also be in response to the amount of resources needed (Ries and Sisk 2004). For instance, when matrix habitats have equal or similar amounts of resources compared to forest fragments, no difference in species abundance or diversity is predicted (Ries and Sisk 2004). However, when resources between matrix habitat and forest fragment are complementary, it is predicted that there will be an increase in abundance near the edge. More specifically, it can be predicted that non-habitat, such as abandoned pasture, surrounding a forest has a low amount of resources, and thus organisms will tend to avoid habitat near edges because being near the edge confers no additional access to resources.

Despite the unique life history characteristics that make amphibians valuable as an indicator taxon and the expectation that they might respond strongly to edges because of their physiological needs and tolerances, relatively few studies have examined edge effects in amphibians (Schlaepfer and Gavin 2001, Toral et al. 2002, Lehtinen et al. 2003, Dixo and Martins 2008). Dixo and Martins (2008) studied edge effect on frogs in a lowland region of Atlantic Forest and found that neutral response of this group to edges in terms of total abundance, diversity, and richness. To explain this result, these authors acknowledged that this response might be associated to seasonality, species life-history traits, and matrix-habitat types that were not compared in the study. Additionally, they did not take into account the direction of the edge, used a limited number of distance categories (edge and 200 m), had a small sample size of four fragments, and used pitfall traps in a direction that might not collect individuals moving parallelly along edges. Thus amphibian response to edge effects in the Atlantic Forest is still highly needed for management and conservation intiatives to protect species that are potentially affected.

Studying the presumed influence of matrix type on forest edge can improve conservation efforts. For example, edge-avoiding species tend to be more prone to extinction than those that do not avoid edges (Lehtinen et al. 2003). The opposite is also true, interior-avoiders are more resistant to extinction in fragments (Lehtinen et al. 2003). Thus, if *Eucalyptus* plantations mitigate the intensity of edge effects, management of the matrix type can benefit edge-avoiding species in fragmented landscape and reduce extinction proneness. Therefore amphibian response to fragmentation effects should be more explored because this characteristic can work as one of the best measures (biological indicator) of environmental quality.

Frog status at Atlantic Forest

The Atlantic Forest harbors approximately 300 endemic frog species (64%), many of which have suffered population declines and local extinctions attributed primarily to habitat changes (Becker et al. 2010, Verdade et al. 2012). Although Brazil currently has 988 recognized species and the highest number of amphibian species per country in the world (Segalla et al. 2014), its anuran richness is still considered to be largely underestimated. In the past five years, more than 60 species were described, and more than a half of them occur within the Atlantic Forest biome (Haddad et al. 2013). New species are increasingly described with the increase in sampling effort in remote areas and microhabitats, such as the pitch plant of Bromeliaceae. Despite of the high biodiversity of anurans in Atlantic Forest and that Brazilian herpetologists have long been fascinated by life histories of amphibians, little is known about the ecology of most species. One of the most studied topics in ecology relates to antipredator behavior. Studies of predator-prey interactions continue to be one of the most fascinating and important aspects of ecological research (Mukherjee and Heithaus 2013). The result of such interest combined with the urge to publish has resulted in an astonishing number of short note publications on anuran defensive mechanisms from the Atlantic Forest but no extensive compilation has been published. While many amphibian species are thought to have declined as a result of habitat loss in the Atlantic Forest, in general population dynamics are poorly documented and understood because of a lack of knowledge of species biology, little to no long-term monitoring, and not least, the enormous size of Brazil and the complexity and diversity of its amphibian species and their habitats (Verdade et al. 2012).

Reports show that many species in mountainous areas of Atlantic Forest are disapearing for not apparently conclusive reasons. Likewise, there is little information on the patterns and trends of the suspected threats throughout most of South American, or the mechanisms by which these factors cause amphibian population declines. Furthermore, it is unclear how or whether specific human activities could be contributing to amphibian declines in remote regions of this biome.

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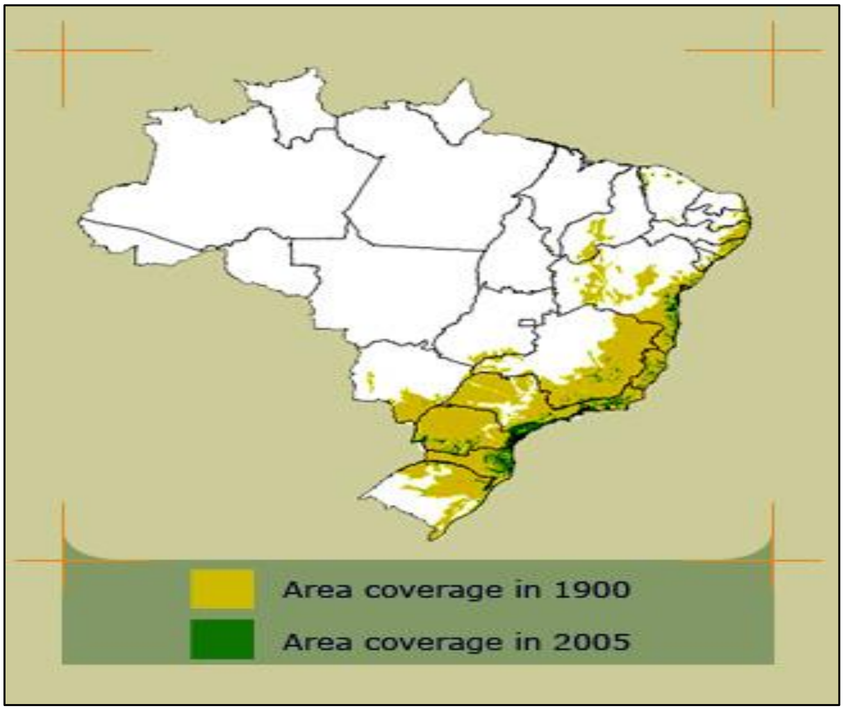

FIG. 1.1. Geographic extension and habitat loss of Brazil's Atlantic Forest between 1900 and 2005.

CHAPTER 2

BREEDING GUILD DETERMINES FROG RESPONSE TO EDGE EFFECTS AND MATRIX TYPES IN BRAZIL'S ATLANTIC FOREST[1]

Abstract

Understanding the response of species with differing life-history traits to habitat edges and matrix types helps predict their occurrence across changing landscape. In Brazil's Atlantic Forest, we evaluated frog richness and abundance by breeding guild across four distances from the edge of a reserve: i) 200 m inside the forest, ii) 50 m inside the forest, iii) at the forest edge, and iv) 50 m inside three different matrix habitats (coffee plantation, non-native *Eucalyptus* plantation, and abandoned pastures). We recorded 622 individual frogs representing 29 species, of which four were undescribed. Breeding guild was the most important variable explaining frog response to edge effects and matrix types. Leaf-litter and bromeliad breeders decreased in richness and abundance from the forest interior toward the matrix habitats. Water-body breeders increased in richness toward the matrix and remained relatively stable in abundance across distances. Number of large trees and bromeliads best explained frog richness and abundance across distances. Richness and abundance across breeding guilds were higher in the rainy season but frog responses were similar across the four distances in the two seasons. Twenty species found in the interior of the forest were not found in any matrix habitat. Across matrix types, leaf-litter species primarily used *Eucalyptus* plantations, whereas water-body species primarily used coffee plantations. Bromeliad breeders were not found inside any matrix habitat. Our study highlights the importance of primary forest for bromeliad and leaf-litter breeders. We propose that water-body breeders use edge and matrix habitats to reach breeding habitats along the valleys. Including life-history characteristics, such as breeding guild, can improve predictions of frog responses to edge effects and matrix types, and can guide more effective management and conservation actions.

Introduction

Rapid habitat loss in the tropics has increased our need to understand how species respond to novel landscape features, such as edge effects and human-modified habitat matrices (Lindenmayer and Franklin, 2002; Ferreira et al., 2012; Almeida-Gomes and Rocha, 2014; Kurz et al., 2014). Due to their great conservation implications, edge effects are one of the most studied topics in landscape ecology; however, because they influence a large number of variables, their role in species occurrences is complex and depends greatly upon the species studied. Examples of the complexities involved in studying edge effects include the wide range of distances that different edge effects can penetrate the forest (Laurance, 2008); the ability of edge effects to change over time with seasonal variation (Ewers and Didham, 2006; Ewers and Banks-Leite, 2013); and the idea that different surrounding matrix types may influence edge effect differently (Ries and Sisk, 2004; Franklin and Lindenmayer, 2009).

The degree of structural similarity between the forest interior and a matrix habitat may be the most important factor influencing species responses to edge and matrix habitats (Kupfer et al., 2006). However, few studies have evaluated the ability of different matrix types to influence edge effects and to harbor different species (Vallan, 2002; Kurz et al., 2014). One can hypothesize that forest-associated species may interpret a matrix habitat with low structural contrast as more suitable than a matrix habitat with high structural contrast compared with the forest (Ries and Sisk, 2004). For example, mature stands of *Eucalyptus* adjacent to primary forest are reported to have greater faunal richness than other agricultural matrices (Demaynadier and Hunter, 1998). This type of information is essential to rank the conservation value of each matrix type according to its influence on species persistence (Kurz et al., 2014).

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[1] This chapter is co-authored by Karen H. Beard and Martha L. Crump

Amphibians might be particularly sensitive to edge effects and matrix habitats because expected changes in temperature, humidity, wind speed, and soil moisture might increase their susceptibility to desiccation. In addition, because frogs use a variety of reproductive habitats, including ponds, streams, bromeliads, and leaf litter, their response to habitat changes is expected to vary across breeding guilds (Zimmerman and Simberloff, 1996; Becker et al., 2010b).

More specifically, studies conducted in the highly disturbed Brazil's Atlantic Forest (14.5% of the area is currently forest remnants) (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2013) show that certain reproductive modes of amphibians are more vulnerable to landscape alterations than others (Becker et al., 2007; Becker et al., 2010a; Ferreira et al., 2012; Almeida-Gomes and Rocha, 2014). For example, because water-body breeders have different life history stages that use different habitats, they are greatly affected by the separation of these habitats (termed "habitat split") due to the risk associated with migrating from upland forest to reproductive habitats in the valleys (Becker et al., 2007; Becker et al., 2010a). Furthermore, bromeliad breeders do not often occur in matrix habitats or small forest fragments because bromeliads are often absent in these habitats (Almeida-Gomes and Rocha, 2014). In a lowland region of Brazil's Atlantic Forest, Pardini et al. (2009) found that forest-specialist leaf-litter breeders tended to avoid edges in large fragments, while Dixo and Martins (2008) found no difference in the richness and abundance of leaf-litter breeders between edges and the interior of large fragments. Dixo and Martins (2008) suggested that the lack of a detectable edge effect on leaf-litter breeders may be due to the different types of matrix habitats surrounding the forest fragments in their study.

Even though most land area across the Atlantic Forest has been converted to other land uses, the use of these different matrix types by frog species and their role on edge effects remains largely unknown. Furthermore, much of the frog diversity of the Atlantic Forest is still being discovered and little is known about frog responses to landscape alteration. The objective of this study was to investigate how frog richness and abundance, particularly across different breeding guilds, respond to different distances from the forest edge and to the three dominant matrix types in a mountainous region of Atlantic Forest. To help understand the mechanisms driving frog responses to these landscape changes, we also investigated how frog richness and abundance are related to habitat characteristics and microclimate variables.

Materials and Methods

Study region

Research was conducted within and around the Reserva Biológica Augusto Ruschi (hereafter REBIO, 19°45'- 20°00' S, 40°27'- 40°38 W; 3,598 ha), in Santa Teresa, Espírito Santo state, Brazil. REBIO is in the northern portion of the Serra do Mar ecoregion in the Atlantic Forest biome and is classified as montane and sub-montane rain forest composed of moist broadleaf trees (Rizzini, 1979; Olson et al., 2001). Santa Teresa was forested until the arrival of European settlers in 1874. Today this municipality has 42% forest cover (Fundação SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais, 2013). The landscape of Santa Teresa is typical of mountainous regions in this biome; forest remnants are mostly restricted to hilltops and the water bodies (i.e. pond, stream, etc.) are located in the valleys that are dominated by different types of human-modified matrix (e.g., coffee plantations, *Eucalyptus* spp. plantations, abandoned pastures, and settlements).

Santa Teresa's climate is classified as Cwa-Cfa according to Köppen-Geiger's classification (Peel et al., 2007). The dry season is mostly from May to August and the rainy season is from September to April. Mean annual precipitation is 1868 mm with highest rainfall in November and lowest in June, when the mean rainfall is less than 60 mm (Mendes and Padovan, 2000). Mean annual temperature is 20°C, with minimum and maximum monthly temperatures averaging 14.3 C and 26.2 C, respectively (Thomaz and Monteiro, 1997).

Sampling design

We established 21 sites (elevational range = 793–908 m) within and around the REBIO. Each site was surveyed once from September to December 2012 (rainy season) and once from June to July 2013 (dry season). Sites comprised seven replicates of each of the three most widespread matrix types in this region (sun-grown coffee plantation, non-native *Eucalyptus* spp. plantation, and abandoned pastures).

At each site, we established a 250-m transect that ran perpendicular to the forest edge, from 50 m inside the matrix to 200 m inside the forest reserve. Along each transect, we surveyed four distances: i) 50 m inside the matrix, ii) at the forest edge, iii) 50 m inside the forest, and iv) 200 m inside the forest. At each distance on each transect, we established two 5 m x 5 m plots (hereafter paired-plots) for measuring frog richness and abundance, microclimate variables, and habitat characteristics.

Sites were placed in and around the REBIO to minimize potential confounding factors, such as fragment area and degree of isolation (Fletcher, 2005). We selected sites that met the following criteria: i) matrix area was at minimum 100 m x 100 m; ii) *Eucalyptus* plantations were between four and seven years old; iii) coffee plantations were all sun-grown (i.e., no shade trees) and at a mature stage (i.e., harvesting stage); and iv) abandoned pastures were between 10 and 20 years old. We avoided selecting sites with human disturbance inside the forest during the last 10 years (e.g., bromeliad harvesting, heavy logging, and cattle).

Frog sampling

We hand-captured frogs in the leaf litter, in bromeliads and on the vegetation up to 2 m off the forest floor during nocturnal surveys from 1800 to 2300 hr. Four people worked simultaneously by moving the leaf litter for 20 minutes to survey each 5 m x 5 m plot. We used a 5 m x 5 m plot size (Jaeger and Inger, 1994) after preliminary fieldwork revealed that it allowed us to capture more frogs per unit time than other tested plot sizes of 8 m x 8 m and 1 m x 2 m (Rocha et al., 2001; Marsh and Haywood, 2010).

We placed captured frogs in moist plastic tubes or plastic bags to prevent dehydration, and later brought them to the laboratory for identification. We released most frogs at the same site the following day. We euthanized some individuals by ventral application of 7.5% to 20% benzocaine and preserved them using 10% formalin before transferring them to 70% ethanol (American and Veterinary Medical Association, 2013; CEBEA/CFMV-Comissão de Ética Bioética e Bem-Estar Animal, 2013). We deposited voucher specimens in the collections at Museu de Biologia Mello Leitão (MBML) and Museu Nacional-Universidade Federal do Rio de Janeiro (MNRJ).

Species traits

We classified each species according to its breeding habitat [bromeliad guild (lays eggs in bromeliads), leaf-litter guild (lays eggs on the forest floor), or water-body guild (lays eggs in pond, river, or stream)]. We based classifications on Haddad et al. (2013) and field observations.

Environmental variables

To measure microclimate variables, we placed a data logger (Onset HOBO U12-012) in each paired-plot to measure air temperature, air relative humidity, and light intensity during the 24 hours prior to frog sampling. We used a digital thermometer pistol to measure leaf-litter temperature from two corners of each plot. We used a portable weather station (Kestrel 2500) to measure wind speed from each paired-plot.

To measure habitat characteristics in each plot, we counted all trees and characterized them according to diameter at breast height (DBH) as: i) large trees (DBH > 15 cm), ii) medium-sized trees (DBH between 5 and 15 cm), and iii) small trees (DBH <5 cm). We counted tank bromeliads (Bromeliaceae) within 2 m height off the forest floor. We measured the leaf-litter depth in the four corners of each plot. We used a spherical densitometer to estimate the percent canopy cover in each plot.

Statistical analysis

We employed generalized linear mixed models (GLMMs) to evaluate how frog richness (number of species) and abundance (total number of individuals) responded to distance from edge (hereafter 'Distance'), breeding guild (hereafter 'Guild'), season, matrix type (hereafter 'Matrix'), and environmental variables (microclimate variables and habitat characteristics). First, we tested 15 models considering the full dataset to evaluate the main effects of 'Distance', 'Guild', 'Matrix', 'Season' and all possible interactions. Second, we tested eight models considering the frogs collected at each distance separately, except in the matrix because of the low sample sizes, to evaluate the effect of 'Guild', 'Matrix', 'Season' and all possible interactions. Finally, we tested another 10 models by taking the best-fitting model from our overall analysis and including each environmental variable as an interaction term to evaluate if any of these variables improved model fit.

For each predictive model, we assessed the effects of the fixed factors using a mixed model with two random effects factors: site within matrix type and distance within site. We specified a Poisson distribution with a log link. These analyses were conducted using the package *lme4*. Because we studied a mountainous region, 'elevation' was included as "offset" in the models to address differences in elevation both across distances within the same transect and across sites.

Models were compared using an information theoretic approach, with lower values of Akaike's information criterion corrected for small sample size (AIC_c) indicating better-fitting models. We also calculated ΔAIC_c (difference in AIC_c for each model from the most parsimonious model) and $wAIC_c$ (AIC_c weight). We considered best-fitting model(s) those with a

$\Delta AIC_c < 2$ (Burnham and Anderson, 2002). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

We found no difference in habitat variables between the paired 5 m x 5 m plots sampled in the same transect, distance from edge, and season (Wilcoxon signed-rank test; package *stats*). Consequently, we summed some variables (tree structure and number of bromeliads) and took the mean of others (leaf-litter depth and canopy cover) from these paired-plots for analysis. We also summed frog richness and abundance found in these paired-plots.

Prior to analysis, we used variance inflation factors (VIF) to assess collinearity among air temperature, relative humidity, light intensity, and leaf-litter temperature using the package *vegan*. We also visually inspected scatterplots using the package *corrgram*. Leaf-litter temperature was excluded because it was correlated with air temperature. Mean, maximum, and minimum measurements of the other microclimate variables were highly correlated and were excluded from the analysis. Instead, we used the range (difference between maximum and minimum) for air temperature (hereafter 'temperature range'), relative humidity (hereafter 'humidity range'), and light intensity (hereafter 'light range') because VIF was smaller than 3. Resulting environmental variables were standardized to a mean of zero and a standard deviation of one to improve convergence of the fitting algorithm and to place the estimated coefficients on the same scale (Zuur et al., 2009).

Due to small sample sizes inside the matrix, we used a Pearson's chi-square exact test ($\chi 2$) to investigate whether richness and abundance of each breeding guild differed across 'matrix type'. We also used Pearson's chi-square exact test to evaluate the difference of richness and abundance between seasons across distances and breeding guilds. We conducted these chi-square tests using a Monte Carlo simulation based on 999 replicates with the package *MASS*. We performed one-way analysis of variance to test for differences of environmental variables across both edges and matrix types. We used package *agricolae* to run Tukey's Honestly Significant

Difference method (Tukey HSD) to control Type I error among pairwise mean comparisons. All analyses were conducted in version 3.0.3 of R software (R Core Team, 2014).

Results

We recorded 622 individual frogs representing 29 species and nine families across the 168 paired-plots (4 distances x 21 sites x 2 seasons) (Table 2.1). We documented a mean of 3.7 (± 4.0) individuals and 2.3 (± 2.1) species per paired-plot. We found four undescribed species: *Adelophryne glandulata* (Lourenço-de-Moraes et al., 2014), *Brachycephalus* sp., *Ischnocnema* cf. *parva* 1 and *Ischnocnema* cf. *parva* 2. We recorded 22 individuals of four bromeliad breeders, 562 individuals of 12 leaf-litter breeders, 37 individuals of 12 water-body breeders, and one individual rock breeder. We recorded 387 individuals of 27 species during the rainy season and 235 individuals of 17 species during the dry season.

'Distance * Guild' was the best-fitting model for frog richness ($wAIC_c$=0.99) and abundance ($wAIC_c$=0.99) across the landscape (Table 2.2). 'Distance * Guild' remained the best-fitting model for richness ($wAIC_c$=0.73) and abundance ($wAIC_c$=0.74) even after excluding the three most abundant species from the dataset (*A. glandulata*, *H. binotatus*, and *I.* cf. *parva* 1 represented 68% of total individuals) (Table 2.3). Furthermore, 'Guild' was the best-fitting model for richness and abundance by analyzing each distance inside the forest separately (Table 2.4). Richness and abundance were higher in the rainy season regardless of 'Distance' or 'Guild'. No environmental variable improved model fit for frog richness or abundance (Table 2.5). Within these environmental models, however, 'Distance * Guild * Large trees' was the best-fitting model for richness ($wAIC_c$=0.97) and 'Distance * Guild * Total bromeliads' was the best model for abundance ($wAIC_c$=0.89) (Table 2.5).

Leaf-litter breeders had higher richness and abundance at every distance compared to bromeliad and water-body breeders (Fig. 2.1; Table 2.1). Bromeliad and leaf-litter breeders decreased in richness and abundance from the forest interior toward the matrix (Fig. 2.1). Water-body breeders increased in richness toward the matrix and remained relatively stable in abundance across distances (Fig. 2.1). The number of large trees and bromeliads increased toward forest interior, whereas the range of microclimate variables tended to decrease toward forest interior (Table 2.6).

Of the frogs collected in the matrix habitats, five were water-body breeders, three were leaf-litter breeders, and one was a rock breeder, totaling 31 individuals of nine species (Table 2.1). Bromeliad breeders were not found inside any matrix habitat. Four species were exclusively found in the matrix of which three were water-body breeders (Table 2.1). Eight and 14 species found in the 50 m and 200 m forest plots, respectively, were not found in any matrix habitat.

Richness of leaf-litter breeders was higher in *Eucalyptus* than in abandoned pastures and coffee plantations, and abundance was higher in both *Eucalyptus* and abandoned pastures than in coffee (Fig. 2.2). Richness and abundance of water-body breeders were higher in coffee than in the other matrix types (Fig. 2.2). Leaf-litter breeders were not found in coffee whereas water-body breeders were found in all three matrix types (Fig. 2.2). The only environmental variables that differed inside the matrices were medium- and large-sized trees, which were higher in abandoned pastures and *Eucalyptus* plantations than in coffee (Tukey HSD, $P<0.05$). There was no significant difference in any environmental variable at edges adjacent to the three matrix types (Tukey HSD, $P>0.05$).

Discussion

The richness and abundance of frogs we studied in the mountainous region of Atlantic Forest varied across distances from forest edge (i.e., edge effects) and across matrix types (i.e. matrix effect). Breeding guild was the most important variable explaining these differences. More specifically, we found that bromeliad and leaf-litter species that do not require breeding habitats outside the forest responded negatively to edges and matrix habitats whereas water-body species that may require breeding habitats in the valleys responded positively or neutrally to edges and matrix habitats. Richness and abundance across breeding guilds were higher in the rainy season but frog responses were similar across the four distances in the two seasons. Across matrix types, leaf-litter species more often used *Eucalyptus* plantations, whereas water-body species more often used coffee plantations. Our data suggest that consideration of breeding habitat requirements can assist in prediction of frog response to both edge effects and matrix habitats (Becker et al., 2010b; Almeida-Gomes and Rocha, 2014).

The increase in richness and abundance of bromeliad and leaf-litter breeders toward the forest interior may be in response to the increase of both large trees and bromeliads toward the forest interior. Similarly, Pardini et al. (2009) showed that forest-specialist leaf-litter breeders prefer the forest interior, which may be attributed to the higher concentration of large trees inside the forest. We also observed a reduction in the range of microclimate variables (i.e. temperature, humidity and light intensity) toward the forest interior, which may be related to the increase in large trees. Trees buffer microclimate and also provide more leaf litter and suitable habitat for reproduction (Didham and Lawton, 1999; Ewers and Banks-Leite, 2013). Furthermore, trees host epiphytic bromeliads, which may contribute to the observed increase of both bromeliads and bromeliad breeders toward the forest interior. Our results suggest that primary forest is more suitable for reproduction for bromeliad and leaf-litter breeders.

We suggest that water-body breeders use edge and matrix habitat because they need to reach water bodies along the valleys (Becker et al., 2010b; Ferreira et al., 2012; Almeida-Gomes and Rocha, 2014). Of the 12 water-body breeding species we collected, nine species were forest specialists (as opposed to open habitat specialist or generalist; Table 2.1), and forest specialists made up 84% of the individual water-body breeders collected. Based on this information, our data suggest that these individuals are moving through these habitats.

Previous studies carried out in habitat fragments in the Atlantic Forest show that forest fragments disjunct from water bodies have lower richness and abundance of water-body breeders compared to forests connected to these reproductive habitats (Becker et al., 2010a; Almeida-Gomes, 2014). Our study, however, was conducted in and around a reserve and thus resources required for water-body breeders are in both inside the forest and in the matrix. The frogs in our study region appear to continue to use water bodies in the valleys outside the reserve despite the risk of migration through a potentially inhospitable habitat. It would be important to determine if this is the case and whether this movement is lowering their populations. The fact that our study recorded only 16% of water-body breeding species ever recorded in Santa Teresa, compared to 57% of bromeliad breeders and 70% of leaf-litter breeders (Rödder et al., 2007; Almeida et al., 2011) indicates that most water-body breeders may be reproducing deeper than 200 m inside the forest reserve, and that perhaps those water-body breeders living near the edge of the reserve have already declined.

Contrary to our prediction, edge effects were not influenced by seasonality. This result suggests that the response of frogs to edge effects may be studied in either of the sampled seasons, although species richness and abundance are higher during the rainy season. This result also indicates that studies during the rainy season may collect better data (i.e. higher counts and fewer zeros). Our study is consistent with most studies in tropical regions in that the rainy season is the reproductive season for most frogs (Watanabe et al., 2005; Ferreira et al., 2012). The dry season is likely less suitable for frog activity due to shorter photoperiod and lower temperature and humidity (Giaretta et al., 1999; Both et al., 2008; Santos-Pereira et al., 2011).

Matrix type had no measurable effect on frog responses or environmental variables in the forest edges or in the forest interior. This is surprising considering the lower abundance of medium- and large-sized trees inside coffee plantations compared to the other matrix types. On the other hand, the breeding guilds used the matrix types differently. Bromeliad and leaf-litter breeders were not found in coffee possibly because coffee plantations in our study are open canopy. Studies have shown that shade-growth coffee plantations are suitable matrix type for frogs across Neotropical ecoregions (Pineda et al., 2005). Surprisingly, coffee was the most used matrix type by water-body breeders. *Eucalyptus* plantation is the most forest-like matrix type in our studied region, which might explain the higher richness of leaf-litter breeders in this habitat. Many studies have pointed out the importance of secondary forests for amphibians as compared to agricultural or plantation matrix types (Tocher et al., 2002; Gardner et al., 2007; Pardini et al., 2009). Abandoned pastures in our region are not becoming secondary forest due to the conversion of secondary forest and other agricultural areas to *Eucalyptus* plantations. This landscape change could be detrimental to water-body breeders, considering that they had the lowest richness and abundance in *Eucalyptus* plantations.

Conclusions

Our results agree with previous suggestions that primary forest is critical for the persistence of most frogs in Atlantic Forest (Pardini et al., 2009; Almeida-Gomes and Rocha, 2014; Lion et al., 2014). The lower richness and abundance of bromeliad and leaf-litter frogs inside the matrix compared to the forest interior suggests that the conversion of the existing natural habitats to any type of matrix will have strong deleterious effects on these breeding guilds. Differences in vegetation structure between forest interior and matrix types helped explain these findings. The fact that water-body breeders are more associated with edge and matrix habitats in our study sites suggests that matrix quality could be important for these species as they migrate toward reproductive habitats located in the valleys. Ferreira et al. (2012) showed that water bodies in the valleys connected to upland forests by forest corridor harbor higher richness and abundance of frogs compared to water bodies surrounded by *Eucalyptus* plantation and human construction. To conserve the various breeding guilds of frogs in Atlantic Forest, we recommend that conservation initiatives focus on maintaining protected areas and improving the connection between upland forested areas and water bodies in the valleys.

The Brazilian Congress recently altered the Forest Act legislation, reducing the minimum width of riparian forest despite scientists' predictions that this will negatively affect frogs (Toledo et al., 2010). We speculate that the reduction in riparian width will increase the distance that water-body breeders will need to travel through the matrix (split distance), and may negatively affect these species (Becker et al., 2010a; Lion et al., 2014). In addition, the Act now allows landowners to reforest previously clear-cut native forest with non-native plants, such as *Eucalyptus*, which we found to be a less utilized matrix type for water-body breeders than traditional coffee plantations. Our results support previous research showing the importance of integrating information about landscape configuration and life-history traits, especially developmental mode, to formulate more effective and ecologically relevant management and conservation strategies (Crump, 2015).

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Table 2.1. Model comparison of frog richness and abundance in relation to 'Breeding guild', 'Distance', 'Matrix type', and 'Season' across 21 sites in the mountainous region of Brazil's Atlantic Forest. Results in bold are the valuable models ($\Delta AIC_c < 2$).

Models	Richness			Abundance		
	AIC_c	ΔAIC_c	$wAIC_c$	AIC_c	ΔAIC_c	$wAIC_c$
Distance * Guild	**570.99**	**0**	**0.99**	**665.19**	**0**	**0.99**
Distance * Guild * Season	585.47	14.48	0	674.31	9.124	0
Null	690.84	119.84	0	891.76	226.57	0
Distance	679.72	108.73	0	872.84	207.65	0
Guild	590.75	19.76	0	699.53	34.34	0
Matrix	694.84	123.84	0	895.80	230.61	0
Season	673.71	102.72	0	856.89	191.70	0
Guild * Matrix	599.38	28.39	0	707.62	42.43	0
Guild * Season	589.18	18.19	0	691.74	26.55	0
Distance * Guild * Matrix	599.39	28.40	0	680.73	15.54	0
Guild * Matrix * Season	611.77	40.78	0	714.25	49.06	0
Distance * Matrix	682.56	111.57	0	877.76	212.57	0
Distance * Season	668.90	97.91	0	843.911	178.72	0
Matrix * Season	681.74	110.75	0	862.94	197.74	0
Distance * Guild * Matrix * Season	697.38	126.39	0	771.989	106.79	0

Table.2.2. Model comparison of frog richness and abundance in relation to environmental variables (microclimate and habitat characteristics). Results in bold are the valuable models (ΔAICc<2).

Models	Richness				Abundance		
	AIC$_c$	ΔAIC$_c$	wAIC$_c$		AIC$_c$	ΔAIC$_c$	wAIC$_c$
Reference model							
Distance * Guild	570.99	0.00	1.00		665.19	0.00	0.99
Model*Env. var.							
Large trees	**579.24**	**0.00**	**0.97**	**Bromeliads**	**667.43**	**0.00**	**0.89**
Light range	587.14	7.90	0.02	Wind	669.64	2.21	0.11
Leaf-litter depth	588.34	9.10	0.01	Large trees	672.95	5.52	0.03
Bromeliads	593.17	13.93	0.00	Small trees	674.19	6.76	0.02
Small trees	594.19	14.95	0.00	Canopy	676.21	8.78	0.01
Temp. range	601.01	21.77	0.00	Leaf-litter depth	676.99	9.56	0.00
Humidity range	597.81	18.57	0.00	Temp. range	678.90	11.47	0.00
Medium-sized trees	600.39	21.15	0.00	Humidity range	679.22	11.79	0.00
Canopy cover	595.54	16.30	0.00	Light range	684.11	16.69	0.00
Wind	599.10	19.86	0.00	Medium-sized trees	693.51	26.09	0.00

Table 2.3. Mean ± Standard deviation of microclimate variables and habitat characteristics by 'Distance' across 21 sites.

Variables (units)	Matrix	Edge	50m Forest	200m Forest
Microclimate variables				
Temp. average (°C)	18.2 ± 1.9	17.4 ± 1.8	16.9 ± 1.7	17.1 ± 1.7
Temp. range (°C)	11.8 ± 4.1	7.2 ± 2.7	5.3 ± 1.9	5.5 ± 2.2
Humidity average (%)	91.6 ± 4.2	92.4 ± 8.9	96.8 ± 3.6	96.6 ± 3.8
Humidity range (%)	31.6 ± 13.9	18.8 ± 9.8	9.8 ± 9.5	10.6 ± 9.7
Light average (lx)	1459.8 ± 968.4	491.5 ± 484.5	119.9 ± 126.6	205.9 ± 330.4
Light range (lx)	13225.4 ± 8091.1	6292.6 ± 5663.6	3071.2 ± 3685.5	2837.5 ± 3384.6
Wind speed (Km/h)	2.4 ± 3.85	1.85 ± 3.6	1.7 ± 3.7	1.5 ± 1.4
Habitat characteristics				
Number of bromeliad	0.02 ± 0.1	1.6 ± 2.3	4.5 ± 5.6	7.4 ± 5.9
Small trees	20.2 ± 9.4	47.8 ± 14.0	42.7 ± 10.2	38.7 ± 8.4
Medium-sized trees	4.1 ± 2.6	10.9 ± 3.5	10.1 ± 2.1	10.1 ± 3.2
Large trees	1.2 ± 1.0	3.3 ± 2.5	4.6 ± 1.6	4.7 ± 1.8
Canopy cover (%)	66.2 ± 25.4	85.4 ± 14.1	91.4 ± 3.3	88.2 ± 11.7
Leaf litter depth (cm)	7.9 ± 2.9	8.6 ± 2.4	10 ± 4.0	12.7 ± 4.2

Table 2.4. List of the 29 species recorded in Santa Teresa municipality, southeastern Brazil, including species traits and abundance by distance from the forest edge. Breeding guild: BR= bromeliad, LL= leaf litter, RW= rock wall, and WB= water body (pond, stream, or river). Forest association: F= forest dependent, O= open-habitat, and G= habitat-generalist. * disregarded in the statistical analysis.

Frog species by family	Breeding guild	Forest association	Abundance by distance				Total abundance
			Matrix	Edge	50m Forest	200m Forest	
Brachycephalidae							
Brachycephalus sp.	LL	F	0	0	1	0	1
Ischnocnema abdita Canedo & Pimenta, 2010	LL	F	0	7	11	23	41
Ischnocnema guentheri Steindachner, 1864	LL	F	7	1	1	0	9
Ischnocnema nasuta (Lutz, 1925)	BR	F	0	0	1	0	1
Ischnocnema oea (Heyer, 1984)	LL	F	0	9	17	18	44
Ischnonema cf. *parva* 1	LL	F	0	11	48	76	135
Ischnonema cf. *parva* 2	LL	F	0	0	1	1	2
Ischnocnema verrucosa Reinhardt and Lutken, 1862	LL	F	0	4	11	14	29
Ischnocnema sp.	LL	F	0	1	0	1	2
Craugastoridae							
Euparkerella tridactyla Izecksohn, 1988	LL	F	0	0	3	4	7
Haddadus binotatus (Spix, 1824)	LL	F	11	47	66	74	198
Cycloramphidae							
Thoropa miliaris (Spix, 1824) *	RW	G	1	0	0	0	1
Zachaenus carvalhoi Izecksohn, 1983	LL	F	0	0	1	2	3
Eleutherodactylidae							
Adelophryne glandulata Lourenço-de-Moraes et al., 2014	LL	F	3	10	44	34	91
Hylidae							
Bokermannohyla caramaschii (Napoli, 2005)	WB	F	1	3	0	2	6
Hypsiboas faber (Wied-Neuwied, 1821)	WB	G	0	2	0	0	2
Hypsiboas semilineatus (Spix, 1824)	WB	F	2	0	0	0	2
Phasmahyla exilis (Cruz, 1980)	WB	F	0	0	0	2	2
Scinax alter (Lutz, 1973)	WB	O	2	0	0	0	2

Scinax arduous Peixoto, 2002	BR	F	0	1	0	0	1
Scinax sp.	WB	F	0	0	1	1	2
Hylodidae							
Crossodactylus sp.	WB	F	0	0	0	5	5
Leptodactylidae							
Crossodactylodes bokermanni Peixoto, 1983	BR	F	0	0	1	1	2
Crossodactylodes izecksohni Peixoto, 1983	BR	F	0	0	0	18	18
Physalaemus crombiei Heyer & Wolf, 1989	WB	F	0	2	0	0	2
Physalaemus cuvieri Fitzinger, 1826	WB	O	2	0	0	0	2
Microhylidae							
Chiasmocleis schubarti Bokermann, 1952	WB	F	0	0	1	2	3
Odontophrynidae							
Proceratophrys boiei (Wied-Neuwied, 1824)	WB	F	0	1	0	0	1
Proceratophrys paviotii Cruz, Prado & Izecksohn, 2005	WB	F	2	1	4	1	8
Total richness			9	15	17	18	-
Total abundance			31	101	213	279	622

Table 2.5. Model comparison of frog richness and abundance in relation to ‘Breeding guild’, ‘Distance’, and ‘Season’, after excluding the three most abundant frog species from the dataset. Results in bold are the valuable models ($\Delta\text{AIC}_c < 2$).

Models	Richness			Abundance		
	AIC_c	ΔAIC_c	$w\text{AIC}_c$	AIC_c	ΔAIC_c	$w\text{AIC}_c$
Distance * Guild	**360.63**	**0**	**0.73**	**445.36**	**0**	**0.74**
Guild * Season	364.07	3.43	0.13	447.76	2.39	0.23
Guild	364.09	3.46	0.13	452.71	7.34	0.01
Guild * Matrix	369.63	9.00	0	453.89	8.52	0
Null	413.72	53.09	0	456.23	10.86	0
Distance	418.28	57.65	0	457.68	12.31	0
Matrix	416.01	55.36	0	530.61	85.24	0
Season	406.39	45.75	0	535.36	89.99	0
Distance * Guild * Matrix	388.55	27.926	0	533.51	88.13	0
Distance * Guild * Season	376.87	16.24	0	519.49	74.13	0
Guild * Matrix * Season	382.64	22.01	0	467.92	22.55	0
Distance * Matrix	424.42	63.79	0	545.29	99.92	0
Distance * Season	415.88	55.25	0	528.13	82.76	0
Matrix * Season	408.02	47.39	0	502.82	57.45	0
Distance * Guild * Matrix * Season	599.41	238.77	0	680.74	235.37	0

Table 2.6. Model comparison of frog richness and abundance in relation to ‘Breeding guild’, ‘Matrix type’, and ‘Season’ for data collected in each of the three distances inside the forest separately. Results in bold are the valuable models ($\Delta AIC_c < 2$).

Models by distance	Richness			Abundance		
	AIC_c	ΔAIC_c	$wAIC_c$	AIC_c	ΔAIC_c	$wAIC_c$
Edge						
Guild	**145.88**	**0.00**	**0.98**	**167.19**	**0.00**	**0.96**
Guild * Season	154.25	8.37	0.02	173.59	6.41	0.04
Guild * Matrix	159.49	13.61	0.00	177.92	10.74	0.00
Matrix	170.85	24.97	0.00	202.64	35.46	0.00
Season	165.84	19.96	0.00	197.16	29.97	0.00
Null	166.33	20.45	0.00	198.09	30.91	0.00
Season * Matrix	174.72	28.84	0.00	203.46	36.27	0.00
Guild * Season * Matrix	194.06	48.18	0.00	210.32	43.13	0.00
50 m forest						
Guild	**179.02**	**0.00**	**0.93**	**215.07**	**0.00**	**0.85**
Guild * Season	184.27	5.25	0.07	217.47	2.40	0.15
Matrix	217.07	38.05	0.00	274.87	59.81	0.00
Season	207.69	28.67	0.00	259.37	44.31	0.00
Null	212.66	33.64	0.00	270.38	55.31	0.00
Guild * Matrix	194.99	15.97	0.00	227.05	11.98	0.00
Season * Matrix	212.23	33.21	0.00	266.09	51.02	0.00
Guild * Season * Matrix	216.10	37.08	0.00	250.10	35.04	0.00
200 m forest						
Guild	**190.38**	**0.00**	**0.95**	**232.07**	**0.00**	**0.85**
Guild * Season	196.27	5.89	0.05	235.65	3.59	0.14
Guild * Matrix	202.59	12.20	0.00	240.51	8.44	0.01
Matrix	222.94	32.55	0.00	314.52	82.46	0.00
Season	219.38	29.00	0.00	299.25	67.18	0.00
Null	223.58	33.21	0.00	314.17	82.10	0.00
Season * Matrix	222.62	32.24	0.00	301.15	69.08	0.00
Guild * Season * Matrix	230.91	40.53	0.00	267.84	35.77	0.00

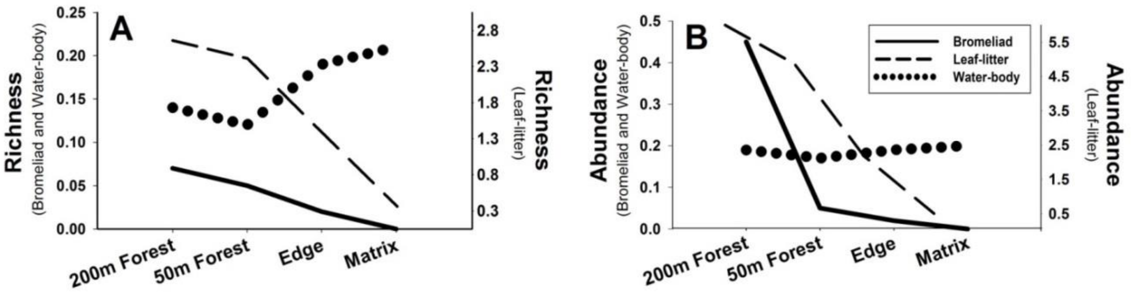

Fig. 2.1. Mean richness (A) and abundance (B) of frogs by breeding guild across distance from the forest edge across 21 sites.

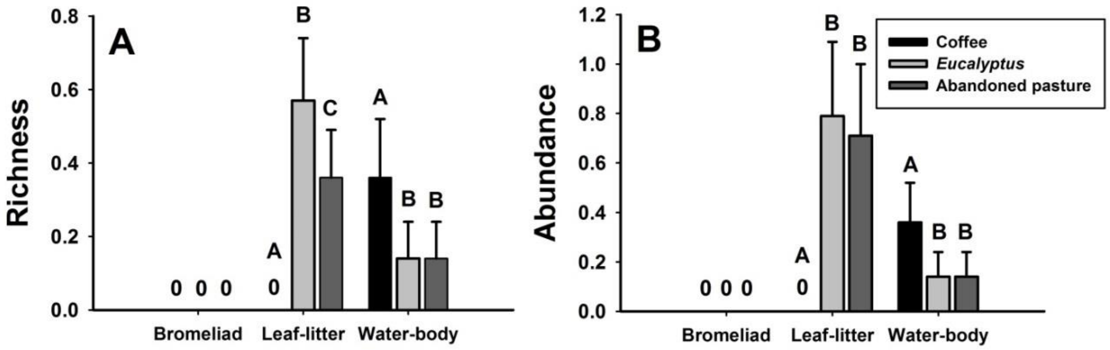

Fig. 2.2. Mean and standard error of richness (A) and abundance (B) of breeding guild inside seven replicates of each matrix type. Means with different letters are significantly different (χ^2; $P < 0.05$).

CHAPTER 3

ANTIPREDATOR BEHAVIOR OF POST-METAMORPHIC ANURANS IN BRAZIL'S ATLANTIC FOREST

Abstract

Predation is one of the most important selective pressures on species life-history traits. We compiled a database of antipredator behaviors of post-metamorphic anurans from Brazil's Atlantic Forest. In total our database comprises 224 records, of which 102 (45%) were collected during our fieldwork, 116 (52%) were compiled from the literature and six (3%) were reported by colleagues. The 224 records represent 165 species, and include 16 families of anurans. Individuals of 164 of the 165 species displayed at least one behavior other than motionless or escape, of which 60 (36%) displayed defensive posture, 23 (14%) actively engaged in defense, and 82 (50%) displayed behaviors of both types. 'Motionless' was the most displayed antipredator behavior followed by 'active escape or fleeing' and 'thanatosis or death feigning'. *Haddadus binotatus*, *Hypsiboas faber*, and *Odontophrynus americanus* displayed 11 behaviors, which was the highest number of behaviors across species. Craugastoridae (mean=7.5), Centrolenidae (mean=7), and Hemiphractidae (mean= 6.7) had the highest mean of antipredator behaviors across families. This database combined with quantitative measurements of morphological and ecological traits is valuable to the advancement of knowledge on evolutionary ecology because life history represents different strategies that evolved to maximize individual fitness.

Introduction

Life history traits represent different strategies that evolved to maximize individual fitness (Vitt 2013, Mesquita et al. 2015). Gathering data on life history traits is crucial for the advancement of several research areas (Mesquita et al. 2015). For instance, Darwin's theory of evolution by natural selection was based on studies of the natural history of organisms (Vitt 2013). Predation has been considered one of the most important selective pressures on life history (Williams et al. 2000). Anurans, for example, have evolved many antipredator behaviors to enhance their chances for survival against a diversity of predators, such as spiders, crabs, insects and vertebrates (Toledo et al. 2007). The diversity of antipredator adaptations in anurans is probably more complex than that of any other terrestrial vertebrate group. These defenses include morphological, behavioral, and/or physiological characteristics that go from motionless to flee (Toledo et al. 2011).

In contrast to the wide variety of antipredator mechanisms in anurans (~30), few extensive studies comprising more than one species have been published (Williams et al. 2000, Toledo et al. 2011). This scenario diverges from other amphibians, such as the widely studied salamanders and newts (Dodd and Brodie Jr. 1976, Brodie Jr 1977). Most studies of defensive mechanisms on anurans are published as short notes due to the sporadic observations mostly done during frog sampling for other purposes (Toledo et al. 2005, Ferreira et al. 2013). Despite receiving little attention, several authors have suggested that behavior may lead the way in adaptation or that behavior acts as a kind of pacemaker for the rate at which evolution occurs (Brodie Jr 1977, Jared et al. 2009).

Studies of predator-prey interactions continue to be one of the most fascinating and important aspects of ecological research (Mukherjee and Heithaus 2013) and Brazilian herpetologists have long been fascinated by life history of amphibian. The result of such interest combined with the urge to publish has resulted in an astonishing number of short note publications on anuran defensive mechanisms from Atlantic Forest. In the present study, we aim to present most records on antipredator behavior elicited from anurans occurring in this biome. For this, we gathered our own data from field research, compiled published literature, and consulted herpetologists for unreported observations.

Materials and Methods

We conducted field research across the Atlantic Forest and tested frog's antipredator behavior in both field and laboratory settings. In a non-systematic standard, antipredator mechanisms were elicited by approaching, handling, lightly prodding and pinching frogs on the head, body, and legs with either plastic forceps or collector's finger (Williams et al. 2000, Toledo et al. 2011, Lourenço-de-Moraes et al. 2014).

We released most frogs at the same site the following day. We selected some specimens and euthanized them by topical ventral application of 7.5% to 20% benzocaine (Association 2013, CEBEA/CFMV 2013); preserved them using 10% formalin before transferring them to 70% ethanol. We deposited voucher specimens in the Zoological Collections of Universidade Estadual de Santa Cruz, Ilhéus (MZUESC), Museu Nacional, Rio de Janeiro, Rio de Janeiro (MNRJ), and Museu de Biologia Mello Leitão (MBML).

In addition to our observations, we compiled records of frog's antipredator behavior from the literature and non-published observations obtained from colleagues. The literature survey was performed in the following databases: Brill online books and journal, Google Scholar, Scientific Eletronic Library Online (SciELO), Scopus, Taylor and Francis Library Online, and Web of Science. In all cases, we used the following keywords: antipredator mechanisms, antipredator behavior, defensive behavior, and defensive strategies combined with either frog or anuran. We also searched specifically the major herpetological journals often used by Brazilian colleagues to publish such topic (Amphibia-Reptilia, Journal of Herpetology, Herpetologica, Herpetological Review, and Herpetology Notes) and consulted the original cross-reference before added them to the database.

We also consulted herpetologist colleagues through emails requesting non-published observations on frog's antipredator behavior. Their observations were included in the database and their names included as "pers. comm." We included reports from both field and laboratory conditions. Our records without precise identification at the species-level (i.e. aff., cf., and gr.) were removed from the database. Taxonomic classification follows Frost (2014).

Except for the behavior "immobility or remaining motionless," all the others behaviors were divided into two major classifications: postures or active defenses and they are in parenthesis in the following list. We classified antipredator behaviors according to the types listed by Haddad et al. (2013): immobility or remaining motionless, crouching down (posture), thanatosis or death-feigning (posture), contracting (posture), chin-tucking (posture), phragmosis (posture), puffing up the body (posture), body raising (posture): a) legs vertically stretched and b) legs laterally stretched, body tilting (posture), stiff-legged behavior (posture), head-up sharp bend (posture), eye-protection (posture), unken reflex (posture), legs interweaving (posture), flipping onto the back (posture), hiding (active defense), digging (active defense), active escape or fleeing (active defense), cloacal discharge (active defense): a) liquid or b) solid, charging, head hitting (active defense), biting (active defense), mouth gaping (posture), tongue protrusion (posture), fighting (active defense), spine aggression (active defense): a) spine-puncturing, b) spine-scratching, c) spine-hurting, phalanx aggression (active defense), regurgitating (active defense), defensive vocalization (active defense), production of secretion (active defense): a) odoriferous, b) adhesive, c) noxious, d) slippery, and poison squirting (active defense).

Results

We compiled a database of antipredator behaviors of post-metamorphic anurans from Brazil's Atlantic Forest (Table 3.1; 3.2; 3.3). In total our database comprises 224 records, of which 102 (45%) were collected during our fieldwork, 116 (52%) were compiled from the literature and six (3%) were reported by colleagues. The 224 records represent 165 species, and include 16 families. Individuals of 164 of the 165 species displayed at least one behavior other than motionless or escape (Fig. 1). Individuals of 60 (36%) displayed defensive posture, 23 (14%) actively engaged in defense, and 82 (50%) displayed behaviors of both types.

“Motionless” (N= 82) was the most displayed antipredator behavior followed by “active escape or fleeing” and “thanatosis or death feigning” (N=72 for each type). The behaviors “head-up sharp bend”, “phalanx aggression”, “poison squirting”, and “tongue protrusion” were not displayed by species listed in our database. Across the displayed behaviors, “flipping onto the back”, “legs interweaving”, “digging”, “charging”, and “regurgitating” were the rarest (N=1) displayed behavior. Fifty species produced “skin secretion”, of which eight released two types of “skin secretion” and 29 produced “skin secretion” that was not classified. Odoriferous substance was the most produced (N= 16 species), followed by noxious (N=7), slippery (N=7), and adhesive (N=2) substances. Twenty species (12%) emitted defensive vocalizations.

Haddadus binotatus, *Hypsiboas faber*, and *Odontophrynus americanus* displayed 11 behaviors, which is the highest number of behaviors across species, including posture, vocalization, and skin secretion. Sixty-one (N=37%) species displayed only a single behavior. Of the 101 species observed during our study, individuals of 74 (73%) species displayed “immobility” or “remained motionless”. Forty species were reported from more than one population. These 40 species displayed at least one different antipredator behavior between populations. Sixty-five (39% of the database) species recorded were Hylidae. Craugastoridae (mean=7.5), Centrolenidae (mean=7), and Hemiphractidae (mean= 6.7) had the highest mean of antipredator behaviors across families.

Discussion

Individuals of most species in our observations remained “motionless” before displaying a posture or any other behavior. Remaining motionless is likely a strategy to avoid observation or detection by a visually oriented predator. This presumably crypsis adaptation is a widespread behavior in anurans and is considered the first line of defense, possibly a precursor to the other displays (Brodie 1977, Toledo et al. 2011). If detected, immobility might reduce the likelihood of further predator attack or reduce the intensity of attack (Brodie 1977). For instance, Toledo et al.

(2011) observed that a predator snake did not prey upon two immobile hylid species. In addition, avian predators ignored immobile salamanders but captured moving salamanders (Dodd and Brodie Jr. 1976). However, the causal basis of the fitness costs of “immobility” is still unclear.

Immobility has presumably further advantage in those frogs that produce antipredator skin secretion. Our results show that the ability to produce skin secretion is widespread across species (N= 50) and families (N= 12) of frogs from the Atlantic Forest. These secretions varied from odoriferous to highly toxic. Odoriferous secretions may have aposematic value because some snakes assess the palatability of the prey prior to attack (Shine 1993). In our observations, most odors were benign to observers, but some odors (e.g. released by *Itapotihyla langsdorffii and Leptodactylus labyrinthicus*) caused unpleasant effects, such as nasal congestion and sneezing. Williams et al. (2000) speculated that if predators learn that an unpalatable prey is associated with a certain odor; they may avoid prey with that odor in the future, even if the odor itself is benign. Adhesive secretions have been reported as an effective mechanism to predation because they may potentially render the predator immobile and/or unable to feed (Williams et al. 2000). Slippery secretions have been successful against tactile predators because they reduce the likelihood of being seized. Although speculative, we believe most of these secretions are potentially efficient defense and inhibit the action of predators. However, only few species from this biome have been assayed for the presence of bioactive compounds (Toledo and Jared 1995, Pires et al. 2002, Jared et al. 2009).

Immobility may also be the precursor of defensive postures, which are displayed by almost all anurans from the Atlantic Forest. Such behaviors include any positioning of the body that might enhance prey chance of surviving contact with predator. It is hypothesized that the sudden change of shape, position and location of the potential prey could startle and disorienting pursuing predators (Brodie Jr 1977). Some species we observed such as bufonids, display “contracting” and “puffing-up the body” to release secretions and direct glands toward the predators (Toledo and Jared 1995, Jared et al. 2009). Several species we observed in leptodactylids, display “body raising with legs stretched” to show blotches or marks of contrasting color on the thighs or flanks (Toledo et al. 2011). Other species such as bufonids, cycloramphids, and hemiphractids display “body raising” and “puffing-up the body” to increase their size (Zocca et al. 2014).

“Thanatosis or death feigning” was the most common type of posture (N= 72 species) displayed by anurans from Atlantic Forest. In fact, thanatosis is widely spread across several terrestrial taxa, in which the animal may dissuade the attack of a potential predator by adopting a posture that gives it the appearance of being dead (Toledo et al. 2011). The frogs in thanatosis often displayed this behavior after they had jumped away from the observer or were handled by the observer (Toledo et al. 2011). In general, individuals can remain in “death feigning” for up to five minutes, and then actively flip to the normal position (i.e. dorsum up) and jump away. Toledo et al. (2011) showed that his type of behavior is more often displayed by presumably non-toxic species. Thanatosis is also a strategy used by some species to show bright coloration on the exposed venter or members, which serve as an aposematic cue to predators (Brodie 1977).

Defensive vocalization was often emitted by many species in Atlantic Forest. Most calls from our observations can be categorized as “distress call” (sensu Toledo et al. 2014) because frog emitted the call when was handled by observer. In only one occasion, we observed “alarm” call; *Gastrotheca megacephala* probably emitted a distress call when apprehended by one of us. This call was interpreted by the other conspecifics as “alarm” because they all stopped calling for about 15 minutes (Lourenço-de-Moraes et al., data submitted). We believe “alarm” call is difficult to be determined because it depends of the response from conspecifics. “Warning” calls serve to warn a potential predator and was emitted only by *Ceratophrys joazeirenses* (Haddad et al. 2013, Toledo et al. 2014). This call is also likely difficult to be determined because most observers do not threaten the frog before capture.

Few frog species from other biomes display the four behaviors not observed in the Atlantic Forest frogs (i.e. “head-up sharp bend”, “phalanx aggression”, “poison squirting”, and “tongue protrusion”). “Head-up sharp bend” has only been observed for the red-eyed Thailand frog, *Leptobrachium smithi* (Chuaynkern et al. 2007). “Phalanx aggression” has been observed for some African arthroleptids (Boulenger 1902). “Poison squirting” has only been observed for *Rhaebo guttatus* (Mailho-Fontana et al. 2014). “Tongue protrusion” has only been observed for *Acanthixalus spinosus* (Perret 1961). It is possible some of these behaviors will be recorded in the future for some species from Atlantic Forest.

Interpopulation variation of antipredator behaviors was observed for many species during our field research. This variation may indicate antipredator behavior is a plastic life history trait that may be a response to local predator pressures. This variation may also indicate that antipredator behavior is probably not a good taxonomic character. Furthermore, antipredator behavior does not appear to be phylogenetically related because most behaviors were displayed by species from different families. These cases of convergences point out the selective advantage of these behaviors and further cautions against the use of defensive mechanisms in taxonomy.

It is noteworthy that the three species that displayed the highest number of behaviors (i.e. *H. binotatus*, *H. faber*, and *O. americanus*) have large distribution across Atlantic Forest. We speculate that the advantage of displaying a large spectrum of defensive mechanism may be associated to distribution range. The many antipredator behaviors displayed by these frogs appear to interact and the total protection is greater than the sum of each of the behaviors alone. It seems that an individual can switch behaviors depending of the threat. For instance, we observed *Gastrotheca megacephala* and *G. recava* escalating the defensive behavior according to the degree of stress imposed by the potential predator (Lourenço-de-Moraes et al., data submitted). Predation involves several phases such as locate identify, approach, subjugate, ingest, and digest prey (Mailho-Fontana et al. 2014). Therefore, the more types of antipredator behavior a species can display, the more likely this species can escape predators. We suggest future studies should evaluate the difference on the number of antipredator behavior across families considering we found certain families displaying many more behaviors and others few behaviors.

In our database, observations done in the field are a large percentage of the reports on antipredator mechanisms in anuran. The potential stress associated with the capture, transport and confinement of anurans may prevent the display of natural behaviors in laboratory. This field of research needs a description of an efficient and reliable method to induce defensive mechanism in anurans, especially under field conditions. Such a method would allow standardization of the inductions across studies and allow direct comparison across taxa and populations.

Our observations from field research considerably increased the number of species reported displaying antipredator behavior. Our database includes records of antipredator behavior for approximately 30% of the species listed for Atlantic Forest (sensu Haddad et al. 2013). Across families from Atlantic Forest, Alsodidae was the only one not represented in our database. This family has only one species, *Limnomedusa macroglossa*, in this biome. It is possible that anurans from Atlantic Forest are one of the most studied globally on this topic. This fact is likely driven by both the admiration of Brazilians for life history and the remarkable work done by some researchers in the previous decades (e.g. C. Jared, C. Haddad, L. F. Toledo and collaborators).

The number of records increased considerably after Toledo et al. (2011) compiled their observations of antipredator behavior for species from this biome. We believe our database provides a unique opportunity to further investigate ecological and evolutionary questions regarding antipredator mechanisms in anuran, especially if combined with quantitative measurements of morphological and ecological traits.

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Table 3.1. Antipredator behavior of post-metamorphic anurans from Brazil's Atlantic Forest. The types of antipredator behavior from 1 to 15 follows Haddad et al. (2013). 1= immobility or remaining motionless, 2= crouching down, 3= thanatosis or death-feigning, 4= contracting, 5= chin-tucking, 6= phragmosis, 7= puffing up the body, 8= body raising: a) with legs vertically or b) laterally stretched, 9= body tilting, 10= stiff-legged behavior, 12= eye-protection, 13= unken reflex, 14= legs interweaving, 15= flipping onto the back. The behavior 11= head-up sharp bend was not observed for species from our dataset.

Ref.	**Taxon**	**Antipredator behavior**													
#		1	2	3	4	5	6	7	8	9	10	12	13	14	15
	Aromobatidae														
1	*Allobates olfersioides*														
	Brachycephalidae														
2	*Brachycephalus ephippium*	x		x				x							
3	*Brachycephalus ephippium*														
4	*Brachycephalus hermogenesi*														
5	*Brachycephalus pitanga*														
6	*Brachycephalus pitanga*														
7	*Ischnocnema abdita*	x		x				x							
8	*Ischnocnema epipeda*	x													
9	*Ischnocnema erythromera*	x		x				x							
10	*Ischnocnema guenteri*	x													
11	*Ischnocnema oea*	x													
12	*Ischnocnema parva*	x		x				x							
13	*Ischnocnema parva sp nov.*	x						x							
14	*Ischnocnema verrucosa*	x		x											
	Bufonidae														
15	*Dendrophryniscus brevipollicatus*	x	x	x											
16	*Dendrophryniscus carvalhoi*	x			x			x							
17	*Dendrophryniscus carvalhoi*			x							x				
18	*Dendrophryniscus proboscideus*				x										
19	*Frostius erythrophthalmus*				x			x							
20	*Frostius pernambucensis*			x	x			x							
21	*Melanophryniscus cambaraensis*														X
22	*Melanophryniscus moreirae*												x		

23	*Melanophryniscus moreirae*										
24	*Melanophryniscus tumifrons*										x
25	*Rhinella cf. crucifer*		x				x				
26	*Rhinella crucifer*	x					x				
27	*Rhinella crucifer*	x					x				
28	*Rhinella granulosa*									x	
29	*Rhinella granulosa*	x			x		x				
30	*Rhinella hoogmoedi*	x			x		x				
31	*Rhinella icterica*						x				
32	*Rhinella jimi*						x		x		
33	*Rhinella marina*				x						
34	*Rhinella ocellata*				x		x				
35	*Rhinella ornata*	x		x			x				
36	*Rhinella ornata*					x					
37	*Rhinella schneideri*	x					x		x		
38	*Rhinella schneideri*				x		x	x			
39	*Rhinella abei*								x		
40	*Rhinella icterica*										
	Centrolenidae										
41	*Vitreorana uranoscopa*	x		x			x				
	Ceratophryidae										
42	*Ceratophrys aurita*										
43	*Ceratophrys joazeirensis*										
44	*Ceratophrys joazeirensis*										
	Craugastoridae										
45	*Eleutherodactylus bilineatus*			x							
46	*Eleutherodactylus bilineatus*			x							
47	*Euparkerella tridactyla*	x						a			
48	*Haddadus binotatus*	x	x	x			x				
49	*Haddadus binotatus*										
50	*Haddadus binotatus*										
51	*Pristimantis paulodutrai*			x							
52	*Pristimantis ramagii*			x							
53	*Pristimantis vinhai*			x							
	Cycloramphidae										

54	*Cycloramphus acangatan*	x			x								x
55	*Cycloramphus acangatan*	x		x	x			x					x
56	*Cycloramphus acangatan*												
57	*Cycloramphus boraceiensis*	x	x										
58	*Cycloramphus brasiliensis*	x		x				x					
59	*Cycloramphus eleutherodactylus*												
60	*Cycloramphus eleutherodactylus*												
61	*Cycloramphus lutzorum*												
62	*Thoropa miliaris*	x		x				x					
63	*Zachaenus carvalhoi*												
64	*Zachaenus carvalhoi*							a					a
65	*Zachaenus parvulus*	x		x				x					
66	*Zachaenus parvulus*										x		
	Eleutherodactylidae												
67	*Adelophryne glandulata*	x		x				x	a				
68	*Adelophryne glandulata*	x											
69	*Adelophryne mucronatus*												
	Hemiphractidae												
70	*Flectonotus ohausi*	x		x	x								
71	*Gastrotheca albolineata*	x	x	x	x			x					
72	*Gastrotheca megacephala*	x		x				x		x			
73	*Gastrotheca recava*	x			x			x		x			
	Hylidae												
74	*Agalychnis aspera*				x								
75	*Aparasphenodon albosignatus*								a	x			
76	*Aparasphenodon arapapa*	x		x	x		x						
77	*Aparasphenodon bokermanni*						x						
78	*Aparasphenodon brunoi*	x			x		x						
79	*Aplastodiscus arildae*				x								
80	*Aplastodiscus arildae*								b				
81	*Aplastodiscus arildae*							x	a	x			
82	*Aplastodiscus callipygius*								a	x			
83	*Aplastodiscus cochranae*											x	
84	*Aplastodiscus cochranae*								a	x			
85	*Aplastodiscus ehrhardti*	x		x	x								
86	*Aplastodiscus ibirapitanga*				x								

87	*Aplastodiscus leucopygius*	x	x					x		
88	*Aplastodiscus leucopygius*									
89	*Aplastodiscus leucopygius*	x						x		
90	*Aplastodiscus leucopygius*								a	x
91	*Aplastodiscus perviridis*								a	x
92	*Aplastodiscus sibilatus*				x					
93	*Aplastodiscus weygoldti*	x								
94	*Bokermannohyla alvarengai*									
95	*Bokermannohyla caramaschi*	x		x				x		
96	*Bokermannohyla circumdata*		x							
97	*Bokermannohyla circumdata*	x	x	x						
98	*Bokermannohyla circumdata*									
99	*Bokermannohyla circumdata*		x							
100	*Bokermannohyla hylax*		x							
101	*Bokermannohyla ibitipoca*				x					
102	*Bokermannohyla luctuosa*									
103	*Bokermannohyla nanuzae*									
104	*Dendropsophus anceps*				x					
105	*Dendropsophus branneri*	x		x				x		
106	*Dendropsophus giesleri*			x						
107	*Dendropsophus haddadi*	x		x						
108	*Dendropsophus microps*	x		x						
109	*Dendropsophus minutus*	x		x				x		
110	*Dendropsophus nanus*	x		x				x		
111	*Dendropsophus sp nov.*	x								
112	*Hypsiboas albomarginatus*									
113	*Hypsiboas albomarginatus*	x		x	x			x		
114	*Hypsiboas albomarginatus*									
115	*Hypsiboas bischoffi*					x				
116	*Hypsiboas bischoffi*					x				
117	*Hypsiboas crepitans*	x		x				x		
118	*Hypsiboas exastis*									
119	*Hypsiboas faber*									
120	*Hypsiboas faber*									
121	*Hypsiboas faber*	x	x	x	x	x		x		
122	*Hypsiboas faber*									
123	*Hypsiboas pardalis*									
124	*Hypsiboas pardalis*	x						x		

125	*Hypsiboas pardalis*								
126	*Hypsiboas pombali*	x			x				
127	*Hypsiboas prasinus*								
128	*Hypsiboas raniceps*	x		x			x		
129	*Hypsiboas raniceps*								
130	*Hypsiboas semilineatus*	x		x	x		x		x
131	*Itapotihyla langsdorffii*			x					
132	*Itapotihyla langsdorffii*	x	x		x				x
133	*Phyllodytes luteolus*			x					
134	*Phyllodytes melanomystax*			x					
135	*Phyllodytes tuberculosus*			x					
136	*Phyllomedusa bahiana*				x				
137	*Phyllomedusa bahiana*					x			
138	*Phyllomedusa burmeisteri*	x			x				
139	*Phyllomedusa burmeisteri*					x			
140	*Phyllomedusa distincta*				x				
141	*Phyllomedusa rohdei*				x				
142	*Phyllomedusa tetraploidea*				x				
143	*Scinax albicans*	x		x			x		
144	*Scinax alter*	x							
145	*Scinax arduous*	x		x	x		x		
146	*Scinax argyreornatus*	x	x	x	x				
147	*Scinax catharinae*	x		x			x		
148	*Scinax flavoguttatus*	x		x					
149	*Scinax fuscomarginatus*	x				x			
150	*Scinax fuscovarius*	x		x			x		
151	*Scinax fuscovarius*								
152	*Scinax granulatus*	x		x					
153	*Scinax hayii*	x		x			x		
154	*Scinax littoralis*	x		x					
155	*Scinax similis*								
156	*Scinax v-signatus*	x		x			x		
157	*Scinax fuscomarginatus*			x			x		
158	*Scinax fuscovarius*			x					
159	*Sphaenorhynchus prasinus*			x					
160	*Trachycephalus mesophaeus*								
161	*Trachycephalus mesophaeus*	x			x		x		
162	*Xenohyla truncata*						x	b	
	Hylodidae								
163	*Megaelosia goeldii*	x		x			x		

164	*Megaelosia goldie*	x		x		x					
165	*Megaelosia massarti*										
	Leptodactylidae										
166	*Adenomera marmorata*	x		x							
167	*Crossodactylodes bokermanni*										
168	*Crossodactylodes izecksohni*	x	x							a	
169	*Leptodactylus chaquensis*	x		x							x
170	*Leptodactylus chaquensis*										
171	*Leptodactylus fuscus*										
172	*Leptodactylus labyrinthicus*						a				
173	*Leptodactylus labyrinthicus*					x					
174	*Leptodactylus latrans*										
175	*Leptodactylus latrans*					x					
176	*Leptodactylus latrans*						b	x			
177	*Leptodactylus marambaiae*				x						
178	*Leptodactylus mystaceus*										
179	*Leptodactylus mystacinus*					x					
180	*Leptodactylus vastus*										
181	*Physalaemus camacan*			x							
182	*Physalaemus crombiei*	x	x	x			x				
183	*Physalaemus erikae*										
184	*Physalaemus erikae*										
185	*Physalaemus kroyeri*			x		x					
186	*Physalaemus marmoratus*						a	x			
187	*Physalaemus olfersii*										
188	*Scythrophrys sawayae*								x		
	Microhylidae										
189	*Chiasmocleis capixaba*			x							
190	*Chiasmocleis schubarti*			x							
191	*Dermatonotus muelleri*					x					
192	*Elachistocleis cf. ovalis*			x							
193	*Elachistocleis erythrogaster*									x	
194	*Elachistocleis ovalis*					x	a				
195	*Elachistocleis ovalis*	x		x							
196	*Myersiella microps*	x		x		x					
197	*Stereocyclops incrassatus*								x		
198	*Stereocyclops incrassatus*								x		
199	*Stereocyclops parkeri*								x		

	Odontophrynidae												
200	*Macrogenioglottus alipioi*				x			x					
201	*Macrogenioglottus alipioi*							x					
202	*Macrogenioglottus alipioi*				x			x					
203	*Macrogenioglottus alipioi*							x	a,b	x			
204	*Odontophrynus americanus*		x					x					
205	*Odontophrynus carvalhoi*				x			x					
206	*Odontophrynus americanus*	x	x	x	x			x				x	
207	*Proceratophrys appendiculata*	x									x		
208	*Proceratophrys appendiculata*										x		
209	*Proceratophrys avelinoi*	x			x								x
210	*Proceratophrys boei*	x		x				x			x		
211	*Proceratophrys boiei*										x		
212	*Proceratophrys boiei*										x		
213	*Proceratophrys boiei*		x										
214	*Proceratophrys cururu*		x					x					
215	*Proceratophrys laticeps*				x								
216	*Proceratophrys laticeps*				x								
217	*Proceratophrys melanopogon*										x		
218	*Proceratophrys paviotii*	x	x	x				x		x	x		
219	*Proceratophrys renalis*			x	x								
220	*Proceratophrys renalis*			x	x								
221	*Proceratophrys renalis*										x		
222	*Proceratophrys schirchi*	x								x			
	Pipidae												
223	*Pipa pipa*												
	Ranidae												
224	*Lithobates catesbeianus*												

Table 3.2. Continuation on antipredator behavior of post-metamorphic anurans from Brazil's Atlantic Forest. The types of antipredator behavior from 16 to 31 follows Haddad et al. (2013). 16= hiding, 17= digging, 18= active escape or fleeing, 19= cloacal discharge: a) liquid or b) solid, 20= charging, 21= head hitting, 22= biting, 23= mouth gaping, 25= fighting, 26= spine aggression: a) spine-puncturing, b) spine-scratching, c) spine-hurting, 28= regurgitating, 29= defensive vocalization, and 30= production of secretion: a) odoriferous, b) adhesive, c) noxious, and d) slippery. The behaviors 24= tongue protrusion, 27= phalanx aggression, and 31= poison squirting were not observed for species from our dataset.

Ref.	Taxon	Antipredator behavior												
#		16	17	18	19	20	21	22	23	25	26	28	29	30
	Aromobatidae													
1	*Allobates olfersioides*	x												
	Brachycephalidae													
2	*Brachycephalus ephippium*	x		x					x	x				
3	*Brachycephalus ephippium*								x					
4	*Brachycephalus hermogenesi*								x					
5	*Brachycephalus pitanga*	x												
6	*Brachycephalus pitanga*								x					
7	*Ischnocnema abdita*			x	x									
8	*Ischnocnema epipeda*			x										
9	*Ischnocnema erythromera*	x		x	x									x
10	*Ischnocnema guenteri*													
11	*Ischnocnema oea*			x										
12	*Ischnocnema parva*			x						x				
13	*Ischnocnema parva sp nov.*			x										
14	*Ischnocnema verrucosa*			x	a									
	Bufonidae													
15	*Dendrophryniscus brevipollicatus*	x		x	x					x				
16	*Dendrophryniscus carvalhoi*			x										
17	*Dendrophryniscus carvalhoi*													
18	*Dendrophryniscus proboscideus*													
19	*Frostius erythrophthalmus*													
20	*Frostius pernambucensis*													
21	*Melanophryniscus cambaraensis*													
22	*Melanophryniscus moreirae*													
23	*Melanophryniscus moreirae*				x									
24	*Melanophryniscus tumifrons*													

25	*Rhinella cf. crucifer*													
26	*Rhinella crucifer*			x	a									
27	*Rhinella crucifer*													
28	*Rhinella granulosa*													
29	*Rhinella granulosa*													
30	*Rhinella hoogmoedi*													
31	*Rhinella icterica*				x									c
32	*Rhinella jimi*													c
33	*Rhinella marina*													
34	*Rhinella ocellata*				x									
35	*Rhinella ornata*	x		x	x					x			x	
36	*Rhinella ornata*													c
37	*Rhinella schneideri*			x									x	
38	*Rhinella schneideri*			x	a		x							
39	*Rhinella abei*													
40	*Rhinella icterica*				a									
	Centrolenidae													
41	*Vitreorana uranoscopa*	x		x						x				x
	Ceratophryidae													
42	*Ceratophrys aurita*							x	x			x	x	
43	*Ceratophrys joazeirensis*							x					x	
44	*Ceratophrys joazeirensis*								x				x	
	Craugastoridae													
45	*Eleutherodactylus bilineatus*								x					
46	*Eleutherodactylus bilineatus*								x					
47	*Euparkerella tridactyla*			x					a					
48	*Haddadus binotatus*	x		x	a				a	x			x	x
49	*Haddadus binotatus*								x				x	
50	*Haddadus binotatus*								x					
51	*Pristimantis paulodutrai*													
52	*Pristimantis ramagii*													
53	*Pristimantis vinhai*													
	Cycloramphidae													
54	*Cycloramphus acangatan*													
55	*Cycloramphus acangatan*			x						x				
56	*Cycloramphus acangatan*				x			x	x				x	
57	*Cycloramphus boraceiensis*							x						
58	*Cycloramphus brasiliensis*	x		x										x

59	*Cycloramphus eleutherodactylus*				x			
60	*Cycloramphus eleutherodactylus*			x	x			
61	*Cycloramphus lutzorum*				x			
62	*Thoropa miliaris*		x	a			x	x
63	*Zachaenus carvalhoi*							
64	*Zachaenus carvalhoi*							
65	*Zachaenus parvulus*		x					
66	*Zachaenus parvulus*							
	Eleutherodactylidae							
67	*Adelophryne glandulata*		x			a		
68	*Adelophryne glandulata*						x	
69	*Adelophryne mucronatus*					b		
	Hemiphractidae							
70	*Flectonotus ohausi*		x					
71	*Gastrotheca albolineata*		x	x				x
72	*Gastrotheca megacephala*		x	a	x	a		
73	*Gastrotheca recava*		x		x	a		
	Hylidae							
74	*Agalychnis aspera*							
75	*Aparasphenodon albosignatus*							
76	*Aparasphenodon arapapa*							
77	*Aparasphenodon bokermanni*							
78	*Aparasphenodon brunoi*							
79	*Aplastodiscus arildae*							
80	*Aplastodiscus arildae*							
81	*Aplastodiscus arildae*			x				a
82	*Aplastodiscus callipygius*							
83	*Aplastodiscus cochranae*							
84	*Aplastodiscus cochranae*							
85	*Aplastodiscus ehrhardti*	x	x	x		x	x	
86	*Aplastodiscus ibirapitanga*							
87	*Aplastodiscus leucopygius*							
88	*Aplastodiscus leucopygius*							a
89	*Aplastodiscus leucopygius*		x					x
90	*Aplastodiscus leucopygius*							
91	*Aplastodiscus perviridis*							
92	*Aplastodiscus sibilatus*							

93	*Aplastodiscus weygoldti*		x						a
94	*Bokermannohyla alvarengai*						a		
95	*Bokermannohyla caramaschi*		x	a		x			x
96	*Bokermannohyla circumdata*								
97	*Bokermannohyla circumdata*		x			x			x
98	*Bokermannohyla circumdata*							x	
99	*Bokermannohyla circumdata*			x			a		a
100	*Bokermannohyla hylax*			x			a		a
101	*Bokermannohyla ibitipoca*								
102	*Bokermannohyla luctuosa*						a		a
103	*Bokermannohyla nanuzae*							x	
104	*Dendropsophus anceps*								
105	*Dendropsophus branneri*	x	x			x			x
106	*Dendropsophus giesleri*								
107	*Dendropsophus haddadi*								
108	*Dendropsophus microps*	x	x	x		x		x	x
109	*Dendropsophus minutus*	x	x			x			
110	*Dendropsophus nanus*	x	x	a		x			a,b
111	*Dendropsophus sp nov.*		x						
112	*Hypsiboas albomarginatus*							x	
113	*Hypsiboas albomarginatus*		x	x					x
114	*Hypsiboas albomarginatus*			x					a
115	*Hypsiboas bischoffi*								
116	*Hypsiboas bischoffi*			x					a
117	*Hypsiboas crepitans*		x			x		x	x
118	*Hypsiboas exastis*						a		
119	*Hypsiboas faber*							x	
120	*Hypsiboas faber*					x			
121	*Hypsiboas faber*	x	x	a		x	x		a,d
122	*Hypsiboas faber*			x			a,b		
123	*Hypsiboas pardalis*							x	
124	*Hypsiboas pardalis*				x				
125	*Hypsiboas pardalis*			x			a,b		a
126	*Hypsiboas pombali*								
127	*Hypsiboas prasinus*			x					
128	*Hypsiboas raniceps*		x	a		x		x	a,d
129	*Hypsiboas raniceps*			x			a		
130	*Hypsiboas semilineatus*		x	x		x			a,d
131	*Itapotihyla langsdorffii*								
132	*Itapotihyla langsdorffii*		x						a,d
133	*Phyllodytes luteolus*								
134	*Phyllodytes melanomystax*								

135	*Phyllodytes tuberculosus*													
136	*Phyllomedusa bahiana*													
137	*Phyllomedusa bahiana*													
138	*Phyllomedusa burmeisteri*													
139	*Phyllomedusa burmeisteri*													
140	*Phyllomedusa distincta*													
141	*Phyllomedusa rohdei*													
142	*Phyllomedusa tetraploidea*													
143	*Scinax albicans*			x										x
144	*Scinax alter*			x										
145	*Scinax arduous*	x		x	x					x				x
146	*Scinax argyreornatus*			x						x				x
147	*Scinax catharinae*	x		x	x				x	x			x	x
148	*Scinax flavoguttatus*			x										x
149	*Scinax fuscomarginatus*	x		x						x				
150	*Scinax fuscovarius*	x		x	a					x				a,d
151	*Scinax fuscovarius*	x			x									
152	*Scinax granulatus*			x						x				x
153	*Scinax hayii*	x		x										x
154	*Scinax littoralis*			x										x
155	*Scinax similis*	x												
156	*Scinax v-signatus*			x	x					x				x
157	*Scinax fuscomarginatus*			x										
158	*Scinax fuscovarius*													
159	*Sphaenorhynchus prasinus*													
160	*Trachycephalus mesophaeus*													b
161	*Trachycephalus mesophaeus*			x						x				x
162	*Xenohyla truncata*													
	Hylodidae													
163	*Megaelosia goeldii*			x						x				x
164	*Megaelosia goldie*			x						x				x
165	*Megaelosia massarti*			x										
	Leptodactylidae													
166	*Adenomera marmorata*	x		x						x				
167	*Crossodactylodes bokermanni*			x										
168	*Crossodactylodes izecksohni*			x							x			
169	*Leptodactylus chaquensis*			x										x
170	*Leptodactylus chaquensis*							x						
171	*Leptodactylus fuscus*				x									

172	*Leptodactylus labyrinthicus*													c
173	*Leptodactylus labyrinthicus*				x						c			a,c
174	*Leptodactylus latrans*					x	x				b			d
175	*Leptodactylus latrans*													
176	*Leptodactylus latrans*										c			c,d
177	*Leptodactylus marambaiae*													
178	*Leptodactylus mystaceus*				x									
179	*Leptodactylus mystacinus*				x									c
180	*Leptodactylus vastus*										c			
181	*Physalaemus camacan*													
182	*Physalaemus crombiei*			x										
183	*Physalaemus erikae*								x					
184	*Physalaemus erikae*								x					
185	*Physalaemus kroyeri*			x										
186	*Physalaemus marmoratus*													c
187	*Physalaemus olfersii*		x											
188	*Scythrophrys sawayae*													
	Microhylidae													
189	*Chiasmocleis capixaba*													
190	*Chiasmocleis schubarti*								x					
191	*Dermatonotus muelleri*													
192	*Elachistocleis cf. ovalis*													
193	*Elachistocleis erythrogaster*													x
194	*Elachistocleis ovalis*													
195	*Elachistocleis ovalis*	x		x						x				d
196	*Myersiella microps*	x		x						x			x	x
197	*Stereocyclops incrassatus*													
198	*Stereocyclops incrassatus*													
199	*Stereocyclops parkeri*													
	Odontophrynidae													
200	*Macrogenioglottus alipioi*													
201	*Macrogenioglottus alipioi*													
202	*Macrogenioglottus alipioi*													
203	*Macrogenioglottus alipioi*				x									
204	*Odontophrynus americanus*				x									
205	*Odontophrynus carvalhoi*			x										
206	*Odontophrynus americanus*	x		x	a					x			x	
207	*Proceratophrys appendiculata*													
208	*Proceratophrys appendiculata*													

209	*Proceratophrys avelinoi*					
210	*Proceratophrys boei*	x		x	x	x
211	*Proceratophrys boiei*					
212	*Proceratophrys boiei*					
213	*Proceratophrys boiei*					
214	*Proceratophrys cururu*					c
215	*Proceratophrys laticeps*					
216	*Proceratophrys laticeps*					
217	*Proceratophrys melanopogon*					
218	*Proceratophrys paviotii*	x				
219	*Proceratophrys renalis*					
220	*Proceratophrys renalis*					
221	*Proceratophrys renalis*					
222	*Proceratophrys schirchi*	x	a			
	Pipidae					
223	*Pipa pipa*		x			
	Ranidae					
224	*Lithobates catesbeianus*				x	

Table 3.3. List of species and their respective reference source.

Ref. #	Taxon	Source
	Aromobatidae	
1	*Allobates olfersioides*	Toledo et al. 2011
	Brachycephalidae	
2	*Brachycephalus ephippium*	our study
3	*Brachycephalus ephippium*	Toledo et al. 2011
4	*Brachycephalus hermogenesi*	Toledo et al. 2011
5	*Brachycephalus pitanga*	Haddad et al. 2013
6	*Brachycephalus pitanga*	Toledo et al. 2011
7	*Ischnocnema abdita*	our study
8	*Ischnocnema epipeda*	our study
9	*Ischnocnema erythromera*	our study
10	*Ischnocnema guenteri*	Haddad et al. 2013
11	*Ischnocnema oea*	our study
12	*Ischnocnema parva*	our study
13	*Ischnocnema parva sp nov.*	our study
14	*Ischnocnema verrucosa*	our study
	Bufonidae	
15	*Dendrophryniscus brevipollicatus*	our study
16	*Dendrophryniscus carvalhoi*	our study
17	*Dendrophryniscus carvalhoi*	Cassimiro et al. 2010
18	*Dendrophryniscus proboscideus*	our study
19	*Frostius erythrophthalmus*	our study
20	*Frostius pernambucensis*	our study
21	*Melanophryniscus cambaraensis*	Haddad et al. 2013
22	*Melanophryniscus moreirae*	Almeida-Santos et al. 2010
23	*Melanophryniscus moreirae*	Toledo et al. 2011
24	*Melanophryniscus tumifrons*	Haddad et al. 2013
25	*Rhinella cf. crucifer*	Toledo 2004
26	*Rhinella crucifer*	our study
27	*Rhinella crucifer*	our study
28	*Rhinella granulosa*	Mângia and Santana 2013
29	*Rhinella granulosa*	our study
30	*Rhinella hoogmoedi*	our study
31	*Rhinella icterica*	Toledo et al. 2011
32	*Rhinella jimi*	Toledo and Jared 1995
33	*Rhinella marina*	Vaz-Silva and Frota 2004

34	*Rhinella ocellata*	Kokubum 2005
35	*Rhinella ornata*	our study
36	*Rhinella ornata*	Toledo et al. 2011
37	*Rhinella schneideri*	our study
38	*Rhinella schneideri*	Zamprogno et al. 1998
39	*Rhinella abei*	Haddad et al. 2013
40	*Rhinella icterica*	Haddad et al. 2013
	Centrolenidae	
41	*Vitreorana uranoscopa*	our study
	Ceratophryidae	
42	*Ceratophrys aurita*	Toledo et al. 2011
43	*Ceratophrys joazeirensis*	Haddad et al. 2013
44	*Ceratophrys joazeirensis*	Toledo et al. 2011
	Craugastoridae	
45	*Eleutherodactylus bilineatus*	our study
46	*Eleutherodactylus bilineatus*	our study
47	*Euparkerella tridactyla*	Ferreira et al. 2013
48	*Haddadus binotatus*	our study
49	*Haddadus binotatus*	Toledo et al. 2011
50	*Haddadus binotatus*	Haddad et al. 2013
51	*Pristimantis paulodutrai*	our study
52	*Pristimantis ramagii*	our study
53	*Pristimantis vinhai*	our study
	Cycloramphidae	
54	*Cycloramphus acangatan*	Lourenço-de-Moraes & Lourenço-de-Moraes 2012
55	*Cycloramphus acangatan*	our study
56	*Cycloramphus acangatan*	Toledo et al. 2011
57	*Cycloramphus boraceiensis*	Hartmann et al. 2003
58	*Cycloramphus brasiliensis*	our study
59	*Cycloramphus eleutherodactylus*	Haddad et al. 2013
60	*Cycloramphus eleutherodactylus*	Toledo et al. 2011
61	*Cycloramphus lutzorum*	Toledo et al. 2011
62	*Thoropa miliaris*	our study
63	*Zachaenus carvalhoi*	Moura et al. 2010
64	*Zachaenus carvalhoi*	Zocca et al. 2014
65	*Zachaenus parvulus*	our study
66	*Zachaenus parvulus*	Rocha et al. 1998

	Eleutherodactylidae	
67	*Adelophryne glandulata*	Lourenço-de-Moraes et al. 2014
68	*Adelophryne glandulata*	our study
69	*Adelophryne mucronatus*	Lourenço-de-Moraes et al. 2014
	Hemiphractidae	
70	*Flectonotus ohausi*	our study
71	*Gastrotheca albolineata*	our study
72	*Gastrotheca megacephala*	our study
73	*Gastrotheca recava*	our study
	Hylidae	
74	*Agalychnis aspera*	our study
75	*Aparasphenodon albosignatus*	Toledo et al. 2011
76	*Aparasphenodon arapapa*	our study
77	*Aparasphenodon bokermanni*	Haddad et al. 2013
78	*Aparasphenodon brunoi*	our study
79	*Aplastodiscus arildae*	Fatorelli and Rocha 2005
80	*Aplastodiscus arildae*	Haddad et al. 2013
81	*Aplastodiscus arildae*	Toledo et al. 2011
82	*Aplastodiscus callipygius*	Toledo et al. 2011
83	*Aplastodiscus cochranae*	Haddad et al. 2013
84	*Aplastodiscus cochranae*	Toledo et al. 2011
85	*Aplastodiscus ehrhardti*	our study
86	*Aplastodiscus ibirapitanga*	our study
87	*Aplastodiscus leucopygius*	Ferrante et al. 2014
88	*Aplastodiscus leucopygius*	Haddad et al. 2013
89	*Aplastodiscus leucopygius*	our study
90	*Aplastodiscus leucopygius*	Toledo et al. 2011
91	*Aplastodiscus perviridis*	Toledo et al. 2011
92	*Aplastodiscus sibilatus*	our study
93	*Aplastodiscus weygoldti*	our study
94	*Bokermannohyla alvarengai*	Toledo et al. 2011
95	*Bokermannohyla caramaschi*	our study
96	*Bokermannohyla circumdata*	Haddad et al. 2013
97	*Bokermannohyla circumdata*	our study
98	*Bokermannohyla circumdata*	Silva et al. 2014
99	*Bokermannohyla circumdata*	Toledo et al. 2011
100	*Bokermannohyla hylax*	Toledo et al. 2011
101	*Bokermannohyla ibitipoca*	Mônico, Alexander (comm pess).
102	*Bokermannohyla luctuosa*	Toledo et al. 2011

103	*Bokermannohyla nanuzae*	Silva et al. 2014
104	*Dendropsophus anceps*	Mônico, Alexander (comm pess).
105	*Dendropsophus branneri*	our study
106	*Dendropsophus giesleri*	our study
107	*Dendropsophus haddadi*	our study
108	*Dendropsophus microps*	our study
109	*Dendropsophus minutus*	our study
110	*Dendropsophus nanus*	our study
111	*Dendropsophus sp nov.*	our study
112	*Hypsiboas albomarginatus*	Figueiredo-de-Andrade et al. 2010
113	*Hypsiboas albomarginatus*	our study
114	*Hypsiboas albomarginatus*	Toledo et al. 2011
115	*Hypsiboas bischoffi*	Haddad et al. 2013
116	*Hypsiboas bischoffi*	Toledo et al. 2011
117	*Hypsiboas crepitans*	our study
118	*Hypsiboas exastis*	Haddad et al. 2013
119	*Hypsiboas faber*	Forti and Bertoluci 2012
120	*Hypsiboas faber*	Haddad et al. 2013
121	*Hypsiboas faber*	our study
122	*Hypsiboas faber*	Toledo et al. 2011
123	*Hypsiboas pardalis*	Haddad et al. 2013
124	*Hypsiboas pardalis*	our study
125	*Hypsiboas pardalis*	Toledo et al. 2011
126	*Hypsiboas pombali*	our study
127	*Hypsiboas prasinus*	Toledo et al. 2011
128	*Hypsiboas raniceps*	our study
129	*Hypsiboas raniceps*	Toledo et al. 2011
130	*Hypsiboas semilineatus*	our study
131	*Itapotihyla langsdorffii*	Mônico, Alexander (pers. comm.)
132	*Itapotihyla langsdorffii*	our study
133	*Phyllodytes luteolus*	our study
134	*Phyllodytes melanomystax*	our study
135	*Phyllodytes tuberculosus*	our study
136	*Phyllomedusa bahiana*	our study
137	*Phyllomedusa bahiana*	Toledo et al. 2011
138	*Phyllomedusa burmeisteri*	our study
139	*Phyllomedusa burmeisteri*	Toledo et al. 2011
140	*Phyllomedusa distincta*	Haddad et al. 2013
141	*Phyllomedusa rohdei*	Haddad et al. 2013
142	*Phyllomedusa tetraploidea*	Borteiro et al. 2014
143	*Scinax albicans*	our study
144	*Scinax alter*	our study

145	*Scinax arduous*	our study
146	*Scinax argyreornatus*	our study
147	*Scinax catharinae*	our study
148	*Scinax flavoguttatus*	our study
149	*Scinax fuscomarginatus*	our study
150	*Scinax fuscovarius*	our study
151	*Scinax fuscovarius*	Toledo et al. 2011
152	*Scinax granulatus*	our study
153	*Scinax hayii*	our study
154	*Scinax littoralis*	our study
155	*Scinax similis*	Toledo et al. 2011
156	*Scinax v-signatus*	our study
157	*Scinax fuscomarginatus*	Toledo 2004
158	*Scinax fuscovarius*	Haddad et al. 2013
159	*Sphaenorhynchus prasinus*	Mônico, Alexander (comm pess).
160	*Trachycephalus mesophaeus*	Haddad et al. 2013
161	*Trachycephalus mesophaeus*	our study
162	*Xenohyla truncata*	Napoli 2001
	Hylodidae	
163	*Megaelosia goeldii*	our study
164	*Megaelosia goldie*	our study
165	*Megaelosia massarti*	Haddad et al. 2013
	Leptodactylidae	
166	*Adenomera marmorata*	our study
167	*Crossodactylodes bokermanni*	our study
168	*Crossodactylodes izecksohni*	our study
169	*Leptodactylus chaquensis*	Lourenço-de-Moraes et al. 2014
170	*Leptodactylus chaquensis*	Toledo et al. 2011
171	*Leptodactylus fuscus*	Toledo et al. 2011
172	*Leptodactylus labyrinthicus*	Haddad et al. 2013
173	*Leptodactylus labyrinthicus*	Toledo et al. 2005; 2011
174	*Leptodactylus latrans*	Haddad et al. 2013
175	*Leptodactylus latrans*	our study
176	*Leptodactylus latrans*	Toledo et al. 2011
177	*Leptodactylus marambaiae*	Siqueira et al. 2006
178	*Leptodactylus mystaceus*	Toledo et al. 2011
179	*Leptodactylus mystacinus*	Toledo et al. 2011
180	*Leptodactylus vastus*	Haddad et al. 2013
181	*Physalaemus camacan*	our study
182	*Physalaemus crombiei*	our study

183	*Physalaemus erikae*	Dias and Solé 2012
184	*Physalaemus erikae*	our study
185	*Physalaemus kroyeri*	Gally et al. 2012
186	*Physalaemus marmoratus*	Toledo et al. 2011
187	*Physalaemus olfersii*	Haddad et al. 2013
188	*Scythrophrys sawayae*	Garcia 1999
	Microhylidae	
189	*Chiasmocleis capixaba*	our study
190	*Chiasmocleis schubarti*	our study
191	*Dermatonotus muelleri*	Tonini, J.F.R. (pers. comm.)
192	*Elachistocleis cf. ovalis*	Toledo 2004
193	*Elachistocleis erythrogaster*	Kwet and Solé 2002
194	*Elachistocleis ovalis*	Kokubum and Menin 2002
195	*Elachistocleis ovalis*	our study
196	*Myersiella microps*	our study
197	*Stereocyclops incrassatus*	Guerreiro et al. 2010
198	*Stereocyclops incrassatus*	Tonini, J.F.R. (pers. comm.)
199	*Stereocyclops parkeri*	Haddad et al. 2013
	Odontophrynidae	
200	*Macrogenioglottus alipioi*	our study
201	*Macrogenioglottus alipioi*	Haddad et al. 2013
202	*Macrogenioglottus alipioi*	our study
203	*Macrogenioglottus alipioi*	Toledo et al. 2011
204	*Odontophrynus americanus*	Toledo et al. 2011
205	*Odontophrynus carvalhoi*	Bezerra et al. 2010
206	*Odontophrynus americanus*	our study
207	*Proceratophrys appendiculata*	our study
208	*Proceratophrys appendiculata*	Haddad et al. 2013
209	*Proceratophrys avelinoi*	Lourenço-de-Moraes & Lourenço-de-Moraes 2012
210	*Proceratophrys boei*	our study
211	*Proceratophrys boiei*	Costa et al. 2009
212	*Proceratophrys boiei*	Toledo 2004
213	*Proceratophrys boiei*	Toledo et al. 2011
214	*Proceratophrys cururu*	Toledo et al. 2011
215	*Proceratophrys laticeps*	our study
216	*Proceratophrys laticeps*	our study
217	*Proceratophrys melanopogon*	Moura et al. 2010
218	*Proceratophrys paviotii*	our study
219	*Proceratophrys renalis*	our study
220	*Proceratophrys renalis*	our study

221	*Proceratophrys renalis*	Peixoto et al. 2013
222	*Proceratophrys schirchi*	our study
	Pipidae	
223	*Pipa pipa*	Toledo et al. 2011
	Ranidae	
224	*Lithobates catesbeianus*	Haddad et al. 2013

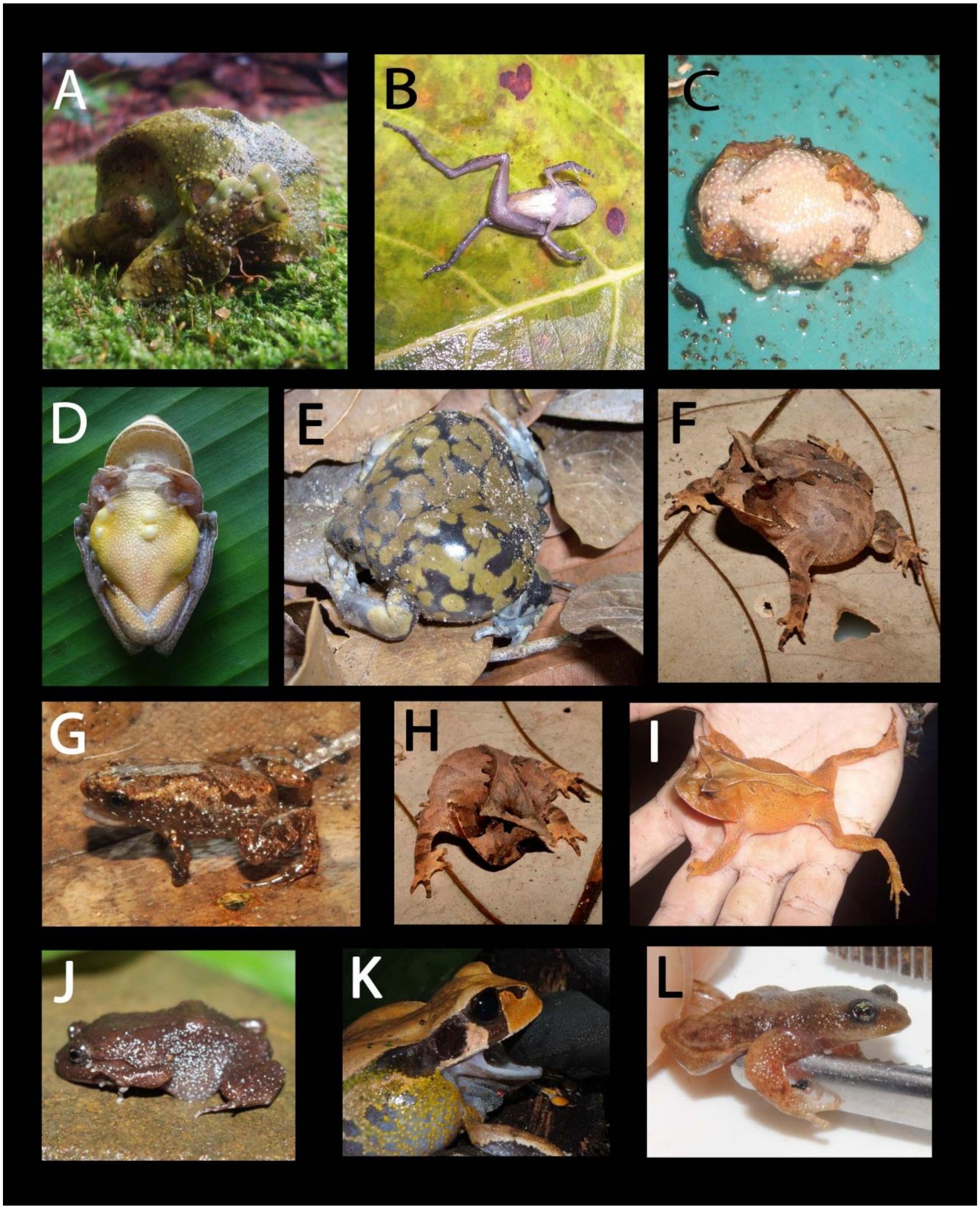

FIG. 3.1. Antipredator behaviors of anurans from Atlantic Forest: A) crouching down of *Itapotihyla langsdorffii*, B) thanatosis of *Pristimantis vinhai*, C) contracting of *Dendrophryniscus carvalhoi*, D) contracting of *Bokermannohyla ibitipoca*, E) puffing-up the body of *Dermatonotus muelleri*, F) puffing-up the body and partial unken reflex of *Proceratophrys paviotii*, G) body

raising with mouth gapping of *Adelophryne glandulata*, H) body tilting of *P. paviotii*, I) stiff legged of *P. boiei*, J) partial unken reflex of *Cycloramphus acangatan*, K) biting of *Gastrotheca megacephala*, and L) spine aggression of *Crossodactylodes izecksohni*. Photos authorship: Alexander Mônico (D), Cássio Z. Zocca (A), João F. R. Tonini (E), Ricardo Lourenço-de-Moraes (B, I, J), Rodrigo B. Ferreira (C, F, G, H, K, L).

CHAPTER 4

THE FIRST BROMELIGENOUS SPECIES OF *DENDROPSOPHUS* (ANURA: HYLIDAE) FROM BRAZIL'S ATLANTIC FOREST[2]

Abstract

We describe a new species, *Dendropsophus bromeliaceus* sp. nov., that was collected on rocky outcrops in the mountainous region of Brazil's Atlantic Forest. The new species is diagnosed by its small size, framed dorsal color pattern, and short membrane in the fifth toe. The diphasic advertisement call is composed of a moderate-pitched two note call (~5 kHz). Phylogenetic analysis based on molecular data indicates *D. bromeliaceus* sp. nov. should not be assigned to any species groups of *Dendropsophus*. Ecologically, *D. bromeliaceus* sp. nov. can be distinguished from its congeners by having a larval phase associated with rainwater accumulated in bromeliads.

Introduction

Dendropsophus is one of the most taxonomically complex genera of hylids due to high intraspecific variation and the morphological similarities among species [1,2,3]. *Dendropsophus* is currently composed of 96 species distributed from Argentina and Uruguay to Mexico [4]. Except for the reversal in *D. decipiens* clade, the only morphological synapomorphy for this group is the lack of labial tooth rows and marginal papillae [5,6].

Twenty-four of the 96 species of *Dendropsophus* occur in the Atlantic Forest biome. It has been over 12 years since a species of *Dendropsophus* has been described for this biome [7]. On the other hand, over the past 12 years, 10 species of *Dendropsophus* have been described in other biomes, particularly the Amazon [8,9,10]. An ecological synapomorphy among all these 96

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[2] This chapter is co-authored by Julian Faivovich, Karen H. Beard, and Jose Pombal Jr.

species is the fact they lay eggs in swamps, ponds, or stream backwaters.

The mountainous region of Brazil’s Atlantic Forest is known for its remarkable diversity and endemism of anurans [11,12]. The region around the municipality of Santa Teresa is one of the most speciose areas for anurans across this biome [13,14,15] but the region’s diversity is presumably far from completely described considering the high rate at which new taxa are being discovered [16,17,18]. Across this region, rocky outcrops are a unique landscape feature (i.e. mostly dome-shaped, shallow soils, rapid water runoff). Bromeliads are the dominant plant in rocky outcrops [19], and are remarkably important because they offer refuge, moisture, and water to their associated biota [20,21,22].

While surveying for frogs inside bromeliads on rocky outcrops in the municipality of Santa Teresa, we found a distinct treefrog jumping out of an epiphytic bromeliad. Here we describe this new bromeligenous species (i.e. larval phase associated with bromeliad [23]), its advertisement and aggressive calls, and study its phylogenetic relationships based on molecular data. We compare this new species to all other congeners and comment on its natural history and conservation status.

Materials and Methods

Study region

Field research was conducted in and around the Reserva Biológica Augusto Ruschi (REBIO, 19º54’S, 40º32’W, datum = WGS84), Santa Teresa, Espírito Santo State, Brazil. Sampled sites range from 745 to 922 meters above sea level (m a.s.l.). The site is in the Atlantic Forest biome, specifically classified as montane and sub-montane rainy forest composed of non-deciduous trees [24].

Santa Teresa’s climate is classified as Cwa-Cfa according to Köppen-Geiger’s classification [25]. The dry season is from May to August and the rainy season is from September to April. [26]. Mean annual precipitation is 1868 mm with highest rainfall in November and lowest in June, when the mean rainfall is less than 60 mm [26]. Mean annual temperature is 20°C, with mean minimum and maximum monthly temperatures of 14.3° C and 26.2° C, respectively [27].

Sampling

We surveyed nine areas with high density of bromeliads during the rainy season of 2012 (August to December) and the dry season of 2013 (June and July). Two of these sites were in rocky outcrops and seven sites were in forest interior. Four collectors visited each site and actively searched inside bromeliads.

We identified the occupied bromeliads and determined their location (epiphyte or ground). We also measured the plant diameter, height, number of leaves, and height from the ground. We used Pearson's chi-square exact test (χ^2) to compare characteristics of bromeliads occupied by the new species using a Monte Carlo simulation based on 999 replicates using the package *MASS* [28].

We euthanized the frogs by ventral application of 7.5% to 10% benzocaine, fixed them in 10% formalin, and preserved in 70% ethanol within one to five days of fixation [29,30]. These specimens were deposited in the collections of Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), State of Rio de Janeiro and the Museu de Biologia Mello Leitão (MBML), State of Espírito Santo, both in Brazil. Prior to fixation, some specimens had tissues samples extracted and stored in 92% ethanol for DNA extraction. Some tadpoles collected from the bromeliads were raised in captivity until metamorphosis to confirm species identification. Vouchers of bromeliads were deposited in the herbarium of MBML.

Morphology

Faivovich et al. [31] recognized nine species groups of *Dendropsophus*: *D. columbianus, D. garagoensis, D. labialis, D. leucophyllatus, D. marmoratus, D. microcephalus, D. minimus, D. minutus,* and *D. parviceps* groups. Herein, we compared the new species with all species of the genus. These specimens used for comparisons and their accession numbers are listed in S1 File.

We used an ocular micrometer in a Zeiss stereomicroscope for most measurements and a caliper with 0.1 mm precision for measurement of snout-vent length. We followed Duellman [32] for morphological terminology: SVL (snout-vent length), HL (head length), HW (head width), ED (eye diameter), TD (tympanum diameter), IOD (interorbital distance), END (eye-nostril distance), IND (internarial distance), THL (thigh length), TL (tibia length), and FL (foot length). Descriptions of coloration of live specimens are based on photographs taken in the field.

Calls recording

We recorded calls using a Marantz PMD-660 digital recorder attached to a Sennheiser ME 64/K6p external directional microphone. We digitalized the calls at a resolution of 16 bits and a sampling rate of 48 kHz. For the bioacoustics analyses, we used Audacity 2.0.5 [33] and the package *Seewave* [34].

We evaluated the following parameters: number of pulses per note; number of notes per call; call, note and pulse duration (milliseconds= ms); interval between calls (ms); and dominant frequency of the note (Hertz= Hz). Advertisement call terminology follows Duellman and Trueb [35]. Call categorization follows Toledo *et al.* [36]. We deposited call recordings at Coleção Científica de Vocalizações de Anfíbios Anuros do Museu Nacional – Universidade Federal do Rio de Janeiro (MNVOC 048/01-06).

We performed one-way analysis of variance (ANOVA) to compare interval of males calling in chorus and alone, and to compare duration and frequency between notes of the advertisement call. Mean ($\bar{X}$) ± Standard deviation (SD) are presented. We performed all the above statistical analyses in the version 3.0.3 of R [37].

Molecular analysis

We extracted DNA from the holotype (MNRJ 85852) and two paratopotypes (MNRJ 85854 and MNRJ 85857) of the new species (GenBank accession number: XXXX). We sequenced the complete 12S rRNA gene and a fragment of the 16S rRNA gene, including the intervening valine-tRNA, using the same primers employed by Faivovich et al. [31]. DNA extraction, amplification, and sequencing methods are those described in a recent paper by Faivovich et al. [38]. We sequenced all samples in both directions. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software SEQUENCHER 3.0 (Gene Codes, Ann Arbor, MI, USA). Complete sequences were edited with BioEdit [39].

We performed a preliminary phylogenetic analysis including a broad diversity of hylids, which indicates the new species belongs to *Dendropsophus* (data not shown). We used sequences of the mitochondrial genes 12S+trna^{VAL}+16S and the dataset by Rivera-Correa & Orrico [9] to explore the relationship of the new species to other species in the genus. This dataset included sequences of 37 of the 96 species of *Dendropsophus* [4], including exemplar species of all species groups currently recognized. Furthermore, it includes 11 outgroup taxa of the genera *Lysapsus*, *Phyllodytes*, *Pseudis*, *Scarthyla*, *Scinax*, *Sphaenorhynchus*, and *Xenohyla*.

We generated static alignments in MAFFT [40]with Q-INS-i strategy (secondary structure of RNA is considered). We performed maximum parsimony analyses using T.N.T Willi Henning Society Edition [41]. We did the searches using the new technology search under search level 50, which included sectorial searches, tree drift and tree fusing [42], and the driven search to hit the best length 100 times. We estimated Parsimony Jackknife absolute frequencies [43] using new technology as well as requesting 5 hits with driven searches, for a total of 1000 replicates.

We performed Bayesian analyses using MrBayes 3.2 [44] as implemented in the Cipress web based platform [45]. The models of molecular evolution were determined for the combined data by gene using Partition Finder 1.01 [46]. We used the GTR+I+G model for 12S and 16S. Bayesian analyses included four independent runs with three heated chains and one cold chain in each run. The MCMC chains were run for 80,000,000 generations and sampled every 1,000 generations. We examined trace plots and effective sample size (ESS) in Tracer v1.5 to determine MCMC mixing and convergence. We removed trees from the first 25% of the samples as burn-in. A consensus of the post-burning trees was visualized in FigTree v1.3.1.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new name contained herein is available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSID (Life Science Identifier) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘‘http://zoobank.org/’’. The LSID for this publication is: urn:lsid:zoobank.org:pub. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Results

Dendropsophus bromeliaceus sp. nov. (Fig. 4.1 and 4.2)

Etymology

The specific epithet “bromeliaceus” refers to the reproductive habit of this species that deposits eggs in bromeliads and have the larva phase spent in the rainwater accumulated in these plants. The suffix “aceus” is a Latin word, meaning “belonging to”.

Common names

We suggest Teresensis' bromeliad treefrog or Pererequinha-de-bromélia-teresensis (in Portuguese). Teresensis refers to the people born in the Municipality of Santa Teresa.

Holotype

MNRJ 85852, adult male, collected from surroundings of Reserva Biológica Augusto Ruschi (19°54'27"S, 40°31'05"W; 878 m a.s.l.), Santa Teresa, State of Espírito Santo, Brazil, on 3 December 2012 by R. B. Ferreira and team (see Acknowledgements).

Paratopotypes

Same locality of holotype: MNRJ 85848, 85851, 85854, 85856, males, collected on 3 December 2012; MNRJ 85857, 85859, males, collected on 10 December 2012; MNRJ 85860-61, male and female respectively, collected on 15 December 2012; MNRJ 85862, male, collected on 10 January 2012; MBML 7712, male, collected on 1 July 2013. Collected nearby Associação do Banestes (19°55'52"S, 40°35'18"W; 764 m a.s.l.): MNRJ 85863, male, collected on 2 October 2012. All specimens collected by R.B. Ferreira and team.

Diagnosis

Dendropsophus bromeliaceus sp. nov. is diagnosable by the following combination of characters: (1) small size (male SVL 16.8 ± 6.6 (16.1-18.4 mm)); (2) framed dorsal color pattern; (3) clearly visible tympanum; (4) reduced membrane on the fifth toe; (5) belly light cream; (6) axillary membrane undeveloped; (7) its finger and toe discs near rounded; (8) absence of cloacal sheath covering entirely the cloacal opening; (9) absence of a white spot under the eye; (10) absence of two whitish lines from snout to sacral region; and (11) the biphasic advertisement call is composed of a two note call, the first note with 3-6 pulses, second note with 4-8 pulses and moderate pitched notes (~5 kHz). Ecologically, *Dendropsophus bromeliaceus* sp. nov. can be distinguished from all other congeners by having a tadpole phase associated with rainwater accumulated in bromeliads.

Description of the holotype

Adult male, SVL 16.7 mm; body moderately robust; head wider than body, widest below eyes, wider than long (HW/HL 1.1); head length representing 35.9% of SVL; snout short, nearly truncate in dorsal and lateral views; eye-nostril distance smaller than eye diameter (END/ED 0.89); *canthus rostralis* indistinct, almost straight; loreal region slightly concave; internarial area slightly depressed; nostrils not protuberant, directed dorsolaterally; interorbital area flat; IOD/ED 1.31; IOD/HW 0.37; eyes large and protuberant (ED/HL 0.31; ED/HW 0.28); pupil horizontal, elliptical; nictitating membrane transparent, its free margin pigmented in the same pattern of the eyelid; distinct supratympanic fold, semi-circular from eye to above the arm insertion; tympanum small (TD/HL 0.16), distinct rounded, separated from the eye; choanae medium size, oval; vomerine odontophores very small; tongue large, codiform, slightly notched behind; vocal slits long, extending from midlateral base of tongue to almost the angle of jaws; vocal sac developed, medium size, and subgular. Arm slender; forearm more robust than arm; arm without fold or fimbria; axillary membrane undeveloped; fingers slender, medium size; relative length of fingers II<III≈V<IV; discs nearly round, small; disc of finger II smaller than others; subarticular tubercles round, most prominent on fingers II and IV; supernumerary tubercles present; a large elliptical inner metacarpal tubercle; a bifid, medium size outer metacarpal tubercle; digital membrane short; webbing formula II trace III 2^{-}—3^{-}IV3^{+}—3^{+}V; nuptial pad unpigmented, acini on the posterior surface of finger II. Hind limbs long and slender (THL/SVL 0.62); no tarsal tubercle or fimbriae; toes moderately slender, medium size; relative length of toes I<II<III≈V<IV; inner metatarsal tubercle small, approximately oval; outer indistinct; toe discs small, round, similar size to the finger discs; subarticular tubercles protruding; tubercles on toes III and IV round; short digital membrane, webbing formula I trace II 3^{-}—$3^{1/2}$ III 3^{+}—$3^{1/2}$IV $3^{½}$ —

3^{-}V. Dorsal skin surfaces, flanks, and throat smooth; skin on belly and ventral surfaces of thighs granular; cloacal opening directed posteriorly, covered by a small sheath dorsally, and surrounding by cloacal tubercles, including a pair below opening cloacal.

Color of the holotype in preservative

General dorsal color light brown; cream wide dorsolateral stripe from behind of eye to inguinal region; a cream mid-dorsal bar from cloacal opening to the level of arm insertion; approximately triangular cream blotch, with apex directed to nostrils from the anterior portion of the eyelids to slightly before the nostrils; lateral areas of the head and flank cream; thigh cream; tibia light brown with two cream blotches; forelimbs grayish. Undersurfaces light cream; gular region, palm of hand, undersurfaces of the thigh and foot cream punctuated with black, more dispersed in gular region. Eye black.

Variation

Measurements of the type series are shown in Table 4.1. The only female (MNRJ 85861) was bigger than males (Table 4.1). Morphology and color pattern are generally concordant with the holotype. The dorsal color pattern in life can be lighter or darker; two specimens are very light, with the dorsal line pattern almost indistinct. The extension of dorsolateral and mid-dorsal stripes may be longer or shorter than the holotype; the dorsolateral stripe can begin on the eye (n=6), and the mid-dorsal stripe can be short, interrupted or reduced to a blotch; the blotch between and anterior to the eyes on the snout can be almost triangular wider in its medial portion. The froglets (MNRJ 85849, 85850, 85853, 85855, and 85858) had mean SVL of 10.7 mm (SD 8.1).

Coloration in life (based on paratopotypes MBML 7712, MNRJ 85857, 85859; Fig. 4.3).

General dorsal color dark brown; metallic dorsolateral stripe from behind of eye to inguinal region; a metallic mid-dorsal bar from above of cloacal opening to the level of arm insertion; approximately triangular metallic blotch, with apex directed to nostrils from the anterior margin of the eyes to slightly before the nostrils; lateral areas of head and flank brown; thigh brown; tibia brown with two or three metallic blotches; forelimbs brown; hidden surfaces of thighs brown or light orange. Undersurfaces light cream; gular region, palm of hand, undersurfaces of thigh and foot cream punctuated with black, more dispersed in gular region. Iris copper.

Froglets have distinct coloration in life compared to adults (Fig. 4.3). Dorsal surfaces of head and body metallic; two parallel dorsal bars formed by interconnected black blotches. Lateral view of head and flank black; thigh black; tibia black with two metallic blotches; forelimbs dark grey.

Comparison with other species

The framed dorsal color pattern distinguishes *D. bromeliaceus* from species of *D. microcephalus* group, except the *D. decipiens* clade. Because of framed dorsal color and small size, the *D. decipiens* clade (except *D. berthalutzae)* is superficially similar to *D. bromeliaceus*. From *D. decipiens, D. haddadi,* and *D. oliveirai,* the new species differs by reduced membrane in the fifth toe (in *D. decipiens*, *D. haddadi*, and *D. oliveirai* membrane reaching the disc in the fifth toe). From *D. berthalutzae,* the new species differs by its dorsal color pattern without an “X”, medium size vocal sac, and membrane in the fifth toe short (*D. berthalutzae* with “X” in dorsal color pattern [47,48]). From species of the *D. microcephalus* group *D. rubicundulus* clade (*sensu* [31]), the new species is distinguished by its framed dorsal color (dorsum dark green in life and violet in preservative [31,49]). Additionally, from *D. araguaya, D. cachimbo, D. cerradensis,* and *D. elianeae,* the new species can be distinguished by its smaller size (male SVL combined 18.9-

25 mm [49,50,51]). *Dendropsophus bromeliaceus* is smaller than *D. bipuntatus, D. coffeus,* D. *gryllatus, D. juliani, D. leali, D. minusculus, D. phlebodes, D. rhodopeplus, D. robertmertensi,* and *D. riveroi* (combined male SVL 19.0-25.5 mm [48,52,53,54,55,56]). From *D. branneri* and *D. werneri,* the new species differs by absence of a white spot under the eye [48,57]. *Dendropsophus meridianus, D. nanus, D. sanborni,* and *D. walfordi* have dorsal pattern with longitudinal stripes or points [48,58]. From *D. pseudomeridianus*, *D. bromeliaceus* differs by absence of two whitish lines from snout to sacral region [59]. From *D. cruzi*, *D. bromeliaceus* can be distinguished by its medium size vocal sac and short membrane in the fifth toe (in *D. cruzi* large vocal sac and membrane in the fifth toe to the disc; see [57]).The new species differs from *D. joannae* by its dorsum without brown marking and without dorsal surfaces of finger and toe discs bright yellow [60]. From *D. mathiassoni* is distinguished by its dorsal pattern (without a distinct dorsal pattern in *D. mathiassoni* [61]. The new species is distinguished from *D. ozzyi*, *D. reichlei*, and *D. shiwiarum* by its undeveloped axillary membrane (developed in these species [8,54,62]). Further, from *D. ozzyi* and *D. shiwiarum* by its finger and toe discs near rounded (pointed discs in *D. ozzyi* and *D. shiwiarum* [8,62]).

Dendropsophus bromeliaceus differs from species of the *D. columbianus* group (SVL combined 24.6-35.8 mm of *D. bogerti*, *D. carnifex*, *D.columbianus*, and *D. norandinus*; see [61,63,64]), the *D. garagoensis* group (combined SVL males 21.3-31.5 mm of *D. garagoensis*, *D. padreluna*, *D. praestans*, and *D. virolinensis*; see [65,66,67]), the *D. labialis* group (combined SVL 26.4-42.0 mm of *D. labialis*, *D. luddeckei*, and *D. meridensis* [61,68,69]), the *D. marmoratus* group (combined males SVL 30.0- 45.0 mm of *D. acreanus*, *D. dutrai*, *D. marmoratus*, *D. melanargyreus*, *D. novaisi*, *D. seniculus*, and *D. soaresi* [48,70,71,72,73,74]), and *D. leucophyllatus* group (combined males SVL 20.0-40.0 mm [48,64,73,75,76]) by its smaller size. Further, the new species is distinguished from species in the *D. columbianus* group by its belly light cream (in the *D. columbianus* group flecked, marbled, or yellow bellies [63,64]);

from the *D. labialis* and *D. marmoratus* groups by its framed dorsal color (green in life and in preserved specimens of the *D. labialis* group and lichenous, both in life and in preserved specimens of the *D. marmoratus* species group [8]. Additionally, *D. bromeliaceus* is distinguished from *D. leucophyllatus* group by absence of a pair of oval pectoral glands (except by *D. anceps*) and hidden surfaces of thighs, groin, and webbing without flash vivid colors (presence of pectoral glands and vivid flash color [9]).

From the *D. parviceps* group, *D. bromeliaceus* differs by its framed dorsal color pattern (lichenous in life and preserved specimen in *D. parviceps* group; see [8]). Additionally, *D. bromeliaceus* is distinguished from *D. bokermanni, D. brevifrons, D. luteoocellatus, D. microps, D. piauiniensis, D. subocularis,* and *D. timbeba* by absence of blotches, spots, or bars on surfaces of thighs and groin; and from *D. bokermanni, D. brevifrons, D. gaucheri, D. koechlini, D. luteoocellatus, D. microps, D. parviceps,* and *D. subocularis* by absence of suborbital bar (see [10,77,78]). Further, it differs from *D. frosti*, *D. grandisonae*, *D. luteoocellatus*, *D. microps*, *D. pauiniensis*, *D. ruschi*, and *D. subocularis* by its smaller size (combined SVL 20.8-33.0 mm [10,48,69,77,79,80,81]). It differs from *D. schubarti* by its smaller eye (HL/ED 3.5; in *D. schubarti* HL/ED 2.5) and larger tympanum (HL/TD 4; in *D. schubarti* 9.5).

The new species is distinct from species of the *D. minutus* group by the absence of a cloacal sheath covering entirely the opening cloacal (present in *D. minutus* group [8]) and by the absence of white supracloacal and tarsal lines (present in species of *D. minutus* group [8]). These same traits also distinguish the new species from *D. stingi* and *D. aperomeus* [82], which are recently considered belonging to *D. minutus* group [83]. These traits also distinguish *D. bromeliaceus* from *D. amicorum* that present such structure and similar to species of the *D. minutus* group, although currently not assigned to any species group [4,84,85]. Further, *D. bromeliaceus* differs from *D. amicorum*, *D. limai*, and *D. stingi* by its smaller size (combined SVL 19-26.2 mm [47,84,85,86]).

The new species is distinguished from *D. minimus* by its clearly visible tympanum, absence of rostral white line and larger size (in *D. minimus* the tympanum is concealed, rostral white line present and SVL 14mm [87]). From *D. miyatai*, *D. bromeliaceus* differs by its clearly visible tympanum and color dorsal pattern without bright red over bright yellow in life (in *D. myatai* tympanum is concealed and dorsal color pattern with bright red and yellow [88]).

Currently, *D. amicorum*, *D. battersbyi*, *D. haraldshultzi*, *D. stingi*, *D. tintinnabulum*, and *D. yaracuyanus* are not included in any species group (see [4,31]). *Dendropsophus amicorum* and *D. stingi* were compared above. From *D. battersbyi*, *D. tintinnabulum*, and *D. yaracuyanus*, the new species is easily separated by its smaller size (combined SVL 19.0-36.6 mm [69,85,89]). *Dendropsophus haraldschultzi* has tuberculate skin on dorsal surfaces, especially dense on the hand and darker longitudinal stripes from the interocular region to the groin [47].

Vocalization

The advertisement and aggressive calls were recorded at the type locality in 12 and 15 December 2012. The air temperature was around 23.2°C and relative humidity was 98% on both nights. The analyses of advertisement call were based on 28 calls of four males. The advertisement call consists of two noted call (diphasic) and has duration of 958-1294 ms ($\bar{X}$ = 1112 ± 87 ms). The first note (note I) has 3-6 pulses ($\bar{X}$ = 4.27 ± 0.827) and duration of 119-362 ms ($\bar{X}$ = 225 ± 67). The second note (note II) has 4-8 pulses ($\bar{X}$ = 5.58 ± 0.945) and duration of 182-379 ms ($\bar{X}$ = 261 ± 51). Nevertheless, analyzing each single note separately, we found that note I is always shorter and with lesser number of pulses than note II ($F_{1,62} = 5.9$; $P < 0.018$). The highest amplitude peak in note I is the first or second pulses and in note II is the third or the fourth pulses (n = 28 calls; 4 males). The spectrogram shows no harmonic structure (Fig. 4.4A) implying that dominant and fundamental frequencies are similar. The dominant frequency is similar between the two notes ($F_{1,66} = 1.2$; $P < 0.276$) and ranges between 4.8-5.6 kHz ($\bar{X}$ = 5.2 ± 0.2).

The interval between calls was different in chorus vs. single calling male ($F_{1,36} = 23.5$; $P < 0.001$). In chorus, each male called in interval between 7.3-14.0 s ($\bar{X} = 9.8 \pm 2.3$; n = 19 calls). Alone, each male call in interval between 4.3-9.5 s ($\bar{X} = 6.8 \pm 1.5$; n = 19 calls). Therefore, males in chorus have lesser calls per minute (range = 6-7 calls) compared to males calling alone (range = 8-9 calls).

Between advertisement calls, *Dendropsophus bromeliaceus* sp. nov. emitted a more complex call consisting of three to four notes (Fig. 4.4B). This call was only emitted by males in neighboring bromeliads, suggesting this is a territorial-aggressive call. A total of six calls of two males were analyzed. This call has duration of 1630-2270 ms ($\bar{X} = 1871 \pm 248$). Because the first and second notes of four-noted calls have similar structure, the data presented below are relative to three-noted call. The first note (note I) has 1-3 pulses and duration of 100-300 ms ($\bar{X} = 167 \pm 75$). The second note (note II) presented 3-4 pulses and duration of 150-250 ms ($\bar{X} = 205 \pm 36$). The third note (note III) presented 4-6 pulses and duration of 210-440 ms ($\bar{X} = 313 \pm 87$). The dominant frequency ranges between 5.3-5.4 kHz ($\bar{X} = 5.4 \pm 73$).

Phylogenetic relationships

Dendropsophus is monophyletic in both parsimony and Bayesian analyses (Jackknife= 79%; posterior probability= 0.84). *Dendropsophus* is composed of several well-supported (Jackknife > 70%; posterior probability > 0.95) sub-clades but the relationships among them need further investigation. The clade *Dendropsophus* + *X. truncata* is recovered in the phylogenetic analyses (Jackknife= 99%; posterior probability= 1). In contrast, the phylogenetic placement of *D. bromeliaceus* sp. nov. is still unclear. In the most parsimonious trees *D. bromeliaceus* sp. nov. is the sister taxon of *D. miyatai* but with 57% Jackknife support (Fig. 4.5A). In the Bayesian tree, the new species is grouped in a polytomy at the basal node of *Dendropsophus* (Fig. 4.5B).

Distribution

Dendropsophus bromeliaceus sp. nov. is known from rocky outcrops in the surroundings of the REBIO Augusto Ruschi at the Municipality of Santa Teresa, mountainous region of State of Espírito Santo, southeastern Brazil (Fig. 4.6). In addition to the two populations we found, colleagues (Lirio, F.C.F, pers. comm.) found another population at a rocky outcrop in Santa Teresa (19°48’23” S; 40°33’13” W; 905 m altitude) but no individual was collected from this population.

Natural history

Dendropsophus bromeliaceus sp. nov. was exclusively found at rocky outcrops with sparse trees of low to medium sizes; the ground was covered by a dense layer of bromeliads and herbaceous plants. Epiphytic bromeliads almost completely covered the tree branches. This vegetation pattern is very distinct from that of the surrounding lower areas, which are shaded due to much higher and thicker trees.

Dendropsophus bromeliaceus sp. nov. is a nocturnal frog with males calling in both rainy (October through December) and dry season (June and July). However the male chorus was less pronounced during the dry season with fewer individuals calling and lesser frequent calls. Tadpoles and froglets were only found in the rainy season. No amplectant pair or eggs were found during our surveys. In a plastic bag, a female of *D. bromeliaceus* sp. nov. laid about 60 eggs (Lirio, F. C. F., pers. comm.).

We found 11 adults, four froglets, and 10 exotrophic tadpoles of *Dendropsophus bromeliaceus* sp. nov. in the rainwater accumulated inside bromeliads (Table 4.2). Calling males and tadpoles were in bromeliads located on the ground up to 5 m above ground. Males called from horizontal leaves and outside the axils of bromeliads. All adults, froglets, and tadpoles were found in the median axils (i.e. basal and central axils were not used). Four calling males were collected from bromeliads with no tadpoles or froglets. Another three calling males were in bromeliads with conspecific tadpoles or froglets.

Vriesea ruschii was the dominant bromeliad at the outcrops and was also the most commonly used plant by *D. bromeliaceus* sp. nov. (Table 4.2). The used terrestrial bromeliads had greater diameter ($F_{1,15} = 58.92$; $P < 0.001$) and height ($F_{1,15} = 28.12$; $P < 0.001$) compared to epiphytes bromeliads. During our samplings, a number of bromeliad species were not occupied by *D. bromeliaceus* sp. nov. such as *Bilbergia* sp., *Edmundoa lindenii*, *Quesnelia strobilispica*, *Neoregelia macrosepala*, *Neoregelia* sp., *Nidularium cariacicaense*, *Nidularium espiritosantense*, *Nidularium* sp., *Vriesea* aff. *atra*, *V. ensiformis*, and *V. vagans*.

Adults of *Dendropsophus bromeliaceus* sp. nov. were not found together in the same bromeliad with their congeners. In one occasion, *D. bromeliaceus* sp. nov. shared the same plant (*Alcantarea extensa*) with another frog species (*Thoropa miliaris*) but they used different axil positions; *D. bromeliaceus* sp. nov. was in a median axil whereas *T. miliaris* was in a basal axil. Although *D. bromeliaceus* sp. nov. and *Scinax arduous* were the most abundant frogs and were frequently found in *Vriesea ruschii*, they did not shared the same plant. In syntopy with *D. bromeliaceus* sp. nov., we also found another 11 frog species inside bromeliads: *Bokermannohyla caramaschii*, *Fritziana fissilis*, *F. goeldii*, *Gastrotheca megacephala*, *Hypsiboas pardalis*, *H. semilineatus*, *Ischnocnema abdita*, *I. epipeda*, *I.* cf. *parva*, *Scinax alter*, and *Scinax arduous*.

Discussion

The monophyly of *Dendropsophus* is supported by several lines of evidence (e.g. morphology, cytogenetic, etc.) [31,90], but the backbone of *Dendropsohus* phylogenetic tree is largely unresolved. Further studies of the genus are needed to clarify the relationships among the major clades.

The dependence of *Dendropsophus bromeliaceus* sp. nov. upon bromeliads to complete its life cycle (reproductive mode = 6, sensus [91]) is an exceptional habit in *Dendropsophus*. The larval phase of most congeners is associated with temporary or lentic water bodies (i.e. ponds and swamps). It is more parsimonious to consider the oviposition in still water as the plesiomorphic oviposition mode in *Dendropsophus* considering the known or inferred oviposition modes of the other genera related to *Dendropsophus*, and the taxonomic distribution in *Dendropsophus* of these modes. Some species of *Dendropsophus* can utilize alternative habitats for depositing eggs. For example, *D. ebraccatus* can lay eggs on vegetation over water body or directly in the water [92]. Also the pond breeder, *D. haddadi* can lay eggs in bromeliads but no tadpoles or froglets were observed [93].

Dendropsophus bromeliaceus sp. nov. used several bromeliad species with a wide range of characteristics. However, the new species seems to avoid many bromeliad species, possibly because they have only the central cup or are not able to store rainwater. *Dendropsophus bromeliaceus* sp. nov. avoided central and basal axils, possibly due to the risk of desiccation and predation and/or disturbance.

The low number of tadpoles per plant (one or two) may indicate *D. bromeliaceus* sp. nov. deposits few eggs per bromeliad or the tadpoles are cannibalistic. Some bromeligenous frogs are known to lay a reduced number of eggs as a way to avoid competition among tadpoles [94]. In others species, tadpoles subsist on the eggs of their own or other species of frogs [95,96].

Dendropsophus bromeliaceus sp. nov. may exhibit tadpole guarding if the tadpoles found in bromeliads with adults are their own progeny. Several bromeligenous species exhibit parental care, which is possibly a response to the evolutionary pressure imposed by the harsh environment and resource limitation inside bromeliads [94].

Our observations suggest *D. bromeliaceus* sp. nov. is an intra- and interspecific territorial species. This behavior is not unusual for bromeligenous frogs, which select and defend their oviposition microhabitats (e.g. *Phyllodytes luteolus* [97,98]; *Crossodactylodes izecksohni* RBF pers. obs.).

Conservation remarks

The most distant populations of *D. bromeliaceus* sp. nov. were about 13.5 km apart. These rocky outcrops are located in private properties surrounding the REBIO Augusto Ruschi. Based on the known distribution of *Dendropsophus bromeliaceus* sp. nov., its extent of occurrence (sensu IUCN 2001) is about 50 km^2. Although *D. bromeliaceus* sp. nov. could be listed as Critically Endangered (CR) under B1a,b and B2a,b IUCN criteria [99], at this time, we recommend that it be listed as Data Deficient due to the lack of knowledge on its exact geographic distribution and populations size. It is likely this species occurs more widely, and possibly inside the REBIO Augusto Ruschi (ca. 3591 ha).

The fact that the current two populations are only known from private properties highlights the vital importance of preserving these forested areas. In addition, these forest areas function as forest corridors for several species [100]. An outreach environmental education program should be implemented by the federal, state and local agencies to safeguard these populations. Furthermore, because rocky outcrops do not attract much agricultural interest, they have frequently been preserved from human impact and have kept their refugia character [19]. This may help this newly described species.

Despite the fact that rocky outcrops may not be converted to agriculture, bromeliad collection from these areas by some local people for yard decoration is a common practice (RBF pers. obs.). *Dendropsophus bromeliaceus* sp. nov. used two bromeliad species (*Aechmea capixabae* and *Vriesea morrenii*) currently listed as vulnerable to extinction in part due to over collected [101]. It is of concern that these bromeliad species may become over collected and may consequently affect bromeligenous frogs across rocky outcrops.

The discovery of this new species emphasizes the importance of this mountainous region for amphibian conservation. Even though Santa Teresa municipality, southeastern Brazil is one of the most sampled areas across the Atlantic Forest, it harbors numerous remote areas still unsampled for frogs. This mountainous region can be considered an important hotspot for anuran and bromeliad conservation due to its high richness and number of endemic species [13,14,102,103]. By including this new species and *Chiasmocleis schubarti* (J.F.R. Tonini pers. comm.), Santa Teresa harbors 94 recognized frog species [13,14] and 107 bromeliad species [102]. However, other frogs and bromeliads are currently being described, making Santa Teresa's biodiversity far from fully appreciated.

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Table 4.1. Measurements of the type series of *Dendropsophus bromeliaceus* sp. nov.. Values presented in millimeters as mean ± standard deviation (range).

	Holotype	Paratopotypes	
Measurement	Male	Males (n=10)	Female (n=1)
Snout-vent length (SVL)	16.7	16.8 ± 6.6 (16.1-18.4)	20.1
Head length (HL)	6.0	5.9 ± 3.52 (5.4-6.5)	6.5
Head width (HW)	6.6	6.4 ± 2.27 (6.0-6.9)	7.2
Eye diameter (ED)	1.9	1.8 ± 1.31 (1.7-2.1)	2.0
Tympanum diameter (TD)	1.0	0.8 ± 1.41 (0.6-1.0)	1.5
Interorbital distance (IOD)	2.5	2.2 ± 1.37 (2.1-2.5)	2.7
Eye-nostril distance (END)	1.7	1.4 ± 1.41 (1.3-1.7)	1.7
Internarial distance (IND)	1.3	1.2 ± 0.09 (1.1-1.4)	1.4
Thigh length (THL)	8.4	8.3 ± 3.25 (7.8-8.6)	10.5
Tibia length (TL)	10.5	8.8 ± 4.59 (7.9-9.3)	11.0
Foot length (FL)	6.4	7.0 ± 4.73 (6.1-7.5)	8.4

Table 4.2. Characteristics of bromeliad species used by *Dendropsophus bromeliaceus* sp. nov.. N = number of bromeliads; PD = plant diameter in cm; PH = plant height in cm; NL = number of leaves; PS = plant height from the soil in m. Frogs (sex or life stage) per bromeliad: A = adult (n=3), F = froglet (n=4), T = tadpole (n=10), M = calling male (n=8); + indicates frogs were in the same bromeliad; / indicates frogs were in different bromeliads. Mean and standard deviation are provided when appropriate.

Bromeliad species	N	PD	PH	NL	PS	Frogs
Aechmea capixabae	1	31	28	14	1.5	M+2T+F
Aechmea lamarchei	1	60	67	13	0	T
Aechmea pineliana	1	70	64	23	0	T
Alcantarea extensa	1	56	62	22	0	M
Neoregelia pauciflora	1	18	15	12	2.0	M+T
Racinaeae spiculosa	3	22 ± 7.8	21 ± 2.6	17 ± 7	2.3 ± 1.0	A/M/M
Vriesea bituminosa	3	14.3 ± 4.7	13.3 ± 4.2	10.7 ± 3.1	2.5 ± 2.2	F+2T/A/T
Vriesea morrenii	2	18.7 ± 2.5	20 ± 2.8	22 ± 2.8	1.85 ± 0.2	M/2T
Vriesea ruschii	4	58.25 ± 19.8	37 ± 12.1	16.8 ± 2.1	0	M+2F/M/A/F
Total	7	38.7 ± 20.1	36.4 ± 20.9	16.7 ± 4.4	1.1 ± 1	

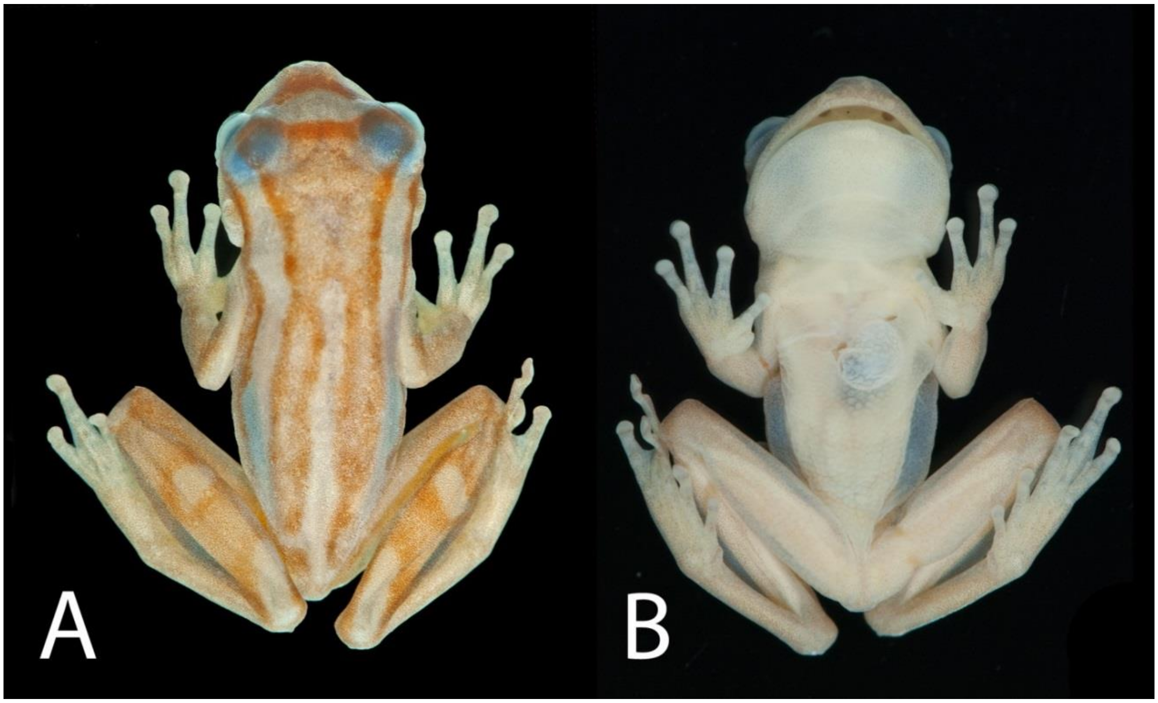

Figure 4.1. Holotype of *Dendropsophus bromeliaceus* sp. nov.. (A) Dorsal and (B) ventral views (MNRJ 85852, SVL 16.7 mm).

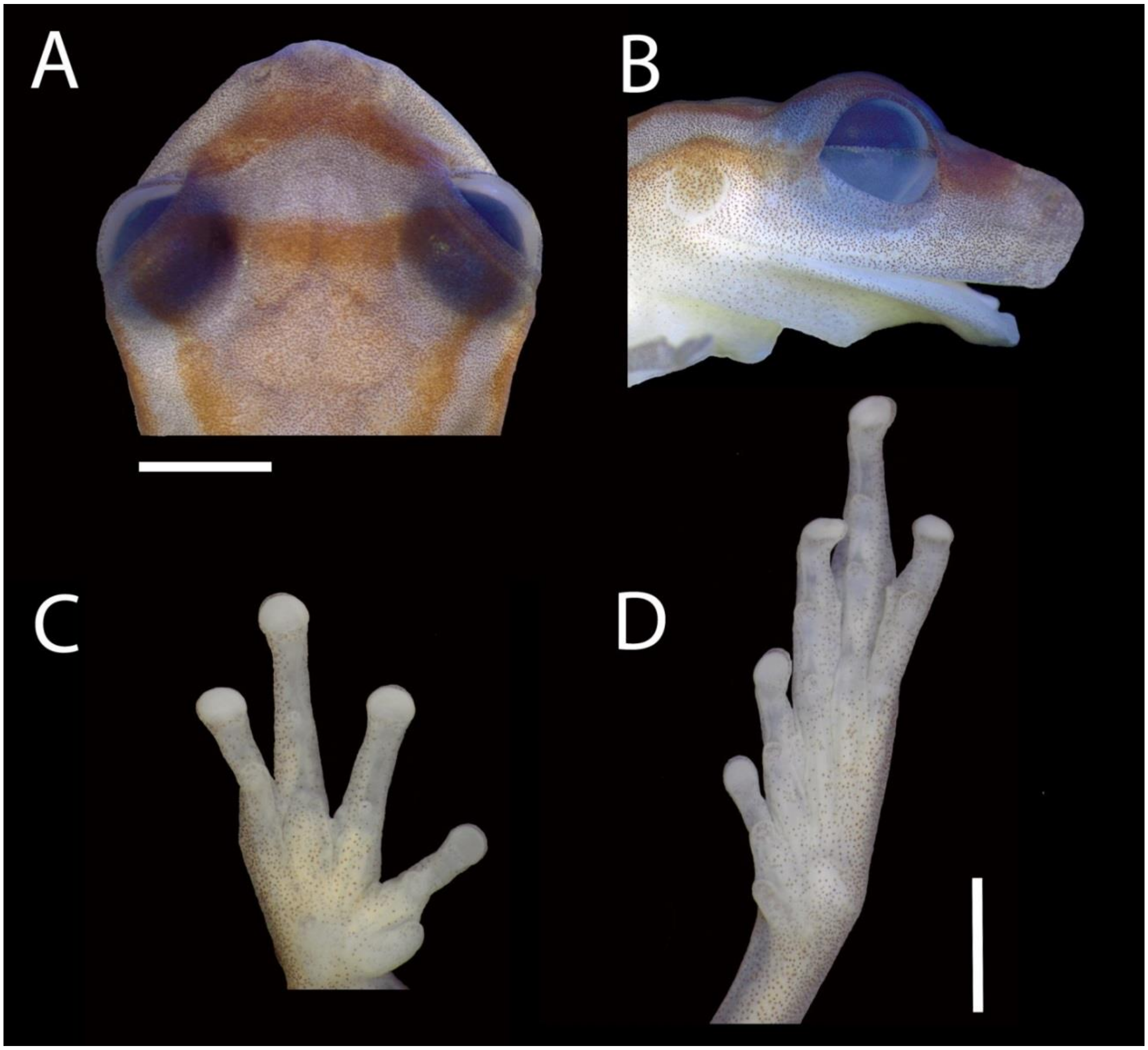

Figure 4.2. Holotype of *Dendropsophus bromeliaceus* sp. nov.. (A) Dorsal and (B) lateral views of head, (C) palmar view of left hand, and (D) plantar view of right foot (MNRJ 85852). Scale bar = 2 mm.

Figure 4.3. *Dendropsophus bromeliaceus* sp. nov. in life. (A) froglet (MNRJ 85855), and (B and C) male paratopotype (MNRJ 7712).

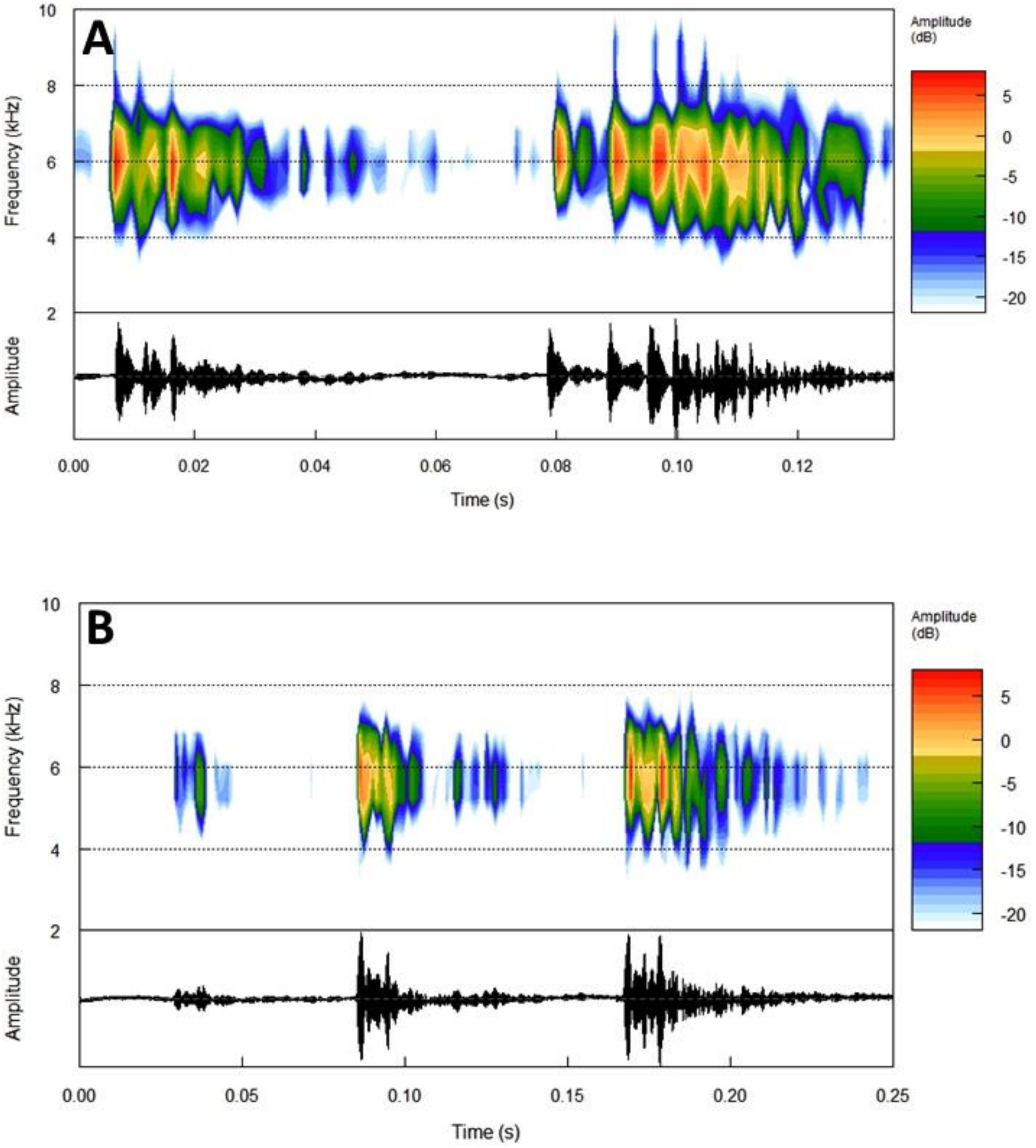

Figure 4.4. Calls of *Dendropsophus bromeliaceus* sp. nov.. (A) Advertisement call and (B) territorial-aggressive call with spectrogram (above) and oscillogram (below). Air temperature was around 23.2°C.

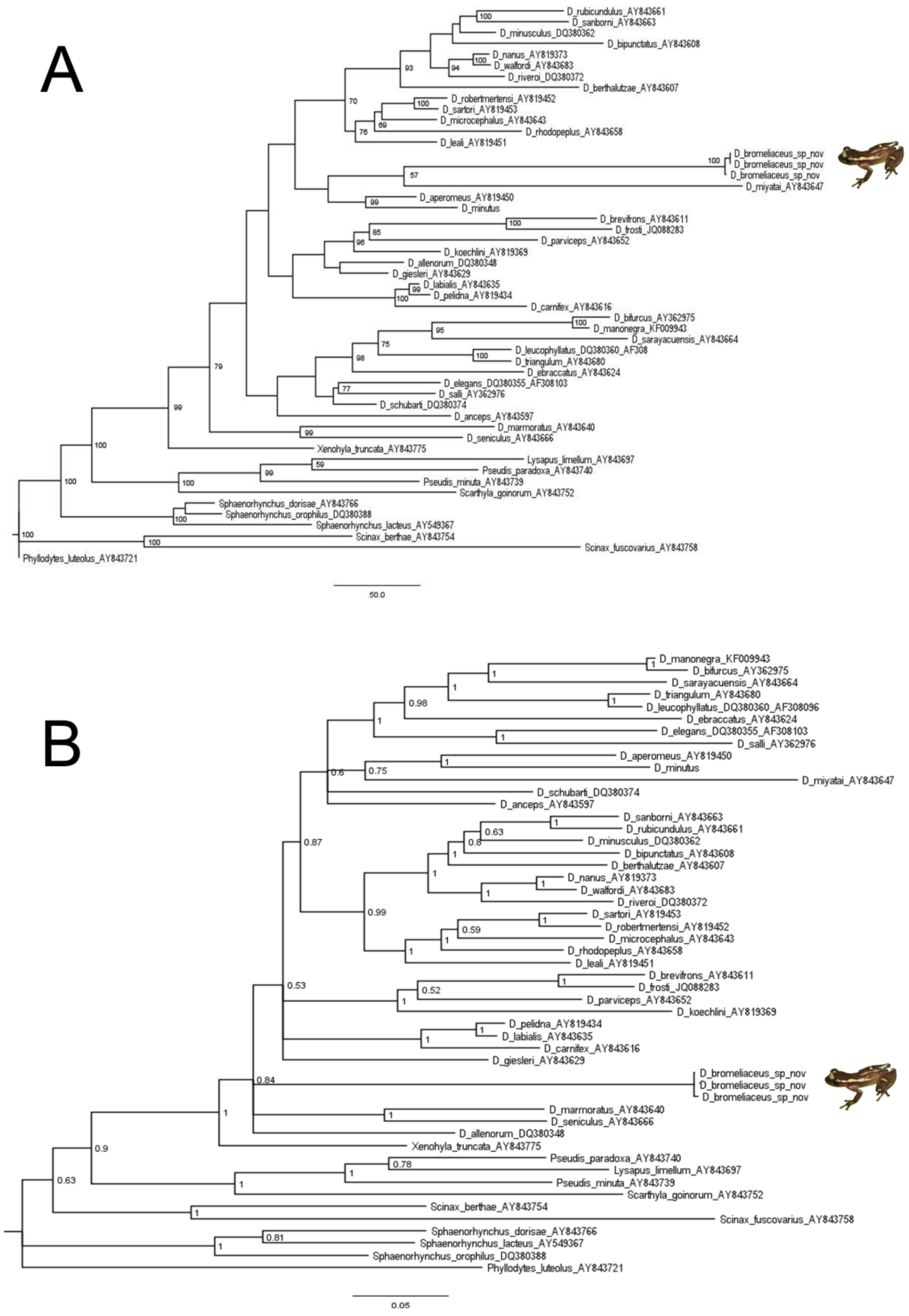

Figure 4.5. Phylogenetic relationship of *Dendropsophus bromeliaceus* sp. nov. (A) Maximum parsimony tree; numbers below nodes indicate Jackknife values > 50 and (B) Bayesian tree; numbers below nodes indicate posterior probability. Both results inferred from the mitochondrial genes 12S+trna^{VAL}+16S (see methods).

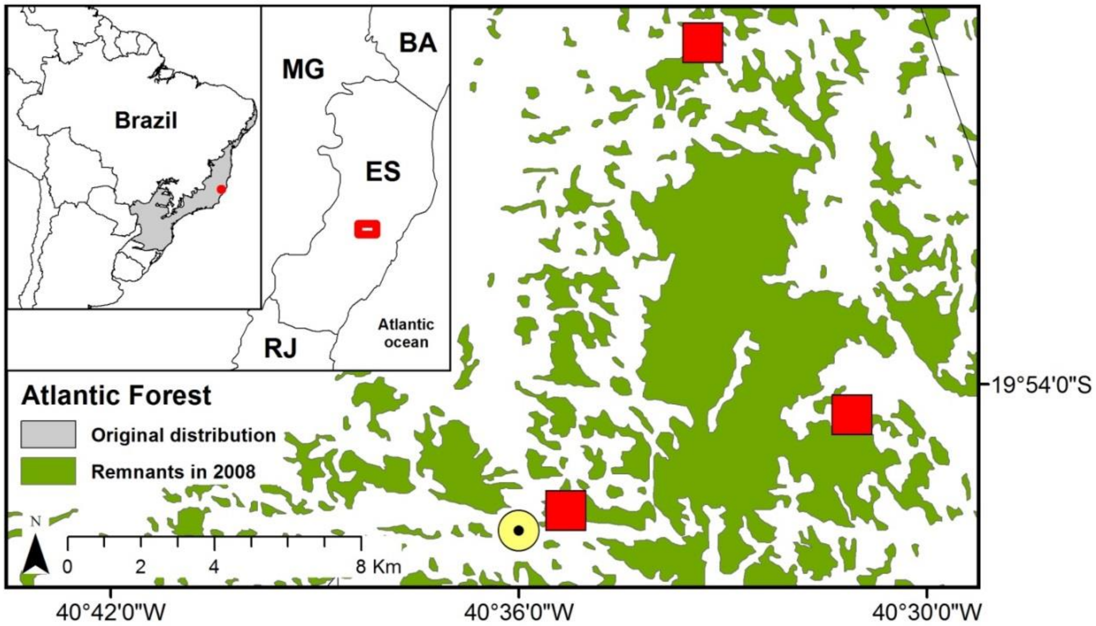

Figure 4.6. Geographic distribution of *Dendropsophus bromeliaceus* sp. nov.. Populations of this new species (red stars) and the city center of Municipality of Santa Teresa (yellow circle), southeastern Brazil. States= BA (Bahia), ES (Espírito Santo), MG (Minas Gerais), and RJ (Rio de Janeiro).

Supporting Information

S1 File. Additional specimens examined. (DOC)

Dendropsophus acreanus: Brazil: Acre: Tarauacá (MNRJ 3971).

Dendropsophus anceps: Brazil: Rio de Janeiro: Cachoeira de Macacu (MNRJ 86722-25).

Dendropsophus araguaya: Brazil: Mato Grosso: Alto Araguaia (MNRJ 17240-41) (paratypes).

Dendropsophus berthalutzae: Brazil: Rio de Janeiro: Duque de Caxias (MNRJ 85196-200); Rio de Janeiro (MNRJ 75053-55).

Dendropsophus bipunctatus: Brazil: Bahia: Ubaitaba (MNRJ 51623-31); Rio de Janeiro: Búzios (MNRJ 82904-23).

Dendropsophus branneri: Brazil, Bahia: Ilhéus (MNRJ 34356-88).

Dendropsophus cachimbo: Brazil: Pará: Cachimbo (MNRJ 17298-99) (paratypes).

Dendropsophus cerradensis: Brazil: Mato Grosso do Sul: Ribas do Rio Pardo (MNRJ 17293) (paratype).

Dendropsophus cruzi: Brazil: Goiás: Mossâmedes (MNRJ 21801-802, 21799-800); Silvânia (MNRJ 21782) (holotype), (MNRJ 18215-16) (paratypes).

Dendropsophus decipiens: Brazil: Rio de Janeiro: Itaguaí (MNRJ 62525-78).

Dendropsophus elegans: Brazil: Espírito Santo: Santa Teresa (MNRJ 30443-44); Rio de Janeiro: Jurubatiba: (MNRJ 66439-40).

Dendropsophus elianeae: Brazil: Mato Grosso: Cáceres (MNRJ 17194-99); Mato Grosso do Sul: Bela Vista (MNRJ 17297) (holotype), (MNRJ 17226-34) (paratypes).

Dendropsophus giesleri: Brazil: Rio de Janeiro: Magé (MNRJ 55244); Nova Iguaçu (MNRJ 86466-89).

Dendropsophus haddadi: Brazil: Espírito Santo: Conceição da Barra (MNRJ 17325) (holotype); Linhares (MNRJ 17078-82) (paratypes).

Dendropsophus jimi: Brazil: São Paulo: Botucatu (MNRJ 21980) (holotype), (MNRJ 21981-89) (paratypes).

Dendropsophus labialis: Colombia: Paramo Bogota (MNRJ 49772).

Dendropsophus leali: Brazil: Rondônia: Forte Príncipe da Beira (MNRJ 3962) (paratype).

Dendropsophus leucophyllatus: Brazil: Tocantins: Araguaína (MNRJ 88535-37).

Dendropsophus marmoratus: Brazil: Amazonas: Barcelos (MNRJ 36241-42).

Dendropsophus melanargyreus: Brazil: Pará: Tucuruí (MNRJ 17786).

Dendropsophus meridianus: Brazil: Rio de Janeiro: Itaguaí (MNRJ 62406-76).

Dendropsophus microcephalus: Colombia: Girardot (MNRJ 21834-40); Costa Rica: Puntarenas (MNRJ 3641, 14636-39).

Dendropsophus microps: Brazil: São Paulo: São José do Barreiro (MNRJ 76654-57).

Dendropsophus minutus. Brazil: Minas Gerais: Sacramento (MNRJ 88598-609); Rio de Janeiro: Nova Friburgo (MNRJ 77141-43); São Paulo: Botucatu (MNRJ 65240-88).

Dendropsophus nahdereri: Brazil, Santa Catarina: São Bento do Sul (MNRJ 3295) (lectotype), (MNRJ 3294, 3296) (paralectotype).

Dendropsophus nanus: Brazil: São Paulo: Botucatu (MNRJ 80017, 81397).

Dendropsophus novaisi: Brazil: Bahia: Maracás (MNRJ 4049) (paratype).

Dendropsophus oliveirai: Brazil: Bahia: Maracás MNRJ 3668).

Dendropsophus ozzyi: Brazil: Pará: Juruti (MNRJ 86921-25) (paratypes).

Dendropsophus phlebodes: Costa Rica: Alajuela (MNRJ 3639, 14635).

Dendropsophus pseudomeridianus: Brazil: Rio de Janeiro: Seropédica (MNRJ 25502) (holotype), (MNRJ 25503-32) (paratypes).

Dendropsophus rhea: Brazil: São Paulo: Pirassununga (MNRJ 17241-46) (paratypes)

Dendropsophus rhodopeplus: Ecuador: Prov. Pastaza. (MNRJ 73360-61).

Dendropsophus rossalleni: Brazil: Amazonas: Itacoatiara, Cairiri (MNRJ 56787-91).

Dendropsophus rubicundulus: Brazil: Minas Gerais: Catas Altas (MNRJ 60611-14).

Dendropsophus ruschii: Brazil: Espírito Santo: Pedra Azul (MNRJ 31548-50); Minas Gerais: Pedra Dourada: (MNRJ 47849-55, 478457).

Dendropsophus sanborni: Brazil: Estado de São Paulo: Ribeirão Branco (MNRJ 18210-11).

Dendropsophus schubarti: Brazil: Rondônia: (MNRJ 3669) (holotype).

Dendropsophus seniculus: Brazil: Espírito Santo: Cariacica (MNRJ 27910-12); Rio de Janeiro: Jurabatiba (MNRJ 88048-58).

Dendropsophus soaresi: Brazil: Piauí: Picos (MNRJ 60083) (holotype).

Dendropsophus tritaeniatus: Brazil: São Paulo: Pirajú (MNRJ 17225).

Dendropsophus walfordi: Brazil: Amazonas: Lago Janauacá (MNRJ 18141-44).

Dendropsophus werneri: Brazil, Paraná, Guaraqueçaba (MNRJ 15608-10), (MNRJ 21843-44); Santa Catarina: Joinvile (MNRJ 1542, 8201-03, 8205, 8207-13); Santa Luzia (MNRJ 2099, 10639-40).

CHAPTER 5

SUMMARY AND CONCLUSIONS

In Chapter 2, I recorded 622 individual frogs representing 29 species, of which four were undescribed species. The richness and abundance of frogs varied across distances from forest edge (i.e., edge effects) and across matrix types (i.e. matrix effect). Breeding guild was the most important variable explaining these differences. More specifically, we found that bromeliad and leaf-litter species that do not require breeding habitats outside the forest responded negatively to edges and matrix habitats whereas water-body species that may require breeding habitats in the valleys responded positively or neutrally to edges and matrix habitats. Richness and abundance across breeding guilds were higher in the rainy season but frog responses were similar across the four distances in the two seasons. Across matrix types, leaf-litter species more often used *Eucalyptus* plantations, whereas water-body species more often used coffee plantations. Bromeliad breeders were not found inside matrix habitats. Our data suggest that consideration of breeding habitat requirements can assist in prediction of frog response to both edge effects and matrix habitats in Brazil’s Atlantic Forest (Almeida-Gomes and Rocha 2014).

In Chapter 3, I showed a compilation of records on antipredator behaviors of post-metamorphic anurans from Brazil’s Atlantic Forest. The 224 records represent 165 species, and include 16 families of anurans. Individuals of most species in our observations remained ‘motionless’ before displaying a posture or any other behavior. Remaining motionless is likely a strategy to avoid observation or detection by a visually oriented predator. Immobility has presumably further advantage in those frogs that produce antipredator skin secretion. Our results show that the ability of producing skin secretion is widespread across species (N= 50) and families (N= 12) of frogs from the Atlantic Forest. These secretions varied from odoriferous to highly toxic. Immobility may also be the precursor of defensive postures, which are displayed by almost all anurans. Such behaviors include any positioning of the body that might enhance prey chance of surviving contact with predator. ‘Thanatosis or death feigning’ was the most common type of posture (N= 72 species) displayed by the studied anurans. Defensive vocalization was often emitted by many species in Atlantic Forest. Most calls from our observations can be categorized as “distress call” (sensu Toledo et al. 2014) because frog emitted the call when was handled by observer. Interpopulation variation of antipredator behaviors was observed for many species during our field researches. It is noteworthy that the three species that displayed the highest number of behaviors (i.e. *H. binotatus, H. faber*, and *O. americanus*) have large distribution across Atlantic Forest. We speculate that the advantage of displaying a large spectrum of defensive behavior may be associated to distribution range. Our observations from field research considerably increased the number of species reported displaying antipredator behavior. Our database includes records of antipredator behavior for approximately 30% of the species listed for Atlantic Forest (sensu Haddad et al. 2013).

In Chapter 4, I described *Dendropsophus bromeliaceus* sp. nov., collected at rocky outcrops of the mountainous region of Brazil’s Atlantic Forest. The new species is diagnosed by its small size, framed dorsal color pattern, medium size vocal sac, and short membrane in the fifth toe. The diphasic advertisement call is composed of a two-note call; first note with 3-6 pulses, second note with 4-8 pulses and moderate pitched notes (~5 kHz). The dependence of *Dendropsophus bromeliaceus* sp. nov. upon bromeliads to complete its life cycle (reproductive mode = 6, sensus Haddad and Prado 2005) is an exceptional habit in *Dendropsophus*. Although the monophyly of *Dendropsophus* is supported by several lines of evidence (e.g. morphology, cytogenetic, etc.) (Faivovich et al. 2005; Suarez et al. 2013), the backbone of *Dendropsohus* phylogenetic tree is largely unresolved and further studies of the genus are needed to clarify the relationships among the major clades. Our phylogenetic and morphological findings confirm *D. bromeliaceus* sp. nov. is a *Dendropsophus*. *Dendropsophus bromeliaceus* sp. nov. used several bromeliad species with a wide range of characteristics. The low number of tadpoles per plant (one or two) may indicate *D. bromeliaceus* sp. nov. deposits few eggs per bromeliad or the tadpoles are oophagus. *Dendropsophus bromeliaceus* sp. nov. may exhibit tadpole guarding if the tadpoles found in bromeliads with adults are their own progeny. Our observations suggest *D. bromeliaceus* sp. nov. is an intra- and interspecific territorial species. Although *D. bromeliaceus* sp. nov. could be listed as Critically Endangered (CR) under B1a,b and B2a,b IUCN criteria (IUCN 2014), we prefer to list it as Data Deficient due to the lack of knowledge on its exact geographic distribution.

I concluded that including life-history characteristics, such as breeding guild, can improve predictions of frog responses to edge effects and matrix types, and can guide more effective management and conservation actions. Primary forest is especially important for the protection of leaf-litter and bromeliad breeders. The fact that water-body breeders are more associated with edge and matrix habitats in our study sites suggests that matrix quality could be important for these species as they migrate toward reproductive habitats located in the valleys. In addition, I conclude that frogs display a wide variety of antipredator behaviors. The database I compiled can be combined with quantitative measurements of morphological and ecological traits to the advancement of knowledge on evolutionary ecology because life history represents different strategies that evolved to maximize individual fitness. Furthermore, the discovery of the *Dendropsophus* species emphasizes the importance of this mountainous region for amphibian conservation. Even though Santa Teresa region, southeastern Brazil is one of the most sampled areas across the Atlantic Forest, it harbors numerous remote areas still unsampled for frogs. Santa Teresa is considered an important hotspot for anuran and bromeliad conservation due to its high richness and number of endemic species (Almeida et al. 2011; Rödder et al. 2007; Wendt et al. 2010). Including this new species and *Chiasmocleis schubarti* (J.F.R. Tonini pers. comm.), Santa Teresa harbors 94 recognized frog species (Almeida et al. 2011; Rödder et al. 2007) and 107 bromeliad species (Wendt et al. 2010). However, other frogs and bromeliads are currently being described, making Santa Teresa's biodiversity far from fully discovered.

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APPENDIX

Coauthor Permission Letters

26 June 2015

Rodrigo B. Ferreira has my permission to include the following manuscript, which has been submitted for publication, of which I was co-author, in his doctoral dissertation.

R. B. Ferreira, K. H. Beard and M. L. Crump. Breeding guilds determine frog's response to edge effects and matrix types in Brazil's Atlantic Forest.

Karen Beard

Karen Beard

26 June, 2015

Rodrigo B. Ferreira has my permission to include the following manuscript, which has been submitted for publication, of which I was co-author, in his doctoral dissertation.

R. B. Ferreira, K. H. Beard and M. L. Crump. Breeding guilds determine frog's response to edge effects and matrix types in Brazil's Atlantic Forest.

Martha L. Crump

Martha L. Crump

26 June, 2015

Rodrigo B. Ferreira has my permission to include the following manuscript, which has been submitted for publication, of which I was co-author, in his doctoral dissertation.

R. B. Ferreira, J. Faivovich, K. H. Beard and J. Pombal Jr.. The first bromeligenous species of *Dendropsophus* (Anura: Hylidae) from Brazil's Atlantic Forest.

Dr. Julián Faivovich

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Karen Beard

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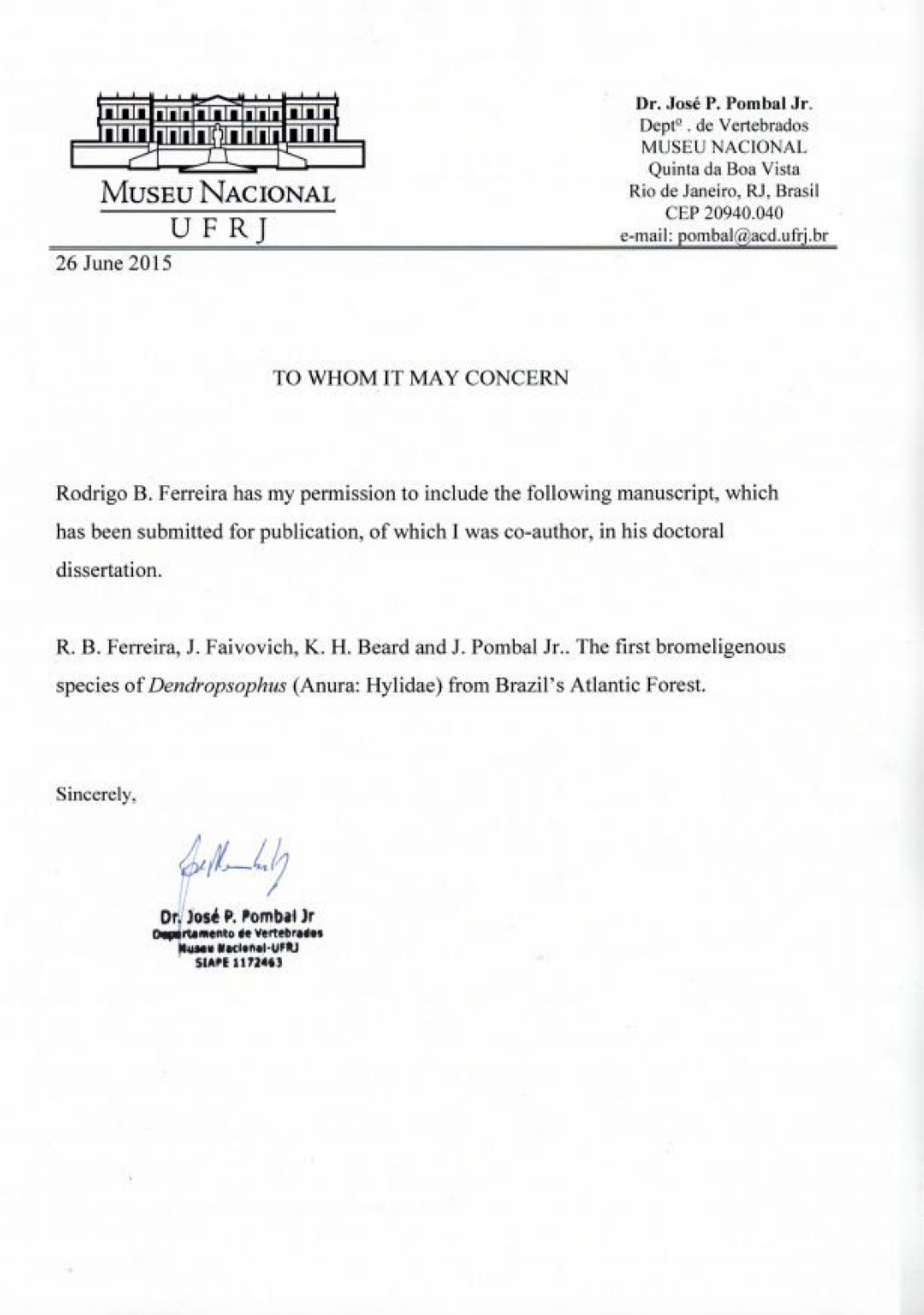

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26 June 2015

TO WHOM IT MAY CONCERN

Rodrigo B. Ferreira has my permission to include the following manuscript, which has been submitted for publication, of which I was co-author, in his doctoral dissertation.

R. B. Ferreira, J. Faivovich, K. H. Beard and J. Pombal Jr.. The first bromeligenous species of *Dendropsophus* (Anura: Hylidae) from Brazil's Atlantic Forest.

Sincerely,

Dr. José P. Pombal Jr
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SIAPE 1172463

Curriculum Vitae

RODRIGO BARBOSA FERREIRA

Position	PhD Candidate in Ecology at Department of Wildland
Resources,	Utah State University, Logan, Utah, USA
Personal Information	Webpage: http://rodrigobferreira.weebly.com/ Cellphone: 435-535-5395 E-mail: rodrigoecologia@yahoo.com.br
Professional Address	Department of Wildland Resources and Ecology Center, Utah
State	University, Old Main Hill, Logan, UT, USA, 84322-5230.
Education	Federal University of Espírito Santo, Brazil. 2003-2008. B.S. Major Biology.

Dissertation title: “Herpetofauna no campus da Universidade Federal do Espírito Santo”.

Research Interests

Ecology of Population, Community and Landscape, Invasive species, Natural History, and Conservation of Amphibians.

Field Work

2012/2013= Santa Teresa, ES, Brazil; 2012= Apalachian’s range, USA; 2008/2010= Domingos Martins and Alfredo Chaves,ES, Brazil; 2006/2010= Vitória,ES, Brazil; 2010= Hawaii, USA; 2007/2008= Alfredo Chaves,ES, Brazil; 2004/2008= Santa Teresa,ES, Brazil; 2005= Germano,MG, Brazil; 2003/2004= Marechal Floriano,ES, Brazil; 2004= Anchieta,ES, Brazil.

Teaching Experience

2012, 2013, 2014 - Conservation Biology at Dept. of Wildland Resources, Utah State University (USU), UT, USA. (Teaching Assistant)

2013- Animal Ecology and Identification at Dept. of Wildland Resources, Utah State University (USU), UT, USA. (Teaching Assistant)

2011 - General Biology at Dept. of Biology, Utah State University (USU), UT, USA. (Teaching Assistant)

2005/2008 - Biology/Chemistry (High School) at “Serviço Social da Indústria” (SESI), ES, BRA. (Teacher)

Technical Activities

2009/2010 - Visiting Scholar at the Insect Pathology Laboratory. Utah State University. USA.

2009/2010 - Laboratory and Field assistant at Ecology Center. Utah State University. USA.

2005 - Environmental Consulting (Rescue Program of Herpetofauna). CEPEMAR. Brazil.

2005 - Environmental Consulting (Studying the Impact on the herpetofauna by the expansion of the mineral-activities extraction). BRANDT. Brazil.

2004 - Environmental Consulting (Evaluation of impacts by construction of a resort). CEPEMAR. Brazil.

Outreach Activities

2013- Columnist in the regional newspaper and webpage “Santa Noticia”- www.santanoticia.com.br

2014- Contest for the local community to decide the common name of a new frog species – Santa Teresa, Espirito Santo, Brazil.

2012-2013- Activities of environmental education with neighbors of Augusto Ruschi Biological Reserve: panflets and stickers distribution, interview, conversation - Santa Teresa, Espirito Santo, Brazil.

2012- Photographic exposition: Bromeligenous from Santa Teresa, Espirito Santo, Brazil- Escola Etevaldo.

2008- Photographic exposition: Frogs from “RPPN Oiutrem”, Espirito Santo, Brazil- RPPN Oiutrem.

2006- Theater presentations for kids: “My Environment”, Espirito Santo, Brazil.

Media Coverage

2014- Newspaper (Jornal Santa Noticia, Jornal o Rio Doce) - The contest for the local community decide the common name of a new frog species.

2014- National TV (Globo News, Globo Rural), State TV (ES TV 1a edição, Jornal do Campo) – The new miniaturized frog species from mountainous region of Atlantic Forest.

Reviewer for Scientific Journals

2014/**present** - Tropical ecology

2014/**present** – Anais da Academia Brasileira de Ciências

2014/**present** – Biological Conservation

2014/**present** - Boletim do Museu de Biologia Mello Leitão

2014/**present** - Natureza Online

2013/**present** - Acta Oecologica

2012/**present** - Amphibia-Reptilia Journal

2012/**present** - Salamandra Journal

2012/**present** - Herpetology Notes

2011/**present** - CheckList Journal

2011 - Journal of Natural History

2012 - North-Western Journal of Zoology

2011 - Belgian Journal of Zoology

2010 - Acta Biologica Colombiana

Honors

2013- Best poster presentation of the VI Congresso Brasileiro de Herpetologia: Tendência ao gigantismo em população insular de *Phyllodytes luteolus* (Anura: Hylidae) no sudeste do Brasil.

2013 - Best Graduate Research Assistant of the year (2013) of Utah State University. Robins Award.

2013 - Best Graduate Research Assistant of the year (2013) of the Quinney College of Natural Resources.

2011 – Best poster presentation of the Graduate Research Symposium: Diet, fecundity, and use of bromeliads by *Phyllodytes luteolus* (Anura: Hylidae) in Southeastern Brazil. Fellowship (U$100).

Grants, Assistantships, and Awards

2014- PhD Completion Funds, Graduate School, Utah State University. Scholarship (U$10,000).

2014- Finishing-up funds, Ecology Center, Utah State University. Scholarship (U$4,000).

2014- PhD scholarship, Centro Nacional de Desenvolvimento Científico e Tecnológico. Scholarship (U$18,000).

2013/2014 - Rufford Small Grant for Conservational Projects- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$9,000).

2013 - Dr. Dinesh and Kalpana Patel Graduate Fellowship. Fellowship (U$5,000).

2013 - Ecology Center Research Award- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$2,500).

2012 - E. E. William Grant, Herpetologist's League- Project: Investigating causes of bromeliad-dwelling frog declines in Brazil's Atlantic rainforest. Fellowship (U$960).

2012 - Ecology Center Research Award- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$4,300.00).

2012/2013- Ecology Center Assistantship Award- Scholarship (U$12,000).

2012 - Smithsonian Institution, National Zoological Park, Center for Conservation Education and Sustainability- Full Scholarship for the Species Monitoring and Conservation course: Amphibian. Scholarship (U$2,000).

2011/2012 - Rufford Small Grant for Conservational Projects- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$9,000).

2011/2012 - Ecology Center Research Award- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$3,500).

2011/2012 - Graduate Senate Research Award- Project: How does matrix-habitat type influence edge effect at Brazilian Atlantic rainforest? A field study on threatened bromeligenous frogs in biodiversity hotspot. Fellowship (U$1,000).

2010/2011 - Berryman Institute- Project: The impacts of introduced greenhouse frogs in Hawaii. Scholarship (U$15,000).

2005/2006 - Programa Petrobrás Ambiental- Project: "Planejando paisagens sustentáveis no corredor central da Mata Atlântica". Undergraduate Scholarship (U$2,000).

Projects

2011/ **present** How do matrix-habitat types influence edge effect at Brazil's Atlantic forest? A field study on frog assemblages in a biodiversity hotspot. ES, Brazil.

2011/**present** Bromeligenous frogs: composition, site selection, and conservation status.

2012/**present** Antipredator behaviors of post-metamorphic anurans.

2010/ 2014 Impacts of the invasive frog *Eleutherodactylus planirostris* on Hawaiian ecosystem. USA.

2008/ 2011 Herpetofauna of "Parque Estadual Pedra Azul" and "PE Forno Grande". ES, Brazil.

2009/ 2010 Ecological aspects of urban herpetofauna, Southeastern Brazil. ES, Brazil.

2008/ 2010 Invasion of Mormon cricket (*Anabrus simplex*): colony development. UT, USA.

2007/ 2008 Ecology of the Herpetofauna in the Oiutrem Private Reserve. ES, Brazil.

2006/ 2008 Road killed Snakes from “Parque Estadual da Fonte Grande”. ES, Brazil.

2005/ 2007 Herpetofauna from “Universidade Federal do Espírito Santo”. ES, Brazil.

2005/ 2006 Designing Sustainable Landscape in Atlantic Rainforest. ES, Brazil.

2003/ 2004 Spatial and Seasonal Distribution of Anurans in Permanent Ponds in Marechal Floriano. ES, Brazil.

Publications

Book Chapter

1. Teixeira, R.L.; **Ferreira, R.B.**; Dantas, R.B., and Pertel, W. Diversidade de Anfíbios Anuros no Entorno da Reserva Augusto Ruschi, Sudeste do Brasil. In: Luciano Azevedo Vieira; André Moreira de Assis. (Org.). Planejando Paisagens Sustentáveis no Corredor Central da Mata Atlântica: uma experiência na região serrana do Espírito Santo. 1 ed. Vitória: Universidade Federal do Espírito Santo, 2007, v. 1, p. 95-100.

Peer-reviewed

1. Lourenço-de-Moraes, R., **Ferreira, R.B.**, Fouquet, A. and Bastos, R. 2014. A new diminutive frog of the genus *Adelophryne* Hoogmoed and Lescure 1984 (Amphibia, Anura, Eleutherodactylidae) from the Atlantic forest of Espírito Santo, Brazil. Zootaxa, 3846(3): 348-360.

2. Lourenço-de-Moraes, R.; Batista, V.G. and **Ferreira, R.B.** 2014. Defensive behaviors of *Leptodactylus chaquensis* Cei, 1950 (Amphibia: Anura: Leptodactylidae). Herpetology Notes, 7: 391-392.

3. Mageski, M.; **Ferreira, R.B.**; Zocca, C.Z.; Teixeira, R.L. and Rodder, D. 2014. The unusual occurrence of a population of *Dendropsophus elegans* (Anura, Hylidae) in an inselberg of southeastern Brazil. Herpetology Notes, 7: 363-365.

4. Zocca, C.Z.; Tonini, J.F.R. and **Ferreira, R.B.** 2014. Uso do espaço por anuros em ambiente urbano de Santa Teresa, Espírito Santo, sudeste do Brasil. Boletim do Museu de Biologia Mello Leitão, 35: 105-117.

5. Zocca, C.Z.; Lirio, F.C.F. and **Ferreira, R.B.** 2014. Observações sobre história natural de *Zachaenus carvalhoi* Izecksohn, 1983 “1982” (Amphibia: Anura: Cycloramphidae). Boletim do Museu de Biologia Mello Leitão, 34: 63-74.

6. Mageski, M.; Silva-Soares, T. and **Ferreira, R.B.** 2014. Hábito bromelígena de *Dendropsophus haddadi*. Boletim do Museu de Biologia Mello Leitão, 34:97-100.

7. Waichert, C.; **Ferreira, R.B.** and Williams, K. 2013. Expansion of distributional records of *Plumarius brasiliensis* Penteado-Diaz (Hymenoptera: Plumariidae) in northeastern of Brazil. Check List Journal, 9(3): 626-7.

8. Poessel, S.A.; Beard, K.H.; Callahan, C.M.; **Ferreira, R.B.** and Stevenson, E. 2013. Biotic acceptance in introduced amphibians and reptiles in Europe and North America. Global Diversity and Biogeography, 22: 192-201.

9. **Ferreira, R.B.**; Beard, K.H.; Petterson, S.; Poessel, S.A. and Callahan, C.M. 2012. Establishment success of non-native reptiles increase with the presence and richness of native congeners. Amphibia-Reptilia, 33: 387-392.

10. **Ferreira, R.B.**; Dantas, R.B. and Tonini, J.F.R. 2012. “Distribuição espacial e sazonal de anfíbios em quatro poças na região serrana do Espírito Santo: influência de corredores florestais.” Iheringia Journal, 102(2): 163-169.

11. **Ferreira, R.B.**; Beard, K.H.; Callahan, C.M. and Poessel, S.A. 2012. Global assessment of establishment success for amphibian and reptile invaders. Wildlife Research, 39: 637-640.

12. **Ferreira, R.B.** and Silva-Soares, T. 2012. Road mortality of snakes at an urban forest area in southeastern Brazil. Boletim do Museu de Biologia Mello Leitão, 29: 5-15.

13. **Ferreira, R.B.** and Lima, C.S. 2012. Anuran hotspot at Brazilian Atlantic rainforest invaded by the non-native *Lithobates catesbeianus* Shaw, 1802 (Anura: Ranidae). North-Western Journal of Zoology, 8(2): 386-389.

14. Freitas, A.M.; Teixeira, R.L. and **Ferreira, R.B.** 2012. Food partitioning between the sympatric lizards *Tropidurus torquatus* and *Ameiva ameiva* in the Atlantic rainforest, northeastern Brazil. Salamandra Journal, 48(2): 63-70.

15. **Ferreira, R.B.**; Schineider, J.A. and Teixeira, R.L. 2012. Diet, fecundity and use of bromeliads by *Phyllodytes luteolus* (Amphibia, Anura, Hylidae) in Southeastern of Brazil. Journal of Herpetology, 46(1): 19-24.

16. Teixeira, R.L.; Barros, E.H.; **Ferreira, R.B.**; Melo, R. M. C. and Salvador-Jr, L. F. 2011. Life history traits of the sand stargazer *Dactyloscopus tridigitatus* (Teleostei, Dactyloscopidae) from a sandy beach in southeastern Brazil. Journal of the Marine Biological Society of the United Kingdom. December 2011.

17. Silva-Soares, T.; Valadares, A.; Koski, D. and **Ferreira, R.B.** 2011. First record of *Aplastodiscus arildae* Cruz and Peixoto, 1985, from Espirito Santo State, Southeastern of Brazil. Herpetology Notes, 4: 255-258.

18. Silva-Soares, T.; Salles, R.; Valadares, A.; **Ferreira, R.B.** and Rocha, C.F. 2011. Continental, insular and coastal marine reptiles from the municipality of Vitória, state of Espirito Santo, southeastern Brazil. CheckList Journal, 7(3): 290-298.

19. Teixeira, R.L. and **Ferreira, R.B.** 2010. Diet and fecundity of *Sphaenorynchus planicola* (Anura, Hylidae) from a coastal lagoon in Southeastern Brazil. Revista Española de Herpetologia, 24:19-25.

20. Silva-Soares, T.; Costa, P.N.; **Ferreira, R.B.** and Weber, L.N. 2010. Description of tadpole of the hylid frog *Scinax belloni* (Faivovich, Gasparini & Haddad, 2010). Zootaxa, 2727: 63-68.

21. **Ferreira, R.B.**, Silva-Soares, T. and Rödder, D. 2010. Amphibians of Vitória, an urban area in Southeastern Brazil. Salamandra, 46(4): 187-196.

22. Pertel, W.; Teixeira, R.L. and **Ferreira, R.B.** 2010. Comparison of diet and use of bromeliads between a bromelicolous and a bromeligenous anurans at an inselberg in the southeastern of Brazil. Caldasia, 32(1): 149-159.

23. **Ferreira, R.B.** and Mendes, S.L. 2010. Herpetofauna composition of the “Universidade Federal do Espírito Santo”. Sitientibus, 10(4): 279-285.

24. **Ferreira, R.B.** and Tonini, J.F.R. 2010. Living holed: *Leptodactylus latrans* occupying crab’s burrows. Herpetology Notes, 3: 237-238.

25. **Ferreira, R.B.**; Silva-Soares, T.; Tonini, J.F.R. and Dantas, R.B. 2010. New records and distribution of a species vulnerable to extinction: *Euparkerella tridactyla* (Anura: Strabomantidae). Herpetology Notes, 3: 57-60.

26. **Ferreira, R.B.** and Teixeira, R.L. 2009. Feeding patterns and use of reproductive habitat of the Striped toad (*Rhinella crucifer*) from southeastern Brazil. Acta Herpetologica, 4(2): 125-134.

27. Teixeira, R.L.; **Ferreira, R.B.** and Rödder, D. 2008. Diversity and abundance variations of anurans at a permanent pond in Suruaca’s Valley, Linhares, Espírito Santo, southeastern Brazil. Amphibia, Germany, 7: 1.

28. Pertel, W.; **Ferreira, R. B.**; Rödder, D. and Teixeira, R. L. 2007. Frösche in und um Bromelien im Atlantischen Regenwald in Espírito Santo Brasilien. Terraria, Germany, 01 jun: 64-69.

29. Rödder, D.; Teixeira, R. L.; **Ferreira, R. B.**; Dantas, R. B. and Guarneire, G. J. 2007. Anuran Hotspots: the municipality of Santa Teresa, Espírito Santo, Southeastern Brazil. Salamandra, 43: 91-110.

30. **Ferreira, R. B**.; Dantas, R. B. and Teixeira, R. L. 2007. Reproduction and ontogenetic diet shifts in *Leptodactylus natalensis* (Anura, Leptodactylidae) from southeastern Brazil. Boletim do Museu de Biologia Mello Leitão, 22: 45-55.

Peer-reviewed short notes

1. Teixeira, R.L.; Ferreira, R.B. and Vrcibradic, D. 2014. Heterospecific amplexus between *Rhinella crucifer* and *Rhinella jimi*. Herpetological Review, 45(4): 683.

2. Ferreira, R.B.; Zocca, C.Z.; Mageski, M. and Lirio, F.C.F. 2014. Limb malformation on *Rhinella crucifer*. Herpetological Review, 45(2): 307.

3. Mageski, M.M.; Falcão, A. and Ferreira, R.B. 2014. Notes on the use of bromeliads by *Hypsiboas semilineatus*. Herpetological Review, 45(1):112-113.

4. Ferreira, R.B.; Hepp, F.; Zocca, C.Z. and Lirio, F.C.F. 2013. Defensive behaviors of *Euparkerella tridactyla*. Herpetological Review, 44(4): 655.

5. Lanschi, F. and Ferreira, R.B. 2012. Predation of *Hemidactylus mabouia*. Herpetological review, 43(1): 133-134.

6. Ferreira, R.B.; Silva-Soares, T. and Rangel, H.R. 2011. Diet of *Leptodactylus latrans* from an urban area, southeastern Brazil. Herpetological Review, 42(1):88-89.

7. Dantas, R. B. and Ferreira, R.B. 2010. Notes on geographic distribution to *Ischnocnema octavioi* (Anura, Brachycephalidae). Herpetological review, 41: 103-104.

8. Ferreira, R.B., Dantas, R.B., Miranda, C.M. and Silva-Soares, T. 2009. Notes on geographic distribution to *Physalaemus signifer* (Anura, Leiuperidae). Herpetological review, 40: 446-447.

9. Silva-Soares, T.; Costa, P.N. and Ferreira, R.B. 2009. Notes on geographic distribution to *Chiasmocleis carvalhoi* (Anura, Brachycephalidae). Herpetological review, 40: 107.

10. Silva-Soares, T.; Costa, P.N. and Ferreira, R.B. 2009. Notes on geographic distribution to *Ischnocnema oea* (Anura, Brachycephalidae). Herpetological review, 40: 108.

11. Vrcibradic, D.; Ferreira, R. B. and Teixeira, R. L. 2005. Notes on geographic distribution to *Phyllomedusa rohdei*. Herpetological Review, 21: 22.

12. Ferreira, R. B. and Vrcibradic, D. 2005. Notes on geographic distribution to *Hyla polytaenia* (Anura, Hylidae). Herpetological review, 36(3): 332-333.

In press

1. **Ferreira, R.B.**; Beard, K.H.; Choi, R. and Pitts, W. Diet of the Greenhouse Frog in Maui, Hawaii. Journal of Herpetology.

2. Teixeira, R.L.; **Ferreira, R.B.**; Silva-Soares, T.; Mageski, M.; Pertel, W.; Rodder, D.; Barros, E.H. and Engler, J.O. Anuran community of a cacao agroecosystem in southeastern Brazil. Salamandra.

3. Mageski, M.M.; **Ferreira, R.B.**; Beard, K.H.; Costa, L.C.; Jesus,P.R.; Medeiros, C.C. and Ferreira, P.D. Bromeliad selection by *Phyllodytes luteolus* (Anura, Hylidae): the influence of plant structure and water quality factors. Journal of Herpetology.

4. Mageski, M.; **Ferreira, R.B.**; Jesus, P.R.; Costa, L.C.; Roper, J.J. and Ferreira, P.D. The island rule in the Brazilian frog *Phyllodytes luteolus* (Anura: Hylidae): incipient gigantism? Zoologia.

Submitted

1. Lacerda, J.V.A., **Ferreira, R.B.**, Souza, G.A., Silva, H.R., and Feio, R.N. On the diagnosis and conservation of the poorly known bromeligenous *Scinax arduous* Peixoto, 2002 (Amphibia, Anura, Hylidae). Zootaxa.

2. **Ferreira, R.B.**; Beard, K.H. and Crump, M. L. Breeding guilds determine frog response to edge effects in Brazil's Atlantic Forest. Biological Conservation.

In preparation

1. Lourenço-de-Moraes, R.; **Ferreira, R.B.**; Castro, T.M.; and Teixeira, R.L. Comparison of diet and reproduction aspects of the invasive lizard *Gymnodactylus darwinii* and the native *Hemidactylus mabouia* from a reforested area in southeastern Brazil.

2. Lourenço-de-Moraes, R.; Mendes, C.C.V.M.; **Ferreira, R.B.**; Zocca, C.Z.; Medeiros, T.; Ruas, D.S.; Rebouças, R.; Toledo, L.F. and Solé, M. Marsupial treefrogs (Hemiphractidae: Gastrotheca) exhibiting escalated defensive behaviors. Herpetological Journal.

3. **Ferreira, R.B.**; Faivovich, J.; Beard, K. H. and Pombal Jr., J.P. and Description of the first bromeligenous species of *Dendropsophus* (Anura, Hylidae) from the mountainous region of southeastern Brazil. PlosOne.

4. Jesus, P.R.; Teixeira, R.L.; Mageski, M.M. and **Ferreira, R.B.** Diet of *Physalaemus crombiei* (Anura: Leptodactylidae) from a coastal lagoon, southeastern Brazil.

5. Targino, M.; **Ferreira, R.B.** and Cruz, C.A. A new species of *Ischnocnema* (Amphibia: Anura: Brachycephalidae) from the mountainous region of Atlantic Forest, Brazil. Zootaxa.

6. Teixeira, R.L.; Mageski, M.M.; Almeida, G.I. and **Ferreira, R.B.** Food division and fecundity of eight sympatric hylids (Amphibia: Anura) in southeastern Brazil.

7. Fagua, J.C.; **Ferreira, R.B.**; Colli, G.; Beard, K. and Ramsey, D. Deforestation promotes the invasion of an open-habitat frog species. Diversity and Distribution.

8. Lourenço-de-Moraes, R.; Batista, V.G.; Affonso, I.P.; Gomes; L.C. and **Ferreira, R.B.** Nested patterns of Neotropical species' composition in urban conservation sites: can these conserve anurans? Herpetological Journal.

9. Santos, M. T. T.; Magalhães, R. F.; **Ferreira, R. B.**; Peixoto, O. L.; Garcia, P. C. A. Taxonomic revision of *Crossodactylodes* Cochran, 1938 (Anura: Leptodactylidae), with redescription of three species and description of a new species. Herpetologica.

10. Santos, M. T. T.; Pezzuti, T. L.; Zaidan, B. F.; **Ferreira, R. B.**; Silva-Soares, T. and Garcia, P. C. A. Larva morphology of the bromeligenous genus *Crossodactylodes* Cochran, 1938 (Anura: Leptodactylidae), with comments on intrafamily relationships. Zoological Journal of the Linnean Society.

11. **Ferreira, R.B.**; Lourenço-de-Moraes, R.; Teixeira, R.L. and Beard, K. Frogs associated to bromeliads in a cacao agroecosystem. North-western Journal of Zoology.

12. Teixeira, R.L.; Britto, R. C.; Bissoli, L.C.P. and **Ferreira, R.B.** Dieta de jovens de *Aparasphenodon brunoi* (Amphibia: Hylidae) de um fragmento de Mata Atlântica no sudeste do Brasil.

13. Mageski, M.M.; **Ferreira, R.B.**; Costa, L.C.; Jesus,P.R.; Medeiros, C.C. and Ferreira, P.D. Diversidade e estruturação espacial da comunidade de anfíbios habitantes de bromélias em área de restinga no sudeste brasileiro. Iheringia.

Communication in Meetings

1. Ferreira, R. B. & Beard, K. H. Frog's assemblies' homogenization in Brazil's Atlantic Forest. 99th Congress of Ecology Society of America, Sacramento, California. 2014.

2. Ferreira, R. B.; Beard, K. H.; Zocca, C.; Lirio, F.C.F.; Barbosa, L. P. Local citizens decide the common name of a new fro species in Brazil. North America Congress for Conservation Biology. 2014.

3. Mageski, M.M.; Ferreira, R.B.; Costa, L.C.; Jesus, P.R.; Campinhos, E.C.; Souza, L.A.R. & Ferreira, P.D. Diversidade e estruturação espacial da comunidade de anfíbios habitantes de bromélias em área de restinga no sudeste brasileiro. III Simpósio sobre Biodiversidade da Mata Atlântica. 2014.

4. Lirio, F.C.F.; Zocca, C.Z.; Ferreira, R.B. Registros de mal-formação de membros em *Rhinella crucifer* (Anura: Bufonidae). III Simpósio sobre Biodiversidade da Mata Atlântica. 2014.

5. Beard, K. H. & Ferreira, R. B.. Matrix-habitat and edge effects on amphibian communities in the Brazilian Atlantic Forest. 26th International Congress of Conservation Biology. 2013.

6. Mageski, M.M; Ferreira, R.B.; Dias, P. Tendência ao gigantismo em população insular de *Phyllodytes luteolus* (Anura: Hylidae) no sudeste do Brasil. VI Congresso Brasileiro de Herpetologia. 2013.

7. Ferreira, R.B. & Beard, K.H. The impact of the introduced *Eleutherodactylus planirostris* on Hawaian Ecossystem. VI Congresso Brasileiro de Herpetologia. 2013.

8. Zocca, C.Z.; Lirio, F.C.F. & Ferreira, R.B. Observações sobre história natural de *Zachaenus carvalhoi* Izecksohn, 1983 "1982" (Amphibia: Anura: Cycloramphidae). VI Congresso Brasileiro de Herpetologia. 2013.

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27. Ferreira, R.B.; Dantas, R.B.; Teixeira, R.L. Ocorrência e dieta de *Sphaenorhynchus planicola* de uma lagoa costeira em Anchieta, Espirito Santo. In: 1º Congresso Brasileiro de Herpetologia, 2004, Curitiba. 1º Congresso Brasileiro de Herpetologia, 2004.

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31. Ferreira, R.B.; Dantas, R.B.; Teixeira, R.L. Aspectos ecológicos de *Phyllomedusa rohdei* em uma lagoa permanente de Nova Venécia, Espírito Santo.. In: 1º Simpósio de Anfíbios da UFRJ, 2004, Rio de Janeiro. Anais do 1º Simpósio de Anfíbios da UFRJ, 2004.

Invited Oral Presentation

1. Ferreira, R.B. and Beard, K.H. Frog response to edge effects and matrix-habitat types. VI Congresso Brasileiro de Herpetologia. 2013.

2. Ferreira, R.B. Edge effect on amphibians. SOS Mata Atlantica. 2013.

3. Ferreira, R.B. Ecological succession. Seminar presentation at Mello Leitao Biological Museum. 2012.

4. Ferreira, R.B. Methods for an effective amphibian sampling. Duas Bocas Biological Reserve. 2012.

5. Ferreira, R.B. How do matrix-habitat types and edge effects influence the community structure of bromeliad-frogs in an anuran hotspot at Brazilian Atlantic rainforest. Utah State University. 2011.

6. Ferreira, R.B. Invasive Herpetofauna on Hawaiian Islands. Simposio de Anfibio (SIMANF). Federal University of Rio de Janeiro. SIMANF (Symposium for the study of amphibians). 2010.

Professional Affiliations

2014/ present	Ecology Society of America
2013/ present	Sociedade Brasileira de Herpetologia
2009/ present	Society for the Study of Amphibians and Reptiles
2011/ present	Conservation Biology
2011/ present	Herpetologists’ League