

Movement ecology and habitat use in males of two species of *Boana* (Anura: Hylidae) during the breeding season

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Abstract. Sharing of space or microhabitat can facilitate coexistence among ecologically similar species. In forests in southern Brazil, the frogs *Boana bischoffi* and *Boana marginata* occur in syntopy. However, little is known about how these species use spatial resource. Our objective was to describe and compare movement patterns, home range and microhabitat of the calling site used by males of these species during breeding season. Individual movement was assessed by marking and recapture of calling males in a home range of temperate Brazilian Atlantic Forest. Both species presented short daily displacement (< 3 m/day) and relatively small home range (< 4 m²). There were differences between the species regarding microhabitat of the calling site use. *Boana marginata* males predominantly used sites closer to water than *B. bischoffi* males, and the latter mainly used microhabitats with higher vegetation density in the lower perch strata. Our data indicate elements of spatial partition between species, which is expected to reduce competition in amphibian aggregations around the same reproductive sites. Also, our data provide relevant information on the spatial ecology of two arboreal species, since most of the available information is about terrestrial species.

Keywords. Home range, Displacement, Space Niche, Spatial Distribution, Space Use

Introduction

In anurans, collective use of reproductive sites such as puddles, ponds and streams has been widely recorded (Wells, 1977). In these places, different species establish their sites for calling, mating and oviposition (Toledo et al., 2003; Wells, 1977). Comparative studies of syntopic species are an excellent opportunity to understand the processes of partitioning and resource use (Pianka, 1973; Schoener, 1974; Heyer et al., 1990). Some analyses of the behavior of these species using daily records of movement and microhabitat use show

a tendency of low overlap in resource use, which could minimize competition and favor coexistence (Oldham and Gerhardt, 1975; Cardoso and Vielliard, 1990; Rossa-Feres and Jim, 2001). Little attention has been addressed to the description of the movements of males within breeding sites. Studies of movement during breeding season bring useful information about reproductive strategies such as the selection of calling site, differences between calling and retreat sites and territoriality (Tozetti and Toledo, 2005; Oliveira et al., 2016).

Movement pattern is closely related to the ability of space sharing between species (Ringleler et al., 2009). Movement allows reaching better places to forage and to find a reproductive partner. At the same time, movements increase the risk of predation and involve a significant energy cost (Lemckert and Shine, 1993). Predation risk, agonistic interactions, territoriality and density of males are a set of habitat elements that lead an individual to stay or leave its calling site (Lemckert and Shine, 1993). To assess short-term movements related to the reproductive period, research studies use the same descriptors used in long-term evaluation of spatial ecology, such as distance traveled per day and home range. One way to complement this data is to insert microhabitat variables such as perch height,

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distance from the water and vegetation cover (Rossa-Feres and Jim, 2001; Sinsch, 2014; Santos *et al.*, 2016). Most of the available data about anuran movements deal with terrestrial species that exhibit bi-dimensional movement patterns (Muths, 2003; Tozetti and Toledo, 2005; Bevier *et al.*, 2006; Caldwell and Shepard, 2007; Pereira and Maneyro, 2016). By monitoring arboreal species of forested habitats, we can reach a more complex set of movements, which includes horizontal and vertical descriptors of their displacements. Arboreal species, such as some hylids, are good models to the study of spatial ecology since they use a wide variety of microhabitats because some of them live on trees but move to the ground level for mating.

In the southern domain of the Atlantic Forest, two frog species (Hylidae; Frost, 2015) are endemic to this biome (Marcelino *et al.*, 2009; Frost, 2015), *Boana bischoffi* (Boulenger, 1887) and *Boana marginata* (Boulenger, 1887). Although they belong to the same group (Faivovich *et al.*, 2004), the two species present some differences in their biology and ecology. While *B. bischoffi* vocalizes predominantly in lentic environments, *B. marginata* uses lotic environments for reproduction (Kwet *et al.*, 2010). However, in situations where a stream originates from a lake, both species can be found vocalizing together (Moser *et al.*, 2019). In addition, *B. marginata* males have a prepollex bone developed into a thorn, which may be used in territorial disputes (Kwet *et al.*, 2010), since several individuals presented fight scars on the dorsum (*pers. comm.*). Such scars were not observed in *B. bischoffi*. Also, there is a mismatch in the knowledge level about those species. There is more information accumulation on *Boana bischoffi* while ecological data on *Boana marginata* are practically nonexistent. Thus, our objective was to describe and compare the spatial biology of calling males of *Boana bischoffi* and *B. marginata* in forest habitats. In our comparisons, we consider their daily displacement patterns, home range and microhabitat use of the calling site.

Materials and methods

Study site.—We conducted the study in subtropical forest environments associated with highland fields in a portion of the Atlantic Forest in the extreme south of Brazil (Figure 1). The sampled habitat portion has the predominance of a vegetation phytophysognomy known as Mixed Ombrophilous Forest, which is dominated by *Araucaria angustifolia* (Araucaria Forest) in the ecoregion of Alto Paraná Atlantic Forest (Dinerstein

et al., 2017). Annual precipitation is 2162 mm with an average annual temperature of 14.5 °C (Backes, 1999; Maluf, 2000). In winter, minimum temperatures are around 0 °C (Maluf, 2000).

We sampled a small stream, connected by a lake, with approximately 100 meters in length in a federal conservation unit (São Francisco de Paula National Forest-FLONA-SFP; 29°25'22.4''S; 50°23'11.2''W) (Figure 1). We selected this stream based on an exploratory pilot study, which revealed that it encompasses a high population density of the target species.

Data collection.—We conducted sampling campaigns between October and December 2016 on 13 nights. We located the calling males through active search (Crump and Scott Jr, 1994), captured them manually, and tagged them with fluorescent subcutaneous labels containing an individual alphanumeric code (*Visible Implant Alpha Tags-Northwest Marine Technology*). The use of alpha tag was carried out with the authorization of the competent Federal Organ, SISBIO (authorization # - 45861-1). We implanted the labels in the lower region of each individual's right leg (Pittman *et al.*, 2008) and released them immediately after in the same capture place. We marked capture points with GPS coordinates and, for a more refined record of the animal's position, we marked the place with a discrete color label. We used visual search to find marked individuals for recapture. We considered each recapture as relocation and used its coordinates to estimate individual movement. We considered each night of searching as one sampling campaign.

Movements' monitoring.—The small distance traveled by the animals between sampling campaigns was smaller than the GPS accuracy level. Because of that, we used a handheld GPS receiver to record only the capture location (initial point of movement) and recorded the distances traveled between recaptures with a measuring tape, using a compass to assess the direction between each recapture point. On each relocation, we recorded the distance (centimeters) and the angle (degrees) in relation to the previous point. This pair of data allowed the creation of a map with a bidimensional representation of the movements of each individual. We plotted these data (distance traveled and degrees between each point) manually in AutoCAD ® 2017. In this way, we were able to map individual movement with greater precision than that obtained by the exclusive use of a handheld GPS receiver.

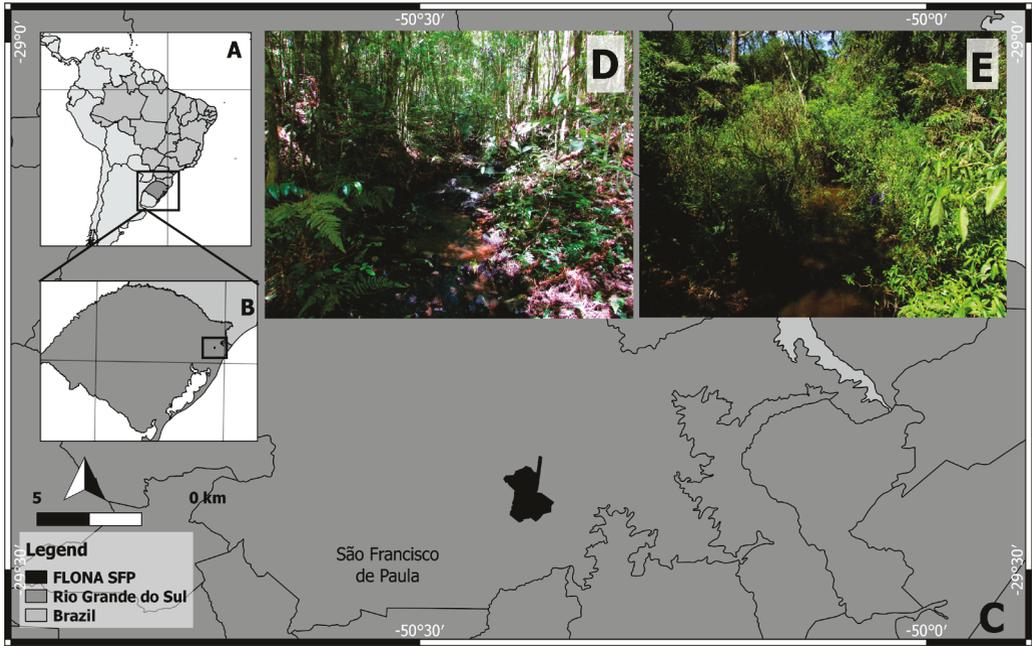


Figure 1. Location of the study area; A: Map of Brazil highlighting the state of Rio Grande do Sul, B: Map of Rio Grande do Sul highlighting the municipality of São Francisco de Paula, C: Map highlighting the São Francisco de Paula National Forest (FLONA – SFP), D and E: Images of the sampled stream.

Microhabitat evaluation.—We considered the calling site as our proxy of microhabitat use. We evaluated the following microhabitat variables for each individual: vegetation cover, individual height relative to the soil (perch height) and distance from the water (Menin et al., 2005; Prado and Pombal, 2005; Wachlevski et al., 2008; Santos et al., 2016). To estimate vegetation cover, we delimited a one-meter-side (1 m²) virtual polyhedron surrounding the amphibian. The polyhedron was divided into three height strata relative to the ground: from 0 to 50 cm, 51 to 150 cm and over 150 cm. We estimated vegetation percentage in each of these strata.

Data analysis.—We calculated the daily displacement (meters/day) and home range (m²) per individual. We used the points from each location to calculate the home range using “Minimum Convex Polygon” (Mohr, 1947; Hayne, 1949) with the Hawth’s Analysis Tools extension (Beyer, 2004) in ArcView (version 10.1; Environmental Systems Research Institute, Inc.). We performed this calculation only for individuals that had been recaptured at least twice per month. For individuals who were recaptured more than twice in all sampling months, we calculated the average of the home range. In this

study, we considered home range as the area in which an individual performs its normal activities during a specified time period (Burt, 1943). We used the Mann-Whitney test to verify whether there was a difference between species regarding recapture rates, home range and distances covered during daily movements. We considered p-values < 0.05 as statistically significant.

Microhabitat use.—We transformed the data recorded in percentages into arcsine degrees (Zar, 2010; Warton and Hui, 2011). We used a collinearity test to eliminate correlated variables. Thus, we only used the distance from water, perch height and medium vegetation in the analyses. To test whether there is a difference between microhabitat use by each species, we used Euclidean distances as a similarity measure, comparing sample units and using data normalization, in a randomization test with 1000 permutations. The probability threshold used for the interpretation of the results was $p < 0.05$. We performed a principal coordinate analysis (PCoA) as an exploratory analysis, where we evaluated the two axes that most explained data distribution. We used the software MULTIV v2.4 (Pillar, 2006) to perform the analyses. We used a One-Way ANOVA to evaluate

whether there were differences in the use of each spatial variable. We used the Levins Standardized Index (Krebs, 1999) to calculate species amplitude niche for the two microhabitat variables (perch height and distance from the water). This index enables comparisons between species since it is limited to a scale of 0 to 1 according to the following equation: $B_{sta.} = (B-1) / (n-1)$, where n represents resource number (categories used), and $B = 1 / \sum p \cdot i^2$, where p represents individual proportion using a given category i of the analyzed resource. Values close to 0 were attributed to specialist behavior, while those close to 1 were attributed to generalist behavior.

Results

We monitored 17 individuals of *Boana marginata* and 11 of *Boana bischoffi*, resulting in 89 and 34 records, respectively. The mean recapture rate was higher for *B. marginata* (5.23 ± 2.52 ; range = 2–11) than for *B. bischoffi* (3 ± 1.26 ; range = 2–5), comprising a significant difference ($N = 18$; $P = 0.04$; $U = 16.5$). Of these, eight individuals of *B. marginata* and five of *B. bischoffi* had two or more registered relocations per month, allowing

the home range evaluation (Table 1). The record of individuals in the exact same capture location, or with a difference of centimeters, was frequent.

Displacement and home range.—We found a positive correlation between the number of points and home range ($N = 12$; *B. marginata*: $P < 0.001$, $r^2 = 0.006$; $N = 6$; *B. bischoffi*: $p = 0.002$, $r^2 = 0.002$). The species *B. marginata* had a displacement of 1.9 ± 2.69 m/day (range = 0.29–10.27 m/day), while the displacement of *B. bischoffi*'s was 1.57 ± 1.32 m/day (range = 0.32–4.7 m/day) (Table 1), comprising a non-significant difference ($U = 58.5$; $p = 0.5$). The average home range of *B. marginata* was 2.45 ± 3.63 m²; ($N = 8$; range = 0.11–10.4m²) and of *B. bischoffi* was 3.19 ± 5.43 m² ($N = 5$; range = 0.005–12.85 m²), another non-significant result ($U = 27$; $P = 0.6$) (Table 1).

Microhabitat use.—The similarity test showed that species use microhabitats differently ($p = 0.01$; difference between groups = 0.18; difference within groups = 0.82). The multivariate analysis indicated a partition of the species along PCoA axes, with the first

Table 1. Table with the main results on the spatial distribution of *Boana marginata* and *B. bischoffi*. For each individual, its number of recaptures, home range and daily displacement are presented.

Species	Code	Recaptures	Home range (m ²)	Daily displacement (m)
<i>B. marginata</i> (N=12)	C84	8	1.90 ± 1.28	1.69 ± 1.30
	C91	4	5.18	1.90
	C93	4	0.16	0.29 ± 0.20
	C95	11	0.11 ± 0.10	0.42 ± 0.20
	C97	4	10.40	1.59 ± 1.89
	I00	8	1.34 ± 1.88	1.74 ± 1.87
	I01	4	-	0.4
	I07	5	-	10.27 ± 5.27
	I15	2	-	1.7
	I02	4	-	2.05 ± 2.19
	I08	7	0.13 ± 0.04	0.95 ± 0.35
I11	4	0.43	0.75 ± 0.42	
Average	-	5.23 ± 2.52	2.45 ± 3.63	1.98 ± 2.69
<i>B. bischoffi</i> (N=6)	C92	5	1.41	1.24
	C94	3	12.85	4.07
	I06	2	1.31	1.75
	I10	2	0.005	0.7
	I13	4	0.38	1.34
	I14	2	-	0.32
Average	-	3 ± 1.26	3.19 ± 5.43	1.57 ± 1.32

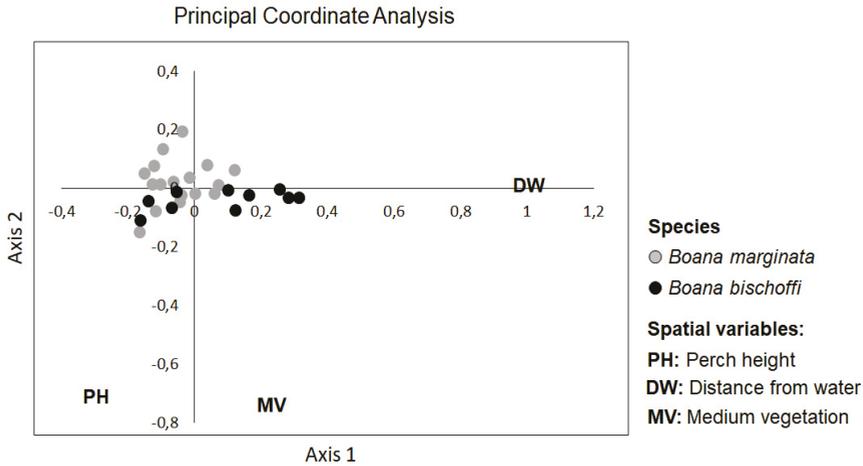


Figure 2. Principal Coordinate Analysis (PCoA) relating microhabitats used by males of *Boana marginata* and *B. bischoffi*. Points represent each species’ microhabitats and the vectors represent variables associated with them.

two PCoA axes explaining 87.4% of data variation (Axis one = 68.9 and axis two = 18.5) (Figure 2). Most of axis 1 variation was related to microhabitat distance relative to the water, while axis 2 was related to perch height and medium vegetation (51 a 150 cm). The microhabitats used by *B. bischoffi* tended to be more distant from the water and with higher vegetation density in the lower strata. On the other hand, *B. marginata* was related to microhabitats closer to the water and with lower vegetation density in all measured strata.

There was no significant difference between species regarding their perch height use (N = 28; F = 1.92; P = 0.17; Table 2). *Boana marginata* used perches at an average height of 50.5 ± 35.6 cm (range = 0–147 cm), and *B. bischoffi* of 62.1 ± 36.2 cm (range = 23–227 cm).

Species differed significantly regarding recorded distance from the water (N = 28; F = 4.88; P = 0.03). On average, *B. marginata* used microhabitats closer to the water (18.5 ± 39.9 cm; range = 0–310 cm) than *B. bischoffi* (47.4 ± 62.4 cm; range = 0–238 cm).

Regarding vegetation cover, microhabitats used by both species differed only in low vegetation density (N = 28; F = 7.19; P = 0.01), with no differences in medium (N = 28; F = 1.27; p = 0.27) and high vegetation (N = 28; F = 0.67; P = 0.42) (Table 2). On average, *B. marginata* used microhabitats with 11 ± 10% of vegetation cover up to 50 cm from the ground (low vegetation), while for *B. bischoffi* density was higher (26 ± 18%).

Spatial niche.—The niche amplitude for perch height was high for both species (*B. marginata* = 0.69 and

Table 2. Microhabitat use. Spatial variables measured for the microhabitats used by males of *Boana marginata* and *Boana bischoffi* during the breeding season.

	Perch height (cm)	Distance from water (cm)	Low vegetation % (0 to 50 cm)	Medium vegetation % (51 to 150 cm)	High vegetation % (> 150 cm)
<i>B. marginata</i> (range)	50.5 ± 35.6 (0–147 cm)	18.5 ± 39.9 (0–310 cm)	11 ± 10% (0–70%)	26 ± 22% (0–80%)	16 ± 19% (0–65%)
<i>B. bischoffi</i> (range)	62.1 ± 36.2 (23–227 cm)	47.4 ± 62.4 (0–238 cm)	26 ± 18% (0–70%)	44 ± 19% (0–80%)	12 ± 19% (0–75%)
Test (p)	1.92 (0.17)	4.88 (0.03)	7.19 (0.01)	1.27 (0.27)	0.67 (0.42)

B. bischoffi 0.59). As for distance from the water, *B. marginata* had a narrow amplitude of 0.14, while *B. bischoffi* had a range of 0.47.

Discussion

The two studied *Boana* species showed similarities in the investigated spatial factors, average distance traveled per day and home range. They were often observed in the same capture sites for several consecutive days. Whenever displacements occurred, they were generally less than three meters/day. This pattern is similar to that recorded to *Hylliola cadaverina* (Harris, 1975) and *Dryophytes versicolor* (Roble, 1979). However, this does not seem to be as common for other hylids, e.g., *Boana faber* (Oliveira *et al.*, 2016), *Dryophytes andersonii* (Freda and Gonzalez, 1986) and *Litoria latopalmata* (Lemckert and Slatyer, 2002), who move relatively greater distances.

Also, the home range of both studied species were small when compared to other species of Bufonidae (Muths, 2003; Caldwell and Shepard, 2007), Ranidae (Bevier *et al.*, 2006) and Hylidae (Oliveira *et al.*, 2016), the home ranges of which varied from 58 m² to 410 m². We found a great variation among individuals in both components (home range and daily displacement) as also observed in other species (Lemckert, 2004; Oliveira *et al.*, 2016). It is likely that this variation occurs due to the different stages in which males go through in the search process and establishment of their calling sites. Males already established in “optimal” sites would tend to perform little to no displacement, while males in the search and/or quarrel phases would be forced to move more. Considering that the energy expenditure during the anurans’ reproductive period is high, mainly due to the vocalizations emitted by the males (Bucher *et al.*, 1982; MacNally, 1984; Taigen and Wells, 1985; Lemckert and Shine, 1993), reducing displacement can be a strategy to save energy reserves. Nevertheless, comparisons between studies should be viewed with caution due to differences in monitoring duration and season (Tozetti and Toledo, 2005). It is important to note that our monitoring was conducted during the breeding season when males tend to displace preferentially around calling sites (Fellers, 1979; Johnson *et al.*, 2007; Oliveira *et al.*, 2016). At this period, males of *Boana faber*, for example, move predominantly around their calling sites, probably to optimize their mating chances and defend their oviposition site (Oliveira *et al.*, 2016), i.e., males of this species are constantly moving around their site, although they do not move away from their

calling site. This same hypothesis may explain the relatively small areas of use recorded for *B. marginata* and *B. bischoffi*.

Although both evaluated species appear to have similar movement patterns, *B. marginata* had a significantly higher recapture rate than *B. bischoffi*. Thus, caution is required when evaluating *B. bischoffi* home range and displacement, since this low recapture rate may suggest that marked specimens are moving far away from the sampling stream. In addition, our data indicate that *B. marginata* is more faithful to the breeding site than its congener. In a study with the hylid *Pithecopus ayeaye*, males had fewer recaptures compared to *B. marginata*, and some individuals showed fidelity to the calling site, being recaptured at the same site several times (Borges *et al.*, 2018), which was also recorded for *B. marginata*. Fidelity to the breeding site is an important spatial biology theme for anurans (Bevier *et al.*, 2006; Pittman *et al.*, 2008). Several studies have observed that fidelity may be associated with different breeding site uses, such as mating (Ritke *et al.*, 1992; Sinsch, 1992; Oswald, 2013; Chechia, 2014), calling (Oldham, 1967; Menin *et al.*, 2004; Caldwell and Shepard, 2007; Tárano, 2009), oviposition (Oliveira *et al.*, 2016) or refuge (Carpenter and Gillingham, 1987; Pittman *et al.*, 2008). The fact that males of *B. marginata* stayed in the same calling site for consecutive months can indicate the high quality of the territory, which could increase their chance to be chosen by females (Bertram *et al.*, 1996; Wogel *et al.*, 2005; Wogel and Pombal Jr., 2007; Borges *et al.*, 2018). In addition, some individuals of *B. marginata* presented scars on their backs, originating from territorial disputes between males, which was not recorded in *B. bischoffi*. Thus, it would be interesting to develop a longer duration study to evaluate whether this recapture rate difference reflects a higher fidelity in *B. marginata* than in *B. bischoffi*.

We verified that *B. marginata* and *B. bischoffi* have obvious differences regarding microhabitat use despite similar movement patterns. In the sampled environment, *B. marginata* predominantly used microhabitats closer to the water and had a narrower niche in this variable than its congener. Most of the *B. marginata* records were made in similar microhabitats (e.g. in this study, 47% of the records were in the distance category of 0 to 25 cm from water), which justifies their small niche amplitude (Krebs, 1999). Thus, this result indicates a specialized use of the stream margins by *B. marginata* males during the reproductive period. This result brings complementary and more detailed information data about characteristics of reproductive sites of *B.*

marginata (Kwet et al., 2010). Regarding vegetation cover, *B. marginata* was shown to use microhabitats with lower vegetation densities than *B. bischoffi*, being more exposed in the environment. High exposure is a behavioral strategy of male vocalizers to win sexual partners (Bernarde, 2012). On the other hand, this behavior also makes them more visible to possible predators (Duellman and Trueb, 1986). Nevertheless, being in a body of water with favorable conditions for its reproduction results in benefits to the species regardless of the high exposure strategy, making the risk of predation tolerable. *Boana marginata* was frequently recorded at lower heights, including on the substrate, while the minimum perch height used by *B. bischoffi* was 23 cm. However, this difference in perch height was not significant. Vocalizing while perched and avoiding the substrate is a behavior already registered for other populations of *B. bischoffi* (Bertoluci and Rodrigues, 2002; Forti, 2009). According to Meserve (1977), the ability of hylids to use three-dimensional space provides a mechanism to reduce competition between congeneric species. Several authors observed this pattern and found a greater overlap of calling sites in anurans that vocalized on the ground or in the water than in perched anurans (Cardoso et al., 1989; Vasconcelos and Rossa-Feres, 2005; Santos and Rossa-Feres, 2007; Silva et al., 2008). Nevertheless, both species used mainly intermediate heights and had high niche amplitude for this variable, which demonstrates a more generalist use of perch height by both species. This result is clear in Figure 2, where perch height had little explanatory power in data distribution.

Our data provide relevant information on the spatial ecology of these species, which are little studied and highly associated with Brazilian forest formations. Although performed as a snapshot, this study provided consistent data on mobility for both species, as well as their distinct associations to microhabitats during the breeding season. These data are important not only in a descriptive context of their natural history but also to assist in decision making during management of one of the most endangered landscapes in South America, the Atlantic forest.

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