

Fragment shape and size, landscape permeability and fragmentation level as predictors of primate occupancy in a region of Brazilian Cerrado

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ABSTRACT. Human activities result in the formation of a mosaic of forest patches within a non-habitat matrix. The response of the local biodiversity to changes in land-use may occur at different scales. It is important to evaluate the effects of the attributes of both the patches and the surrounding landscape on the occupancy of forest patches by animal populations. Here, we assessed the predictive potential of local (basal area, tree density), patch (size, shape) and landscape scale (total area of forest, number of patches, matrix permeability, patch proximity) variables on the occupancy of forest patches by the syntopic primates *Alouatta caraya*, *Sapajus libidinosus* and *Callithrix penicillata* in the city of Goiânia in the Cerrado region of central Brazil. We used playback to survey primate populations in 22 focal patches and assessed the landscape within a 1000 m buffer zone around each site. In *A. caraya*, occupancy was influenced by the shape of the focal patches, the amount of forest and fragmentation level of the landscape. Focal patch size and the permeability of the matrix were the principal determinants of the occupancy of *S. libidinosus*. None of the predictors influenced patch occupancy in *C. penicillata*, and the structure of the vegetation did not influence occupancy in any of the species. The preservation of as many forest patches as possible, both large and small, as well as gallery forests, and the enhancement of matrix permeability will be essential for the long-term conservation of the syntopic primates of the Cerrado of central Brazil.

Keywords: primate syntopy; patch occupancy; matrix; forest fragmentation; playback.

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Introduction

Human activities and increasing rates of urbanization have led to the progressive degradation of the environment and the loss of natural vegetation, which converts continuous forest cover into a fragmented landscape dominated by small and isolated patches of forest (Soulsbury & White, 2015; Goudie, 2018). This process provokes ecological disturbance at different habitat scales (Lyra-Jorge, Ribeiro, Ciochetti, Tambosi, & Pivello, 2010). At a local scale, patches may be impoverished, for example, through edge effects, the simplification of the fauna, the loss or local extinction of plant species (Tabarelli, Silva, & Gascon, 2004) or also the homogenization of the composition of the vegetation (Lôbo, Leão, Melo, Santos, & Tabarelli, 2011). At the patch scale, habitat patches may become progressively smaller and more isolated, while at a landscape scale, they may disappear altogether (Fahrig, 2003). The occupation of these forest patches by animal populations will depend on the dynamics of the exploitation of the resources available in the patches themselves and the surrounding matrix (Santos, Chiarello, Ribeiro, Ribeiro, & Paglia, 2016), which will influence the resilience of the populations or their susceptibility to extinction (Arroyo-Rodríguez et al., 2017; Borges-Matos, Aragón, Silva, Fortin, & Magnusson, 2016; Brady, McAlpine, Possingham, Miller, & Baxter, 2011). Ultimately, the socioecology of the species may also influence patch occupation patterns. Depending on the social system and dispersal dynamics of the species, individuals may either disperse systematically from their natal group or disperse secondarily between groups (Izar et al., 2012; Jack & Fedigan, 2004).

Most primate populations are either already undergoing the synergistic effects of the process of landscape fragmentation or will do so in the not-too-distant future (Estrada et al., 2017). These impacts can modify the distribution of the primate populations within the landscape, and are influenced by both the composition of the landscape matrix and the vertical structure of the vegetation in the patches (Arroyo-Rodríguez & Dias, 2010; Boyle & Smith, 2010; Mbora & Meikle, 2004). A number of studies have highlighted the importance of features of the vegetation structure, such as basal area, and canopy cover and height for the distribution and abundance of primate populations (Arroyo-Rodríguez & Mandujano, 2006). The drivers of primate occupancy in any landscape may depend on key elements of the local habitat, such as the amount of canopy, which is especially important to forest-dwelling species, as observed by Sales, Hayward, and Passamani (2016) in *Callicebus nigrifrons*. Anzures-Dadda and Manson (2007) also found a positive correlation between the presence of *Alouatta palliata* and the abundance and size of patches, canopy height, and abundance of corridors. However, occupancy is not determined solely by the attributes of the patches themselves, but also by the characteristics of the surrounding matrix (Anderson, Rowcliffe, & Cowlishaw, 2007; Hasui et al., 2017), so the presence of primate populations appears to depend on the overall configuration of the landscape (Arroyo-Rodríguez & Fahrig, 2014). For example, Sales et al. (2015) assessed the effects of forest patch size and connectivity on changes in occupancy, extinction and colonization rates following environmental change over time in two native Brazilian primates. These authors found that the black-tufted marmoset (*Callithrix penicillata*) presented a rapid response to habitat change, given that its occupation of the landscape is best explained by its current attributes, especially connectivity, resulting in an equilibrium with the present-day landscape. On the other hand, the response of the black-fronted titi monkey (*Callicebus nigrifrons*), which is dependent on the forest canopy, suffered a time-lag effect, because current occupation patterns are related to the past attributes of the landscape (especially fragment size).

The structure and composition of the landscape matrix can also influence the dynamics of primate populations both within and among forest patches (Benchimol & Peres, 2013). Habitat loss limits the availability of resources in patches (Estrada & Coates-Estrada, 1996), and may stimulate the exploration of the matrix (Mandujano, Escobedo-Morales, & Palacios-Silva, 2004) by animals searching for resources and moving to new patches (Asensio, Arroyo-Rodríguez, Dunn, & Cristóbal-Azkarate, 2009). Thus, the exploitation of resources from the matrix may mitigate the effects of habitat loss and relativize the structural connectivity of the landscape, making it more functional (Pardini, Souza, Braga-Neto, & Metzger, 2005; Ricketts, 2001). The success of primate populations in a fragmented landscape may thus depend on the complex interaction of a range of factors at different spatial scales, including patch size, quality, and structure, the composition of the matrix, and the ability of the animals to exploit the patches (Arroyo-Rodríguez, Cuesta-del-Moral, Mandujano, Chapman, Reyna-Hurtado, & Fahrig, 2013a; Carretero-Pinzón, Defler, McAlpine, & Rhodes, 2017; Silva, Ribeiro, Hasui, Costa, & Cunha, 2015).

It is imperative to understand how different primate species respond to changes in the landscapes they occupy because the species–landscape relationship depends strongly on landscape variables and the regional context (Galán-Acedo, Arroyo-Rodríguez, Estrada, & Ramos-Fernández, 2018). The populations of coexisting primate species, in particular, constitute a challenge for the determination of the environmental predictors of their potential success or failure in a fragmented landscape (Arroyo-Rodríguez & Dias, 2010; Peres & Janson, 1999). It is also important to identify the specific factors and the most appropriate spatial scale of analysis applicable to each case (Arroyo-Rodríguez et al., 2013a; Arroyo-Rodríguez, González-Perez, Garmendia, Solà, & Estrada, 2013b; Arroyo-Rodríguez & Fahrig, 2014). The rural-urban landscape gradient is an opportune scenario, given that the intensity of the matrix has negative effects on the richness and abundance of mammals (Brady, McAlpine, Miller, Possingham, & Baxter, 2009; Brady et al., 2011; Estrada, Raboy, & Oliveira, 2012). The understanding of the factors that determine the patch occupancy permits the comprehension of the environmental demands of the primates found in fragmented landscapes and the more systematic identification of the local, patch and landscape scale attributes that are of the highest priority for the development of conservation strategies (Carretero-Pinzón et al., 2017; Pozo-Montuy, Serio-Silva, & Bonilla-Sánchez, 2011). This approach should provide more reliable guidelines for the development of effective conservation measures that include both the species themselves and specific features of the environment, to ensure the survival of populations over the medium to long term (Chapman & Peres, 2001; Marsh et al., 2003).

The syntopic primates of the Brazilian central Cerrado coexist in forest patches within a fragmented landscape, providing an appropriate context for the assessment of the issues on patch occupancy outlined above. Although little is known about the relationships established between these primates and the landscape and patch characteristics, we can propose a number of predictions on the characteristics of the behavioral ecology of these species. As a generalist species, the marmosets would be less sensitive to the landscape and local degradation and would not be affected by the anthropogenic matrix (Sales et al., 2015; Secco, Grilo, & Bager, 2018). As the capuchin monkeys live in large groups, they would need larger patches with a well-preserved structure (Fragaszy, Visalberghi, & Fedigan, 2004). Howler monkeys appear to tolerate small patches (Bicca-Marques, 2003), but because they are folivorous-frugivorous, they would also need well-structured patches. All three species would likely benefit from the greater proximity between the patches in the landscape, and greater permeability, which usually favors movements within the landscape (Martensen, Pimentel, & Metzger, 2008). Our general hypothesis is that habitat loss and fragmentation will affect differentially the occupation of patches by the different primate species. In the present study, we investigated the effects of local, patch, and landscape scale attributes on the occupancy of forests by the black-and-gold howler monkey (*Alouatta caraya*), the brown capuchin (*Sapajus libidinosus*), and the black-tufted marmoset (*Callithrix penicillata*) within a rural-urban gradient. We analyzed variables including vegetation structure (basal area, tree density), patch size and shape, and landscape composition/configuration (total area of forest, number of patches, matrix permeability, and patch proximity). We aimed to identify the habitat attributes and the spatial scale most relevant to the conservation of these primate populations.

Material and methods

Study area

We surveyed 22 forest patches in the city of Goiânia (16°40' S, 49°16' W), which is located in the Cerrado biome of central Brazil. We randomly selected forest patches with an area of at least 5 ha, divided approximately equally among four size classes, i.e., 5–20, 20–40, 40–100, and 100–110 ha (Figure 1). We consider this division of classes to have the most homogeneous possible distribution of patches within the whole city. We avoided patches smaller than 5 ha because they were areas with highly degraded vegetation and the most potential risk for the field team. We confirmed the spatial independence of the study areas using the Average Nearest Neighbor test (ratio = 1.12), which measures the distance between each patch centroid and the centroid of its nearest neighbor. This ratio is calculated as the observed average distance divided by the expected average distance (based on a hypothetical random distribution of the patches within the area). If the value of the ratio is less than 1, the fragments are clustered, but if it is greater than 1, the fragments are well dispersed (Mitchell, 2005). In addition, as the buffer zones established around the focal patches did not overlap (see landscape classification section, below), they were considered to be independent sample units.

Primate surveys

We surveyed the primate populations of the focal patches between November 2010 and July 2011 using vocal playbacks. To provide a representative sample of each patch, we adjusted sampling effort to patch size, with the smallest patches (5–20 ha) being visited twice, the next largest patches (20–40 ha) three times, and the next largest (40–100 ha), four times, while the largest patches (100–110 ha) were surveyed five times. We used the recordings of long-calls and alarm vocalizations from the Emmons project (Emmons, Whitney, & Ross Jr., 1998) and those recorded in Brazil in other study sites, kindly provided by our colleagues. We used the Audacity® software v. 1.3.9 to clear background noise and cut the tracks. During each visit, we played recordings along transects at three different times of day (7:00–9:00h, 11:30–13:30h, and 16:00–18:00h). In order to survey the maximum possible area within each patch, we established longitudinal transects at regular intervals throughout each forest and chose three equidistant points (as far as possible) along the transect to broadcast the playbacks (Figure 2). During each playback session, we broadcast a 15-min. call twice for each species, separated by a 5-min. interval of silence.

We conducted playbacks until we obtained a response from the target species or, when there was no response, until the end of the planned survey schedule. Once a species was detected, either by playback, visual observation or vestiges (feces on the ground, in the case of *A. caraya*), we removed its vocalization

from the playback sequence. We considered a patch to be occupied by a species if we detected the presence of at least one individual. The playbacks were emitted using a portable loudspeaker (24.5 cm × 21 cm × 35 cm) containing two Pioneer speakers (6 × 9 TS-A6983S), coupled to an LG CD player (LSC500UN), and a H-Buster amplifier (600 W HBM-T200 TRANSPower), powered by a car battery (12V, 45A).

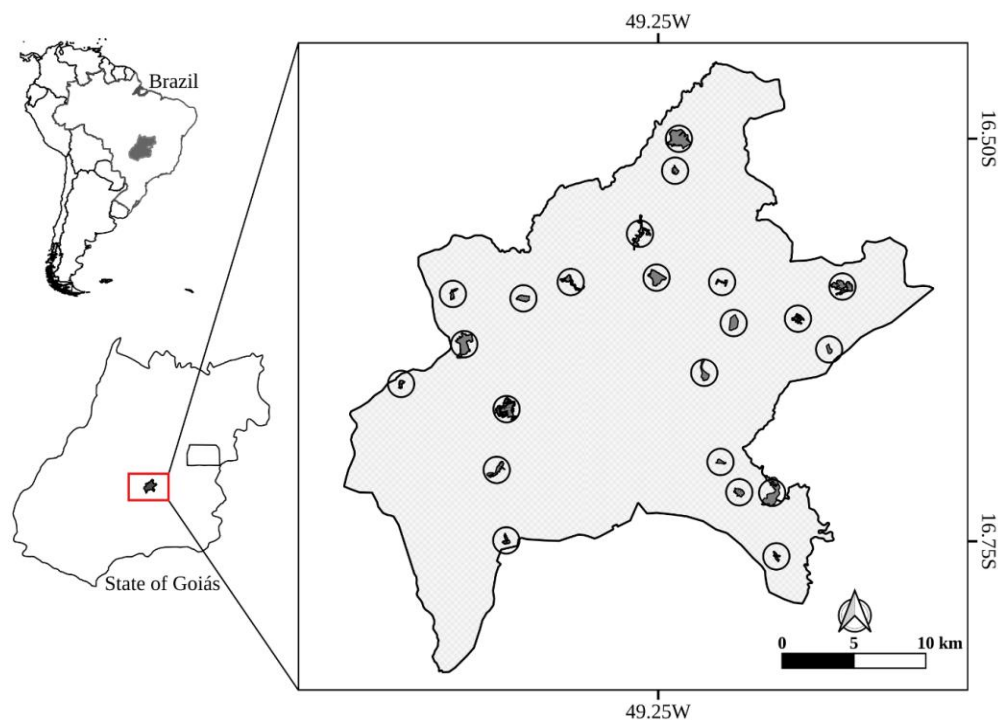


Figure 1. Location of the 22 focal forest patches in the city of Goiânia, Goiás state, Brazil.

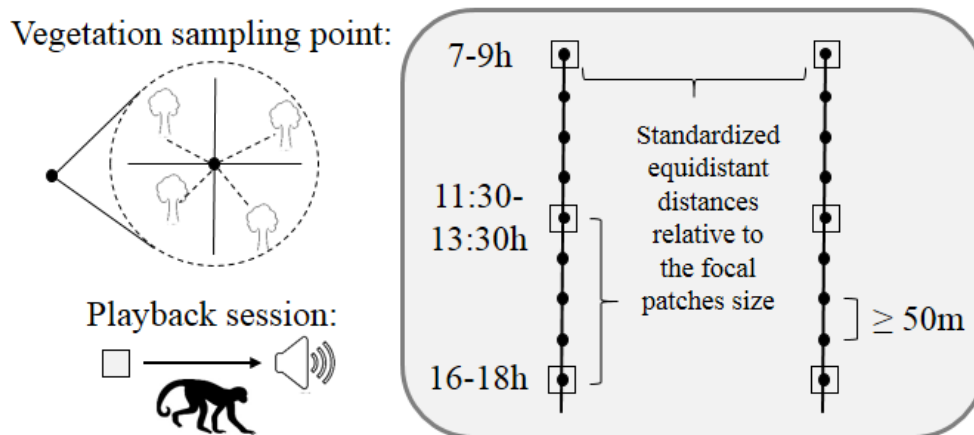


Figure 2. Diagram of vegetation structure sampling and the playback sessions conducted in the focal forest patches in the city of Goiânia, Goiás state, Brazil.

We validated the playback survey by preliminary pilot tests in patches not included in the study, in which presence of species was known. This allowed us to confirm the high degree of responsiveness of the species to the playbacks. We also investigated the presence of primates in each focal patch through interviews with local residents and/or other persons found in the vicinity of the patch, who were at least 18 years old. We conducted 185 interviews, 3–11 per patch (informed consent form certified by the Ethics Committee of the *Universidade Federal de Goiás*, approval n° 377/2010). During the interviews, we questioned the subject on the presence of primates in the focal forest, and used color photographs of different primate species, including species that are not present in the study region, to test the veracity of the information provided.

We tested the reliability of the survey methods by comparing the results of the playback surveys and interviews using a Pearson Chi-square test. The presence of *A. caraya* ($X^2 = 46.2$, $df = 1$, $p < 0.001$) and *S.*

libidinosus ($X^2 = 59.3$, $df = 1$, $p < 0.001$) was reported significantly more frequently in interviews at sites where the species were also detected in the playback surveys. This relationship was not significant in *C. penicillata* ($X^2 = 3.1$, $df = 1$, $p = 0.07$), however, possibly because of the high occupancy rate recorded for this species.

Local attributes

We sampled the vegetation structure of the patches using the Point-Centered Quarter Method, or PCQM (see Cottam & Curtis, 1956). We selected sampling points randomly at 50-m intervals along the transects used for the playback surveys. In general, the number of transects corresponded to the number of visits to each patch. The total length of the transects was not fixed, although we standardized the sampling effort as far as possible by distributing the transects evenly across the area of each fragment. The number of points sampled per patch varied according to its size class, with 15 points being sampled in the smallest patches (5–20 ha), 20 points in the next largest patches (20–40 ha), 25 points in the next largest (40–100 ha), and 30 points in the largest patches, of 100–110 ha (Figure 2).

In the PCQM, each point is defined as a sampling unit, and the area surrounding the point is divided into four 90° quarters (quadrants). We defined the quadrants at each point by throwing a cross randomly onto the ground, and then, within each quadrant, we identified the tree nearest to the center of the cross with a circumference at breast height (CBH) of at least 15 cm. For each tree identified in this way, we measured the distance to the center point (point–plant distance) and the CBH. We selected randomly 60 of total trees sampled in the PCQM's per patch to standardize the vegetation samples. We squared the mean point–plant distance to obtain the quadrant area and estimate the density of trees per hectare. We calculated the mean basal area from the CBH values.

Landscape attributes

We conducted a supervised classification by visual inspection (ESRI ArcGIS 9.3) using a fine resolution orthophotograph (0.6m) to determine the land cover within a 1000-m radius of the center of each focal patch. We considered this size of radius so that the landscape established around the focal patches were represented adequately for all the species and the buffer zones did not overlap with each other. We also considered the dispersal capacity in the matrix of congener species to those monitored in the present study (Glander, 1992; Mandujano et al., 2004). The land cover of a given area was assigned to one of six categories: forest, pasture, cropland, human settlement, non-forest vegetation, and water. We calculated the size of each focal patch, and its shape and the proximity index using 800 m as the specified distance from the focal patch (McGarigal, Cushman, & Ene, 2012). The proximity index increases as the neighborhood is occupied increasingly by patches of the same type, and as these become close to each other and more contiguous (or less fragmented) in their distribution. We also calculated the area and number (fragmentation level) of all the forest patches observed within the landscape (Fragstats v. 4.2), as well as the permeability matrix index (PI), based on Arroyo-Rodríguez et al., (2013b). The PI is calculated by multiplying the percentage of each land cover category within the landscape by its relative permeability. The permeability of a given type of land cover was defined by the similarity of its vegetation structure with that of the forest, weighted as follows: 1 (water, lowest permeability), 2 (human settlement), 3 (cattle pasture), 4 (cropland), 5 (non-forest vegetation) and 6 (forest, highest permeability). The PI values recorded in the present study ranged from 16.6 (100% of the matrix composed by water) to 100 (100% of the matrix composed by forest).

Data analysis

We used logistic regressions to test which patch and landscape characteristics best predicted patch occupancy by the different primate species sampled by playback survey. We selected the link-function binomial and the logit model, given that our response variable has the discrete probability distribution of the number of occurrences and non-occurrences of the species, and the logit function, which linearizes a logistic curve, is the most adequate for the general linear model fitting (Chatterjee & Hadi, 2006). To test for collinearity, we determined the Pearson correlation coefficient between all predictor variables (Table 1), and calculated the Variance Inflation Factor (VIF) for each predictor (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Correlations of over 0.8 were considered to be collinear (Tabachnick & Fidell, 2013), but no values this high were recorded in the present study. Values of VIF of over 4 indicate possible collinearity, and values above 10 indicate strong collinearity (Quinn & Keough, 2002).

Table 1. Pearson correlation coefficients among local, patch and landscape attributes used as occupancy predictors by *Alouatta caraya*, *Sapajus libidinosus* and *Callithrix penicillata* in the focal forest patches in the city of Goiânia, Goiás state, Brazil. * $p < 0.05$.

	Density	Size	Shape	Forest area	Number of patches	Matrix permeability	Proximity
Basal area	-0.48*	-0.31	0.18	0.23	-0.04	0.07	-0.07
Density		-0.13	0.20	-0.25	-0.03	-0.25	-0.35
Size			0.15	-0.15	0.03	0.60*	0.77*
Shape				-0.11	0.28	0.39	0.05
Forest area					0.30	0.29	0.23
Number of patches						0.18	0.22
Matrix permeability							0.59*

We tested three models based on (i) m1: local attributes (basal area and density), (ii) m2: patch metrics (size and shape), and (iii) m3: landscape metrics (forest area, number of forest patches, matrix permeability, and proximity). We tested the full models, but we do not present the results here because all the models presented a series of fundamental problems, including high levels of multicollinearity and low model fit. We adopted the Akaike Information Criterion for Second-Order Bias Correction (AICc) to select the most parsimonious model that contained the variables with the highest power of discrimination to determine the probability of patch occupancy by each primate species. This criterion is appropriate for samples of reduced size, and defines the best models as those with delta (Δ_i) values of between 0 and 2. Models with a Δ_i value of 4–7 are considered to be poorly supported, while Δ_i values higher than 10 essentially have no support (Burnham & Anderson, 2004).

We also used the corrected Akaike weight (wAICc) to assess uncertainty in the model selection. We used hierarchical partitioning to measure the specific importance of each variable in the best models. This approach quantifies independent correlation (R^2) of each predictor variable with the response variable (Chevan & Sutherland, 1991). The variables that independently accounted for a greater proportion of the variance than expected by chance were identified by randomization. For each randomization, the values in each independent variable are randomized independently, resulting in a matrix of values, on which a hierarchical partitioning is run. In relation to the randomized matrix, the function provides a summary table listing the observed values and its 95th and 99th percentile values. We ran this analysis in R v. 3.4.1 (R Core Team, 2017) using the packages bbmle (Bolker, 2017), hier.part (Walsh & Nally, 2013), car (Fox et al., 2019), MASS (Ripley et al., 2019), and AICcmodavg (Mazerolle & Linden, 2019). Statistical significance was set at the $p = 0.05$ probability level, although p values marginally higher than 0.05 were also discussed. We consider the best models to be those that presented an association between significant (or marginally significant) p values and Δ_i AIC values of up to approximately 4 (Burnham & Anderson, 2004). We used R^2 as a complementary approach (Chevan & Sutherland, 1991) to support the understanding of the relationship between the different metrics and species occurrence.

Results and discussion

We recorded the presence of all three primate species within the study landscape. The most common species was *C. penicillata*, which was recorded in 91% ($n = 20$) of the focal patches, followed by *S. libidinosus* and *A. caraya*, which were both found in 45% of the patches ($n = 10$) patches (Table 2). The analyses indicated that the patch (m2) and landscape (m3) models provided the most parsimonious explanation for the occupation of patches by *A. caraya* and *S. libidinosus* (Table 3; Table 4). In the case of occupancy by *S. libidinosus*, patch size and the permeability of the landscape matrix were the most important metrics, both having a positive effect. The occupancy of *A. caraya* was positively related to the number of forest patches in the landscape and to the focal patch shape, and negatively related to the amount of forest in the landscape. The focal patch shape and the amount of forest in the landscape had a marginally relationship (p value approximately 0.05). By contrast, none of the predictors had any clear influence on patch occupation by *C. penicillata*, which was presumably due to the widespread distribution of this species within the landscape.

Table 2. Area, Brazilian Cerrado phytophysiognomies, and primate occurrence records of the focal forest patches in the city of Goiânia, Goiás state, Brazil.

Site	Area (ha)	Phytophysiognomy	Primate occurrence		
			<i>Alouatta caraya</i>	<i>Callithrix penicillata</i>	<i>Sapajus libidinosus</i>
17	6.1	Riparian and Dry forest	1	1	0
29	7.1	Riparian and Dry forest	1	1	0
9	7.5	Cerrado <i>sensu stricto</i> , Riparian and Dry forest	0	1	0
20	7.7	Cerrado <i>sensu stricto</i> , Riparian and Dry forest	0	1	0
1	8.8	Cerrado <i>sensu stricto</i> , Riparian and Dry forest	0	1	0
26	9.7	Riparian and Dry forest	1	1	0
13	13.0	Dry forest	0	1	1
18	13.5	Riparian and Dry forest	1	1	0
5	14.6	Riparian and Dry forest	0	0	1
10	21.1	Riparian and Dry forest	0	1	1
14	22.8	Dry forest	0	1	0
2	23.9	Riparian and Dry forest	0	1	0
24	25.3	Dry forest	0	1	0
21	33.2	Cerradão, Riparian and Dry forest	1	1	0
7	35.7	Riparian forest	1	1	1
19	44.5	Dry forest	0	1	1
3	46.5	Dry forest	1	0	1
23	64.2	Riparian and Dry forest	0	1	1
28	73.3	Riparian and Dry forest	1	1	1
12	76.9	Riparian and Dry forest	1	1	0
25	95.0	Riparian and Dry forest	1	1	1
4	107.0	Riparian and Dry forest	0	1	1

Table 3. Models used to evaluate the predictability of forest patch occupancy by *Alouatta caraya*, *Sapajus libidinosus* and *Callithrix penicillata* in the landscape of Goiânia, Brazil, based on local, patch and landscape attributes. The best models are highlighted in bold types, and R² is only presented for the best models.

Species / Spatial scale	Model	Predictor	Parameter	Z	p	VIF	Δi AICc	wAICc	R2
<i>Alouatta caraya</i>									
Local	m1	Basal area	-0.0001	-0.032	0.97	1.1	6.0	0.04	
		Density	-0.0005	-0.331	0.74	1.1			
Patch	m2	Size	0.002	0.181	0.85	1.0	0.0	0.87	9.2
		Shape	1.358	1.691	0.09	1.0			90.8
Landscape	m3	Forest area	-0.138	-1.775	0.07	1.7	4.7	0.08	52.2
		Number of patches	0.653	1.922	0.05	1.8			45.5
		Matrix permeability	0.021	0.329	0.74	1.3			0.9
		Proximity	-0.006	-0.367	0.71	1.5			1.3
<i>Sapajus libidinosus</i>									
Local	m1	Basal area	-0.006	-1.428	0.15	1.4	6.6	0.02	
		Density	-0.001	-1.004	0.31	1.4			
Patch	m2	Size	0.059	2.173	0.02	1.2	0.0	0.69	85.7
		Shape	-0.783	-1.128	0.25	1.2			14.3
Landscape	m3	Forest area	0.016	0.293	0.76	1.1	1.8	0.28	3.2
		Number of patches	-0.811	-1.629	0.10	2.4			18.6
		Matrix permeability	0.245	2.182	0.02	2.2			68.3
		Proximity	0.003	0.188	0.85	1.4			9.8
<i>Callithrix penicillata</i>									
Local	m1	Basal area	-0.003	-0.688	0.49	1.2	0.0	0.66	
		Density	-0.003	-1.307	0.19	1.2			
Patch	m2	Size	0.002	0.087	0.93	1.0	1.7	0.27	
		Shape	0.366	0.400	0.68	1.0			
Landscape	m3	Forest area	-0.096	-1.100	0.27	2.2	4.9	0.05	
		Number of patches	0.255	0.512	0.60	1.2			
		Matrix permeability	-0.124	-0.945	0.34	1.0			
		Proximity	0.084	1.077	0.28	2.0			

The three primate species presented distinct levels of occupancy within the study landscape in the Brazilian Cerrado. Howlers and capuchins were both encountered in less than half of the focal patches, whereas the marmosets were found in almost all of them. Within the rural-urban landscape gradient, the

howlers and capuchin monkeys may have a more restricted occupation of the landscape in comparison with the marmosets, whose ample distribution and ecological plasticity has been documented in other urban centers (Duarte & Young, 2011; Goulart, Teixeira, & Young, 2010) and in remnants of the original forest (Hilário & Ferrari, 2015). This may indicate a significant difference in the landscape requirements of howlers and capuchins in the anthropogenic matrix of the Brazilian Cerrado, in comparison with the marmosets (Hoffman & O’Riain, 2012).

Table 4. Mean, standard deviation (SD), minimum (Min), and maximum (Max) values of local, patch and landscape attributes among the focal forest patches in the city of Goiânia, Goiás state, Brazil.

Scale	Metric	Mean \pm SD	Min–Max
Patch	Size	34 \pm 30	6 – 107
	Shape	2 \pm 1	1 – 8
Landscape	Forest area	15 \pm 13	0 – 54
	Number of patches	4 \pm 2	1 – 8
	Matrix permeability	54 \pm 9	35 – 70
	Proximity	25 \pm 44	0 – 170

Specific patch metrics and landscape attributes influenced patch occupancy by howlers and capuchins. Patch size and matrix permeability were important predictors of capuchin occupancy. Under natural conditions, capuchins live in large groups (12 to 27 individuals), with relatively large home ranges, of 161 ha, on average (Fragaszy et al., 2004). Where habitats have been fragmented and impoverished, larger patches may increase the potential for the occurrence and persistence of capuchin populations (Carretero-Pinzón et al., 2017; Mota, Leite, & Martins, 2018). Given the ability of capuchins to cross open areas in the landscape matrix (T. O. Grande, personal observation), in addition, a more permeable matrix would also facilitate access to adjacent forest patches, amplifying the range of resources available to a resident capuchin group (Hendges, Melo, Gonçalves, Cerezer, & Cáceres, 2017; Silva et al., 2015). In this scenario, dynamic capuchin groups would be able to exploit more effectively resources distributed heterogeneously or seasonally within the fragmented landscape.

Capuchins are likely to be prevalent and persist over the long term in more rural landscapes in comparison with less hospitable urban landscapes, given the greater potential for dispersal among patches and groups (Estrada et al., 2012), as well as their considerable behavioral and ecological flexibility. In an analysis of the similarity of mammal communities among isolated forest patches in the fragmented landscape of the southwestern Cerrado, medium- and large-sized mammals (including *S. libidinosus*) were able to move between patches regardless of the size, degree of isolation or vegetation structure of these forest remnants (Cáceres, Nápoli, Casella, & Hannibal, 2010). In this case, movement would be facilitated by the permeability of the pasture matrix. A number of other studies (Michalski & Peres, 2005; Sorensen & Fedigan, 2000) have also recorded other species of capuchins moving over large distances in fragmented landscapes, often along unconnected corridors in both grassland and degraded forest habitats.

For the howlers, patch shape and the number and area of forest patches appear to be the principal predictors of occupancy. The more irregular its shape, the greater the probability of the occurrence of howlers in the patch. In the study region, fragments of gallery forest tend to be the most irregularly shaped. Howlers may be associated with gallery forests due to both the resources they offer and their connectivity, given that the anthropogenic matrix tends to be less permeable (Arroyo-Rodríguez et al., 2013b). Howlers were prevalent in areas with a high level of fragmentation, but a smaller total area of forest. This may reflect the tolerance of these monkeys to habitat loss and fragmentation, which typically results in a reduction of the area of forest and an increase in the number of patches (Fahrig, 2003). While habitat fragmentation may limit the dispersal capacity of *A. caraya* (Oklander, Kowalewski, & Corach, 2010; Oklander & Corach, 2013), a larger number of more closely-spaced patches may facilitate movements by providing stepping-stones of habitat (Clarke, Collins, & Zucker, 2002; Pozo-Montuy et al., 2011), especially considering the ability of the howlers to move over the ground (Serio-Silva, Ramírez-Julián, Eppley, & Chapman, 2019). It is important to note, however, that this apparent tolerance of habitat loss and fragmentation may actually represent the delayed or time-lagged extinction of populations (Michalski & Peres, 2005; Sales et al., 2015). While howler populations may persist in the short term, then, even in disturbed patches, both occupancy and overall density may decline over the medium to long term (Zunino, Kowalewski, Oklander, & González, 2007).

In contrast with the other two species, no significant influence of any predictor was found on patch occupancy by *C. penicillata*. In patches of native vegetation of the Brazilian Atlantic forest and Cerrado, Sales et al. (2016) also observed a high occupancy level for marmosets, which did not exhibit a clear relationship with any predictors at either a local or landscape scale. This might be accounted for by the considerable ecological flexibility of the marmosets of this genus (Abreu, De la Fuente, Schiel, & Souto, 2016; Amora, Mendes, & Ferrari, 2013), which allows them to colonize successfully both open and disturbed forests. Black-tufted marmosets are highly opportunistic, and may maintain a high reproductive output, even in extremely degraded habitats, which contributes to their adaptability to urban development (Vilela & Del-Claro, 2011). The ability of these marmosets to survive in urban habitats may be determined, in part, by their capacity to exploit readily-available resources, such as cultivated fruit trees and garbage (Goulart et al., 2010; Miranda & Faria, 2001; Secco et al., 2018; Vilela & Faria, 2002). This species also has a considerable dispersal capacity, being able to move short distance across the ground between forest patches or even individual trees, which may act as stepping-stones within the urban matrix.

The local scale attributes did not influence the probability of occupancy of any of the primate species. All three species used features of the anthropogenic matrix, such as gardens, orchards, and plantations, to obtain resources or move between patches (T. O. Grande, personal observation; Arroyo-Rodríguez et al., 2013b; Pozo-Montuy et al., 2011), which may contribute to their persistence in patches of varying structure and conditions (Cáceres et al., 2010; Michalski & Peres, 2005). The plant diversity or the variation in the availability of food sources in the rural-urban landscape (Arroyo-Rodríguez & Dias, 2010) may also contribute to patch occupancy in these primates (Boyle & Smith, 2010; Cristóbal-Azkarate, Veà, Asensio, & Rodríguez-Luna, 2005; Zunino, González, Kowalewski, & Bravo, 2001). In this case, a more systematic analysis of the availability of resources in both the forest patches and the surrounding matrix would be essential for a more definitive understanding of the determinants of habitat use by primates in this landscape.

Restoring landscapes to compensate for habitat loss and fragmentation is a major challenge for conservation planning. *A priori*, conservation measures should focus on the current conditions that most favor the target species or group of organisms. While all the species analyzed in the present study are considered to be tolerant to habitat disturbance (Lessa, Alves, Geise, & Barreto, 2012), we demonstrated that certain specific features of the landscape may be potentially more important for the conservation of this group in the context of the rural-urban habitat gradient of the central Brazilian Cerrado. The results of the present study indicate clearly that the preservation of remaining patches, both large and small, and in particular the gallery forests, as well as ensuring matrix permeability, are priority measures for the conservation of all three primate species. If habitat loss and fragmentation continue at present rates, however, the persistence of populations in local patches will certainly be challenged (Arroyo-Rodríguez & Dias, 2010; Hendges et al., 2017).

The preservation of large forest patches would better safeguard wildlife habitat, and could eventually support reintroduction projects (Arroyo-Rodríguez & Mandujano, 2009; Chiarello, 2000), whereas smaller ones can play an important role as stepping stones, increasing landscape connectivity (Pardini et al., 2005; Tulloch, Barnes, Ringma, Fuller, & Watson, 2016). It will also be important to maintain legally-sanctioned areas, including obligatory areas of permanent preservation, such as gallery forests, which will be fundamental to the persistence of mammals associated with riparian forest, such as *A. caraya*, as shown in the present study (Galetti et al., 2010; Johnson, Saraiva & Coelho, 1999). Maintaining or even increasing the permeability of the matrix, which could be achieved by the planting of hedgerows or even isolated trees (Estrada et al., 2006), would contribute to the movement capacity and foraging potential of the species within the landscape (Arroyo-Rodríguez et al., 2013b; Arroyo-Rodríguez et al., 2017; Kennedy, Zipkin & Marra, 2017). Our findings contribute to the development of landscape-specific management strategies that will guarantee the conservation of primate populations facing high levels of habitat fragmentation.

Conclusion

This study assessed the effects of local, patch, and landscape scale attributes on the occupancy of forests patches by the *Alouatta caraya*, *Sapajus libidinosus*, and *Callithrix penicillata*, in a fragmented landscape within the Cerrado, Brazil. The main results were that the occupancy of the *A. caraya* was influenced by the shape of the focal patches, the amount of forest and fragmentation level of the landscape. In *S. libidinosus*,

focal patch size and the permeability of the matrix were the principal determinants of the occupation, while for the *C. penicillata* the occupancy was not determined by none of the predictors evaluated.

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