

Spatiotemporal ecology of two Neotropical herbivorous mammals

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Abstract. On this study, we used camera traps in a Semi deciduous Seasonal Forest, northeast of Brazil, to estimate the frequencies of occurrence of two Neotropical herbivorous mammals: the spotted paca (*Cuniculus paca*) and the tapeti (*Sylvilagus brasiliensis*), analyzing their seasonal variations of spatial distribution. We also characterized the activity pattern of the species and their seasonal variation. The herbivorous frequencies of occurrence were constant during all the seasons. In general, both species were mostly active at night. However, between the rainy and dry season, we identified differences in spotted paca activity peaks. Here we present one of the first studies on the tapeti, whose ecology is understudied. Our results also show a general view of the spotted paca and tapeti behavior strategies to seasonal variations. Due to the scarce food resource in the dry season, possibly these herbivorous need to search for different kinds of food available IFS around.

Key-Words. *Cuniculus paca*; *Sylvilagus brasiliensis*; Agroforestry mosaic; Distribution patterns; Activity patterns.

INTRODUCTION

At seasonal climatic environments, the main resources availability reduces because of increasing dry season (Thrash *et al.*, 1995). Thus, when resources become scarce, animals are forced to aggregate near them (Valeix *et al.*, 2007). Consequently, species tend to exhibit behavioral adjustments to deal with these adverse conditions (Thrash *et al.*, 1995; Ferregueti *et al.*, 2017). Behavior is a variable phenotype resulting from interaction between environmental changes and the animal's internal state (Morgan, 2004). In this sense, the combination of seasonal variations in the environmental conditions such as temperature and availability of food can also cause changes in species activity patterns (Pita *et al.*, 2011). Daily activity patterns of many tropical animals are known in general terms (*i.e.*, whether a species is mostly nocturnal or diurnal) (*e.g.*, Emmons & Feer, 1997) but details of these patterns are less well described.

The spotted paca *Cuniculus paca* (Linnaeus, 1766) and tapeti *Sylvilagus brasiliensis* (Linnaeus, 1758) are Neotropical herbivorous mammals and sympatric in most of their distributions (AMCELA *et al.*, 2008; Emmons, 2016). The spotted paca

lives in different forest types, such as mangroves, semi deciduous forests and savannas (Oliveira & Bonvicino, 2011). It occurs mainly at gallery forests close to rivers and other bodies of water, where it builds its own burrow or rests in shelters of other species (Emmons, 2016; Figueroa-de-León *et al.*, 2017). The spotted paca is a territorial and solitary animal and it is eventually seen in pairs (Pérez, 1992). Its activity pattern is predominately nocturnal (Michalski & Norris, 2011; Dias *et al.*, 2018) and its diet could vary according to seasonality. It is an opportunistic herbivorous with preference to fruits (Pérez, 1992; Dubost & Henry, 2006).

The tapeti is a generalist mammal occupying from deciduous and secondary forests to open areas (Chapman & Flux, 1990). It commonly lives at transition environments among forests, open fields and the edge of watercourses (AMCELA *et al.*, 2008; Reis *et al.*, 2011). It has crepuscular and nocturnal habit and its diet is based on fruits, leaves, roots and seeds. (Reis *et al.*, 2011). Although it has been commonly recorded at wildlife inventories and most of tropical forest sites are included into its occurrence area, its ecology has unfortunately been neglected (Silva Júnior *et al.*, 2005; Dantas *et al.*, 2016; Andrade & Hernández, 2017).

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Thus, it is fundamental to understand the behavioral adjustments of these herbivores to environmental changes. Our objectives were: 1) Evaluate the seasonal variation of the frequency of occurrence and distribution of spotted paca and tapeti, in a semi deciduous forest; 2) Characterize their activity patterns, and investigate possible changes in temporal activity between rainy and dry seasons.

MATERIAL AND METHODS

Study area

We conducted this study at a semi deciduous Atlantic forest patch of ~ 400 ha with different stages of succession, including patch of the oil palm *Elaeis guineensis* Jacq. and secondary vegetation (capoeira). The area belongs to Federal Institute of Education, Science and Technology of Sergipe (IFS), São Cristóvão (Fig. 1). The region presents hot and humid weather with the rainy season from March to August (autumn and winter) (INPE, 2018). The average annual rainfall is of 1,500 mm, and 73% of this volume falls during the wet season, following historical data from the Secretaria de Estado do Meio Ambiente e dos Recursos Hídricos of Sergipe. The fragment is located within the metropolitan region of Aracaju, the Sergipe state capital, and it is surrounded by a matrix of mixed farmland.

Sampling

We sampled a total of 33 camera sites (*i.e.*, our sampling units), randomly selected within of the forest patch. The mean distance between two simultaneously active cameras was 665 m. One camera was placed at each site for 32 consecutive days in mean and operated for 24 h. Due to the limited number of cameras, we rotated cameras among sites within patch. Specifically, we deployed cameras at 2 sites for 32 consecutive days (on average), then we moving cameras to another 2 sites within the patch. We repeated this process until all 33 sites were sampled. Unfortunately, on two occasions had stolen equipment problems, which compromised our sampling effort. We carried out this study during 21 months from July 2015 to August 2017. We did not use baits to attract animals. We defined as frequency of occurrence (FO) of spotted paca and tapeti the number of independent records for each species divided by the total sampling effort (in days), during the entire study.

Data analysis

Although the studied species have average home ranges lower than 4 ha (Swihart, 1986; Benavides *et al.*, 2017), we tested whether the species FO would be correlated with the distances between the camera sites. As

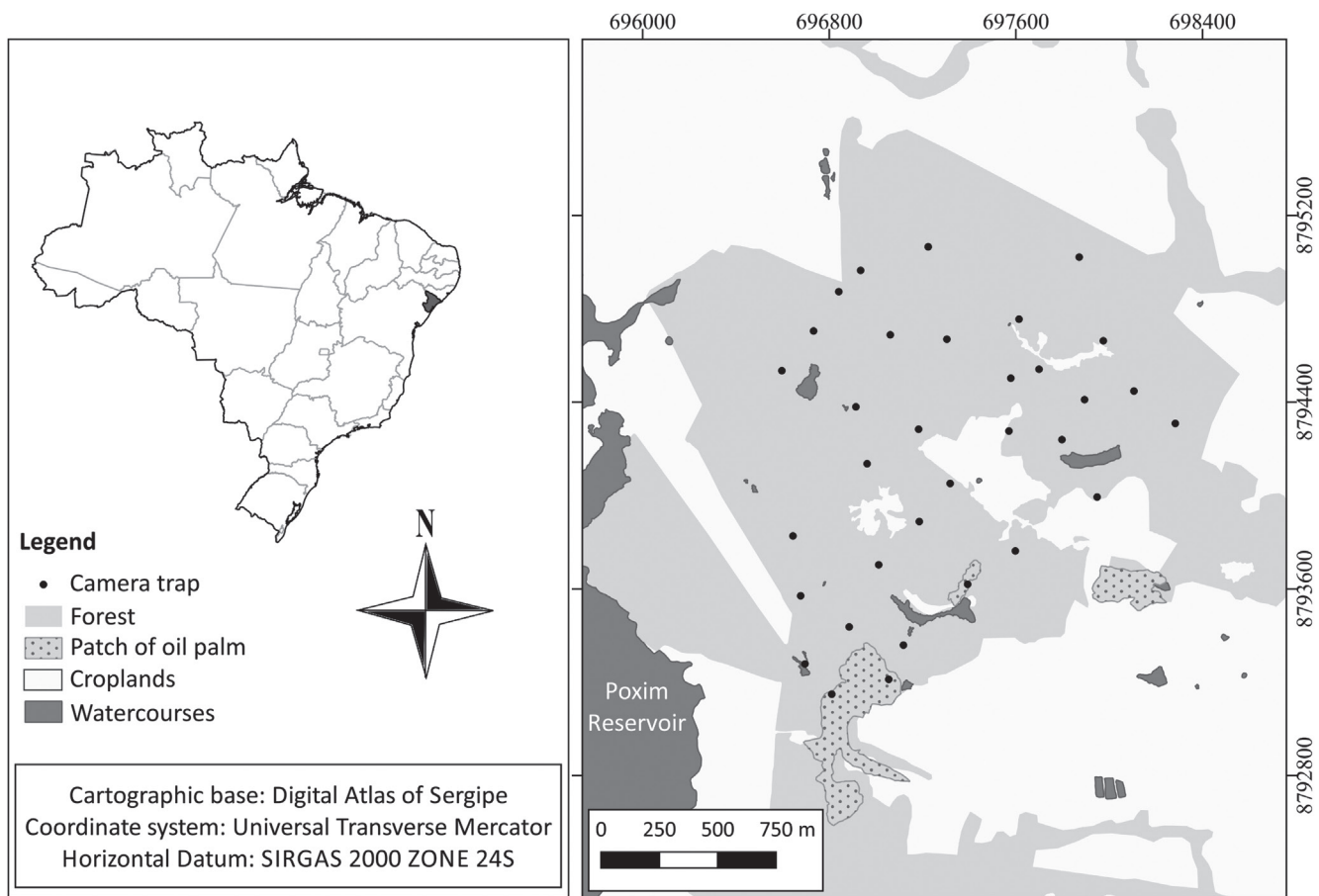


Figure 1. Forest Fragment location at the Federal Institute of Sergipe (IFS), São Cristóvão, SE. The insertion at the top-right hand corner represents the Brazilian territory with a highlight to Sergipe state (on dark gray).

the distance from camera sites not was highly correlated with the frequency of occurrence that from both spotted paca and tapeti ($r = -0.09$; $p = 0.58$ and $r = 0.22$; $p = 0.21$ respectively), we treated the camera trap sites as sampling units, assuming that the catch rates were independent due to their spacing.

We also assumed that all the capture events of the species ≥ 1 h of interval were independent (Goulart *et al.*, 2009; Dias *et al.*, 2018). To verify the variation of the species occurrence between the wet and dry season, we plotted maps to illustrate the individual distributions of spotted paca and tapeti. Additionally, we verified possible seasonal differences in the FO of each species through the nonparametric Mann-Whitney test (U).

To describe the activity pattern of the species, we turned the activity records of each species into solar time, with the objective of adjusting the real time to the circadian cycle of the species (Linkie & Ridout, 2011). We used the sunrise and sunset time of the study site to define the time adjustment and its transformations, through the Tropsolar 5.0 Software (Cabús, 2015). We categorized the activity of each target species as being predominantly nocturnal when most of the activity occurred between 1 h after the sunset and 1 h before the sunrise. For strictly nocturnal species, we considered the ones whose activity periods were exclusively recorded during the night (Dias *et al.*, 2018, 2019a). We defined the cathemeral period occurring between 1 h before and after sunrise and sunset (see Massara *et al.*, 2018).

Through the time records, we determined the general activity pattern of spotted paca and tapeti in the IFS. We determined the diurnal cycle distribution of the camera traps records of each species using circular statistics, which tests if the set of angles (the records for each hour of the day) is evenly distributed (Zar, 2010). We verified the uniformity of the circular distribution of the collected records during the study period using Rayleigh Test (Z) through the Oriana software 4.01 (Kovach Computing Services, Anglesey, UK). Using the Overlap package (Meredith & Ridout, 2014), we estimated the density of the activity of each species using the kernel density, a nonparametric approach that evaluates the probability function of the density of a random variable (Worton, 1989) through R software (R Development Core Team, 2017). To complement this analysis, we compared the 24-hour cycles of the species between rainy and dry seasons using the Mardia-Watson-Wheeler test (W), run in Oriana 4.01 (Kovach Computing Services, Anglesey, UK).

RESULTS

We had 106 records of spotted paca and 69 of tapeti (totaling 175 independent records). The spotted paca frequency of occurrence between the rainy season (FO = 0.07) and the dry season (FO = 0.12), was not significantly different (U = 190.5; $p = 0.25$). However, its distribution was limited only at a few sites during the dry season (Fig. 2). We also did not find differences on the tapeti frequency of occurrence (U = 183; $p = 0.43$) be-

Table 1. Rayleigh's uniformity test (Z) for the temporal activity; value of Z tabulated for significance level of 0.05 ($Z_{critical}$), based on the number of independent records (N) collected for each species. The classification of the activity was based on the proportion of observations in each period of the circadian cycle.

Species	Z	p	$Z_{critical}$	N	Distribution	Activity
Rainy season						
Spotted paca	24.4	5.6×10^{-11}	2.97	41	Non-uniform	Strictly nocturnal
Tapeti	15.3	2.3×10^{-7}	2.98	50	Non-uniform	Predominantly nocturnal
Dry season						
Spotted paca	29.8	1×10^{-12}	2.98	65	Non-uniform	Predominantly nocturnal
Tapeti	6.8	6.5×10^{-4}	2.95	19	Non-uniform	Predominantly nocturnal

tween the rainy season (FO = 0.09) and the dry season (FO = 0.03). Its distribution followed the same pattern previously observed for spotted paca in this work (Fig. 2).

The Rayleigh Test (Z) showed that the daily activity of the two species did not followed a uniform distribution (Table 1). In general, the small herbivorous presented activity predominately nocturnal (observations > 60%). During the rainy season, only the spotted paca presented an activity pattern strictly nocturnal (100% of the records). Despite the predominantly nocturnal pattern (88%), tapeti presented a considerable crepuscular activity with 22% of the records in this period. During the dry season, the spotted paca was mostly active at night (92% of records), but with some records at crepuscular periods (8%). The tapeti activity followed similar pattern to the rainy season, with 79% of their records during the nocturnal period.

The W Test showed significant differences among the circadian distributions of the spotted paca between rainy and dry season (W = 7.74; $p = 0.02$; Fig. 3A), but there were no differences on the distribution of the daily records of the tapeti between seasons (W = 2.67; $p = 0.26$; Fig. 3B).

DISCUSSION

The frequency of occurrence of the small herbivorous did not vary with the climatic seasonality at the study site, suggesting that the spotted paca and tapeti abundances were constant during the year. Although, our sample design did not allow us to estimate the real abundance of species, studies indicate that there is a correlation between the photographic rate measured in terms of traps/day and the abundance of the animals (Carbone *et al.*, 2002). In fact, both as spotted paca and tapeti could reproduce from two to three times a year (Chapman & Flux, 1990; Pérez, 1992). These breeding taxes could explain our results for the constant frequencies of occurrence found during this study.

We identified a seasonal variation on the species distribution at IFS. During the rainy season, numerous small lagoons were found as well as a great diversity of fruits, such as *Byrsonima* sp. L., *Eugenia candolleana* DC., *Genipa americana* L. and *Licania tomentosa* Benth, *Talisia esculenta* (A. St.-Hil.) Radlk. This could benefit the wide

use of the area by the mammals. On the other hand, during the dry season, only the greatest lagoons had water and just few arboreal species could bear fruits, such as *Mangifera indica* L. and the oil palm *Elaeis guineensis* Jacq. Considering the water availability as a relevant factor on the structure of mammal communities, due to its influence on the species distributions (Ferregueti *et al.*, 2017; Dias *et al.*, 2019b), a variation on its availability could influence the distribution of the small herbivorous at IFS, mainly the spotted paca. Thus, the spotted paca selectively used the forest fragment at IFS, during the dry season, probably due to the reduction of the superficial water sources. The proximity to permanent watercourses has been described as a key-variable for the selective

use of burrows by spotted paca (Figuroa-de-León *et al.*, 2017). In the same way, hydric bodies have been the main habitats elements related to the reproduction of this rodent. (Figuroa-de-León *et al.*, 2017). Therefore, the low lagoons availability during the dry season reflects on the reduction of its distribution at IFS.

Alternatively, the low fruits availability during the dry season can also explain the reduction on the spotted paca and tapeti distributions. Some studies showed that food availability drives the spatial behavior in small mammals (Schradin & Pillay, 2006; Cooper & Randall, 2007; Quirici *et al.*, 2010). Spotted paca and tapeti feed largely on fruits; however, these species are opportunistic and could adjust their diet according to seasonal

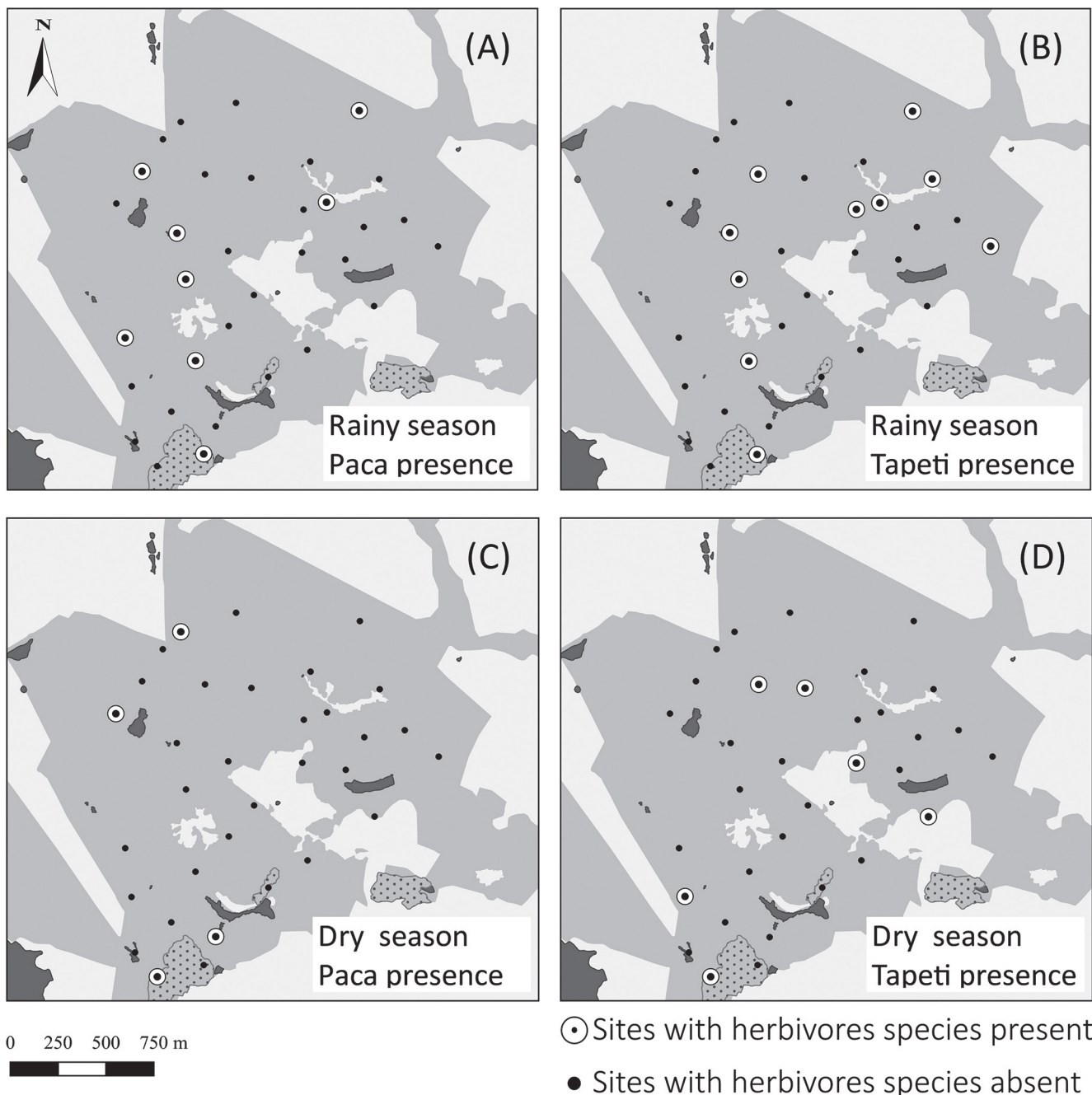


Figure 2. Individual distributions of spotted paca and tapeti at a forest fragment at IFS, São Cristóvão, SE, Brazil. We collected the data through camera traps records at 33 sample sites from July 2015 to August 2017. The presence of each species was inferred from species camera trap records from each sample site, while the absence of the species was inferred by the lack of these records.

variations of the food availability (Dubost & Henry, 2006; Reis et al., 2011). Nonetheless, during the dry season, the spotted paca was mostly active at sites close to oil palm patches *Elaeis guineensis* Jacq and to the forest fragment edge. Although it was described as typical of the forest (Pérez, 1992; Oliveira & Bonvicino, 2011), in agroforestry systems in the Bolivian Amazon, Benavides et al. (2017) showed that the species tended to be more abundant at agricultural crops than in secondary forests. This corroborates with the distribution of this rodent at IFS during the dry season, once the surrounding matrix is mostly composed by sugar cane and corn fields and orchards of species of fruit trees, such as *Anacardium occidentale* L., *Passiflora edulis* Sims, *Annona squamosa* L., *Malpighia emarginata* DC. and *Annona muricata* L., that bear fruits at different periods of the year and they could represent an important food resource for spotted paca in this season. The tapeti is more flexible than spotted paca in the habitat use. It lives typically at open areas, forest edges and it could live at perturbed areas (Silva Júnior et al., 2005; Reis et al., 2011). Therefore, during the rainy season, when the native fruits are available, the tapeti occurs more in the forest interior but during the dry season, it tends to be more frequent at the forest edge sites, probably due to its search for alternative food resources.

The activity pattern for spotted paca and tapeti found here corroborates with previous studies that indicated a predominately-nocturnal activity for these species (Blake et al., 2012; Dias et al., 2018). During the rainy season, the

spotted paca was strictly nocturnal, while tapeti was predominately nocturnal. On this season, the spotted paca presenting a peak of activity at 00:00 h and the tapeti showed a constant activity during the nocturnal period. During the dry season, the spotted paca shifted its activity pattern, exhibiting a bimodal pattern with peak periods of activity at 03:00 h and 20:00 h. This seasonal variation on the spotted paca activity could be due to the low food availability during the dry season, making the species to increase its activity period during the night for searching food.

Here we present one of the first studies on the tapeti, whose ecology is understudied. Our results also show a general view of the spotted paca and tapeti behavior strategies to seasonal variations. Due to the scarce food resource in the dry season, possibly these herbivorous need to search for different kinds of food available IFS around.

Given that the spotted paca and tapeti could be considered as a target group for the conservation efforts due to its influence on the community diversity and structure, just as on the plants recovering through the seed dispersion and predation (Wright et al., 2000). Future studies should be done at areas with different degree of disturbances in order to evaluate the influence of habitat perturbation on these species behavior. In addition, trophic data can provide additional information on the ecology of these mammals.

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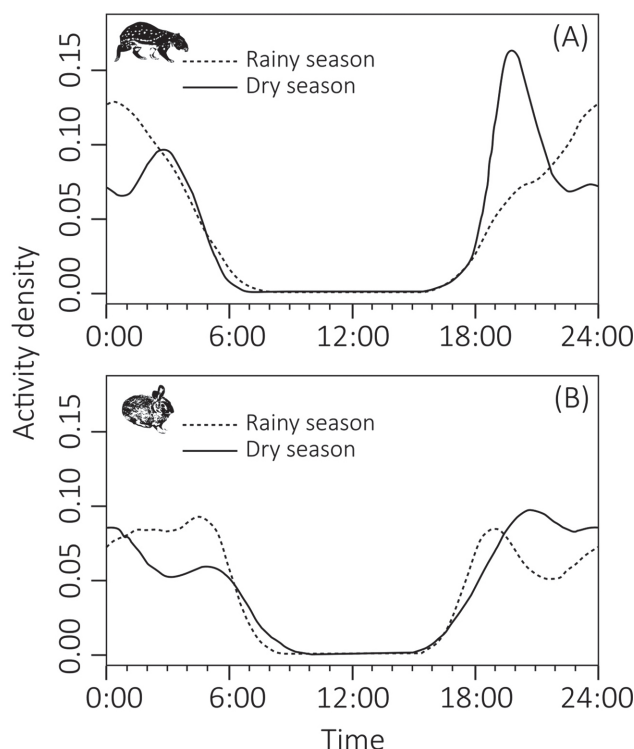


Figure 3. Activity density pattern of the spotted paca (A) and tapeti (B) during the rainy and dry seasons, at a forest fragment, IFS, São Cristóvão, SE, Brazil. The X-axis shows the time of the day. During the rainy season, the average sunrise time was at 06:15 and average sunset time at 17:45. For the dry season, the average sunrise time was at 05:45 and the average sunset time was at 18:15.

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