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Temporal and spatial segregation between mammal predators and their prey in a Brazilian Conservation Unit (PARNASO)

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Abstract

Time and space are niche dimensions that allow local coexistence of predators and their prey. Daily activity patterns are a crucial component of mammalian ecology and behavior, and temporal avoidance is often being regarded as the most important mechanism of coexistence among species. However, temporal overlap alone does not define the vulnerability of the prey or the preference of the predator, since there must also be spatial segregation, which can alleviate possible hostile interactions among animals. In this study, we tested whether there are any significant differences between temporal and spatial activity patterns of predators (*Leopardus wiedii* and *Puma concolor*) and prey (*Sylvilagus brasiliensis*, *Cuniculus paca* and *Didelphis aurita*). We used the camera-trapping data to test if the predator's species had less occurrence than expected by chance in Parque Nacional da Serra dos Órgãos (PARNASO), a protected area of the Brazilian Atlantic Forest. We used a measure of spatial segregation (C-score) and a Kernel Density Function to determine predators and preys time of activity and whether a pair of species occurred simultaneously. In addition, we calculated a coefficient of overlap between predators and prey. We found low values of C-Score in all analyses, which means high spatial co-occurrence and lack of spatial segregation among predators and their potential prey. Also, the Kernel Density Function showed that predators had more cathemeral activity while prey were mainly nocturnal. We thus show that temporal segregation is more important than spatial segregation in the study area. Our results suggest that predators are most likely to adjust their activity patterns based on the behavior of their main prey rather than to avoid competition with other species.

Key words: Brazilian Atlantic Forest, Competition, Neotropical mammals, theory of niche.

1. INTRODUCTION

One important mechanism of coexistence among species is temporal segregation (e.g. Bianchi et al. 2016; Marinho et al. 2020). Temporal segregation generally occurs with weaker species being active at times of the day when there is a lower probability of encountering a stronger competitor (Polis et al. 1989). This strategy contributes to the avoidance of hostile encounters among animals, which minimizes competition levels, reduces the chance of intraguild predation (killing and sometimes eating potential competitors) and reduces interspecific killing among mammalian carnivores (Marinho et al. 2020). Evaluating temporal segregation between species is thus fundamental to understand how species interact in highly diverse environments.

Species can also differentiate their niches by consuming different prey or using other parts of the environment (Castillo-Ruiz et al. 2012). Therefore, biotic factors causing niche shifts include predator-prey relationships (Hut et al. 2012). Temporal "overlap" between predators and prey can lead to predators being able to hunt prey (Guiden et al. 2019). Conversely, temporal niche shifts can enable prey species to avoid times of increased predation risk (Castillo-Ruiz et al. 2012; Hertel et al. 2017). According to Schoener (1974), predators are more likely to show more variation in temporal patterns compared to other groups, because they are active at different times of the day. That is, predators can be cathemeral (their active behavior varies between day and night). On the other hand, prey can be nocturnal to avoid predators.

Temporal overlap alone does not define the vulnerability of the prey or the preference of the predator, as there could also be spatial segregation (Marinho et al. 2020). Spatial segregation refers to a coexistence mechanism where individuals display differential use of space. Previous research has shown that spatial segregation may be more important than temporal segregation alleviating possible hostile interactions among individuals of carnivore species such as *Puma concolor* and *Panthera onca* (Contreras-Díaz et al. 2021), Thus, the high overlap of daily activity among species does not always mean that they will meet, because they may use different environments (Marinho et al. 2020). In addition, optimal foraging theory predicts that animals will search and exploit food resources in a way they can maximize net energy intake while reducing costs (MacArthur and Pianka 1966; Botts et al. 2020). However, in the predator-prey relationship, prey should avoid risky locations even when it compromises energy intake (Lima 2002; Eriksen et al. 2011). Despite its importance, the theory of how predation affects species spatial and temporal activity patterns is much less developed than the competition theory (Schoener 1974).

In this study, we evaluate temporal and spatial activity patterns of predators and their prey in one study area of the Brazilian Atlantic Forest. We tested if there are any significant differences among the daily activity patterns of predators (*Leopardus wiedii* and *Puma concolor*) and prey (*Sylvilagus brasiliensis*, *Cuniculus paca* and *Didelphis aurita*), expecting to find temporal and spatial segregation between them. We used null models to test if their spatial co-occurrence is less than expected by chance. We then used the Kernel Density Function to analyze predator and prey time of activity.

2. MATERIAL AND METHODS

2.1. Study area

The study area is the Parque Nacional da Serra dos Órgãos, a Protected Area (PA) that is part of the Mosaico da Mata Atlântica Central Fluminense (MCF), located on the State of Rio de Janeiro. The Protected Area is located in a region with the highest species richness of mammals (384) recorded in the Southeast region (Figueiredo et al. 2021). Camera traps (Tigrinus and *Bushnell*) were distributed in 21 stations, each containing two camera traps facing each other (Figure 1). The stations were approximately three kilometers apart. Camera traps were active for 120 days, working 24 hours a day, from May 27 to September 24, 2013.

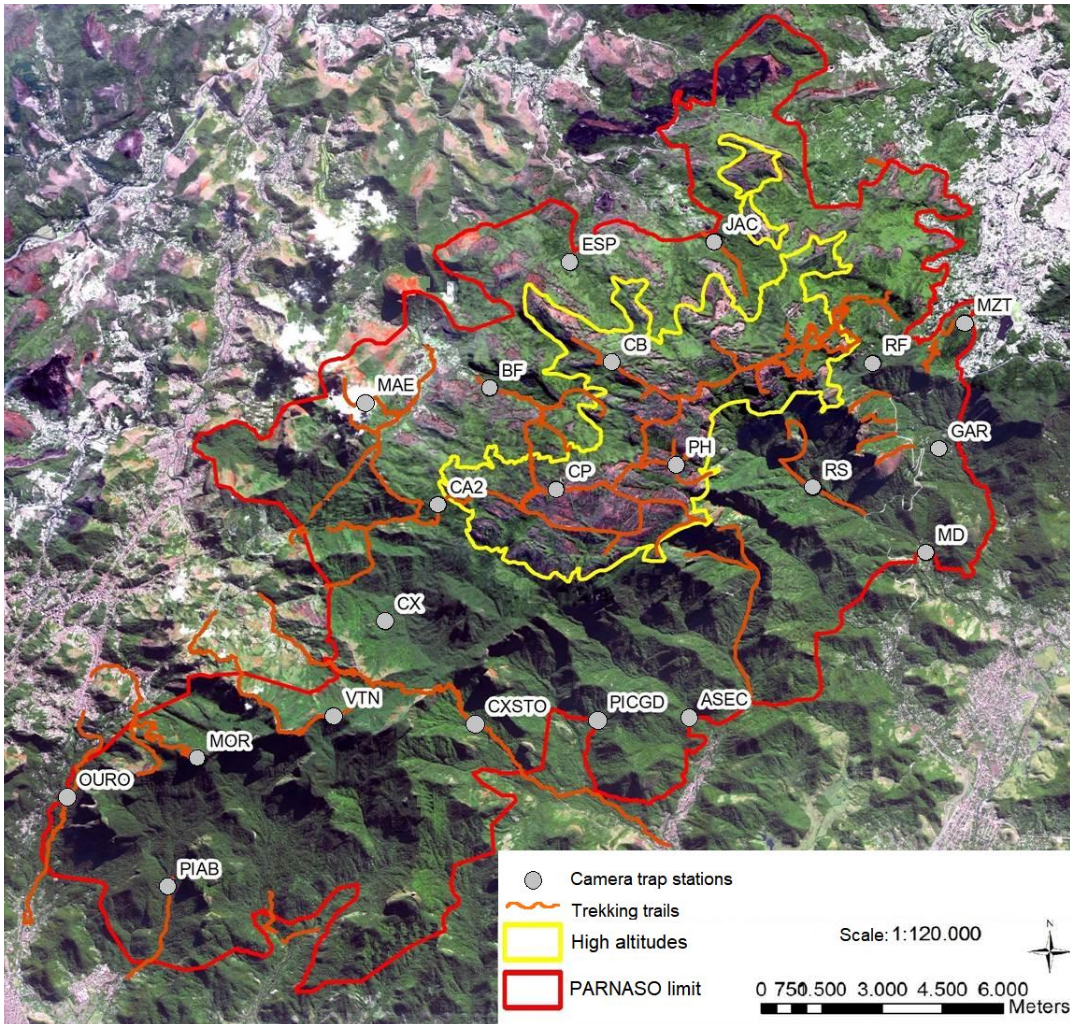

FIGURE 1. Limits of Parque Nacional da Serra dos Órgãos, Brazil, with the camera traps stations. The acronyms next to the camera trap stations are the names given to each trail so they could be identified in the database.

2.2 Data analysis

To analyze spatial and temporal overlap between predators and prey, we chose the five species with most records (*S. brasiliensis* with 23 records, *C. paca* with 59 records, *Didelphis aurita* with 163 records, *L. wiedii* with nine records, *P. concolor* with 29 records). Two of them are predators (*P. concolor* and *L. wiedii*) and the other three are prey (*S. brasiliensis*, *C. paca* and *D. aurita*). Following Marinho et al. (2018), we discarded records of each species captured at the same station at intervals of less than one hour to minimize the risk of recording the same individual twice.

We used a spatial segregation index (C-score) to determine whether a pair of species occurred simultaneously. C-score (CU) is calculated by the formula $CU = (R_i - S) \times (R_j - S)$, where R_i represents the number of sites where species i occurs, R_j is the number of sites where species j occurs, and S corresponds to the number of sites where both occur together (Varzinczak et al. 2016). The C-Score ranges from 0 (when the two species are maximally aggregated) to a maximum of R_iR_j (when both species are maximally segregated, not sharing any sites) (Gotelli; Hart; Ellison 2015). If the C-Score observed is higher than expected by chance, this means that the community is structured by interspecific interactions (Varzinczak et al. 2016). Usually, this approach is used to test the importance of interspecific competition, but it can also be used to test other interactions such as predation. We used a Null model to determine whether the individuals' occurrence at each station was lower than expected by chance. The function of the Null model is to randomize ecological data, producing new random patterns. These will be as expected if there is no biological cause interfering with the environment (Varzinczak et al. 2016). Raw data was randomized with EcoSim software 1.1 (http://www.garyentsminger.com/ecosim/), which creates random species pairs occurring together. We then compared the simulations with the real data to infer whether biological factors, such as species avoiding a location because of potential predators, influence species occurrence.

To find out the probability of predators and prey leaving their hideout at certain time intervals from 00:00 to 23:59, we calculated a Kernel Density Function for each species using R (version 3.6.3). In the Kernel Density Function plots of each species, a dotted line was drawn that divides the day between 6:00 am and 5:00 pm, with the night being considered between 5:01 pm and 5:59 am. Day and night periods were chosen based on sunrise and sunset times during the data collection period May 27 to September 24, 2013.

We also computed the coefficient of overlap between prey and predator species using the *Overlap* package (version 0.3.4; Ridout & Linkie, 2009) in R. The shaded areas in the Overlap plots represent the times species are found in the environment. The coefficient of overlap between two species, Δ, is the area lying under the kernel density curves. The closer Δ is to 1, the more aggregated the distribution of species are. The value considered for Δ was Dhat1. Dhat1 is calculated from density vectors estimated at time intervals t equally spaced between 0 and 2π. It is the recommended estimator when the number of samples is less than 50 because it compares curves at evenly spaced points (Ridout & Linkie, 2009). The Δ (Dhat1) and the confidence intervals are presented in each overlap plot. The 95% confidence intervals of the coefficient of overlapping (Δ) were calculated using smoothed bootstrap with 10,000 resamples (Meredith & Ridout, 2021).

3. RESULTS

The C-Score metric did not differ from what would be expected by chance for all the co-occurrence patterns analyzed between predators and prey (Table 1 - 2). Therefore, we did not find evidence of spatial segregation among species.

TABLE 1. Results of C-Score to test the influence of *P. concolor* on occurrence of potential prey (*S. brasiliensis*, *C. paca* and *D. aurita*) on Parque Nacional da Serra dos Órgãos, Teresópolis, RJ. (Obs – observed; Exp – expected; NS – not significant).

		S. brasiliensis	*C. paca*	*D. aurita*
C-Score	Obs	27.10	36.00	72.00
	Exp	27.25	36.10	72.15
	p-value	NS	NS	NS

TABLE 2. Results of C-Score to test the influence of *L. wiedii* on occurrence of potential prey (*S. brasiliensis*, *C. paca* and *D. aurita*) on Parque Nacional da Serra dos Órgãos, Teresópolis, RJ. (Obs – observed; Exp – expected; NS – not significant).

		S. brasiliensis	*C. paca*	*D. aurita*
C-Score	Obs	18.00	36.10	72.15
	Exp	18.15	36.20	72.30
	p-value	NS	NS	NS

The Kernel Density Function plots suggest that prey (*S. brasiliensis*, *D. aurita* and *C. paca* have a primarily nocturnal habit (Figure 3a-c) and appear at night 96% of the time. Conversely, *P. concolor* has a more cathemeral habit (Figure 3d), whereas *L. wiedii*, a small predator, also has a more nocturnal habit and makes 70% of its appearances at night (Figure 3e).

According to the Overlap plots, the mean time of activity overlap between *L. wiedii* and *S. brasiliensis* was 70% and it varied between 50% and 90% according to the confidence interval estimate (Figure 3a). The mean overlap time between *L. wiedii* and *C. paca* was only 35% and it varied between 20% and 50% (Figure 3b). The overlap between *L. wiedii* and *D. aurita* was 56% (Figure 3c). *P. concolor* did not appear to have any significant differences in the time of activity overlap with the three prey species. The overlap between *P. concolor* and *S. brasiliensis* was 47%, *P. concolor* and *C. paca* was also 47% and *P. concolor* and *D. aurita* was 48% (Figure 3 d,e,f).

4. DISCUSSION

Our results suggest that there is no spatial segregation among predators and prey in PARNASO. The lack of difference between observed and simulated C-Score (Tables 1 and 2) shows less segregation between species, indicating higher co-occurrence. Our results are different from those with evidence of spatial segregation between predators and prey (Currier 1983; McBee and Baker 1982; Goulart et al. 2009). No spatial segregation means that the distribution of prey is not influenced by the spatial distribution of predators. However, we show that temporal segregation can be the main driver in the predator-prey relationships analyzed.

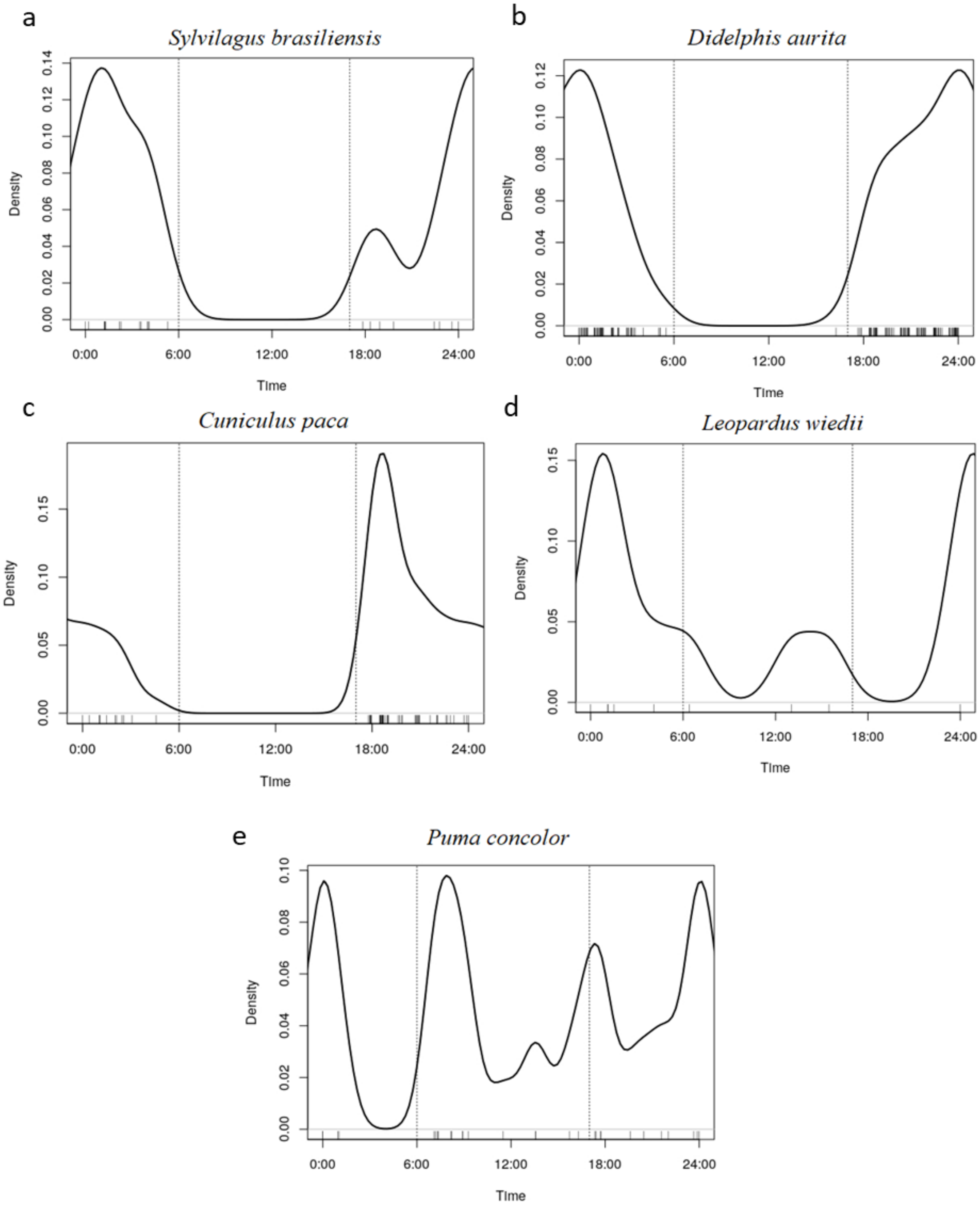

FIGURE 2 Kernel Density Function of *L. wiedii* and prey (a-c) and *P. concolor* and prey (d-f) species analysed in this study.

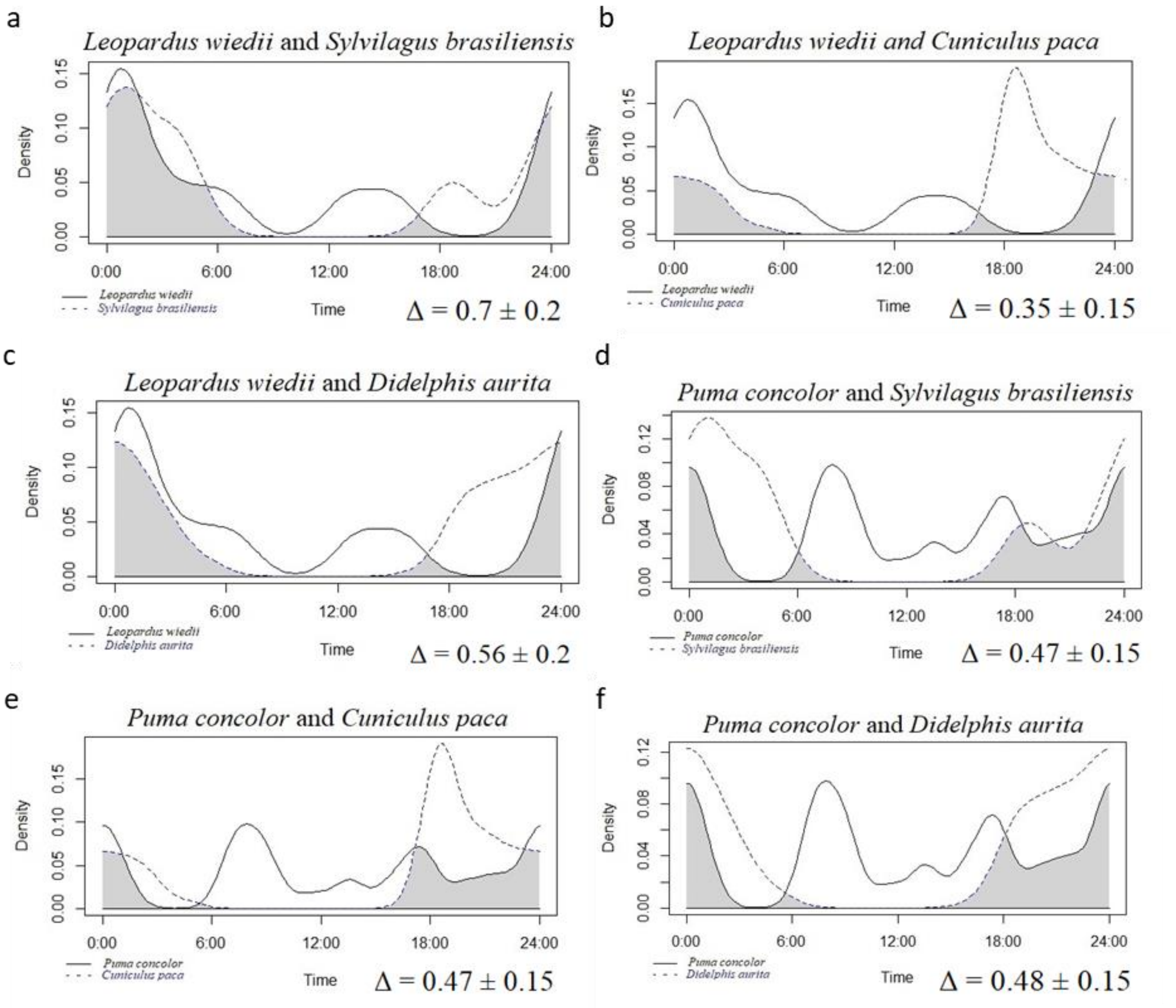

FIGURE 3. Activity patterns overlap between *L. wiedii* and prey (a-c) and between *P. concolor* and prey (d-f) species analysed in this study.

Our results show that prey species follow a nocturnal pattern while predators tend to be cathemeral. As stated by Smythe (1987), the agouti (*C. paca*) is a nocturnal Neotropical Forest mammal, in accordance with the results of this study. Also, according to Dias et al. (2019) and García-R et al. (2019), agouti is strictly nocturnal during the rainy season and predominately nocturnal during the dry season, when our data was collected. We found that *S. brasiliensis*, *D. aurita* and *C. paca* made 96% of its appearances at night. Small mammals are mostly nocturnal but have some activity during the day, and medium-sized mammals are primarily nocturnal (Nagy Reis et al. 2017), whereas predators have a much more cathemeral habit. In our study, *L. wiedii* made 70% of its appearances at night, whereas *P. concolor* only showed nocturnal habits 50% of the time.

We also found evidence of differential activity patterns between predator species. Compared to *P. concolor*, *L. wiedii* showed a more nocturnal habit, in accordance with the results of Botts et al. (2020). Smaller predators can change their behavior and time of activity to avoid competition with larger predators, as has been shown for species such as of the oncilla (*Leopardus tigrinus*), who changes its behavior depending on the presence of margay (Nagy-Reis et al. 2017). There's also the possibility that large predators can get out any time of the day because they are top chain species and do not face any predation threats. The cathemeral pattern in pumas has been previously documented (e. g. Massara et al. 2018, Botts et al. 2020). Their cathemeral behavior increases predator encounter with a larger variety of prey, enlarging their trophic niche (Scognamillo et al. 2003; Di Bitetti et al. 2010, Martín et al. 2013, Botts et al. 2020). The main components of puma's diet are deer, paca, armadillos, peccaries, and lagomorphs (De Oliveira 2002; Botts et al. 2020).

We show that predators have different time of interactions with prey. According to the Overlap plots, the time of activity overlap between *L. wiedii* and *S. brasiliensis* was 70%, and between *L. wiedii* and *C. paca*, only 36%. *P. concolor* did not appear to have any significant difference in the time of activity overlap with the three prey species, which means it can be more generalist (Currier 1983). Because *L. wiedii* seems to be more specialist, its nocturnal behavior may be to synchronize its time of activity with their main prey. The synchronism of the time of activity between predator and prey has been previously found in carnivores, especially felids (e. g. northern oncilla, Marinho et al. 2018; puma and jaguar, Weckel et al. 2006; Harmsen et al. 2011; Foster et al. 2013). On the other hand, we found *P. concolor* to be more generalist, having approximately 50% of time overlap with the three studied prey species. Some authors have suggested that the activity patterns of pumas are determined by the daily activity patterns of their prey species (Emmons 1989; Núñez et al. 2000, Scognamillo et al. 2003; Harmsen et al. 2011; Botts et al. 2020). These studies found a significant overlap in activity between *P. concolor* and their main prey, supporting the theory that predators adjust their activity to optimize energy intake and reduce energy expenditure when foraging.

Our results also suggest that predators are most likely to adjust their activity patterns based on the behavior of their main prey rather than to avoid competition with other species. Future studies should evaluate how activity patterns are affected by anthropogenic disturbances, which can change what and when animals eat, and how species interact with each other (Massara et al. 2018). In our study area, the Atlantic Forest degradation has caused a biome reduction of more than 80%, currently leaving, a forest cover of 13% (Ribeiro et al. 2009; Souza et al. 2020). Nevertheless, only about 9% of the biome is fully protected by Protected Areas (PAs) (Lira et al. 2021). The reduction of prey populations via illegal hunting activities and deforestation can, therefore, increase intraguild competition between predators (Botts et al. 2020). Tropical predator–prey relationships can be disrupted by illegal hunting and exaggerated deforestation, resulting in an unbalanced ecosystem where generalists such as *P. concolor* might benefit while specialists, such as *L. wiedii*, can become disproportionately affected. Future studies evaluating the relationship between human pressures and prey activity patterns could help to understand how to allow the protection of top predators in these highly threatened landscapes.

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