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ACTIVITY PATTERNS AND TEMPORAL SEGREGATION OF MEDIUM- AND LARGE-SIZED MAMMALS IN TRÊS PICOS STATE PARK AND GUAPIAÇU ECOLOGICAL RESERVE, BRAZILIAN ATLANTIC FOREST

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Abstract: Species coexistence relies on niche partitioning, where species utilize different niche dimensions, such as time and space, to minimize interspecific competition and predation. This study aimed to describe the activity patterns and prey-predator dynamics of medium and large-sized mammals in two Protected Areas, Guapiaçu Ecological Reserve and Três Picos State Park, Rio de Janeiro, Brazil. Using camera traps deployed across 42 stations for a total of 200 camera-trap days, we recorded 1,502 detections of 10 mammal species. Prey species accounted for the majority of records, with Didelphis aurita (588 detections) being the most frequently observed. Among predators, the puma (Puma concolor) had the highest number of detections (113). The results revealed variation in activity patterns among the recorded species, with some being primarily diurnal, others nocturnal — most of them prey species — and P. concolor exhibiting cathemeral activity. These patterns suggest temporal segregation as a potential mechanism to reduce predation risk and interspecific competition. These findings contribute to understanding how ecological factors shape species behavior and coexistence in biodiverse tropical regions.

Keywords: camera-traps; circadian behavior; niche dimensions; predation; species coexistence

INTRODUCTION

The ecological niche is characterized by all potential combinations of biotic and abiotic environmental factors where a species occurs, thereby utilizing resources and influencing its surroundings (Begon *et al.* 2006). Hutchinson's perspective (1957) views the niche as a species' dynamic position within a local community, shaped by its biotic and abiotic needs and interactions with other species (Polechová & Storch 2008). These interactions among species can lead to predation, interspecific competition, and other ecological dynamics (Polechová & Storch 2008). Therefore, species attempt to adopt the strategy of niche partitioning, which consists of dividing or partitioning resources to avoid interspecific competition (Schoener 1974). For example, mammals can leave their den at different times of day, adopting the strategy of temporal segregation in order to avoid predation (Frey *et al.* 2017, Mugerwa *et al.* 2017, Botts *et al.* 2020).

Temporal segregation is a strategy often employed by mammals to avoid competition and minimize predation risk. Prey species can reduce encounters with predators by leaving their dens during times of lower predation risk, which may also influence predator activity patterns (Castillo-Ruiz *et al.* 2012, Hertel *et al.* 2017, Botts *et al.* 2020, Rheingantz *et al.* 2016). Temporal segregation was expected to be found in this study, based on the niche partitioning theory (Schoener 1974). Temporal segregation can be particularly pronounced in diverse ecosystems. Predators in these regions exhibit temporal plasticity, adjusting their activity to environmental conditions and prey availability (Eisenberg 1981). Prey species, in turn, often adapt to these pressures by becoming more nocturnal to minimize encounters with predators (Schoener 1974, Leão *et al.* 2022). For example, in tropical forests of Costa Rica, Botts *et al.* (2020) found that smaller felids such as the ocelot (*Leopardus pardalis*), margay (*L. wiedii*), and oncilla (*L. tigrinus*) were mostly nocturnal, whereas diurnal prey species such as agoutis (*Dasyprocta leporina*) and coatis (*Nasua nasua*) displayed contrasting activity patterns, suggesting that temporal segregation may help reduce predator-prey encounters. However, it is crucial to recognize that these adaptations are not solely in response to predation pressures; they also reflect the species' physiological and morphological constraints (Carscadden *et al.* 2020).

The Brazilian Atlantic Forest is a tropical and subtropical forest biome located along the Atlantic coast of Brazil, extending into parts of Paraguay and Argentina. Characterized by high levels of endemism and biodiversity, it is considered one of the world's most threatened biodiversity hotspots due to historical deforestation and habitat fragmentation (Myers *et al.* 2000, Ribeiro *et al.* 2009). With over 384 mammal species, including a significant number of endemics, the region offers a unique opportunity to observe how interspecific competition and predation shape the niche partitioning and activity patterns of its inhabitants (Figueiredo *et al.* 2021).

The objective of this study is to analyze the temporal distribution of terrestrial mammals within two Protected Areas (PAs) in Rio de Janeiro State, Brazil. The results were interpreted in the light of how temporal segregation may reduce predation risk and minimize interspecific competition. The probability distribution of species over time was modeled through Kernel Density Function, to investigate potential temporal segregation between them. Species were divided into two categories: prey and predators. Prey were expected to exhibit predominantly nocturnal behavior as a strategy to avoid predators (Eisenberg 1981). In contrast, predators were hypothesized to be cathemeral, allowing them to broaden their niche and increase opportunities to encounter prey (Eisenberg 1981). These predictions align with previous studies suggesting that temporal niche partitioning reduces competition (Amarasekare 2003) and predation risk (Rioux *et al.* 2022) in diverse ecosystems (*e.g.* Lear *et al.* 2021, Grabowski *et al.* 2024).

MATERIAL AND METHODS

Study area

This study was conducted in two ecologically connected protected areas encompassing the Três Picos State Park (PETP) and the Guapiaçú Ecological Reserve (REGUA), which are located in the mountainous region of Rio de Janeiro State, Brazil (22.3798°S – 42.73201°W). The study area spans the municipalities of Cachoeiras de Macacu and Teresópolis. The PETP protects an area of 651 km², with altitudes ranging from 100 meters to over 2,300 meters, including the highest peak of the Serra do Mar mountain range (Vieira & Gramani 2015). The steep slopes of the Serra do Mar have historically hindered human occupation, allowing many forested areas to remain preserved or abandoned, which has facilitated the creation of conservation units throughout the mountain range. Consequently, our study area is not isolated within the landscape. To the north, it connects with the Macaé de Cima Environmental Protection Area, which further links to Desengano State Park. To the south, the PETP is contiguous with two other protected areas, namely the Serra dos Órgãos National Park and the Tinguá Biological Reserve. The REGUA is located within the PETP and reaches up to 400 m in elevation, whereas the broader PETP area spans altitudes up to 1,400 m in the study region. Despite some loss of connectivity due to fragmentation, the entire Serra do Mar Biodiversity Corridor is considered *a priori*ty area for biodiversity conservation (MMA 2017). The vegetation of the study area is classified into Lowland Dense Rainforest (right above sea level), Submontane Dense Rainforest (lower mountain slope) and Montane Dense Rainforest (highest altitudes of the forest) (Veloso *et al.* 1992) (Figure 1).

Mammal camera-trapping

Camera-traps (35 Bushnell Trophy Cam Aggressor 119875 and seven ScoutGuard SG560C) were used to identify medium and large mammal species (> 1 kg) in three trails, classified as A, B and C, with altitudes ranging from 200 to 1400 meters above sea level. The cameras operated continuously, without interruption, for 200 camera-trap days, from autumn to spring (between April 1st and October 17th, 2018). Each trail (A, B, and C) was surveyed using 14 cameras, with two cameras installed along the altitudinal range at intervals of every 200 meters above sea level (Figure 1). Each sampling point had two cameras, one in the trail and one off the trail, approximately 50 m apart from each other. Di Bitetti *et al.* (2014) recommend combining on-road and off-road camera placements to achieve a more comprehensive survey. Their study highlighted that camera placement significantly influenced species detection, with on-road cameras recording a different subset of species compared to off-road placements, likely reflecting differences in habitat use.

The cameras were installed approximately 0.5 m above the ground, tied in tree trunks, to optimize the detection of mammals, which often move close to the forest floor. This height ensures that the cameras capture the target species' natural behaviors while minimizing the risk of missing ground-dwelling animals that may not trigger higher-placed sensors. Additionally, placing cameras at this height reduces interference from branches, leaves, and wind, enhancing the accuracy of detection by infrared sensors (Wearn & Glover-Kapfer 2017). They were programmed to trigger continuously using high-sensitivity infrared sensors, recording 30-second videos with no interruptions between the end of one video and the start of the next upon sensor activation. This continuous monitoring approach allowed for a more efficient detection of species presence (Wearn & Glover-Kapfer 2017), as the videos facilitated species identification through the analysis of frames extracted from the footage.

To minimize the risk of duplicate recordings of the same individual, records of each species captured at the same station within intervals of less than one hour were excluded (Marinho *et al.* 2018, Leão *et al.* 2022). Subsequently, species with enough records for meaningful statistical analyses were selected. The number of records used in this study was determined based on the recommendations of Seaman *et al.* 1999, which suggest a minimum of 30 records per species for reliable analysis. Exceptions were made for *Tamandua tetradactyla* (16 records) and *Eira barbara* (27 records), as their inclusion was justified by the Kernel Density Function results, which exhibited behaviors consistent with expected patterns. The following species were included in the analysis: prey *Didelphis aurita*, *Dasyprocta leporina*, *Dasypus novemcinctus*, *Guerlinguetus brasiliensis*, *Cuniculus paca*, *Tamandua tetradactyla*, predators *Puma concolor*, *Leopardus pardalis*, *Leopardus wiedii*, and *Eira barbara* (Harmsen *et al.* 2011; Harmsen *et al.* 2018; Gonçalves 2023).

Statistical analysis

For the temporal analysis, the Kernel Density Function was calculated for each species using the 'kdensity' package in R (version 3.6.3). Daytime was defined as 6:00 am to 6:00 pm, and nighttime as 6:00 pm to 6:00 am, based on sunrise and sunset times during the study period (April to October 2018), when the cameras were active. These definitions were used to calculate the percentages of the animals' activity times.

Subsequently, the overlap package (version 0.3.4, Ridout & Linkie 2009) in R was employed to compute the overlap coefficient between the studied species. Based on the database containing the timestamps of animal records at each camera-trap location, a Kernel Density Function graph was generated. The overlap package in R was used to compare the Kernel Density Function graphs of two species, calculating the percentage of temporal overlap between them. Δ (Dhat) is a measure of temporal activity overlap between two species. Its value ranges from 0 to 1, where 0 indicates no overlap in activity (completely distinct temporal patterns) and 1 represents complete overlap (identical activity patterns). This metric allows us to assess the

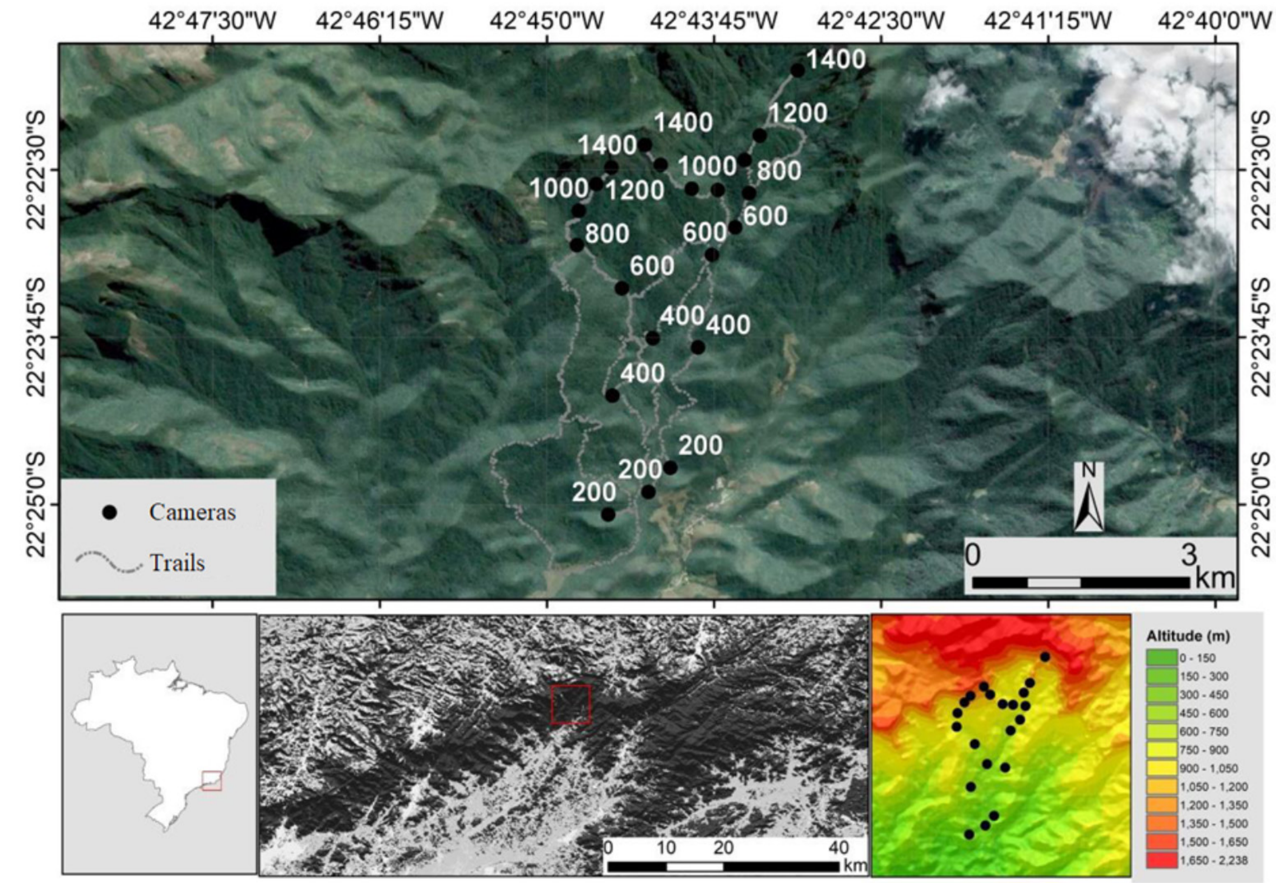

Figure 1. Study area along the altitudinal range in the two ecologically connected protected areas Três Picos State Park (Parque Estadual dos Três Picos - PETP) and Guapiaçu Ecological Reserve (Reserva Ecológica do Guapiaçu - REGUA) in Rio de Janeiro State, Brazil. The REGUA occupies lower elevations within the park, reaching up to 400 m, while sampling sites across the PETP extend to elevations of approximately 1,400 m. The dataset was collected between April 1st and October 17th, 2018, and each point represents a camera-trap station. In the first figure, white numbers represent the altitudinal elevation of each trail used.

degree of temporal segregation or synchronization between species, which is particularly useful for understanding predator-prey interactions and competition dynamics. For sample sizes under 50, Dhat1 provides the most accurate estimates. In contrast, Dhat4 is recommended when both samples exceed a size of 50 (Meredith *et al.* 2024). Dhat4 was utilized for comparisons involving *P. concolor* and *D. leporina*, *P. concolor* and *G. brasiliensis*, *P. concolor* and *D. aurita*, *P. concolor* and *C. paca*, and *P. concolor* and *D. novemcinctus*. All other analyses were conducted using Dhat1.

RESULTS

A total of 1,502 detections were recorded across the ten analyzed species. Prey species accounted for the majority of records, with *Didelphis aurita* being the most frequently detected (588 records), followed by *Dasyprocta leporina* (229), *Dasypus novemcinctus* (185), *Guerlinguetus brasiliensis* (166), *Cuniculus paca* (106), and *Tamandua tetradactyla* (16). Among predators, *Puma concolor* had the highest number of detections (113), followed by *Leopardus pardalis* (37), *Leopardus wiedii* (35), and *Eira barbara* (27).

The studied species reveals discernible behavioral patterns: the prey species *G. brasiliensis* (55% of apparitions during the daytime - between 6:00 am and 6:00 pm), and the top predator *P. concolor* (54% of apparitions during the daytime) exhibited a cathemeral habit. *P. concolor* activity were around 8:00 am and 6:00 pm. Prey species (Figure 2) such as *C. paca* (96%), *D. novemcinctus* (92%), *D. aurita* (91%), and *T. tetradactyla* (84%) predominantly exhibited nocturnal behavior. Among predators (Figure 3), *L. pardalis* was also primarily nocturnal, with 80% of

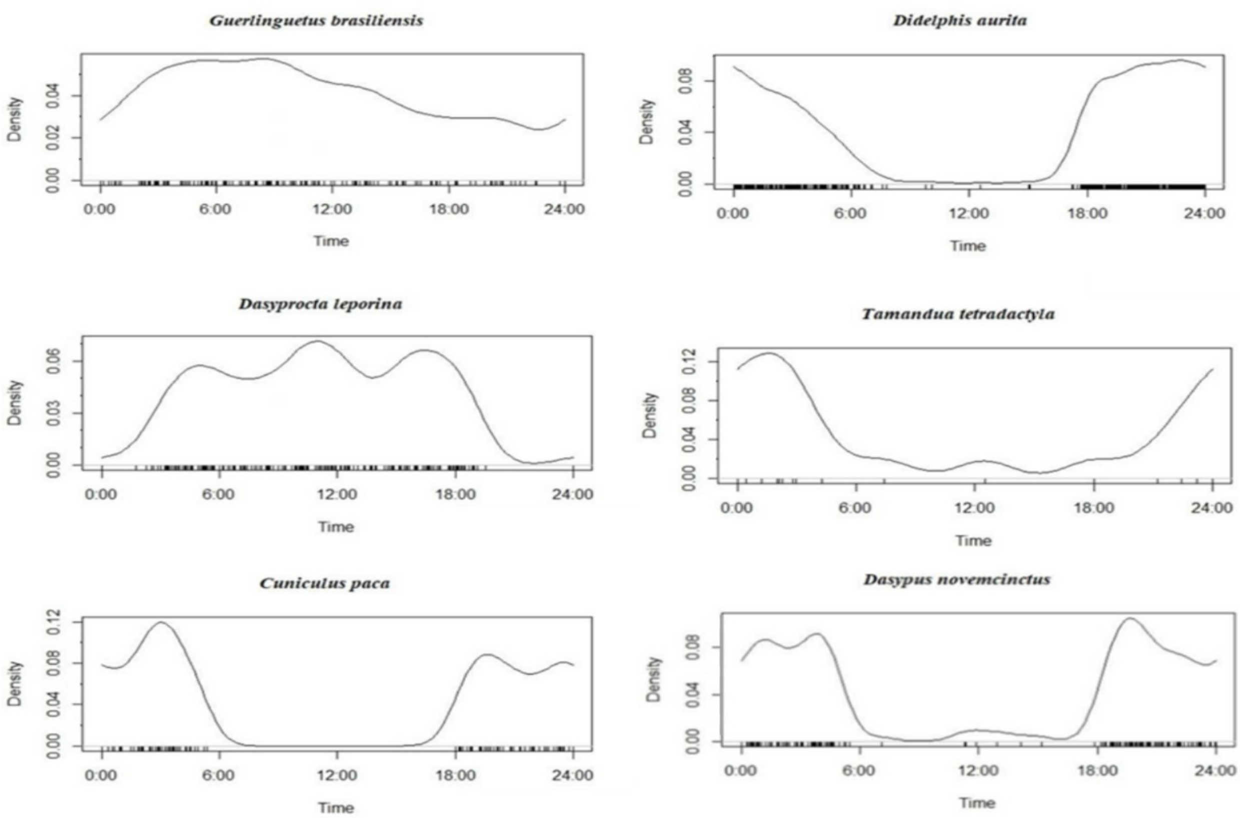

Figure 2. Kernel Density Function of prey — *G. brasiliensis, D. aurita, D. leporina, T. tetradactyla, C. paca, D. novemcinctus*, respectively — recorded with camera-traps in the Brazilian Atlantic Forest between April and October 2018. Each tick mark above the x-axis represents a camera-trap detection (record) of an individual.

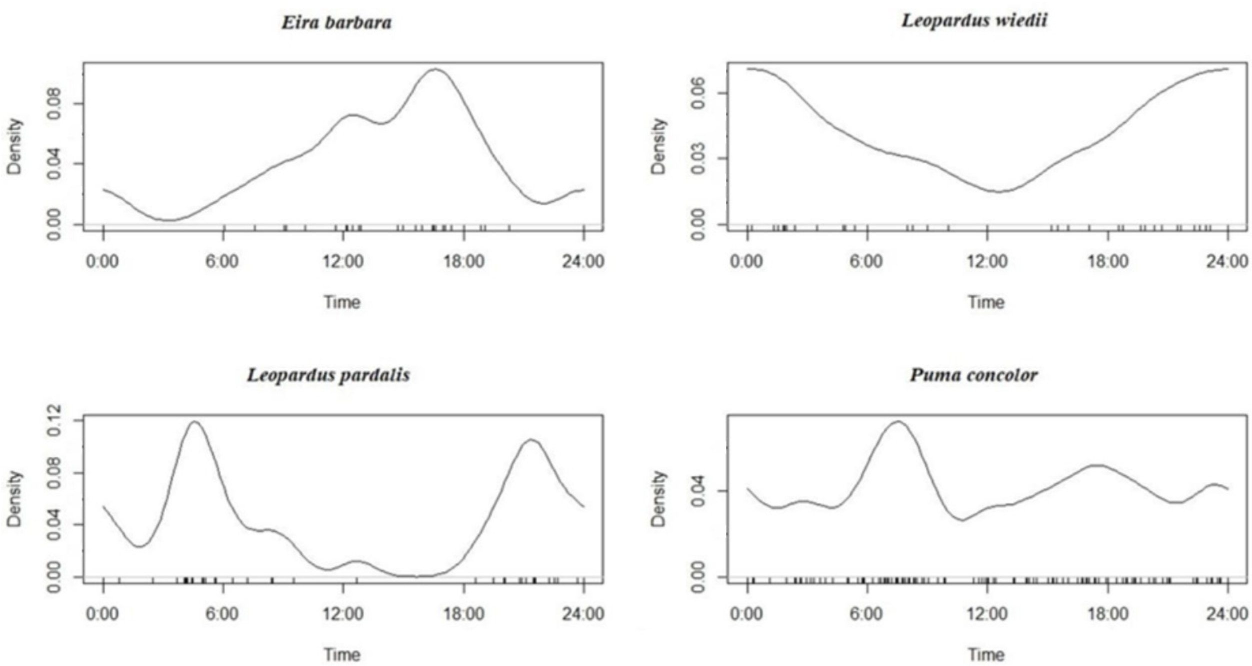

Figure 3. Kernel Density Function of predators — *E. barbara, L. wiedii, L. pardalis, P. concolor*, respectively — recorded with camera-traps in the Brazilian Atlantic Forest between April and October 2018. Each tick mark above the x-axis represents a camera-trap detection (record) of an individual.

Table 1. Temporal overlap percentages between mammalian predators and their potential prey species. Higher values indicate greater synchrony in activity patterns, which may suggest increased encounter rates and predation opportunities.

Predator	Prey	Temporal overlap (%)
P. concolor	*G. brasiliensis*	83
P. concolor	*D. leporina*	73
L. wiedii	*D. aurita*	76
L. wiedii	*D. novemcinctus*	74
L. wiedii	*C. paca*	72
L. wiedii	*T. tetradactyla*	72
L. wiedii	*G. brasiliensis*	71
L. pardalis	*D. novemcinctus*	70
L. pardalis	*D. aurita*	67
L. pardalis	*C. paca*	66
E. barbara	*D. leporina*	73
E. barbara	*G. brasiliensis*	65

Table 2. Temporal overlap percentages between predator species. These values reflect the degree of overlap in activity patterns, which may influence interspecific competition or avoidance behaviors among sympatric carnivores.

Predator 1	Predator 2	Temporal overlap (%)
L. wiedii	*L. pardalis*	72
P. concolor	*L. wiedii*	75
P. concolor	*E. barbara*	66

its activity recorded at night. This species showed distinct activity peaks, occurring just before dawn and around 10:00 pm. The predator *L. wiedii* was predominantly nocturnal, with 69% of its activity occurring at night and only sparse daytime records. The species displayed a surge in activity around midnight. *E. barbara* (74% of apparitions during the daytime) was identified as a diurnal predator, and rarely appeared before 6:00 am and after 6:00 pm. Prey *D. leporina*, with 71% of apparitions during the daytime, exhibited more diurnal habits than other prey species did.

Analyzing the graphs depicting species overlap yields the following observations (Tables 1 and 2; supplementary material - Figures 1 to 5): regarding the overlap coefficient involving the top predator, *P. concolor*, the highest overlap coefficients were 83% between *P. concolor* and *G. brasiliensis*, and 73% with *D. leporina*. The highest overlap coefficients between *L. wiedii* and various nocturnal species were as follows: *L. wiedii* and *D. aurita*, 76%; *L. wiedii* and *D. novemcinctus*, 74%; *L. wiedii* and *C. paca*, 72%; *L. wiedii* and *T. tetradactyla*, 72%; and *L. wiedii* and *G. brasiliensis*, 71%. The highest overlap coefficients between *L. pardalis* and nocturnal prey species were as follows: 70% with *D. novemcinctus*, 67% with *D. aurita*, and 66% with *C. paca*. *E. barbara* presented a relatively low percentage of overlap with nocturnal species as evidenced by low overlap percentages. On the other hand, the predator showed a greater overlap with cathemeral and diurnal species: *E. barbara* and *D. leporina*, 73%; and *E. barbara* and *G. brasiliensis*, 65%. *L. wiedii* and *L. pardalis* had a high overlap coefficient (72%). *P. concolor* had a high overlap with *L. wiedii* (75%) and *E. barbara* (66%).

DISCUSSION

Prey species were expected to be predominantly nocturnal, using temporal segregation as a strategy to reduce the likelihood of being predated. Predators, on the other hand, were expected to exhibit cathemeral activity, as they likely experience lower predation pressure — in the case of mesopredators — or none at all — as with top predators such as the puma — allowing them to broaden their temporal overlap with prey (Schoener 1974, Leão *et al.* 2022). The results indicate that this hypothesis was only partially supported. While some prey species displayed the expected nocturnal behavior, others exhibited cathemeral (*Guerlinguetus brasiliensis*) or diurnal (*Dasyprocta leporina*) habits. Among predators, the margay and the ocelot were found to be nocturnal, whereas the tayra (*Eira barbara*) exhibited diurnal behavior. It is important to note that nocturnal behavior in prey does not necessarily indicate a direct avoidance of specific predators, but rather a general adaptation to reduce predation risk (Lima & Dill 1990).

Temporal overlap analysis provided further insights into these interactions. *P. concolor*, the top predator, showed higher overlap coefficients with prey species possessing cathemeral or diurnal habits, whereas lower coefficients were observed with nocturnal prey. In contrast, the margay exhibited greater overlap with nocturnal prey compared to the puma. Additionally, *L. wiedii* showed a notable overlap with the cathemeral species *G. brasiliensis* (71%) but a lower overlap with the diurnal species *D. leporina* (55%). These patterns suggest that predator temporal activity aligns with prey availability (Nagy-reis *et al.* 2019). The ocelot displayed activity peaks around 5:00 pm and 9:00 pm, leading to lower overlap coefficients, even with nocturnal prey. Furthermore, the mesopredator exhibited relatively low overlap with cathemeral and diurnal prey. The overlap between the tayra (diurnal) and the ocelot (nocturnal) was only 36%, highlighting the contrast in their temporal habits.

The findings of this study align with prior research on felid coexistence and activity patterns in Neotropical forests, particularly in the Atlantic Forest. Santos *et al.* (2019) emphasized the significance of prey availability and temporal partitioning in modulating felid coexistence, demonstrating that prey abundance is a more critical determinant of habitat use than interspecies interactions. These insights complement our results, where temporal activity patterns and overlap coefficients underscore the role of prey dynamics in shaping predator-prey interactions. For instance, in the Atlantic Forest, the ocelot displayed strong associations with small-bodied prey, mirroring findings from our study area that highlight prey availability as a driver of activity patterns among predators and prey.

Moreover, Santos *et al.* (2019) observed that smaller predators such as margay and jaguarundi (*Herpailurus yagouaroundi*) exhibited distinct activity peaks, possibly to reduce direct competition with the ocelot, a pattern also detected in our study with species such as margay and the tayra. This further corroborates the hypothesis that temporal niche partitioning is a vital strategy for coexistence within these biodiverse ecosystems.

These patterns indicate that temporal segregation plays a significant role in reducing inter- and intraspecific competition, whereas temporal overlap may adjust based on predation pressure and prey availability. These findings emphasize the complexity of predator-prey interactions, suggesting that behaviors such as cathemerality or diurnality among prey can influence temporal dynamics within these communities.

G. brasiliensis, one of the most studied Neotropical squirrel species, is typically known for its diurnal habits according to Mendes *et al.* (2019) and Gomes Rocha *et al.* (2022). However, in the present study, the squirrel displayed a significant number of records during the night, indicating a cathemeral behavior that deviates from the previous findings mentioned above.

D. leporina has been consistently documented in previous studies as exhibiting diurnal habits (*e.g.*, Ferreguetti *et al.* 2018), which aligns with the findings of the present study. Previous research by Emmons & Feer (1997) revealed two distinct activity peaks: one in the early morning and another in the late afternoon. Similarly, Ferreguetti *et al.* (2018) observed no activity during the hottest hours of the day, between noon and 1:30 pm. In contrast, our study identified three peaks of activity: one before 6:00 am, one before noon, and one before 6:00 pm. Notably, we also recorded significant activity between noon and 1:30 pm, which diverges from previous findings.

This divergence may be explained by the cooler temperatures in the study area's mountainous environment, which likely enable *D. leporina* to remain active during periods that are typically too hot in lower-altitude or urban regions. These localized environmental conditions, including temperature variations driven by altitude, highlight the flexibility of the species' activity patterns across different habitats. For *G. brasiliensis*, which is a forest-dependent species, habitat characteristics such as canopy cover, resource availability, and temperature gradients are known to influence behavior (Mendes *et al.* 2019, Gomes Rocha *et al.* 2022). Cooler climates in montane regions, as well as variations in forest structure and food resource distribution, may support more flexible activity patterns, including the nocturnal behaviors observed in this study. There are different conditioning factors according to specific environments that stimulate the activity time of a species (Erkert *et al.* 1976, Marques & Fábian 2018).

The diurnal species *E. barbara* presented an activity peak before 6:00 pm, followed by a smaller peak at noon. These findings align with the study by Villafañe-Trujillo *et al.* (2021), which observed similar activity patterns in regions near the equator, where *E. barbara* displayed early morning activity, a peak around noon, and a gradual decrease thereafter. Although the current study was conducted at a different location within the southern hemisphere, it further supports the diurnal activity pattern of

E. barbara, with some variations in timing and number of peaks.

The margay and the ocelot exhibited nocturnal behavior, which was consistent with findings from previous studies. Di Bitetti *et al.* 2010 found that the margay is strictly nocturnal, whereas the ocelot is nocturnal but presents some activity during the day. In this study, both cats showed some diurnal activity, despite their nocturnal habits, and *L. pardalis* was more nocturnal than *L. wiedii*. Perhaps these species may exhibit mainly nocturnal behavior to temporarily avoid the top predator *P. concolor* during daytime, thereby avoiding competition through the strategy of temporal niche partitioning. According to the results of Valeix *et al.* (2007), the temporal niches of smaller species are influenced by interference competition from behaviorally dominant larger species. The 'pardalis effect' refers to how the ocelot, as the predominant mesocarnivore, shapes the dynamics of smaller predator communities in tropical America. This influence typically manifests through niche partitioning, where smaller felids adjust their spatial or temporal activity to avoid interactions with *L. pardalis*, or through intra-guild predation, where the ocelot directly suppresses populations of smaller spotted cats. As *L. pardalis* populations decline, there is often a corresponding increase in the population density of smaller felids (De Oliveira *et al.* 2010, De Oliveira *et al.* 2022). This study found no evidence of the 'pardalis effect' through temporal segregation, as there was significant temporal overlap (72%) between the ocelot and the margay. The lack of expected temporal segregation may be explained by spatial segregation. In the study area, both cats occupy distinct altitudinal ranges, with *L. pardalis* being found between 200 and 600 meters above sea level and *L. wiedii* between 600 and 1400 meters (Leão 2024). Additionally, we can argue that this spatial segregation likely reduces competitive interactions, serving as an alternative mechanism to temporal segregation. By avoiding each other spatially, species eliminate the need for temporal segregation, as they occupy distinct areas (Schoener 1974). While this study focused primarily on temporal segregation, spatial segregation can also play a role in minimizing hostile interactions within and between species. By partitioning habitats, individuals can reduce interference competition (Shigesada *et al.* 1979) and predation risk (Galliez & Fernandez 2012).

In conclusion, species are not randomly distributed across time, demonstrating that temporal segregation is a key strategy for niche partitioning. By adjusting their activity patterns, prey species reduce the likelihood of encountering predators, as most of them exhibit predominantly nocturnal behavior. Similarly, temporal segregation minimizes direct competition among predators by allowing species to utilize different periods of the day (Eisenberg 1981). For instance, while *L. pardalis* and *L. wiedii* display overlapping nocturnal behavior, the top predator, *P. concolor*, exhibits cathemeral activity, and the omnivorous tayra is primarily diurnal. These distinct activity patterns highlight the role of temporal segregation in facilitating coexistence and align with the study's hypothesis.

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