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Article

Daily and seasonal activity patterns of a felid assemblage in a forest-grassland mosaic in southern Brazil

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ABSTRACT. The mechanisms of ecological segregation involved in the coexistence between Neotropical felids are the key to support strategies for conservation. Due to their inconspicuous and elusive behavior, camera trapping constitute a strategic, non-invasive method to study these species. The present work aimed to evaluate the daily and seasonal activity patterns of four felid species: *Leopardus guttulus* (Hensel, 1872), *L. pardalis* (Linnaeus, 1758), *L. wiedii* (Schinz, 1821) and *Puma concolor* (Linnaeus, 1771), in the Papagaios-de-Altitude Private Protected Area, state of Santa Catarina, southern Brazil. Data were collected from January 2018 to December 2019, using 25 sites of camera traps among the study area. We collected 624 independent records from *L. guttulus* (108), *L. pardalis* (55), *L. wiedii* (77) and *P. concolor* (384) in a sampling effort of 12,266 camera-traps/day. All species analysed showed a non-uniform distribution of daily activity, when considering the two years. We report the peak of seasonal activity for all species between the months of June and September, coinciding with the Araucaria nut harvest in the study area, and with the increase in populations of small rodents. We also report a high overlap between the activity patterns of the four species. The daily and seasonal activity patterns of the species in this study seem to reflect the intrinsic dynamics of the Araucaria Forest, as well as possible adaptations to prey availability.

KEYWORDS. Camera traps, Felidae, Atlantic Forest, circadian rhythm, Private Protected Area.

RESUMO. Padrões de atividade diários e sazonais de uma assembleia de felinos em um mosaico de floresta-campo no sul do Brasil. Os mecanismos de segregação ecológica envolvidos na coexistência entre felídeos neotropicais são a chave para subsidiar estratégias para sua conservação. Por apresentarem comportamento inconspícuo e esquivo, as armadilhas fotográficas constituem um método não invasivo estratégico para estudá-los. O presente trabalho buscou avaliar o padrão de atividade diário e sazonal de quatro espécies de felídeos: *Leopardus guttulus* (Hensel, 1872), *L. pardalis* (Linnaeus, 1758), *L. wiedii* (Schinz, 1821) e *Puma concolor* (Linnaeus, 1771), na RPPN Papagaios-de-Altitude, no estado de Santa Catarina, sul do Brasil. Coletamos os dados através de 25 sítios de armadilhas fotográficas na área de estudo. Obtivemos 624 registros independentes de *L. guttulus* (108), *L. pardalis* (55), *L. wiedii* (77) e *P. concolor* (384) em um esforço amostral de 12.266 armadilhas/dia. Todas as espécies analisadas apresentaram distribuição de atividade diária não uniforme, quando considerados os dois anos. Relatamos o pico de atividade sazonal de todas as espécies entre os meses de junho a setembro, coincidindo com a safra de pinhão na região, e com o aumento nas populações de pequenos roedores. Também relatamos uma alta sobreposição entre os padrões de atividade das quatro espécies. A atividade diária e sazonal das espécies neste estudo parece refletir as dinâmicas intrínsecas da Floresta Ombrófila Mista, além de possíveis adaptações à disponibilidade de presas.

PALAVRAS-CHAVE. Armadilhas fotográficas, Felidae, Mata Atlântica, ritmo circadiano, RPPN

Wild felids are indispensable in regulating and maintaining the ecological structure of neotropical forests, acting as top predators or mesopredators (Roemer *et al.*, 2009; Estes *et al.*, 2011). Felids show high morphological and functional similarity, given the relatively recent divergence of the clade, dating from the late Miocene (Morales & Giannini, 2010). The high similarity among these predators is a factor that could increase agonistic interactions (Pianka, 1974), which include indirect competition for food resources and home range, and in more extreme cases, interspecific predation (Di Bitetti *et al.*, 2010; Oliveira & Pereira, 2014; Santos *et al.*, 2019). The niche complementarity hypothesis (Schoener, 1974) states that there must be differences in the use of at least one resource dimension (spatial, temporal or trophic) by competitor species, in order to reduce agonistic events. One of the most used forms of ecological partition between carnivores is temporal segregation (Schoener, 1974), which aims to reduce intraguild competition, especially between animals of similar body size or diet (Di Bitetti *et al.*, 2010).

Analyzing the activity patterns of sympatric species is the first step to evaluate possible differences in their temporal niche. The daily and seasonal activity patterns of mammals are shaped by a range of factors including environmental conditions, prey availability, social interactions or between competitors (Zielinski, 1986; Beltrán & Delibes, 1994; Foster *et al.*, 2013; Botts *et al.*, 2020). The temporal segregation strategy as a mean of coexistence is a recurring theme in the study of Neotropical felids (Oliveira-Santos *et al*., 2012; Graipel *et al*., 2014; Massara *et al*., 2018; Santos, 2019; Nagy- Reis *et al.*, 2019). However, it is still incipient for the state of Santa Catarina, Brazil, which is entirely distributed in the threatened Atlantic Forest biome.

Given the high degree of fragmentation of the Araucaria Forest and natural grasslands on the Santa Catarina plateau, human influence represents a serious threat to wild felids. Understanding the activity patterns of these species is essential to elucidate their responses to environmental conditions and exogenous disturbances, and its implications for conservation. In the Papagaios-de-Altitude Private Protected Area, five species of felids are found: *Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803), *Leopardus guttulus* (Hensel, 1872), *L. pardalis* (Linnaeus, 1758), *L. wiedii* (Schinz, 1821) and *Puma concolor* (Linnaeus, 1771), the majority is considered threatened species by the Brazilian National Red List (Ministério do Meio Ambiente, 2022). The threatened species are *H. yagouaroundi*, *L. guttulus* and *L. wiedii*, while *P. concolor* and *L. pardalis* are not considered threatened.

The objective of this study is to characterize aspects of the ecology of felids in the Papagaios-de-Altitude Private Protected Area, with emphasis on their patterns of daily and seasonal activity, over a period of two years. We hypothesized that this felid assemblage would present temporal segregation, with low activity overlap between the four species.

MATERIAL AND METHODS

Study area. The Papagaios-de-Altitude Private Protected Area is located in the state of Santa Catarina (SC), southern Brazil. It is inserted within the rural matrix of the municipality of Urupema (27°56’42.87”S, 49°54’55.33”W), a plateau region in which accour the largest remnants of the Araucaria Forest in the state, one of the most threatened phytophysiognomies of Brazilian Atlantic Forest (Martinez *et al*., 2021) (Fig. 1). It comprises an area of 36.07 hectares, the largest portion of which is covered by Upper Montane Araucaria Forest. There are also areas with a predominance of tree fern (*Dicksonia sellowiana* (Presl.) Hook.) and natural grasslands, with peat bogs and herbaceous vegetation associated with rocky outcrops.

The area is located at an average altitude of 1,418 meters above sea level, belonging to the Cfb climate (marine temperate) according to the Köppen-Geiger classification. The average annual temperature is 13.5 °C. Temperatures below 5 °C are common throughout all months of the year, with a strong presence of frost mainly between April and November. The average annual rainfall is 1,656 mm (EPAGRI/CIRAM, 2022).

Camera trapping. Data were collected from records of 25 camera traps, which are in the image database of Papagaios-de-Altitude Private Protected Area maintained by Projeto Charão (AMA/ICB-UPF), during the period from January 2018 to December 2019. The number of camera traps used in monitoring progressively increased in this period, from 10 to 25 in total. The additional cameras were installed during the first semester of 2019. All camera traps installed remained active simultaneously for 24 hours in all months sampled, and there was no pause or interval in monitoring. We performed a review of traps and exchange of memory cards at an average interval of 30 days. No baits were used.

We programmed the 25 camera traps (Bushnell Trophy Cam) for hybrid function (photo and video). Triggering speed was set to 0.5 seconds, the duration of each video was set to 10 seconds, and the interval time between each capture was 5 seconds. The camera traps were installed between 30 and 50 centimeters from the ground, respecting an interval of 100 to 400 meters between each installation site (Fig. 1). The sites were selected by previous found of wild mammals evidences (feces, marks on trunks or footprints), seeking to contemplate the greatest diversity of environments within the Papagaios-de-Altitude Private Protected Area.

The set of images containing felid records were separeted and identified. We selected those referring to the species: *Herpailurus yagouaroundi*, *Leopardus guttulus*, *L. pardalis*, *L. wiedii* and *Puma concolor*. For each record, we evaluated the following aspects: camera positioning location (georeferenced); date; time; image quality and format (photo/video) and species identification. We did not differentiate individuals.

Data analysis. To investigate the activity patterns of the felids at the Papagaios-de-Altitude Private Protected Area, we applied a pre-selection of one-hour independence between the records, considering the proximity of the camera traps. Records of the same species at immediately adjacent points (distance of 250 meters or lower), within the same one-hour interval, were accounted as a single record. We calculated the capture success through the ratio between the number of independent records of each species and the sampling effort, multiplied by 100, according to Srbek-Araujo & Chiarello (2007). Subsequently, we performed circular analyses, with the Rayleigh Test of Uniformity in the “circular” package version 0.4-93 (Agostinelli & Lund, 2017) in the R software (R Core Team, 2020). Circular analysis was performed both for the distribution of activity over 24 hours of the day, as well

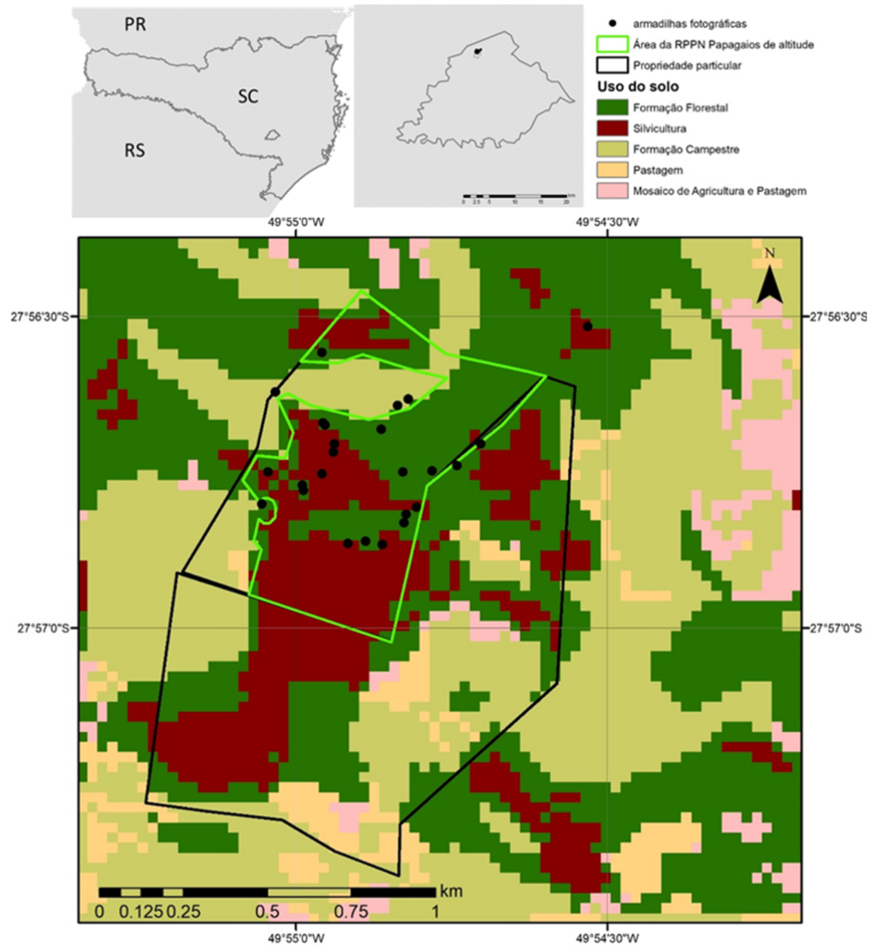

Fig. 1. Study area: Papagaios-de-Altitude Private Protected Area in Urupema, Santa Catarina, Brazil. On the top-right panel, colors indicate the type of soil-use in the area and its limits. The black dots in the map indicate the location of the camera traps.

as over 12 months of the year, in which the information of hours and months were converted to radians (ranging from 0 to 2 π). In this analysis, by means of the indicative arrow in the circular histograms, we observe the angular mean (μ) and mean vector length (r), where values closer to 1 indicate a high concentration of data close to the mean, while values closer to zero indicate a low concentration. A significant value for the Rayleigh's Test of Uniformity ($p < 0.05$) indicates non-uniform distribution, where records are concentrated in a certain time interval. A non-significant value ($p \geq 0.05$) does not refute the null hypothesis of uniformity, with no activity peak concentrated at any time interval. Circular analysis performed with the number of records obtained throughout the year was used to assess the existence of differential patterns among months, relating them to the seasons of the year. We compared the results using Watson's Two-sample Test of Homogeneity (U^2), also included in the "circular" package. This test was performed comparing the activity patterns of different species in the same year, and between the same species in different years.

To analyze the daily activity of the species, we used all the records selected for the years 2018 and 2019. For the seasonal activity, we standardized the sampling effort within the same analyzed year, so that all months of the same year had the same number of active camera traps. For the year 2018, we selected 10 camera traps, and for 2019, we selected 16.

Species were classified as diurnal (<15% of records at night), nocturnal (>85% of records at night), mostly diurnal (15–35% of records at night), mostly nocturnal (65-85% of records at night), or cathemerals (the ones that do not fit the limits considered for the previous categories), according to Romero-Muñoz *et al.* (2010). We considered as night the entire period from the mean time of sunset in the study region (18:40h) until sunrise (06:36h), and day as the period after sunrise (06:37h) until sunset (18:39h). Data was obtained through the Sunrise and Sunset platform (https://sunrise-sunset.org/), which shows the exact time of sunrise and sunset in the study area.

Additionally, we estimated the similarity of the daily activity between the species, using the "overlap" package version 0.3.4 (Ridout & Linkie, 2009). We considered the overlap coefficients (Dhat1 for sample sets < 70; Dhat4 for sample sets ≥ 70). Dhat1 and Dhat4 values closer to 1 indicate high activity overlap, while values close to zero indicate low overlap. We calculated confidence intervals through 1,000 bootstrap resamplings. These results were correlated with the daily luminosity periods recorded for the study area. We added the mean of sunrise and sunset times in the area to the daily activity histograms for each species, thus illustrating the relationship between the luminosity periods in the area and the activity of the felids.

RESULTS

We obtained a total of 624 independent records (n_{2018}= 315, n_{2019} = 309) including 108 records of the species *Leopardus guttulus* (n_{2018}= 57, n_{2019}= 51), 55 records of *L. pardalis* (n_{2018}= 25, n_{2019}= 30), 77 records of *L. wiedii* (n_{2018}= 30, n_{2019}= 47) and 384 records of *Puma concolor* (n_{2018}= 202, n_{2019}=182). The number of records for *Herpailurus yagouaroundi* was much lower than the others (n_{total}= 8) , and we chose not to include it in the analysis. The total sampling effort was 12,266 cameras/day (2018= 5,424 cameras/day, 2019= 6,842 cameras/day). Regarding capture success, for the two years together, we obtained values of 0.88% for *L. guttulus* (2018= 1.05%, 2019= 0.74%), 0.45% for *L. pardalis* (2018= 0.46%, 2019= 0.44%), 0.63% for *L. wiedii* (2018= 0.55%, 2019= 0.69%) and 3.13% for *P. concolor* (2018= 3.72%, 2019= 2.66%). All species analyzed showed non-uniform distribution of daily activity, when considering both years (Fig. 2). However, this was not the pattern found for *L. guttulus* and *L. wiedii* in 2018 and for *L. pardalis* in 2019 (see below more details in species items).

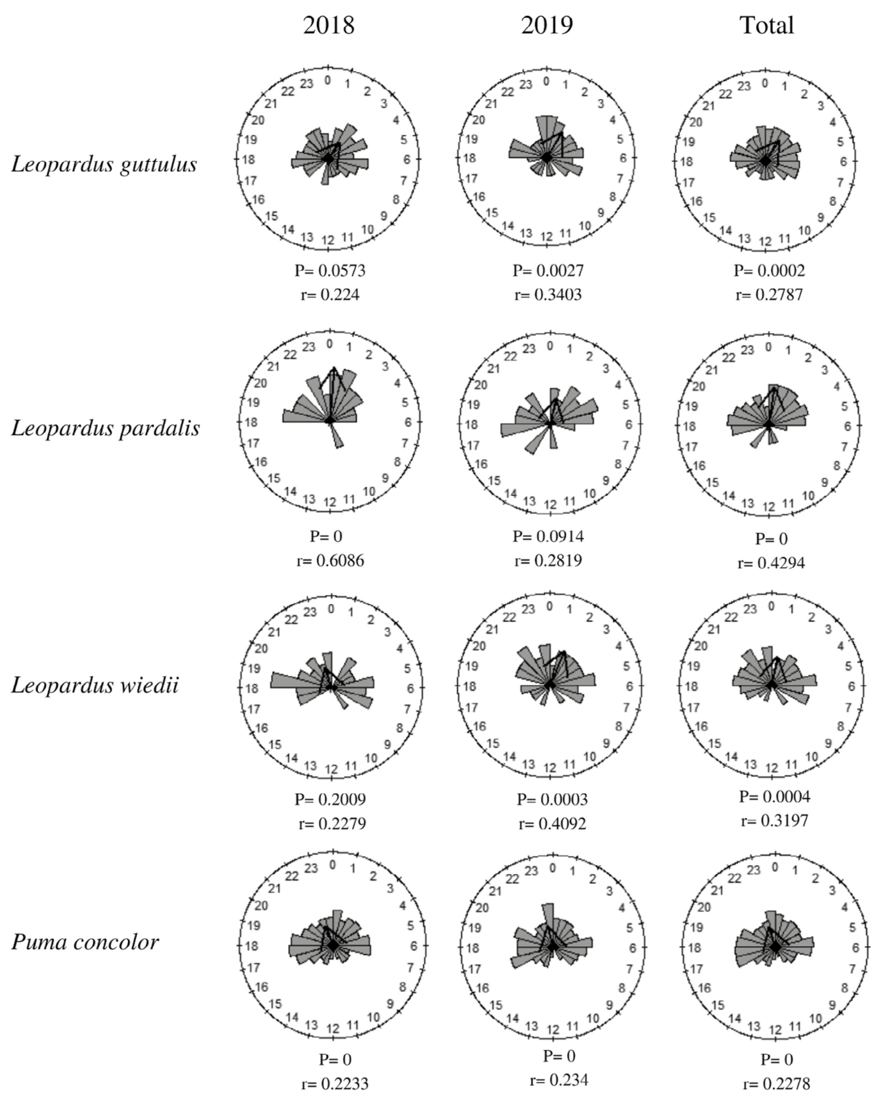

Fig. 2. Circular histograms with distribution and frequency of daily activity of *Leopardus guttulus*, *L. pardalis*, *L. wiedii* and *Puma concolor* in Papagaios-de-Altitude Private Protected Area, Santa Catarina, Brazil. The black arrows on each graph indicate the direction of the mean angle (μ). Each graph also exhibits the values of P and mean vector length (r).

Regarding seasonal activity patterns, we analyzed 543 independent records (n_{2018}= 246, n_{2019}= 297) . Of these, 72 refer to *L. guttulus* (n_{2018}= 23, n_{2019}= 49), 47 to *L. pardalis* (n_{2018}= 18, n_{2019}= 29), 64 to *L. wiedii* (n_{2018}= 21, n_{2019}= 43) and 360 to *P. concolor* (n_{2018}= 184, n_{2019}= 176). The highest frequency of records occurred in winter, between June and September (Fig. 3).

Leopardus guttulus. We classified the habit of *L. guttulus* as cathemeral (Tab. I), with non-uniform activity (Rayleigh's Test= 0.278, $p < 0.001$) and high dispersion of the records over 24 hours of the day in relation to the mean vector, indicated between 02:00h and 03:00h (Fig. 2). The species presented a large peak of activity in the interval between 00:00h and 08:00h, and a smaller one between 18:00h and 19:00h. We found no significant difference in the daily activity patterns of this species between the two sampled years (U^2= 0.0569, p> 0.10). We observed that *L. guttulus* was more active between June and July, showing a non-uniform distribution throughout the year (Rayleigh Test= 0.335, $p < 0.001$) and high dispersion of records. When analyzing the 2018 and 2019 data separately, we observed that this pattern was maintained, and that the species showed a non-uniform distribution in the two years (Fig. 3) and there was no significant difference between the years (U^2= 0.1011, $p > 0.10$).

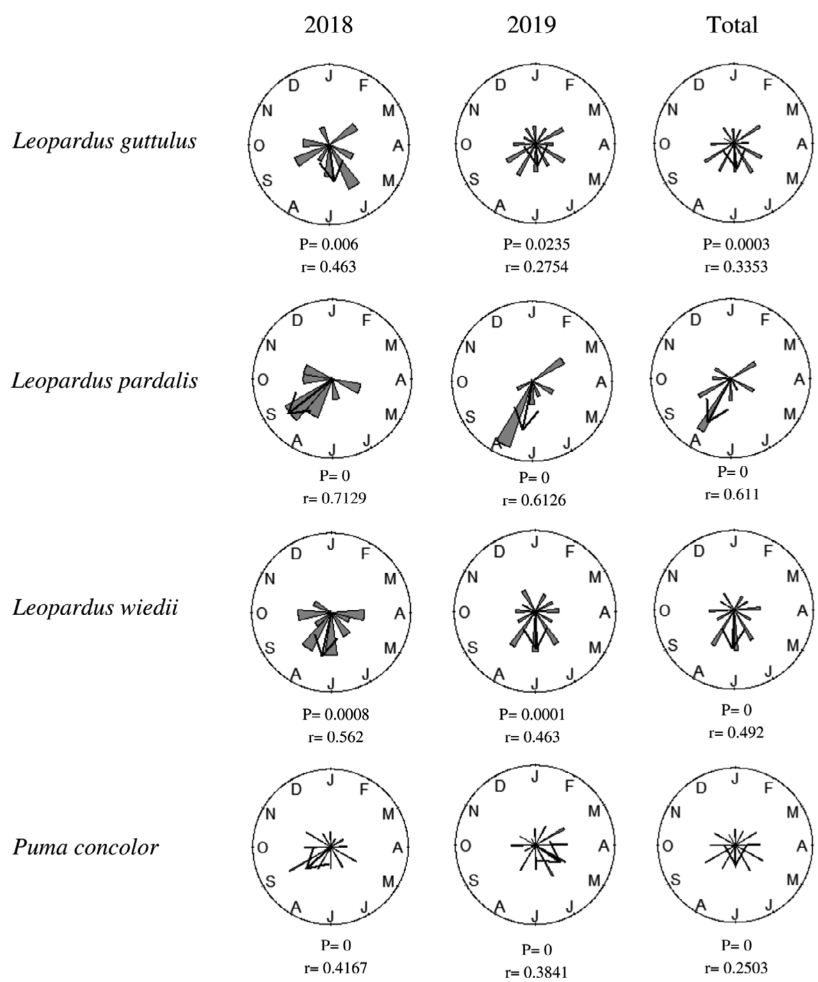

Fig. 3. Circular histograms with distribution and frequency of the seasonal activity of *Leopardus guttulus*, *L. pardalis*, *L. wiedii* and *Puma concolor* in Papagaios-de-Altitude Private Protected Area, Santa Catarina, Brazil. The arrows on each graph indicate the direction of the mean angle (μ). Each graph also exhibits the values of P and mean vector length (r).

Tab. I. Distribution of records of each species, in percentage, for each period (day and night) at Papagaios-de-Altitude Private Protected Area in Urupema, Santa Catarina, Southern Brazil.

	L. guttulus	*L. pardalis*	*L. wiedii*	*P. concolor*
Day	35.19	16.36	32.47	37.76
Night	64.81	83.64	67.53	62.24

Leopardus pardalis. We classified the habit of *L. pardalis* as mostly nocturnal (Tab. I), with non-uniform activity (Rayleigh Test= 0.429, $p < 0.001$), and peak of activity concentrated between 00:00h and 03:00h, with high dispersion of records in relation to the mean vector, indicated between 00:00h and 01:00h (Fig. 2). We found a significant difference in the daily activity patterns of this species between the two sampled years (U^2= 0.2502, p< 0.05). Concerning the seasonal distribution of activity, throughout the entire sampled period, we observed that *L. pardalis* had the highest activity between July and August (Rayleigh Test= 0.611, $p < 0.001$) and an intermediate dispersion of records throughout the year, in relation to the mean. Analyzing 2018 independently, we found that there was a peak of activity of the species during the month of September, and that there was a high concentration of records in relation to the mean vector. In 2019, we observed a pattern similar to the result obtained for the total period (Fig. 3). Species patterns in 2018 and 2019 differed significantly (U^2= 0.2963, $p < 0.01$).

Leopardus wiedii. This species had mostly nocturnal habits (Tab. I), with non-uniform activity (Rayleigh Test= 0.319, $p < 0.001$), and a peak of activity concentrated between 21:00h and 06:00h, with high dispersion of records in relation to the mean, indicated between 00:00h and 02:00h (Fig. 2). We found no significant difference in the daily activity patterns of this species between the two sampled years (U^2= 0.1612, p> 0.05). As for the seasonal distribution of activity, throughout the entire sampled period, we observed that *L. wiedii* was more active between the months of July and August, with a non-uniform distribution throughout the year (Rayleigh Test= 0.492, $p < 0.001$) and high dispersion of records. By independently analyzing the records for 2018, we found that the pattern was similar to that found for the total period (Fig. 3). However, in 2019 we recorded a peak of activity for the species between the months of June and July, with an intermediate dispersion of records throughout the year. It was not sufficient to differentiate the patterns between the two years (U^2= 0.0508, $p > 0.10$).

Puma concolor. The habit of *P. concolor* was cathemeral (Tab. I), with a non-uniform activity (Rayleigh Test= 0.227, $p < 0.001$). This species showed several peaks of activity, with high dispersion of records over 24 hours, in relation to the mean (Fig. 2). We found no significant difference in the daily activity patterns of this species between the two sampled years (U^2= 0.0678, p> 0.10). Regarding the seasonal distribution of activity, throughout the entire sampled period, we observed that *P. concolor* was more active during the months of July and August, showing a non-uniform distribution throughout the year (Rayleigh Test= 0.250, $p < 0.001$) and a high dispersion of records. Independent analysis of the 2018 records revealed a different pattern, showing a peak between August and September. In 2019, the peak of activity occurred between the months of May and June (Fig. 3). The difference between the two years was significant (U^2= 1.3815, $p < 0.001$).

Pairwise comparisons. We performed the Watson's Two Sample Test of Homogeneity to assess differences in daily activity patterns between pairs of species. Regarding the whole period, only *L. pardalis* and *P. concolor* showed a significant difference (U^2= 0.27, p< 0.01). The other pairs presented only slight and non-significant differences: *L. guttulus* and *L. pardalis* (U^2= 0.1195, p> 0.10); *L. guttulus* and *L. wiedii* (U^2= 0.0664, p> 0.10); *L. guttulus* and *P. concolor* (U^2= 0.163, p> 0.05); *L. wiedii* and *L. pardalis* (U^2=0.1328, p> 0.10); *L. wiedii* and *P. concolor* (U^2= 0.1194, p> 0.10). Results for each year separately can be accessed in Supplementary Material 1 (S1).

Watson's Test was also performed to pairwise comparisons in the seasonal activity patterns between species. Regarding the whole period, significant differences were found for the pairs of species: *L. guttulus* and *L. pardalis* (U^2= 0.5087, p< 0.001); *L. guttulus* and *L. wiedii* (U^2= 0.2044, p< 0.05); *L. pardalis* and *L. wiedii* (U^2= 0.3326, p< 0.01); *L. pardalis* and *P. concolor* (U^2= 0.8746, p< 0.001); *L. wiedii* and *P. concolor* (U^2= 0.4792, p< 0.001). Only *L. guttulus* and *P. concolor* showed a non-significant difference (U^2= 0.1778, p> 0.05). Results for each year separately can be accessed in Supplementary Material 2 (S2).

Daily activity overlap. We observed that the four species showed high overlap of daily activity (Fig. 4), but with distinct peaks of activity. The largest activity overlaps between species were *Leopardus guttulus* and *L. wiedii* (Dhat4= 0.84; Confidence Interval [CI]: 0.8 - 0.98); *L. guttulus and Puma concolor* (Dhat4 = 0.83; CI: 0.78 - 0.93) and *L. wiedii and P. concolor* (Dhat4 = 0.84; CI: 0.79 - 0.95). We observed a high overlap of activity between *L. guttulus* and *L. pardalis* (Dhat1= 0.79; CI: 0.73 - 0.9) and *L. pardalis* with *L. wiedii* (Dhat1= 0.79; CI: 0, 7 - 0.93). *L. pardalis* and *P. concolor* presented the lowest coefficient of overlap in our study (Dhat1= 0.77; CI: 0.68 - 0.87).

DISCUSSION

Our results indicate predominantly nocturnal activity patterns for two species of *Leopardus* (*L. pardalis and L. wiedii*), while *Puma concolor* and *L. guttulus* behaved as cathemerals. However, the species showed slight differences in daily activity patterns between years, especially *L. pardalis*, in which the difference was significant. We found high coefficients of overlap between the daily activity patterns of all four species. Additionally, we observed a similar pattern of seasonal activity for all species, with the highest peaks concentrated between the months of June and September. Pairwise comparisons indicated differences between the seasonal activity patterns of most pairs of species, when considering the two years.

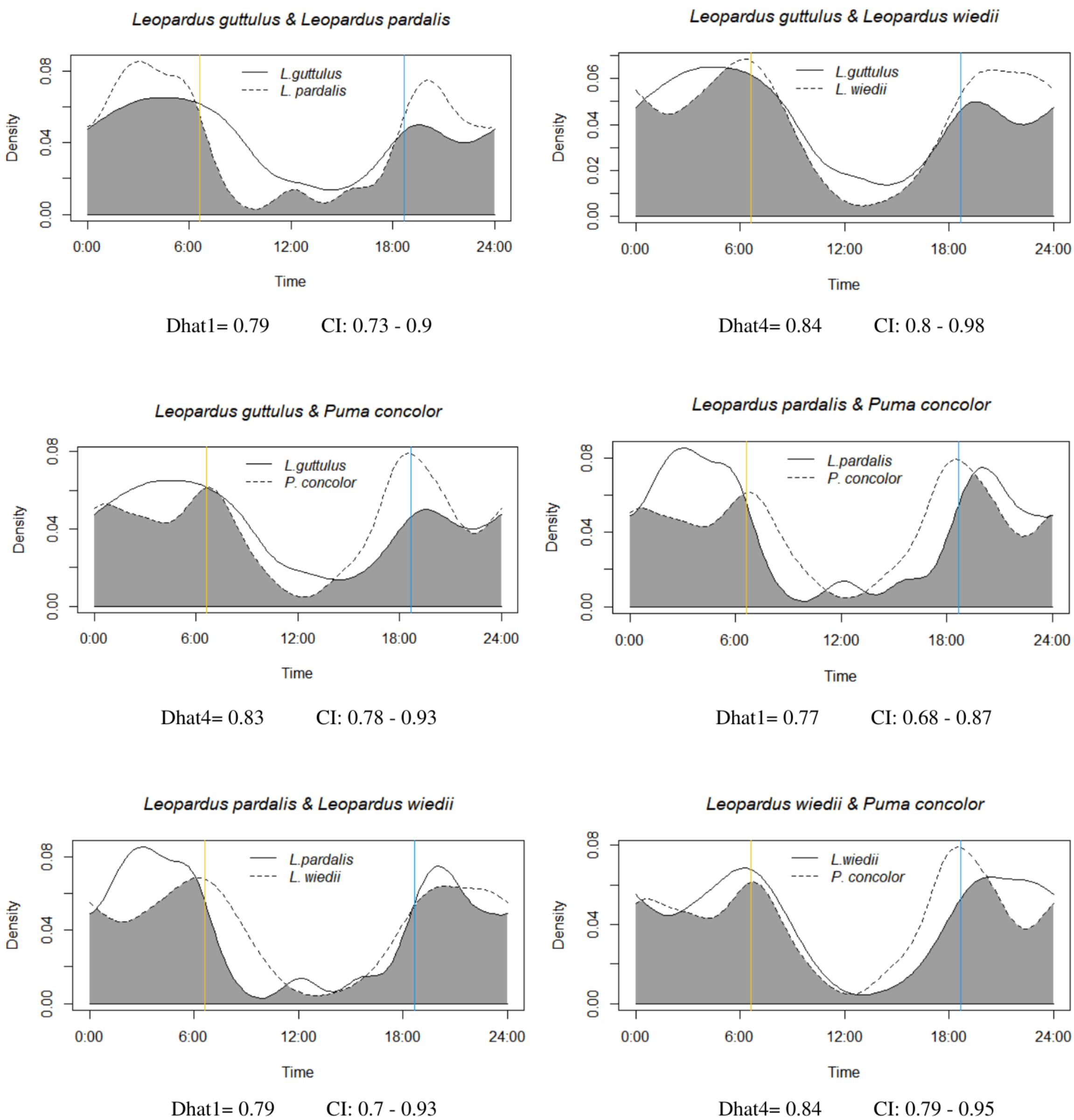

Fig. 4. Overlap of daily activities between the pairs of the four felid species found in the Papagaios-de-Altitude Private Protected Area in Urupema, Santa Catarina, southern Brazil. The area colored in gray indicates the overlapping of daily activity in each species pair. The parallel lines in each graph indicate the mean time of sunrise (yellow) and sunset (blue) in the study region. Below each graph is the coefficient of overlap for each pair of species, and the confidence interval.

The cathemeral behavior of *L. guttulus* found in our study, with peaks of nocturnal activity, corroborates previous studies of this species in other regions. According to OLIVEIRA-SANTOS *et al.* (2012) and NAGY-REIS *et al.* (2019) the species may present a cathemeral behavior in the presence of other felids. LINCK *et al*. (2021) suggest that *L. guttulus* may modulate their activity in order to reflect the activity of their prey, showing a more nocturnal activity in the warmer months of the year. Similar pattern has been documented for *L. tigrinus* (previously considered as the same species as *L. guttulus*) in the Caatinga biome, showing a large peak of activity before dawn and a smaller one at midnight (PENIDO *et al*., 2017) and it is suggested that the nocturnal behavior of the species is more likely reflecting temperature extremes and the activity of potential prey, rather than influenced by intraguild interactions (PENIDO *et al*,. 2017). CRUZ *et al*. (2018) also identified a mostly nocturnal activity pattern of this species associated with sites with an anthropic presence. Cathemeral species may be able to adjust their activity pattern to local conditions (DI BITETTI *et al*., 2010), which could explain the pattern exhibited by *L. guttulus* in our study.

Leopardus wiedii showed a mostly nocturnal behavior, as it is documented in previous knowledge from this species (Hernández-Sánchez & Santos-Moreno, 2020; Horn *et al.*, 2020). According to Sunquist & Sunquist (2002), the nocturnal behavior is likely related to the activity of their prey, since *L. wiedii* consumes mainly small rodents (Oliveira, 1994; Rocha-Mendes *et al*., 2010; Bianchi *et al*., 2011) that are mostly active at night. Hernández-Sánchez & Santos-Moreno (2020) also described a mostly nocturnal activity for *L. wiedii* and suggested that this pattern could be influenced by prey availability. Horn *et al.* (2020) found similar pattern in the Brazilian southernmost Atlantic Forest, where the species was strictly nocturnal even in the human-altered landscapes.

Our results indicate that *L. pardalis* behaved as mostly nocturnal in the study area. Nagy-Reis *et al*. (2019) described a similar pattern for the Brazilian southeastern Atlantic Forest, and found a high overlap between the activity of *L. pardalis* and their potential prey. The predominantly nocturnal activity was also described in Araucaria forest by Marques & Fábian (2018), where the activity was reduced after daybreak and increased between one and two hours before nightfall, similar to our findings. There are evidences of *L. pardalis* increasing their nocturnal activity to avoid human presence (Cruz *et al.*, 2018), however, the nocturnal behavior is an expected result for this species even in undisturbed areas (Kolowski & Alonso, 2010). The daily activity patterns of *L. pardalis* differed significantly between years, showing lower concentration of records close to the mean in 2019 comparing to 2018. This difference might be caused by inter-annual variations in environmental and ecological conditions, however the nocturnal behavior of the species is maintained in both years.

In our study, *P. concolor* exhibited cathemeral behavior, with several peaks of activity, which is consistent with previous studies in South America. In the Green Corridor of Misiones province, Argentina, and contiguous areas of Brazil, *P. concolor* is active during the entire day, with a peak of activity in the early morning (Di Bitetti *et al.*, 2010). This pattern was also found for *P. concolor* in a tropical montane forest of Costa Rica (Botts *et al*., 2020), where the species co-exist with four other felids. This study emphasized that prey availability is more important than intraguild competition in determining the activity patterns of the felid assemblage. The role of food resource in modulating *P. concolor* activity patterns is also described by Foster *et al*. (2013) in four Brazilian biomes, where both *P. concolor* and *Panthera onca* showed intensive nocturnal and crepuscular activity, with high coefficients of overlap.

All pairs of species analyzed in the present study exhibited high coefficients of daily activity overlap. Hernández-Sánchez & Santos-Moreno (2020) reported a high activity overlap between *L. tigrinus* and *L. pardalis* (Dhat1= 0.76); between *L. tigrinus* and *P. concolor* (Dhat1= 0.79) and between *L. pardalis* and *P. concolor* (Dhat1= 0.74-0.77), that are very similar to our findings. The authors pointed out that prey diversity and availability at the site facilitated temporal overlap between felid species. Furthermore, we found that the overlap of the daily activity of *L. pardalis* and *P. concolor* was the lowest in our study, with very different peak times. This pattern may suggest an attempt by *L. pardalis* to avoid encountering *P. concolor*, as observed in previous studies (Massara *et al.*, 2018; Finnegan *et al*., 2021). However, Herrera *et al*. (2018) found high overlap coefficients among the two felids, and suggested that space use or prey availability may have a main role in determining their activity patterns. In the same study, the two species also differed in their peaks of activity and showed different degrees of nocturnality, which was also observed in the Papagaios-de-Altitude area.

Studies have shown that the diet overlap of felid species is variable and influenced by morphological and behavioral differences, in addition to environmental factors and prey availability (Martins *et al*., 2008; Kasper *et al*., 2016; Nagy-Reis *et al*., 2019). The broad habitat and diet profile of these animals contributes to greater plasticity, and may allow them to adapt locally to available resources. In more restricted and fragmented landscapes, space could become a limiting factor, forcing smaller species to temporarily segregate with top predators. However, we consider that the connectivity of the Papagaios-de-Altitude with an adjacent area, the Complexo Serra da Farofa Private Protected Area, with a similar phytophysiognomy and an area of approximately 4,987 hectares, may facilitate the activity overlap of these species. Felids tend to occupy a wide home range and benefit from the set of interconnected environments, which support an abundance of resources for each species (Ashrafzadeh *et al*., 2020).

When comparing the seasonal activity patterns between pairs of species, we found that most pairs showed significant differences. However, all species showed the highest peak of activity concentrated between the months of June and September, a period that corresponds to winter in the southern hemisphere. During these months, Araucaria (*Araucaria angustifolia* (Bertol.) Kuntze) nuts fall in the Araucaria Forest. The nuts are an important food resource for the fauna, mainly birds and small rodents. The winter period is scarce in zoochoric fruits in the forests (Vieira & Paise, 2006; Paise & Vieira, 2005), and the Araucaria nut has a high energy content, especially of starch and protein (Rosado *et al*., 1994), presenting a high relevance for the maintenance of animal populations. Small rodents are especially influenced by this dynamic, since their populations can present an abrupt increase in their densities correlated with the high availability of food resources (Alho & Pereira, 1985; Greenwood, 1985; Orland & Kelt, 2007; Prevedello *et al*., 2013). Furthermore, it is known that rodents are important predators of the Araucaria nut, also acting as dispersers (Vieira & Iob, 2009). Studies show the increase in the abundance of small rodents linked to the Araucaria nut harvest in southern Brazil (CADEMARTORI *et al*., 2004; PAISE, 2005), starting from June to August, and which tends to decline at the beginning of September, period when seed fall ceases (CADERMATORI *et al*., 2004). These data overlap with the higher frequencies of felids in the Papagaios-de-Altitude Private Protected Area.

According to OLIVEIRA (1994) and ROCHA-MENDES (2010), small and medium-sized rodents are prey of great importance in the diet of all species present in our study. The abundance of prey is a factor that can promote convergence in use of habitat among felids (SANTOS *et al*., 2019) and their activity patterns usually overlap with that of their potential prey, maximizing the probability of encounters and minimizing energy expenditure during hunting (EMMONS & FEER, 1997; FOSTER *et al*., 2013, PORFIRIO *et al.*, 2016). Thus, it is likely that the peak activity of the felids in the study area has a positive correlation with the Araucaria nut supply, and the presence of small rodents that benefit from it.

The camera trapping method was efficient to elucidate the patterns of daily and seasonal activity of the species in the study area, as well as their similarities. In our study, the species with the lowest capture success was *L. pardalis*, which is explained by its strong association with the water resource and its surroundings (WOLFF *et al*., 2019), reducing the chance of capture by cameras further away from this location. Furthermore, *P. concolor* was the species from which we obtained the most records. Studies report that the body mass of animals affects recording success, because larger species have higher probability of triggering the cameras (TOBLER *et al*., 2008; LYRA-JORGE *et al.*, 2008). Therefore, *P. concolor* may present the higher number of records as a consequence of its larger size, in comparison to the other felids in our study.

Our study elucidated the daily and seasonal activity patterns of felids in a protected area of the Santa Catarina plateau, indicating a high overlap of activity between the species. Our findings corroborate previous knowledge from the daily activity patterns of the species, likely reflecting environmental conditions and the activity of prey. Furthermore, we emphasize the correlation between the seasonal activity peak of the felids and the Araucaria nut harvest in the study area, possibly associated with the increase in the occurrence of small rodents. We did not find evidence of temporal segregation between the felids in the Papagaios-de-Altitude Private Protected Area. Further research, such as for spatial and trophic use, are needed to elucidate the mechanisms of ecological segregation of felids at the site.

Supplementary material

Supplementary Material 1. Results from the Watson's Two Test of Homogeneity (U^2) to assess differences in the daily activity patterns between pairs of species in the Papagaios-de-Altitude Private Protected Area.

Supplementary Material 2. Results from the Watson's Two Test of Homogeneity (U^2) to assess differences in the seasonal activity patterns between pairs of species in the Papagaios-de-Altitude Private Protected Area.

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