Spatial distribution and daily activity patterns of three carnivore species in temperate grasslands of southern Brazil and northern Uruguay

Distribuição espacial e padrões de atividade diária de três espécies de carnívoros em pastagens temperadas do sul do Brasil e norte do Uruguai

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ABSTRACT
In the temperate grasslands of southern Brazil and northern Uruguay, three species of mesopredators have similar size, are in the same guild, and they seem to tolerate anthropogenic modifications. Sympatric species from the same trophic guild tend to divide resources both spatially and temporally to facilitate coexistence. The aim of this study was to determine the patterns of the periods of daily activity and habitat use through different detection and occupancy models, of *Cerdocyon thous* (crab-eating fox), *Lycalopex gymnocercus* (pampas fox) and *Leopardus geoffroyi* (geoffroy's cat) in the mosaic of landscapes of anthropic domain in the Uruguayan Savanna ecoregion, through camera trap records. A total of 66 cameras were installed, divided into the 3 main environments, with a distance of 2 km between each camera to maintain the independence of the records, achieving a real sampling effort of 4,756 trap nights. The three mesocarnivores considered in this study were predominantly nocturnal. *Cerdocyon thous* presented a vesperal-nocturnal activity pattern, being sunset the moment of highest activity, in contrast, *L. gymnocercus* presented highest activity at sunrise, being crepuscular-nocturnal. These opposite daily activity patterns among foxes species have not been recorded in other regions. With respect to *L. geoffroyi*, these specie presented a mostly nocturnal activity pattern. Regarding the use of habitats by the species after applying different models, the highest probability of detection and occupation of *C. thous* and *L. geoffroyi* was in the native forest environment and for *L. gymnocercus* was the natural grassland. Even the preference of *L. geoffroyi* for the native forest environment, these species presented a certain degree of

adaptability for habitats with alterations produced by agricultural activities. The results obtained represent a very important contribution to the region in which this study was carried out, as well as allowing us to compare the results with other studies with these species in other regions.

Keywords: carnivores, activity patterns, spatial distribution, temperate grasslands.

RESUMO
Nos campos temperados do sul do Brasil e do norte do Uruguai, três espécies de mesopredadores têm tamanho semelhante, pertencem à mesma guilda e parecem tolerar modificações antropogênicas. As espécies simpátricas da mesma guilda trófica tendem a dividir os recursos espacial e temporalmente para facilitar a coexistência. O objetivo deste estudo foi determinar os padrões dos períodos de atividade diária e uso do habitat, por meio de diferentes modelos de detecção e ocupação, de Cerdocyon thous (raposa-caranguejeira), Lycalopex gymnocercus (raposa-dos-pampas) e Leopardus geoffroyi (gato-do-mato-pequeno) no mosaico de paisagens de domínio antrópico na ecorregião da Savana uruguaia, por meio de registros de armadilhas fotográficas. Foram instaladas 66 câmeras, divididas nos três ambientes principais, com uma distância de 2 km entre cada câmera para manter a independência dos registros, alcançando um esforço real de amostragem de 4.756 noites de armadilhas. Os três mesocarnívoros considerados neste estudo eram predominantemente noturnos. Cerdocyon thous apresentou um padrão de atividade vespertino-noturno, sendo o pôr do sol o momento de maior atividade; em contrapartida, L. gymnocercus apresentou maior atividade ao nascer do sol, sendo crepuscular-noturno. Esses padrões opostos de atividade diária entre as espécies de raposas não foram registrados em outras regiões. Com relação à L. geoffroyi, essa espécie apresentou um padrão de atividade predominantemente noturno. Com relação ao uso de habitats pelas espécies após a aplicação de diferentes modelos, a maior probabilidade de detecção e ocupação de C. thous e L. geoffroyi foi no ambiente de floresta nativa e, para L. gymnocercus, foi no pasto natural. Mesmo com a preferência de L. geoffroyi pelo ambiente de floresta nativa, essas espécies apresentaram certo grau de adaptabilidade a habitats com alterações produzidas por atividades agrícolas. Os resultados obtidos representam uma contribuição muito importante para a região em que este estudo foi realizado, além de nos permitir comparar os resultados com outros estudos com essas espécies em outras regiões.

Palavras-chave: carnívoros, padrões de atividade, distribuição espacial, pastagens temperadas.

1 INTRODUCTION

One of the traditional approaches in ecology regarding species that live in sympatry and that, in turn, belong to the same guild, is the tendency to divide the use of resources, thus facilitating their coexistence (Schoener 1974). The three most important parameters commonly used to characterize overlap and determine resource partitioning are diet, space use, and time use (Pianka 1974).

The carnivorous mammals analyzed in this study belong to the group of mesopredators, that is, species belonging to the order Carnivora, located at an intermediate trophic level (Prugh et al. 2009). In general, these species must adjust their behavior to increase the success of prey capture, since they have to face strong competitive pressure within the guild (Ritchie and Johnson 2009, Oliveira and Pereira 2013). The activity pattern, for example, is basic information of the natural history of the species (van Schaik and Griffiths 1996, Manfredi et al. 2011), it is decisive to determine the overlap between sympatric species (Halle 2000), to reduce competition between each other (Loveridge and Macdonald 2003) and also to influence their foraging success (Lockard 1978).

Determining the pattern of activity is also important to understand how species use space by estimating, for example, habitat use. One way to do this is by using occupancy models, which estimate the proportion of sites in which a species occurs, while simultaneously estimating the probability of detection (when the probability of detection is <1), through repeated sampling of each site (MacKenzie et al. 2002, Mackenzie 2006, Bailey et al. 2014). However, modeling the presence of carnivores is potentially complex, as they are affected not only by biological traits specific to each species, but also by environmental factors such as habitat quality, landscape structure, and resource availability (Di Bitetti et al. 2006, Sarmento et al., 2011; Gálvez et al., 2013), in addition to suffering consequences from a variety of anthropogenic threats (Long et al. 2011, Pia et al. 2013).

In the region of grasslands and subtropical fields that extends from the extreme south of the state of Rio Grande do Sul, including all Uruguay (Olson et al. 2001), human activities have extensively modified the natural habitats of both prairie and native forest, making the region one of the most threatened environments on the continent (Dinerstein et al. 1995, Bilenca and Miñaro 2004). Mesopredator species such as the canids *Cerdocyon thous*, *Lycalopex gymnocercus* and the felid *Leopardus geoffroyi*, are species that are closely related to the main productive activity of this grassland region, such as livestock, agriculture and poultry farming.

All three species are classified as “Least Concern” by the International Union for Conservation of Nature (IUCN) (Lucherini 2015, 2016; Pereira et al. 2016). *Cerdocyon thous*, is a medium-sized, nocturnal-crepuscular mammal (Di Bitetti et al. 2009) with a geographic range that goes from the north of South America, covering a large part of the territory of Brazil to the north of Argentina and Uruguay. It is found in all habitats, including the open ones (Bossi et al. 2019) and its population is considered stable (Lucherini 2015). On the other hand, *L. gymnocercus* is also a medium-sized mammal, found in eastern Bolivia, western Paraguay, Uruguay, southeastern Brazil, and central and northern Argentina. It is associated with open habitats (Bossi et al. 2019) and has a variable activity pattern (Lucherini and Luengos Vidal 2008), becoming more diurnal in areas where *C. thous* is abundant to avoid this likely superior competitor (Di Bitetti et al. 2009). Lastly, *L. geoffroyi*, is a small, solitary Neotropical cat. It is considered abundant in most of its distribution, which goes from Bolivia and the extreme south of Brazil to the extreme south of America. It is known to have a nocturnal activity pattern (Manfredi et al. 2011; Pereira et al. 2015; Tirelli et al. 2019) and studies in the region and in Argentina, the country that occupies the largest proportion of its distribution, indicate that the species is tolerant and perhaps sometimes favored by habitat alteration and may persist alongside cattle raising and agriculture.

In this context, the objective of this study was to determine the activity patterns and habitat use of three species of mesocarnivores, in the mosaic of environments in the Uruguayan savannah ecoregion. Being the specific objectives, to determine the pattern of daily activity and to model the detection and occupation of the species: *C. thous*, *L. gymnocercus* and *L. geoffroyi*.

2 MATERIALS AND METHODS

Study area.- This study was carried out in northeastern Uruguay and southwestern Brazil, within the Uruguayan Savanna region (Fig. 1) (Dinerstein et al. 2015). It is an ecoregion of grasslands and subtropical savannahs that extends from the extreme south of the state of Rio Grande do Sul, including all of Uruguay (Olson et al. 2001). The study area presents a landscape composed of a mosaic of forests, grasslands, and mountain ranges, in a prairie matrix (Evia and Gudynas 2000). Sampling design and data collection.- Camera traps of three different models were used to obtain data: Zeroglow 10M™ (Scoutguard®), sg2060-k 20 MP™ (Scoutguard®) and Trophy Cam™ (Bushnell®). Eleven sampling sites distributed in the localities were determined: Artigas, Tacuarembó, Salto, Quaraí, Cacequi, Alegrete and Rosário do Sul. Six cameras were installed at each site, two in each of the three types of environments identified as characteristic and predominant in the study area: native forest, natural grassland and anthropic environment (Forestry: pine, eucalyptus, rice and soy). 66 cameras were installed, equally distributed among the three environments as mentioned above (Fig. 1). The cameras were installed at a distance of at least 2 km from each other, at a height between 40 and 50 cm above the ground, and were programmed to record 20-second videos. They were active 24 hours a day for a period between 2 and 5 months (depending on the possibilities of access due to the pandemic), during the spring-summer period of 2020 and 2021, between the months of October and March. Bait was not used to attract the animals.

Information on environmental variables linked to the environment of each of the cameras was obtained. Four measurements of the height of the vegetation were taken at 15 meters from the camera in the north, south, east and west directions, using a hypsometer (Vertex IV HS102). These measurements were then averaged, obtaining a single height value per camera point. Canopy cover (in percentage) was also measured, at the same points, to the north, south, east and west, using the Canopy Capture application (available on the App Store), measurements that were then averaged to obtain a single value of canopy cover, same way that was done with the height of the vegetation.

Once the data collection time had elapsed, the cameras were collected and the memory cards (Kingston Micro SD 64 GB) analyzed. The videos were processed and analyzed using the Timelapse 2 software (Version 2.3.3.7; Greenberg 2013), generating a matrix for each of the cameras, totaling 66 spreadsheets. Then, a single excel matrix was created with the information from all the spreadsheets (where the following were taken into account: time, date, point, class, order, family, genus, species, number of individuals, etc.).

From this single matrix, the data was filtered and a registration rate matrix was constructed for each of the three species: *C. thous, L. gymnocercus,* and *L. geoffroyi*. Which was then processed using R software (R Development Core Team 2015).

Activity patterns.- First, an average was determined for the time of sunrise and sunset during the sampling period (spring-summer). It was calculated based on data from the site https://www.sunrise-and-sunset.com/ for each of the 11 locations where the cameras were installed and then an average was made for the entire study area.

The daily activity pattern for each of the species was elaborated using records taken at intervals of one hour that were then analyzed by circular statistics using the Oriana 4.0 software (Kovach 2019). In the analysis, the Rayleigh Test was applied to see the uniformity of the results.

Once the activity pattern of each species was obtained, the temporal overlap coefficient (Δ) was calculated using the “overlap” package (Ridout and Linkie 2009) within the R software (R Development Core Team, 2015). These analyzes were performed using Kernel density, this method considers each record as a random sample from an underlying continuous distribution (Ridout and Linkie 2009; Foster et al. 2013). The degree of overlap was measured pair by pair between the three carnivore species: *C. thous - L. gymnocercus*; *C. thous-L. geoffroyi*; *L. gymnocercus - L. geoffroyi*. The value of the coefficient varies between 0 (no overlap) and 1 (complete overlap) (Ridout and Linkie 2009).

Habitat use - From the records of the species, a percentage of occurrence was also analyzed by each one with respect to the different environments. Elaborating a table for each species with the records by environment. The historical matrices of each of the species were imported into the R software (R Development Core Team 2015), together with the respective values of the variables of each site, mentioned in the previous paragraph. For the independence of the records, a period of 24 hours was determined as the minimum limit between each record of the same species per camera.
Then, different occupancy models were applied for each of the species, in order to estimate the probabilities of both detection and occupancy of these in the study area (Mackenzie et al. 2006). The models were based on variables obtained in the field and in the different environments that were sampled. For the detection, the variables considered were the "Vegetal cover of the canopy" at the point where each camera was installed and the previously averaged "Vegetation height" per point, both obtained in the field. While for the occupation, the different environments were used as categories: native forest, natural grassland and anthropic environment.

Models were built using the "unmarked" statistical package (Fiske and Chandler 2015) in R software (R Development Core Team 2015). Detection was modeled first, where detectability is estimated from the frequency of detections per site, taking imperfect detectability into account (Mackenzie et al. 2006). The variables measured in the field and the different environments where the cameras were located were used. Different models were developed for each species including the detection variables mentioned above, and a null model. The different detection models were classified using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). Those with $\Delta AIC \leq 2$ from the upper model were considered adjusted (Burnham and Anderson 2002).

Then, for the elaboration of the occupancy models, the best detection model was used (MacKenzie et al. 2006; De Wan et al. 2009). Which included the different environments as categorical variables, where a null model was also developed. Then, the different occupancy models were ranked according to the AIC value, where those in which the ΔAIC value was less than or equal to two ($\Delta AIC \leq 2$) were considered the best (Burnham and Anderson 2002). Starting from the best, the effect of each variable was evaluated both in the probability of detection and in the probability of occupation.

Once the models were developed, the "backTransform" function was applied to them within the "unmarked" package, to obtain the probability of detection and occupation of each of the species in the study area.

3 RESULTS

Data collection - The total sampling effort was 4,756 trap nights. Where 227 records of *C. thous*, 137 of *L. gymnocercus* and 32 of *L. geoffroyi* were obtained.

Activity pattern.- All mesopredators were predominantly nocturnal, presenting a non-uniform activity pattern (Table 1). *Cerdocyon thous* presented a peak of activity between 6:00 p.m. and 7:00 p.m., being the average time of its activity at 8:00 p.m. (Fig. 2). On the other hand, *L. gymnocercus* showed a peak of activity opposite to *C. thous*, between 06:00 and 08:00, the mean time of its activity being 06:00 (Fig. 3). The species presented a tendency to have a higher registration rate in the stations located in the natural grassland, than in native forest and anthropic environment (Table 2). As for *L. geoffroyi*, the specie showed a peak of activity between 9:00 p.m. and 11:00 p.m., with the mean time of activity being approximately 10:30 p.m. (Fig. 4).

Overlap - Regarding activity comparisons between the three species of mesopredators, it can be seen that there is a medium overlap between all of them, classified as moderate (Monterroso et al. 2014). When overlapping the activity pattern between *C. thous* and *L. gymnocercus*, it is possible to observe that despite having opposite peaks of activity (Fig. 5), they present a coefficient of overlap in their daily activity of 62% (Δ̂=0.62 (0.52-0.71 CI)). Regarding the comparison between *C. thous* and *L. geoffroyi*, the highest overlap coefficient was obtained, 71 % (Δ̂=0.71 (0.56-0.82 CI)). Both species presented a nocturnal vesper activity pattern (Fig. 6). The lowest overlap coefficient was obtained when comparing the species, *L. gymnocercus* and *L. geoffroyi*, 55 % (Δ̂=0.55 (0.41-0.68 CI)). Both presented opposite peaks of activity, as happened with *C. thous* and *L. gymnocercus* (Fig. 7).

Habitat use - *Cerdocyon thous* presented a tendency to have a higher registration rate in stations located in native forest (52.86%), than in natural grasslands (43.17%) and anthropic environment (3.96%). On the other hand, *L. gymnocercus* presented a tendency to have a higher registration rate in the stations located in the natural grasslands (60.58%), than in native forest (23.35%) and anthropic environment (16.05%). Meanwhile, *L. geoffroyi* presented a tendency to have a higher registration rate in stations located in native forest (81.25%), than in natural grasslands (6.25%) and anthropic environment (12.5%).

Regarding detection and occupancy models, for *C. thous* the best detection models (ΔAIC ≤ 2) that fit the species include "Canopy Cover" (det2) and the combination of "Canopy Cover " plus the "Vegetation Height" (det3) (Table 2). Regarding the probability of occupation, the model that best fit the species was the null model (Ocu1). However, all models were adjusted and presented ΔAIC values ≤ 2 (Table 3). The second best model was the one that combined the variable "Canopy Coverage" plus the environment "Native Forest" (Ocu2), followed by the model that integrated "Plant Coverage" and "Anthropic Environment" (Ocu3), and finally the model with the "Canopy cover" and the environment "natural grassland" (Ocu4). In the Ocu 1 model, the probability of occupancy is null (does not include variables) and the "Canopy cover" presented a negative trend for detection (beta = - 0.421, SE = 0.1052, z = - 4.0, P(>| z|) = 6.28e-05). Ocu2, a positive trend for the "Native Forest" environment in terms of occupancy (beta = 0.80, SE = 0.726, z = 1.10, P(>|z|) = 0.271) and negative for "Canopy Cover", with respect to the probability of detection (beta = -0.43, SE = 0.105, z = -4.11, P(>|z|) = 3.98e-05). Ocu3, a negative trend for "anthropic environment" for occupation (beta = -0.544, SE = 0.609, z = -0.894, P(>|z|) = 0.3714) and also negative for "Canopy cover" in the detection (beta = -0.425, SE = 0.105, z = -4.04, P(>|z|) = 5.24e-05). Ocu4, a negative trend regarding the probability of occupation for the "Campo" environment (beta = -0.116, SE = 0.625, z = -0.186, P(>|z|) = 0.852) and also negative for the detection with respect to "Canopy cover" (beta = -0.421, SE = 0.1051, z = -4.01, P(>|z|) = 6.11e-05).

For *L. gymnocercus*, all the detection models applied presented a ΔAIC value ≤ 2 (Table 4). The best being the one that includes the variable "Vegetation height" (det1), followed by the model that includes the combination of "Vegetation height" plus "Canopy cover" (det3). As with the detection models, all occupancy models were fitted (Table 5). However, the best was the one that includes the "Height of the vegetation" (Ocu1), followed by the one that combines the "Height of the vegetation" plus the environment "anthropic environment" (Ocu3), then the one that includes the "Vegetation height" and the environment “Native Forest” (Ocu2) and finally the one that combines the variables "Vegetation height" and the environment “natural grassland” (Ocu4). In the Ocu1 model, the probability of occupancy is null (it does not include variables) and the “Vegetation height” presented a positive trend for detection (beta = 0.13, SE = 0.0684, z =1.89, P(>|z|) = 5.81e-02). Ocu3, a negative trend for "Anthropic environment" in terms of occupation (beta = -0.153, SE = 0.634, z = -0.242, P(>|z|) = 0.80873) and positive for "Vegetation height" , with respect to the probability of detection (beta = 0.13, SE = 0.0684, z = 1.9, P(>|z|) = 5.8e-02). Ocu2, a positive trend for the "Native Forest" environment for occupation (beta = 0.143, SE = 0.617, z = 0.232, P(>|z|) = 0.81687) and also positive for the "Vegetation Height" in detection (beta = 0.13, SE = 0.0684, z = 1.9, P(>|z|) = 5.80e-02). Ocu4, a positive trend regarding the probability of occupation for the " natural grassland" environment (beta = 0.00565, SE = 0.637, z = 0.00887, P(>|z|) = 0.99292) and also positive for detection with with respect to the "Vegetation Height" (beta = 0.13, SE = 0.0684, z = 1.89, P(>|z|) = 5.81e-02).

Finally, for *L. geoffroyi*, the best model that was adjusted to the species was the one that includes the variable “Vegetation height” (det1), followed by the one that combines the “Vegetation height” plus the “Vegetation cover”. canopy” (det3). They were the only models that presented a ΔAIC value ≤ 2 (Table 6). Regarding the occupancy models, the one that best fit was the one that includes the variable “crop” (Ocu3) (Table 7). In which, the variable "Vegetation height" (beta = 0.424, SE = 0.116, z = 3.65, P(>|z|) = 2.63e-04) presented a positive trend with respect to the probability of detection and “Anthropic environment” (beta = 1.293, SE = 0.683, z = 1.89, P(>|z|) = 0.0582) a positive trend for the probability of occupation.

4 DISCUSSION

In general, the activity pattern is a result of adaptations for predation, because predators must synchronize their activity with that of their prey (Theuerkauf et al. 2003; Jenny and Zuberbühler 2005; Eriksen et al. 2011). However, this pattern also exhibits temporal differences by species in the use of similar niches (Kasper et al. 2007). From which, it should also be noted that the use of habitat by different species is based on behavioral requirements and physiological/biological requirements (Swihart et al. 1988), and there is usually a clear relationship between the size of the home range of a species, its body mass and diet, with the relationship mediated by landscape productivity (Gehrt and Fritzell 1997; Gompper and Gittleman 1991), where environmental spatial complexity can also promote coexistence when both specialist species and as generalists (Simon 1974).

Regarding the pattern of daily activity, in this study *C. thous* presented a pattern of activity mostly vesperal-nocturnal, presenting a peak of activity at dusk. This result is similar to that obtained by Bianchi et al. (2016) in the Central Pantanal area in Brazil, unlike the study carried out by Kasper et al. (2007) in the "Parque Estadual do Turvo" in Rio Grande do Sul, in which the species was preferably nocturnal and in the studies carried out by Di Bitetti et al. (2009) in the Argentine Northeast and Maffei et al. (2007) in the Bolivian Dry Chaco, where the species presented a mostly nocturnal and crepuscular activity pattern and the study carried out in Northeast Brazil in a remnant of the Caatinga by Dias and Bocchiglieri (2016), where the species was strictly nocturnal.

On the other hand, *L. gymnocercus* presented a peak of activity at dawn, with its daily activity pattern being mostly crepuscular-nocturnal. This result is also similar to that obtained by Bianchi et al. (2016) in the Central Pantanal area in Brazil for this species, which can also be compared with the bimodal night/day pattern obtained by Di Bitetti et al. (2009) in the Argentine Northeast, unlike the one carried out by Maffei et al. (2007) in the Bolivian Dry Chaco, in which the species showed a tendency to have a nocturnal pattern.

Despite the fact that the overlap with respect to the daily activity pattern of the canids presented high values (62%), we must highlight the periods of activity with opposite peaks in time since they were not recorded in other studies, marking a new precedent for future jobs. These opposite peaks perhaps suggest that the species are acting in a complementary way, facilitating the coexistence between both since they are species that are in sympatry. It is said that two species live in sympatry or can be sympatric when their respective distribution areas coincide in whole or in part (Galán et al. 2013). Supporting this suggestion, according to the study carried out in northeastern Argentina by Di Bitetti et al. (Di Bitteti et al. 2009), *L. gymnocercus* becomes more diurnal in areas where *C. thous* is found and when both species must coexist in the same environment, it is *L. gymnocercus* that modifies its daily activity to avoid encounters with other species. Unlike what was stated in the study carried out by Maffei and collaborators, which did not reveal differences in the activity patterns of these species (Maffei, et al. 2007). The fact that *L. gymnocercus* resorts to this interspecific avoidance mechanism may be linked to its smaller size since it is a species that tends to feed alone, finding itself at a competitive disadvantage with *C. thous* (Di Bitetti et al . 2009). In relation to the aforementioned, another very important aspect must also be taken into account and highlighted, these species of canids have a preference for different environments. The differences in the physical appearance of the two species also point to adaptations to different environments, since *C. thous* has relatively shorter legs, snout and ears than *L.gymnocercus*, morphological characteristics typical of species that live in forests (Langguth 1975). *Cerdocyon thous* has generally been associated with forests, forest edges, and wooded savannas (Berta, 1982; Courtenay and Maffei 2004), while *L. gymnocercus* has been associated mainly with grasslands (Lucherini et al. 2004; Lucherini and Luengos Vidal 2008;), which was also reflected in this study, being native forest the environment with the highest number of records of *C. thous* and natural grasslands of *L. gymnocercus*.

Supporting the records that were obtained from each species in the different environments, when applying the detection and occupancy models, it was possible to observe that although both species of foxes used all the types of habitats monitored in our study, they did so to a different degree. "Native forest" being the environment with the highest probability of both detection and occupation for *C. thous* and the environment "Natural grassland" for *L. gymnocercus*. These results are reflected from the fact that in the different models, the variable "Native forest" presented a positive trend in terms of the probability of occupation for *C. thous*, however, the variable "Canopy cover" presented a negative trend in terms of the probability of occupation for *C. thous*. regarding the probability of detection. This may be associated with an increase in detection capacity in forest edges and wooded savannas (Berta, 1982; Courtenay and Maffei 2004) that do not have very dense vegetation.

However, despite the results obtained, in studies carried out in central Brazil, C.thous used all available environments in proportion to their availability (Jácomo et al. 2004), selecting more open areas of natural grasslands (Juarez and Marino 2002).

Regarding *L. gymnocercus*, the variable "Grassland" presented a positive trend in terms of the probability of occupation for the species, while the variable "Vegetation height" presented a positive trend for the probability of detection. In this case, the variable "Grassland" suggests a greater probability of occupation by the species in open environments, on the other hand, the variable "Vegetation height" is associated with the height of the grasslands, suggesting that the height in the vegetation would probably be associated with the species' need for shelter. Supporting the information already known, in which the species is described as grassland, but that it can also inhabit savannahs and open forests (Redford and Eisenberg 1992; García and Kittlein 2005; Vieira and Port 2007; Lucherini and Luengos Vidal 2008).

Regarding "Anthropic environment", this presented a negative trend for the probability of detection and occupation for both species of foxes, suggesting that this environment may present a threat to them. This result differs from that mentioned in other studies, where *C. thous* was shown to be more tolerable to altered environments (Courtenay and Maffei 2004; Lemos et al. 2011), taking into account that they are environments with another anthropic use. On the other hand, in the case of *L.*

gymnocercus, it has been previously recorded that altered environments do represent a threat to the species (Lucherini and Luengos Vidal 2008).

Unlike the two fox species, which had opposite peaks of activity at dusk and dawn, for *L. geoffroyi*, the species exhibited a mostly nocturnal pattern of activity in our study area. These results are similar to those previously reported by Johnson and Franklin (1991) in Patagonia, Pereira (2009) in central Argentina, Cuellar et al. (2006) in the Bolivian Chaco, Manfredi et al. (2011) and Castillo et al. (2008) in the Humid Pampas and Johnson and Franklin (1991) in the Magellanic subpolar forest. This daily pattern could be related to a greater activity and/or vulnerability of the main prey species (small rodents and birds) of *L. geoffroyi* in this region (Manfredi et al. 2004) and despite the high overlap that it presented with the two species of foxes, being 71% with *C. thous* and 55% with L. gymncoercus, their daily pattern does not interfere in the activity of these species.

When applying the different models, already mentioned above, to *L. geoffroyi*, as with *L. gymnocercus*, the variable "Vegetation height" also had a positive trend for the detection of this species, although in this case the variable is associated with the height of the vegetation of the "native forest" environment where it presented a greater number of records. On the other hand, this species was associated with "anthropic environment", the results showed a positive influence of this variable in terms of the probability of occupation of the species, the latter is in accordance with what is mentioned in other studies, where it is shown that the specie presents a certain degree of adaptability to habitat alterations produced by agricultural activities (Castillo et al. 2008; Cuellar et al. 2006; Pereira et al. 2011, 2012; Manfredi et al. 2012). However, the environment with the largest number of records by the species was "Native Forest", agreeing with and confirming results obtained in other studies regarding this result (Manfredi et al. 2006, 2012; Pereira et al 2012; Castillo et al 2019).

With regard to open areas such as the "natural grassland" environment, these do not seem to be suitable for the species (Caruso et al. 2016; Manfredi et al. 2012; Tirelli et al. 2019).

Several factors contribute to habitat selection by a species as noted above, but the most influential for this species is likely to be relative prey availability (Harper 2007; McNab 1963). Small mammals have been described as the main prey of *L. geoffroyi* in several studies (Bisceglia et al. 2008; Guidobono et al. 2016; Manfredi et al. 2004).

5 CONCLUSION

From the discussion of the results obtained in this study, we can say that these constitute a very important contribution to the region, revealing the pattern of activity, use of habitat and the application of detection and occupancy models of three species of mesocarnivores, information that allows us to know a little more about them and from which it is also possible to compare the results with studies carried out in other regions. Another reason why knowing the behavior of these species in the region is important is because they have an intimate relationship with our main productive activities, being permanently identified as predators of sheep and poultry (González and Martínez 2010).

How was it possible to observe, regarding the activity pattern, the three mesopredators considered in this study were predominantly nocturnal, corroborating previous knowledge of these species in other regions (Maffei et al. 2007; Bianchi et al. 2016; Castillo et al. al. 2019). However, something that we must highlight are the opposite peaks between the two species of foxes, something that has not been recorded in another region, becoming the starting point for future studies, allowing the generation of new hypotheses about the daily activity pattern of these species. This also reaffirms and reflects the need and lack of research work regarding mesopredators in the region.

Another important point of the results of this work is that we can say that these also show us the importance they have and what the mosaic of environments that make up the region represents, since they are areas that provide food and valuable shelter to species during the day and indicate that these environments are essential areas for wildlife. Highlighting the fact that many times the limits between forests and grasslands can be poorly defined. For these reasons, the incorporation of these findings in the conservation planning of these environments must be relevant to ensure the persistence not only of these species but of the entire community of wild mammals in the region.

TABLES

Tabla 1.- Valores del Test de Rayleigh para cada especie.

Especie	Rayleigh Test
Cerdocyon thous	0.3549; P<0,05
Lycalopex gymnocercus	0.3549; P<0,05
Leopardus geoffroyi	0.3781; P<0,05

Tabla 2.- Resultado de los distintos modelos de probabilidad de detección (p) para *C. thous* (Alt.veg = Altura de la vegetación; Cob = Cobertura de dosel).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
det2	p (Cob) ~ ψ (1)	3	1228.05	0.00	6.4e-01	0.64
det3	p (Alt.veg + Cob) ~ ψ (1)	4	1229.24	1.19	3.6e-01	1.00
det1	p (Alt.veg) ~ ψ (1)	3	1242.05	14.00	5.9e-04	1.00
det0	p (1) ~ ψ (1)	2	1298.29	70.24	3.6e-16	1.00

Tabla 3: Resultado de los distintos modelos de probabilidad de ocupación (ψ) para *C. thous* (Cob = Cobertura de dosel; Bosque = Bosque Nativo; AA = Ambiente antrópico; Camp = Campo).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
ocu1	p (Cob) ~ ψ (1)	3	1228.05	0.00	0.38	0.38
ocu2	p (Cob) ~ ψ (Bosque)	4	1228.70	0.65	0.27	0.65
ocu3	p (Cob) ~ ψ (AA)	4	1229.25	1.20	0.21	0.86
ocu4	p (Cob) ~ ψ (Camp)	4	1230.02	1.97	0.14	1.00

Tabla 4: Resultado de los distintos modelos de probabilidad de detección (p) para *L. gymnocercus* (Alt.veg = Altura de la vegetación; Cob = Cobertura de dosel).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
det1	p (Alt.veg) ~ ψ (1)	3	920.16	0.00	0.39	0.39
det3	p (Alt.veg + Cob) ~ ψ (1)	4	921.27	1.11	0.22	0.61
det2	p(Cob)~ ψ(1)	3	921.41	1.25	0.21	0.81
det0	p(1)~ψ(1)	2	921.60	1.44	0.19	1.00

Tabla 5: Resultado de los distintos modelos de probabilidad de ocupación (ψ) para *L. gymnocercus* (Alt = Altura de la vegetación; Bosque = Bosque Nativo; AA = Ambiente antrópico; Camp = Campo).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
ocu1	p (Alt) ~ ψ (1)	3	920.16	0.00	0.47	0.47
ocu3	p (Alt) ~ ψ (AA)	4	922.10	1.94	0.18	0.65
ocu2	p (Alt) ~ ψ (Bosque)	4	922.10	1.95	0.18	0.83
ocu4	p (Alt) ~ ψ (Camp)	4	922.16	2.00	0.17	1.00

Tabla 6: Resultado de los distintos modelos de probabilidad de detección (p) para *L. geoffroyi* (Alt.veg = Altura de la vegetación; Cob = Cobertura de dosel).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
det1	p (Alt.veg) ~ ψ (1)	3	414.04	0.00	0.6801	0.68
det3	p (Alt.veg + Cob) ~ ψ (1)	4	415.58	1.54	0.3146	0.99
det2	p (Cob)~ ψ(1)	3	425.10	11.06	0.0027	1.00
det0	p (1)~ψ(1)	2	425.14	11.11	0.0026	1.00

Tabla 7: Resultado de los distintos modelos de probabilidad de ocupación (ψ) para *L. geoffroyi* (Cob = Cobertura de dosel; Bosque = Bosque Nativo; AA = Ambiente antrópico; Camp = Campo).

Modelo	Fórmula	Número de parámetros	AIC	Delta	Peso de AIC	Peso acumulativo
ocu3	p (Cob) ~ ψ (AA)	4	412.34	0.00	0.50	0.50
ocu1	p (Cob) ~ ψ (1)	3	414.04	2.09	0.17	0.89
ocu4	p (Cob) ~ ψ (Camp)	4	414.43	2.09	0.17	0.89
ocu2	p (Cob) ~ ψ (Bosque)	4	415.29	2.95	0.11	1.00

Tabla 8: Probabilidad de detección y ocupación de las especies en toda área de estudio.

Especie	Detección %	Ocupación %
C.thous	3,9%	63,7%
L.gymnocercus	5,9%	27,2%
L.geoffroyi	1,66%	41%

LEYENDA FIGURAS

Figura 1: Mapa Área de estudio - Sabana Uruguayense. Mapas: A - América del Sur; B - Sitios muestreados en Brasil y Uruguay; C - Esquema cámaras trampa: dos cámaras en el ambiente “Bosque nativo”; dos cámaras en el ambiente “Campo natural”; dos cámaras en el ambiente

"Cultivo". En los mapas B y C los puntos negros representan las cámaras trampa, el área naranja la Sabana Uruguayense, mientras que la línea amarilla delimita la frontera entre Uruguay y Brasil.

Figura 2: Distribución circadiana de la actividad de *C. thous* durante las horas del día. Los histogramas azules muestran la distribución de la actividad de la especie, el vector la media (μ) junto con el desvío estándar 99%.

Figura 3: Distribución circadiana de la actividad de *L. gymnocercus* durante las horas del día. Los histogramas azules muestran la distribución de la actividad de la especie, el vector la media (μ) junto con el desvío standard 99%.

Figura 4: Distribución circadiana de la actividad de *L. geoffroyi* durante las horas del día. Los histogramas azules muestran la distribución de la actividad de la especie, el vector la media (μ) junto con el desvío standard 99%.

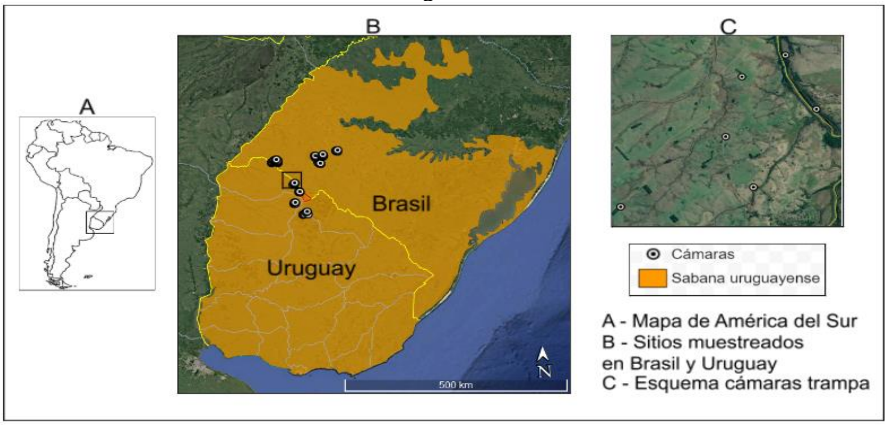
Figura 5: Gráfica de superposición de actividad circadiana entre *C. thous* y *L. gymnocercus*. La línea sólida representa la estimación de la densidad de kernel para *C. thous*, mientras que la punteada lo hace para *L. gymnocercus*. Las líneas azules representan el promedio calculado para el amanecer y atardecer para el área de estudio, mientras que, el coeficiente de superposición está representado por el área gris.

Figura 6: Gráfica de superposición de actividad circadiana entre *C. thous* y *L. geoffroyi*. La línea sólida representa la estimación de la densidad de kernel para C. thous, mientras que la punteada lo hace para *L. geoffroyi*. Las líneas azules representan el promedio calculado para el amanecer y atardecer para el área de estudio, mientras que, el coeficiente de superposición está representado por el área gris.

Figura 7: Gráfica de superposición de actividad circadiana entre *L. gymnocercus* y *L. geoffroyi*. La línea sólida representa la estimación de la densidad de kernel para L. gymnocercus, mientras que la punteada lo hace para *L. geoffroyi*. Las líneas azules representan el promedio calculado para el amanecer y atardecer para el área de estudio, mientras que, el coeficiente de superposición está representado por el área gris.

FIGURAS

Figura 1



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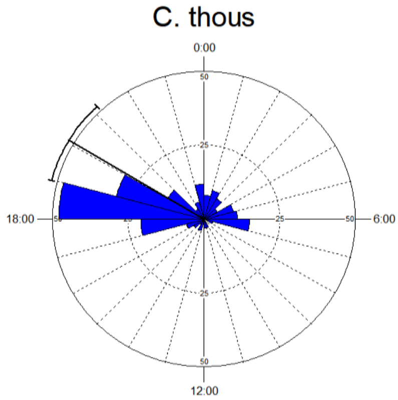

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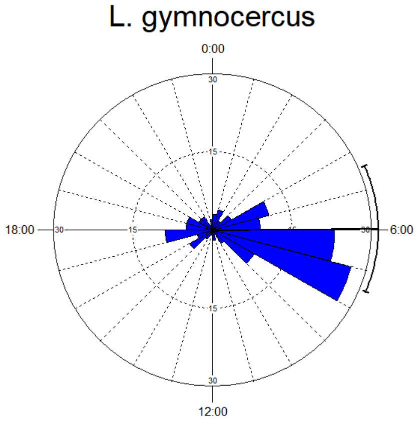

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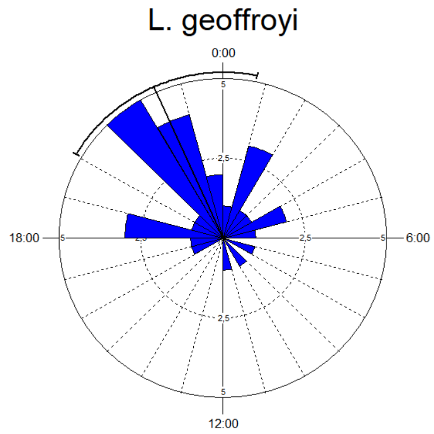

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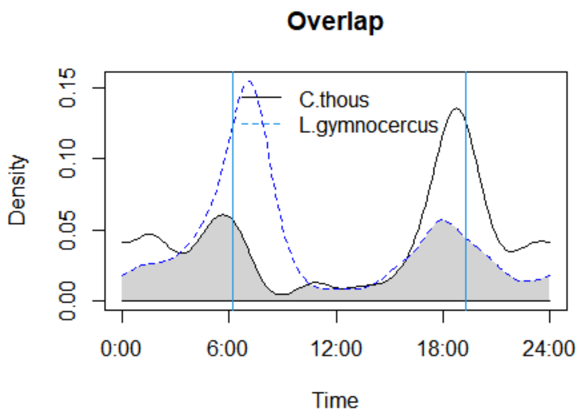

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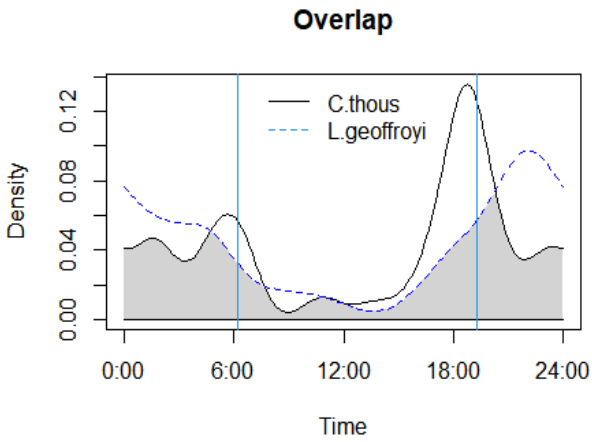

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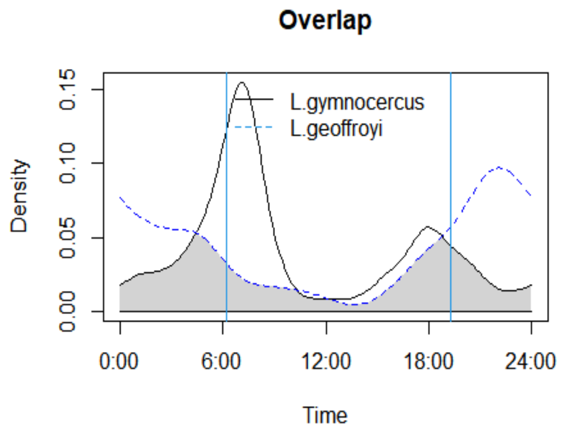
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L.gymnocercus
L.geoffroyi
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0.05
0.10
0.15
0:00
6:00
12:00
18:00
24:00
Time