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Habitat use and densities of two sympatric foxes in the Mburucuyá National Park (Iberá Wetlands ecoregion, Argentina) during the winter season

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Abstract. In Argentina, two fox species —*Lycalopex gymnocercus* and *Cerdocyon thous*— are generally considered abundant and coexist across various natural, transitional and anthropogenic environments. However, studies on habitat use and population size estimation in sympatric areas remain scarce. Their low densities, elusive behavior and morphological similarities make them particularly difficult to study. The Mburucuyá National Park (Corrientes, Argentina), which conserves terrestrial ecosystems within the Iberá wetlands region, served as the study site for assessing habitat use based on density estimates. Surveys were conducted between May and August 2015, during both diurnal and nocturnal periods, along 12 linear transects spanning three habitat types: mesophilous forest, mesophilous grassland and *Butia yatay* savanna. Fox detections were analyzed using the hierarchical distance sampling (HDS) method, applying a probability function to model detection distances perpendicular to the transect centerline. A total of 63 fox detections were recorded over a sampling effort of 103.8 km. Of these, 37 detections were identified as *L. gymnocercus* (51.4% in savanna, 29.7% in forest and 18.9% in grassland), while 26 detections corresponded to *C. thous* (73.1% in savanna). The mean population density was estimated at 0.27 individuals/km² for *L. gymnocercus* and 0.50 individuals/km² for *C. thous*. No statistically significant differences were found between species or across habitat types within each species. The findings of this study will contribute to understanding species coexistence, enable comparisons with other sympatric populations and help assess carnivore responses to varying anthropogenic pressures.

[Keywords: *Cerdocyon thous*, *Lycalopex gymnocercus*, protected area]

Resumen. Uso de hábitat y densidades de dos especies de zorros simpátricos en el Parque Nacional Mburucuyá (ecoregión Esteros del Iberá, Argentina) durante la estación invernal. En la Argentina, dos especies de zorros, *Lycalopex gymnocercus* y *Cerdocyon thous* —consideradas abundantes— solapan sus distribuciones en diversos ambientes naturales, transicionales y antropogénicos. Sin embargo, los estudios sobre el uso del hábitat y la estimación del tamaño poblacional en áreas de simpatría son escasos. Su baja densidad, comportamiento evasivo y similitudes morfológicas dificultan su identificación y estudio. El Parque Nacional Mburucuyá (Corrientes, Argentina), que preserva ecosistemas terrestres dentro de la región de los humedales del Iberá, fue seleccionado como sitio de estudio para evaluar el uso del hábitat de estas especies a partir de estimaciones de densidad. Los relevamientos se llevaron a cabo entre mayo y agosto de 2015, en períodos diurnos y nocturnos, a lo largo de 12 transectas lineales distribuidas en tres tipos de hábitat: bosque mesófilo, pastizal mesófilo y sabana de *Butia yatay*. Las detecciones obtenidas se analizaron mediante el método de muestreo jerárquico por distancia (HDS), aplicando una función de probabilidad para modelar la detección de individuos a distancias perpendiculares a la línea central de la transecta. Se registraron 63 detecciones de zorros tras un esfuerzo de muestreo de 103.8 km. De estas, 37 correspondieron a *L. gymnocercus* (51.4% en la sabana, 29.7% en el bosque y 18.9% en el pastizal), mientras que 26 se atribuyeron a *C. thous* (73.1% en la sabana). La densidad poblacional media se estimó en 0.27 individuos/km² para *L. gymnocercus* y 0.50 individuos/km² para *C. thous*. No se encontraron diferencias estadísticas significativas entre especies ni entre hábitats dentro de cada especie. Los resultados de este estudio contribuirán a comprender la coexistencia de estas especies, facilitarán las comparaciones con otras poblaciones en simpatría y permitirán evaluar sus respuestas a distintos niveles de impacto antropogénico.

[Palabras clave: *Cerdocyon thous*, *Lycalopex gymnocercus*, área protegida]

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Introduction

South America has the highest canid diversity in the world. These species typically occupy the top predator or mesopredator niches in their respective communities, engaging in hunting or scavenging to obtain vertebrate and/or invertebrate prey (Castelló and Sillero-Zubiri 2018). In addition to hunting, most canids also feed on fruit (Wallace et al. 2010; Bay Juliá et al. 2024) and, along with other frugivore species, play a key role in seed dispersal (Armenda-Mendez et al. 2020). To conserve these predators and their ecological roles, knowledge of distribution, abundance, habitat use and population dynamics is essential to develop wildlife management and conservation plans (Schmitz 2007).

Five species of canids inhabit Argentina (Teta et al. 2018), including the Pampas fox (*Lycalopex gymnocercus*, Fischer 1814) and the crab-eating fox (*Cerdocyon thous*, Linnaeus 1766). Both species have overlapping distributions in southeastern Brazil, eastern Bolivia, northern Uruguay, western Paraguay and northern Argentina (Sillero-Zubiri et al. 2004). *Lycalopex gymnocercus* and *C. thous* have omnivorous and opportunistic diets, including small mammals, birds, reptiles, insects and fruits. Both species are categorized as Least Concern in Argentina, but their populations are affected by hunting and poaching, traffic accidents, habitat loss and infectious diseases (Cirignoli et al. 2019; Luengos et al. 2019). Regarding habitat use, *L. gymnocercus* is found in open and arid environments (Maffei et al. 2007), as well as in grasslands, including pajonales (Viera and Port 2007). In contrast, *C. thous* is primarily associated with forested environments (Maffei et al. 2007). Some authors have observed that this species shows a preference for a wide range of environmental conditions, suggesting that it may be considered a habitat generalist. For example, it has been identified as a generalist species in the Brazilian Cerrado, with records in cultivated areas, grasslands, savannas and various types of forests (Trovati et al. 2007; Viera and Port 2007), while in Emas National Park (Goiás State, Brazil), there is evidence indicating a preference for grasslands (Jácomo et al. 2004). In Argentina, both *L. gymnocercus* (Luengos Vidal et al. 2019) and *C. thous* (Di Bitetti et al. 2009; Cirignoli et al. 2019) were recorded in woodlands, shrublands and grasslands.

Regarding density data, some studies reported densities of *L. gymnocercus* ranging from 0.03 individuals/km^2 in the Tornquist Provincial Park (38°03′ S - 62°00′ W) in Buenos Aires (Luengos Vidal 2004; Lucherini and Luengos Vidal 2008) to 1.8 individuals/km^2 in the Bañados of the Izozog of the Bolivian Chaco (19°-21° S - 61°-62° W) in Boliva (Ayala and Noss 2000); and for *C. thous*, from 0.7 to 1 individuals/km^2 in Chiquitania forest (17°00′37′′ S - 62°00′00′′ W) of Bolivia (Maffei and Taber 2003), with an intermediate data set from 0.78 to 0.8 individuals/km^2 of Brazil in the Pantanal de Nhecolandia, Corumba (19°24′16′′ S - 57°02′85′′ W) (Rocha 2006) and Itapuã State Park, Rio Grande do Sul (30°22′ S - 51°02′ W) (Faria-Corrêa et al. 2009), respectively.

However, studies on habitat use and population size estimates of *C. thous* and *L. gymnocercus* in sympatric areas are scarce due to their low densities, elusive behavior and similar fur (Wallace et al. 2010). In Argentina, both species coexist in the Iberá ecoregion (12000 km^2), part of the Mesopotamian region within the vast Paraná river basin (Orfeo 2012). In Corrientes, Di Bitetti et al. (2009) studied both fox species in the Iberá Nature Reserve. They found higher frequencies of *C. thous* in the gallery forests and thickets, away from people and livestock, while *L. gymnocercus* was more frequent in anthropogenic grasslands. The coexistence of these species in this region is possibly due to their similar body size, which reduces the risk of predation and intraguild killing, as well as their different habitat use patterns in shared landscapes (Di Bitetti et al. 2022). Another comparative study in the Iberá National Park (Portal San Nicolás, 28.1282 S - 57.4346 W; 16780 ha, Corrientes, Argentina) reported that both species are nest predators. *Cerdocyon thous* was responsible for 11 predation events and *L. gymnocercus* for three, together accounting for 50% of predation events on *Alectrurus risora*, an endangered grassland bird (Browne et al. 2023). This behavior suggests that both species exploit common trophic resources. Bay Jouliá et al. (2024) found a high degree of trophic niche overlap between *L. gymnocercus* and *C. thous* in three protected areas of Corrientes, demonstrating the dietary plasticity of both species, even across small geographical variations. This finding confirms the ability of both species to coexist non-competitively in different ecosystems in terms of the trophic niche dimension, or suggests the possibility of niche partitioning in an as-yet unexplored dimension.

The Iberá ecoregion encompasses the Mburucuyá National Park, an ideal study site

for obtaining comparative data on the habitat use and population densities of *L. gymnocercus* and *C. thous* when occurring in sympatry. Therefore, our objectives in this study were to: 1) determine the habitat use of *L. gymnocercus* and *C. thous* in the Mburucuyá National Park, a protected area where both species coexist; 2) estimate the densities of both species, and 3) evaluate which variables influence their detection probability and density in these protected environments of the Iberá wetlands of northeastern Argentina.

Materials and Methods

Study area

The study was carried out at the Mburucuyá National Park (hereinafter, MNP; 27°58′ - 26°05′ S and 57°59′ - 58°08′ W), which is a 17086 ha conservation unit within Iberá wetlands in Corrientes province, Northern Argentina (Figure 1), and includes plant species from the Humid Chaco, Espinal and Paranaense ecoregions (Cabrera 1976; Dinerstein et al. 2017). In this park, three main types of habitats are present and protected: 1) mesophilous forests characterized by forest fragments with predominance of *Ocotea acutifolia* and *Schinopsis balansae* (2720 ha); 2) mesophilous grasslands (tall and low grasslands) of *Elionurus muticus* and *Andropogon lateralis* in 'lomadas' (i.e., small hills) and *A. lateralis* and *Sorghastrum agrostoides* in low areas with floodable soils (2500 ha), and 3) savannas of *Butia yatay* (tall palms higher than 15 m) in higher hills (1010 ha) (Arbo 2004; Fontana 2017; Oyarzabal et al. 2018).

The remaining area of the national park is characterized by estuaries, flooded grasslands, streams and approximately 188 lagoons (Arbo 2004). The climate, relative isolation and immense floristic diversity with the consequent supply of nutrients, generate an extremely rich and varied fauna (Lipori and De Oto 2012). Climate is humid and subtropical, with rainfalls ranging between 37.5 and 206.6 mm and an average daily temperature between 16.03±0.9 °C during the winter months with few frosts (June-August) and 25.6±1.4 °C during the summer months (November-February) (Contreras et al. 2018).

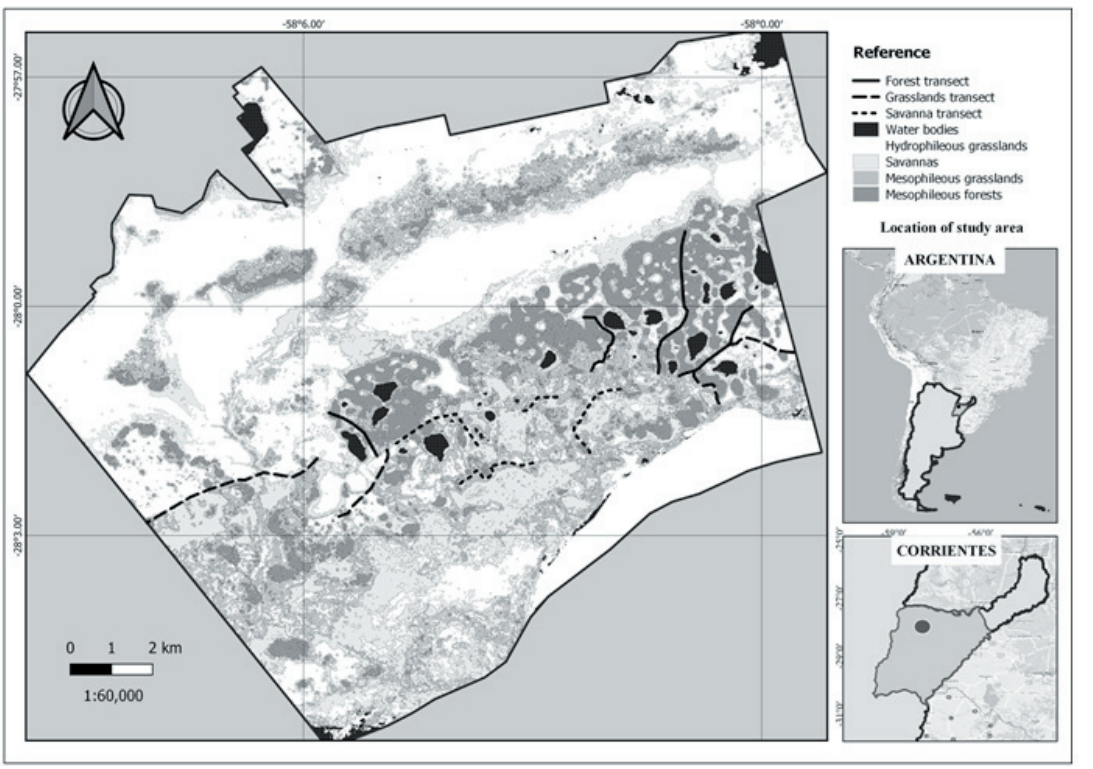

Figure 1. Location of study area and line transects surveyed for estimating density of *Lycalopex gymnocercus* and *Cerdocyon thous* in the Mburucuyá National Park, Corrientes, Argentina.

Figure 1. Ubicación del área de estudio y transectas relevadas para estimar la densidad de *Lycalopex gymnocercus* y *Cerdocyon thous* en el Parque Nacional Mburucuyá, Corrientes, Argentina.

Data collection

Between May and August 2015 (winter season), we determined habitat use and estimated densities of *L. gymnocercus* and *C. thous* using the distance sampling method (Buckland et al. 1993) based on sighting data from the study area. Due to the short sampling period (4 months), our study populations can be considered closed, with stable territories and with no change due to births or mortalities. The short study time period was utilized by other researchers exploring similar issues in canids, for example *Vulpes vulpes* (Sarmento et al. 2009). The location of transects was designed through stratified random sampling, considering three habitat types (mesophilous forest, mesophilous grasslands and savannas of *B. yatay*). Overall, 12 line transects, four per habitat (Figure 1) and with lengths varying between 1.2 and 4.2 km (Table 1) were surveyed. Following previously reported peaks of daily activity for both foxes in this wetland (Di Bitetti et al. 2009), daytime and night-time sampling periods were established from 06:00 to 12:00 h, and from 19:00 to 00: 00 h, respectively. Powerful flashlights (Maglite, one candle, model USA) were used for nighttime detections, and in 70% of them the individuals were photographed (Nikon Coolpix, 40X optical zoom). The photographs were utilized for re-confirming identification and/or for register of individual´s the health or behavioral status (including observations of movement, feeding, or other behaviors).

Temporally, each transect was surveyed at least twice and up to eight times within the study period, depending on climatic variation (i.e., it was impossible to access some trails during June and July due to sectors flooded by intense rains) or logistic limitations (i.e. compliance with the method assumptions, logistic and security of observers). Two observers traveled transects established for each habitat type, walking at an average speed of 1.5 km/h. Sampling effort per transect varied between 2 to 4 h depending on the transect length and number of detections. During a census, once a fox was detected, the following data were recorded: perpendicular distance to the center line of transect (x), time, species, number of individuals, social status (solitary, pair), sex, age (adult and juvenile) and additional observations on behavior, including those pertaining to parental care, reproduction, feeding and foraging. The juvenile category included those foxes accompanied by an individual with a larger body size, possibly one of the parents, or individuals with a small body size that moved alone. The sex of individuals is distinguished by the observation of the genitals when urinating in males or the presence of dilated breasts in lactating females. In general, each detection lasted a few minutes, and in some cases, the observation was extended to a maximum time of 10 minutes, after which the transect route was continued.

Data analyses

Habitat use and densities of *L. gymnocercus* and *C. thous* were calculated via the distance sampling method (Buckland et al. 1993) based on the perpendicular sighting distances of each fox from the transect line (x) by modeling the

Table 1. Characteristics of line transects surveyed to estimate density of *Lycalopex gymnocercus* and *Cerdocyon thous* in three habitat types within the Mburucuyá National Park, Corrientes, Argentina. s: Solitary. p: Pair. Ad: Adults; J: Juvenile.

Tabla 1. Características de las transectas estudiadas para estimar la densidad de *Lycalopex gymnocercus* y *Cerdocyon thous* en tres tipos de hábitats del Parque Nacional Mburucuyá, Corrientes, Argentina. s: Solitario. p: Pareja. Ad: Adultos. J: Juvenil.

Habitat type	Transect ID	Transect length (km)	Number of repeats	Total effort (km surveyed)	Records obtained	
					L. gymnocercus	*C. thous*
Mesophilous forests	1	1.9	2	4.3	1s (Ad)	1s (Ad)
	2	2.0	5	10.0	3s, 1p (Ad)	4s (Ad)
	3	3.7	3	11.7	3s, 1p (Ad)	
	10	2.0	3	6.0	2p	
Mesophilous grasslands	4	1.2	8	9.6	1s (Ad)	1s (Ad)
	5	1.5	2	3.0		
	6	2.4	4	9.6	4s (Ad)	1s (Ad)
	12	4.2	2	9.0	2p (Ad)	
Savannas of *Butia yatay*	7	2.2	3	6.6	2s (Ad)	
	8	1.7	6	10.2	10s (9Ad,1J)	7s (Ad)
	9	2.2	4	8.8		8s, 1p (Ad)
	11	2.5	6	15.0	6s, 1p (Ad)	2s, 1p (Ad)

detection function, g(x) (i.e., the probability of detecting a given fox that is x distance from the transect line) (Thomas et al. 2002). A fundamental premise of this methodology is the assumption that all foxes located on the transect center line are detected with absolute certainty, that is to say, g(0) is equal to one (Buckland et al. 1993). Additionally, two distance criteria between detections were employed to guarantee the independence of the data set. Firstly, a minimum distance of 5 km was established between transects of the same habitat. Secondly, each observer examined and recorded data from a single side of transect, thus avoiding the counting of the same animal on multiple occasions.

The density (D) of *L. gymnocercus* and *C. thous* was calculated using the equation

$$D = n / 2 \hat{u} L \qquad \text{Equation 1}$$

where n is the number of detections, û is the effective strip width and L is the transect length (Thomas et al. 2002). It is recommended that a minimum of 40 independent detections be used, although smaller samples (up to 20 detections) can also generate robust estimates (Buckland et al. 1993). A Hierarchical Distance Sampling was applied to estimate density (Chandler et al. 2011) using software R unmarked package (Fiske and Chandler 2011).

We investigated whether the detectability and density of *L. gymnocercus* and *C. thous* were influenced by the time of day (day vs. night sampling), vegetation type at the site scale and proximity to water bodies. Specifically, these covariates were quantified as follows: A) the proportion of detections during night sampling (Sn); B) the proportion of vegetation cover in the upper stratum (Vc). This was estimated as the proportional cover of the vegetation strata across 10 plots per transect, of 4x4 m (in mesophilous grasslands and savannas of *B. yatay*) or 25x25 m (in mesophilous forests), in accordance with the methodology proposed by Mota et al. (2014); C) vegetation type (C), defined as the area (in km^2) covered by the specific habitat type considered (i.e., mesophilous forests, mesophilous grasslands or savannas of *B. yatay*) within a plot encompassing 350 m on either side of the transect line, and D) proximity to water bodies (Wd), defined as the mean minimum distance of water bodies from the transect line.

The covariates C and Wd were extracted from Landsat 8 satellite images (30-m resolution) using Google Earth Pro version 7.3.3. These variables are relevant for the probability detection and presence of both species of foxes, especially the time zone that may be related to activity patterns (Di Bitteti et al. 2009), the type of vegetation to habitat use and the proximity to water bodies can be open areas between types of vegetation for hunting certain types of prey such as reptiles, a behavior reported for *C. thous* by Ruiz Garcia et al. (2020) in the study area.

The influence of covariates was assessed from 54 models for both detection probabilities and densities of foxes in the MNP (Table 2). The models were analyzed with different robust functions (semi-normal, hazard-rate, negative exponential) and classified into

Table 2. Proposed models to determine detection probabilities and densities of *Cerdocyon thous* and *Lycalopex gymnocercus* in the PNM (Corrientes, Argentina), winter season 2015. C: Vegetation type cover. Vc: Vegetation cover of upper stratum. Wd: Proximity to water bodies. Sn: Detections during night sampling.

Tabla 2. Modelos propuestos para determinar probabilidades de detección y densidades de *Cerdocyon thous* y *Lycalopex gymnocercus* en el PNM (Corrientes, Argentina), temporada invernal 2015. C: Cobertura del tipo de vegetación. Vc: Cobertura vegetal del estrato superior. Wd: Proximidad a cuerpos de agua. Sn: Detecciones durante muestreos nocturnos.

Models (analyzed with different robust functions semi-normal, hazard rate, negative exponential)		
Null models: detection: ~1, density: ~ 1		
model semi -normal: ~1 ~1	model hazard rate: ~1 ~1	model negative exponential: ~1 ~1
Null models for detection: detection: ~1, density: ~ covariates		
model[1]: ~1 ~C	model[2]: ~1 ~C + Vc	model[3]: ~1 ~Wd
Null models for density: detection: ~ covariates, density: ~1		
model[4]: ~Sn ~1	model[5]: ~Vc ~1	model[6]: ~Sn + Vc ~1
Non-null models: detection: ~ covariates, density: ~ covariates		
model[7]: ~Sn ~C	model[8]: ~Sn ~C + Vc	model[9]: ~Sn ~Wd
model[10]: ~Vc ~C	model[11]: ~Vc ~C + Vc	model[12]: ~Vc ~Wd
model[14]: ~Vc ~C + Wd	model[15]: ~Vc + Sn ~C + Vc	
model[16]: ~Vc + Sn ~Wd	model[17]: ~Vc + Sn ~C + Wd	

different categories: null models, null models for detection, null models for density and non-null models (Miller et al. 2019). The best models were selected using the Akaike Information Criterion (AIC) through the fitsDSmodel function in the AICc modavg package (Mazerolle 2020). The detection function was calculated for the selected model with the lowest AIC, and subsequently, the density function and its predictions for each transect and habitat type (within a 95% confidence interval) were determined for both fox species. Comparisons between *L. gymnocercus* and *C. thous* densities within each habitat and the density of each species between habitat types were assessed using ANOVA or Kruskal-Wallis tests. Finally, we performed a comparison between the average densities of each species without considering habitat type using Wilcoxon-Mann-Whitney tests for comparison with other studies. These analyses were performed using R software (2020) and a significance level of 5%.

Results

We covered a total of 103.8 km with similar sampling distances in each habitat type (forest: 32 km; grassland: 31.2 km; savanna: 40.6 km; X^2=0.46; degrees of freedom (df)=2; P-value=0.10), and we obtained 63 fox detections (Table 1). Thirty-seven detections corresponded to *L. gymnocercus* (51.4% in savanna, 29.7% in forest and 18.9% in grasslands) and 26 to *C. thous* (73.1% in savanna, 19.2% in forest and 7.7% in grasslands). The number of foxes per detection varied between 1 and 2 individuals in the three habitats analyzed, except for *C. thous* in forests and grasslands where the records were from a single individual. The recorded *L. gymnocercus* individuals were mostly adults, including 29 solitary individuals plus one young solitary individual and seven pairs. After data truncation (10%, 33 detections), the detection probability were between 0 and 2 m (Supplementary material-Figure S1). The data was not normally distributed. All *C. thous*, recorded were adults (24 solitary individuals and two pairs). The *C. thous* detections were between 0 and 20 m (Supplementary material-Figure S1). The analysis of the detection probabilities to the distance of the transect center line presented an outlier detection value at 50 m in transect 9, which was excluded. There were no significant differences between fox species in the detectability of solitary individuals (X^2=0.41, df=1, P-value=0.10) or pairs (X^2=0.09, df=1, P-value=0.10).

The probability of detection and density of *L. gymnocercus* were determined with half-normal model (detection: ~0.66; density: ~-0.08*C-0.05*Vc; AIC=89.82, k=4) and for *C. thous* with an exponential model (detection: ~1.37; density: ~0.16+0.08*C-0.07*Vc; AIC=78.31, k=4). Probability detection of *L. gymnocercus* varied randomly and its density was negatively influenced by habitat coverage and the percentage of vegetation cover in the upper stratum. Density estimation of *C. thous* was positively influenced by habitat coverage and negatively by the vegetation cover of the upper stratum.

The estimated mean density was 0.27 individuals/km^2 for *L. gymnocercus* (n=9, range: 0.05-0.73 individuals/km^2, median=0.24, sd=0.22) and 0.50 individuals/km^2 for *C. thous* (n=7, range: 0.10-1.09 individuals/km^2, median=0.37, sd=0.34) (Supplementary material-Table S1). Non-significant differences were found in the densities of each fox species among habitat types (Figure 2), as well as between species (Wilcoxon-Mann-Whitney test: $n_{L.\ gymnocercus}$= 9, $n_{C.\ thous}$=7, Z=-1.32, P=0.20).

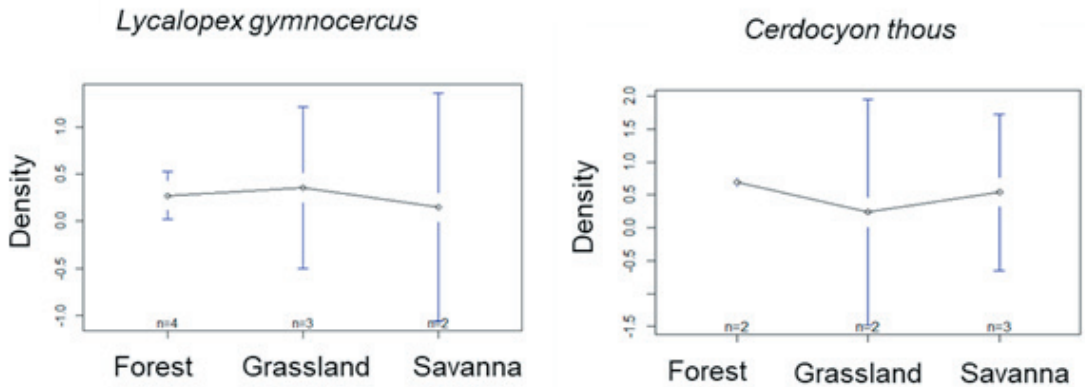

Figure 2. Comparative of densities between habitats for each fox species with Tukey test.

Figure 2. Comparación de las densidades de cada especie de zorro entre hábitats con la prueba de Tukey.

Discussion

Our study in the MNP provides the first study of habitat use based on density estimates of *L. gymnocercus* and *C. thous* living in sympatry in a protected area of the Iberá Wetlands. Similar densities were found for both species in the three habitats analyzed (mesophilous forests, mesophilous grasslands and savannas of *B. yatay*), with mean densities of 0.27 individuals/km^2 for *L. gymnocercus* and 0.50 individuals/km^2 for *C. thous*. However, some trends indicated higher densities in certain habitats (Supplementary material-Table S1). Our model for density showed a positive influence of habitat cover within the MNP for *C. thous* and a negative influence for *L. gymnocercus*, which could be related to differential habitat use between species. Therefore, the results of our study show an inverse relationship between the density and the cover of the upper vegetation layer. Similar variations in the recording frequencies of these species in different habitats (forest and savannas) were also identified in other study areas within the Iberá wetlands (Di Bitetti et al. 2009, 2022). This would indicate a tendency for *C. thous* to prefer closed habitats, such as forests and savannas with palm trees, and *L. gymnocercus* to prefer open habitats, such as grasslands. Indeed, we found a relatively higher density of *C. thous* in forests (0.70 individuals/km^2) and *L. gymnocercus* in grasslands (0.35 individuals/km^2) within the MNP supporting the hypothesis of Di Bitteti et al. (2009) about spatial niche partitioning between these species in the Iberá wetlands. Additionally, relatively high densities of *C. thous* have been observed in Bolivian cloud forests (Maffei and Taber 2003), which supports the hypothesis that this species utilizes more these environments. However, other authors have proposed an alternative hypothesis, suggesting that *C. thous* exhibit generalized patterns of habitat use, including their regular presence in disturbed environments (Trovati et al. 2007; Vieira and Port 2007) and a tendency to utilize grasslands and savannas (De Almeida Jácomo et al. 2004) in Brazil.

Regarding *L. gymnocercus*, this species has been observed in open and arid environments in Bolivia (Maffei et al. 2007), as well as in grasslands in Brazil (Vieira and Port 2007; Faria-Corrêa et al. 2009), a habitat similar to that recorded for Argentina. In sympatry with *C. thous*, *L. gymnocercus* would still select open areas such as grasslands, unlike the former species, which is restricted to the use of wooded areas (Lucherini et al. 2004). In our study, the density of *C. thous* was low in tall grasslands, whose dominant herbaceous plants (which can reach up to 2 m and cover up to 90%) could restrict its movement or hinder its foraging ability. However, *L. gymnocercus* seems to be a species better adapted to this type of habitat due to its relatively slender body (Lucherini 2016; Castelló and Sillero-Zubiri 2018). Its presence in the forested areas of the MNP could be due to its use as a passage between more open environments (grasslands and palm groves), due to the heterogeneity of the landscape.

Although the methodologies used to estimate fox densities differed between study sites, and thus comparisons should be made with caution, mean densities estimated in the MNP for each species were found to be lower than mean densities obtained at other distribution sites, as reported by (Ayala and Noss 2000; Maffei and Taber 2003; Luengos Vidal 2004; Rocha 2006; Lucherini and Luengos Vidal 2008; Faria-Corrêa et al. 2009). Consequently, we proceed with caution when comparing data in order to maintain consistency in the averaging process. In Brazil, a comparable investigation in regions where these species occur in sympatry reported an estimated density of 0.78 individuals/km^2 for *C. thous*. This estimate was not provided for *L. gymnocercus* due to the limited number of detections of this species (Faria-Corrêa et al. 2009). The low densities observed in our study may be indicative of the populations in the MNP representing peripheral or marginal distributions relative to the proposed distributions for each species (Lucherini 2015, 2016). This could result in population sizes and densities that are smaller than those observed in central populations (Mayr 1963; Brown 1984). In this regard, the MNP site is situated within the northernmost and easternmost range limit of *L. gymnocercus* and the southernmost range limit of *C. thous* (Cirignoli et al. 2019; Luengos Vidal et al. 2019). Furthermore, the lower densities could also be associated with the high percentage of aquatic environments in the MNP (64%), which in rainy seasons increases the areas prone to flooding, potentially reducing the availability of optimal habitats for both foxes, and displacing populations outside the limits of the protected area and increasing contact with threat factors. Among the threat factors, frequent road kills of both fox species were observed in the MNP, the presence of domestic dogs and habitat disturbance due to livestock, forestry and rice production activities (Romero 2018), or overcrowding conditions that could

promote the exchange of zoonotic diseases (Natalini et al. 2021).

In this regard, we suggest focusing future studies on how the degree of environmental heterogeneity and fragmentation affects the population size of these species and other ecological aspects such as diet, feeding movement and activity patterns. Therefore, the habitat use and demographic data provided by this study constitutes a basis to understand species coexistence, to make comparisons with other populations of these species living in sympatry and to evaluate the responses of these carnivores in areas under anthropogenic impacts.

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