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Trophic ecology of *Cerdocyon thous* and *Lycalopex gymnocercus* within the Iberá Ecoregion in Argentina

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This study analyzed the diet, trophic niche overlap, and resource selection of two sympatric foxes, *Cerdocyon thous* and *Lycalopex gymnocercus*, in Mburucuyá National Park, a protected area within the Iberá Ecoregion, Argentina. Between December 2014 and November 2015, a total of 293 scat samples were analyzed, with 44% identified as *C. thous* and 56% as *L. gymnocercus*. The analysis revealed 11 plant species and 27 animal taxa that were consumed by both foxes. The results suggest that both species are hypocarnivorous and have overlapping trophic niches throughout the year, although they exhibit seasonal variations in their trophic amplitudes. During the winter months, when fruit availability was low, both species displayed more active foraging behavior. This selective foraging was evidenced by their consumption of specific palm species, which likely represent a critical nutritional source. Although insects and arachnids (weighing between 0.1 and 10 grams) were their most common prey, meso and small mammals constituted approximately 90% of the consumed biomass due to their larger size. Further research should focus on the trophic plasticity of these foxes in other environments and on quantifying the nutritional contributions of different food sources. Comparing these findings from a protected area to those from anthropogenically disturbed environments will be crucial for understanding the species´ conservation needs.

Keywords: Canids, coexistence, food availability, Mburucuyá National Park, resource partitioning, trophic overlap.

Este estudio analizó la dieta, la superposición de nichos tróficos y la selección de recursos de dos zorros simpátricos, *Cerdocyon thous* y *Lycalopex gymnocercus*, en el Parque Nacional Mburucuyá, un área protegida dentro de la Ecorregión Iberá, Argentina. Entre diciembre de 2014 y noviembre de 2015, se analizaron un total de 293 muestras de heces, de las cuales el 44% se identificaron como de *C. thous* y el 56% como de *L. gymnocercus*. El análisis reveló 11 especies de plantas y 27 taxones de animales que fueron consumidos por ambos zorros. Los resultados sugieren que ambas especies son hipocarnívoras y presentan superposición de nichos tróficos a lo largo del año, aunque muestran variaciones estacionales en sus amplitudes tróficas. Durante los meses de invierno, cuando la disponibilidad de fruta era baja, ambas especies mostraron un comportamiento de búsqueda de alimento (forrajeo) más activo. Este forrajeo selectivo se evidenció por su consumo de especies de palmeras específicas, lo que probablemente representa una fuente nutricional crítica. Aunque los insectos y arácnidos (con un peso entre 0,1 y 10 gramos) fueron sus presas más comunes, los meso y pequeños mamíferos constituyeron aproximadamente el 90% de la biomasa consumida debido a su mayor tamaño. Es necesario que la investigación futura se centre en la plasticidad trófica de estos zorros en otros entornos y en cuantificar las contribuciones nutricionales de las diferentes fuentes de alimento. La comparación de estos hallazgos de un área protegida con aquellos de ambientes sujetos a perturbación antropogénica será crucial para comprender las necesidades de conservación de las especies.

Palabras clave: Cánidos, coexistencia, disponibilidad de alimento, Parque Nacional Mburucuyá, partición de recursos, superposición trófica.

The competitive exclusion principle, states that competitors using identical resources cannot coexist (Hardin 1960). Competitive exclusion can manifest either as exploitative competition, where species vie directly for limited resources, or as apparent competition, which is mediated by shared natural enemies (Johnson and Bronstein 2019). To avoid it, sympatric species often differentiate their use of available resources, a phenomenon known as niche differentiation (Kooyers *et al.* 2017). Niche partitioning fundamentally explains how different species within a community divide and use space and resources to reduce interspecific competition, thus allowing for their coexistence (Pianka 1986; Petalas *et al.* 2021; Říha *et al.* 2025). To study these dynamics, ecologists measure niche overlap, which assesses the degree of shared resource use between species, facilitating the analysis of potential competition (Colwell and Futuyma 1971; Hurlbert 1978). From an ecological perspective, coexistence depends on morphological, physiological and/or behavioral divergences. These differences can lead to differential resource utilization or spatial or temporal variation in the use of similar resource (Schoener 1974). Furthermore, at finer spatial scales, variations in resource use by a species have been directly linked to greater niche overlap or partitioning (Anderson *et al.* 2011; Ávila-Nájera *et al.* 2020).

Given their phylogenetic proximity and morphological similarities (Xiaoming *et al.* 2004), canids (Carnivora, Canidae) are an ideal subject for this analysis. In

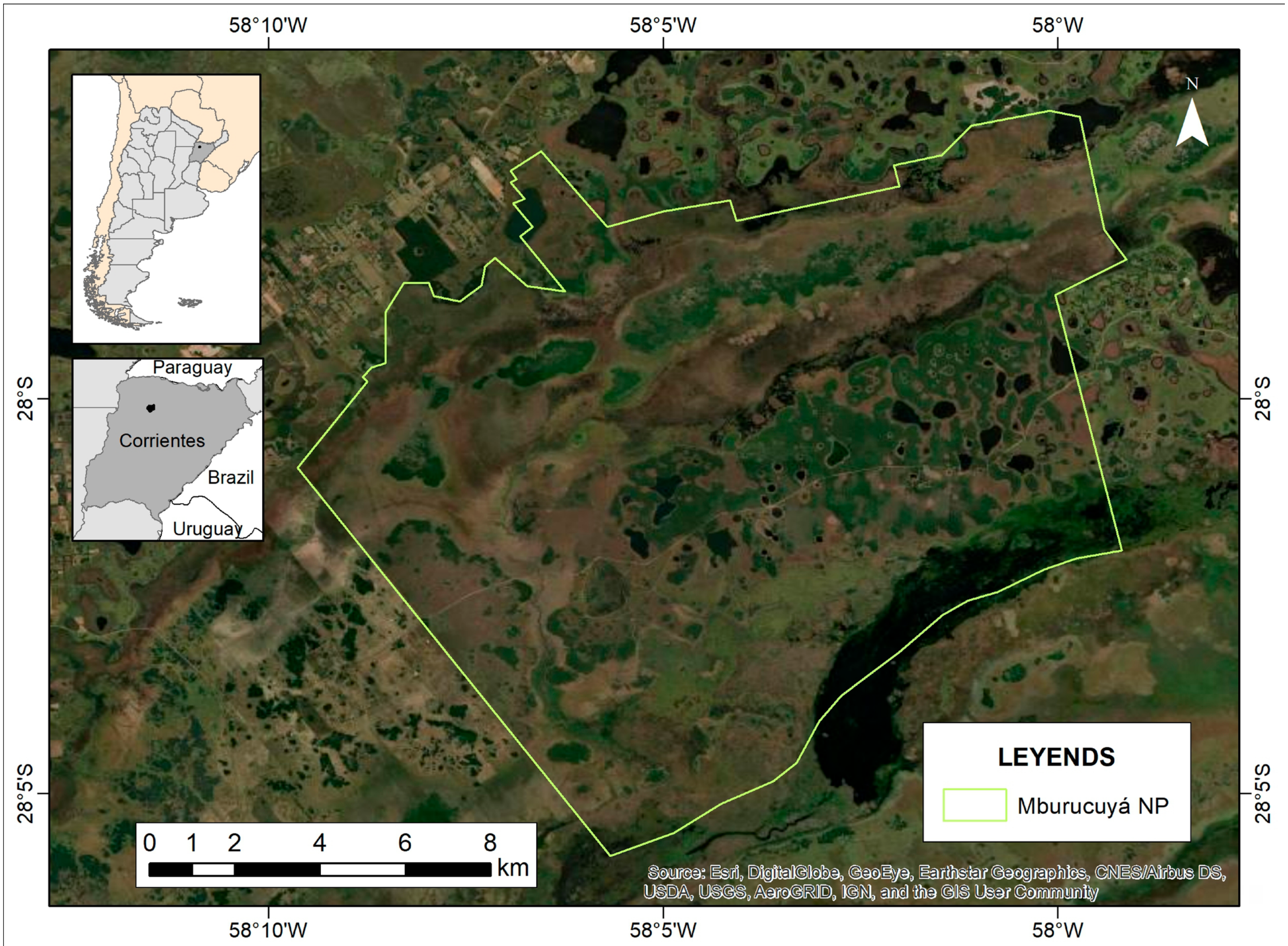

Figure 1. Study Area. Geographical location of Mburucuyá National Park (Corrientes, Argentina).

northeastern Argentina, two sympatric species with similar characteristics coexist: the crab-eating fox *Cerdocyon thous* (Linnaeus, 1766) and the pampas fox *Lycalopex gymnocercus* (G. Fischer, 1814). Both foxes are medium-sized, with *C. thous* weighing 4.5–8.5 kg (head-body length 54–77.5 cm) and *L. gymnocercus* weighing 3–8.2 kg (head-body length 44–72 cm) (Castelló 2018). As opportunistic omnivorous, their diets include a wide range of food items, including fruit, carrion, and prey ranging from such as ungulates, armadillos, capybaras, small mammals, birds, reptiles, amphibians, crustaceans, and insects (Sillero-Zubiri *et al.* 2004; Luengos Vidal *et al.* 2019).

The geographical ranges of these foxes overlap considerably (Sillero-Zubiri *et al.* 2004; Di Bitteti *et al.* 2009). The distribution of *C. thous* extends from northern Colombia and Venezuela to a substantial portion of Brazil, eastern Bolivia, Paraguay, Uruguay, and on to northern Argentina. It is highly resilient, able to utilize a wide variety of environments, including savannas, swamps, mesophileous forests, lowlands within the Amazon rainforest zone, and anthropogenic areas such as plantations, agricultural fields, and/or regenerating developments (Eisenberg and Redford 1999; Courtenay and Maffei 2004). However, its presence in anthropogenic areas, such as plantations and agricultural fields, highlights its tolerance for disturbed habitats, though this resilience often comes at the cost of increased exposure to zoonotic diseases, such as severe scabies (Oliveira *et al.* 2025). In turn, the distribution of *L. gymnocercus* ranges from southern Bolivia and Brazil to Chile, Paraguay, Uruguay, and Argentina, reaching as far south as Tierra del Fuego (Luengos Vidal *et al.* 2019). Due to the potential for competition in their overlapping habitats, studying these species in sympatry offers a valuable opportunity to investigate the mechanisms facilitating their coexistence (Bossi *et al.* 2018).

Several studies have compared the ecological niche of *C. thous* and *L. gymnocercus* in both Brazil and Argentina (Vieira and Port 2007; Di Bitetti *et al.* 2009; Faria-Corrêa *et al.* 2009; Bossi *et al.* 2018; Di Bitteti *et al.* 2022; Bay-Joulià *et al.* 2024; Romero *et al.* 2025). Focusing on the niche complementarity hypothesis which posits that some niche dimensions are partitioned when there is high overlap in another (Schoener 1974). Vieira and Port (2007) found a high degree of dietary overlap, between these foxes in

Table 1: Occurrence data and percentage obtained from the diet composition of canids, *Cerdocyon thous* and *Lycalopex gymnocercus,* in Mburucuyá National Park, Corrientes, Argentina (2014-2015). References: O, occurrence; OP, occurrence percentage.

	Cerdocyon thous **(scat samples: 129)**			***Lycalopex gymnocercus*** **(scat samples: 164)**		
FLESHY FRUIT PLANTS	**Count**	**O**	**OP**	**Count**	**O**	**OP**
Syagrus romanzoffiana	108	15	7.65	36	11	5.7
Butia yatay	161	34	17.35	239	44	22.8
Bromelia serra	15	7	3.57	14	6	3.11
Ocotea acutifolia	885	28	14.29	370	16	8.29
Eugenia uniflora	38	2	1.02			
Ficus luschnathiana	818	20	10.20	320	9	4.66
Citrus	5	3	1.53	4	3	1.55
Chrysophyllum gonocarpum	22	2	1.02			
Chrysophyllum marginatum	200	1	0.51	975	7	3.63
Psidium guajava	15	2	1.02	3	1	0.52
Solanaceae	35	2	1.02	80	2	1.04
ANIMAL CATEGORIES						
INVERTEBRATES						
Gastropoda						
Pomacea canaliculata				11	3	1.55
Crustacea						
Trichodactylus kensleyi	4	4	2.04	3	3	1.55
Arachnidae						
Ixodidae	3	1	0.51	1	1	0.52
Scorpiones cf. *Bothriurus* sp.	3	3	1.53	1	1	0.52
Araneae				1	1	0.52
Insecta						
Mantidae	1	1	0.51			
Acrididae	96	28	14.29	63	29	15.03
Gryllidae				1	1	0.52
Tettigonidae				2	1	0.52
Lepidoptera	3	3	1.53			
Formicidae				1	1	0.52
Scarabeidae	6	5	2.55	14	9	4.66
Cicindelinae	2	2	1.02			
Carabidae	1	1	0.51			
Unidentified beetle	3	3	1.53	1	1	0.52
Other unidentified insects	61	3	1.53	26	6	3.11
VERTEBRATES						
Unidentified fish	1	1	0.51	1	1	0.52
Unidentified reptiles	2	2	1.02	2	2	1.04
Colubridae				1	1	0.52
Lacertilia	2	2	1.02			
Eggs	1	1	0.51			
Unidentified small birds	1	1	0.51	1	1	0.52
Passeriforme				8	8	4.15
Mammals						
Cavia aperea	1	1	0.51	2	2	1.04
Hydrochoerus hydrochaeris	2	2	1.03	2	2	1.04
Unidentified small mammals	7	7	3.57	7	7	3.63
Unidentified medium mammals	9	9	4.59	13	13	6.74
TOTAL	2511	196	100	2203	193	100

the Aparados da Serra National Park (Southeastern Brazil, 29°10'S, 50°25'W), whilst they partitioned habitat use over time and space: *C. thous* exhibited a more nocturnal activity pattern and was observed more frequently at forest edges, in grasslands, and on roads, whereas *L. gymnocercus* was more prevalent in open areas (Vieira and Port 2007). Likewise comparative diet analysis across three protected areas in northeastern Argentina (Mburucuyá National Park, Portal de San Nicolás, and Rincón de Santa María Natural Reserve) also evidenced high degree of niche overlap among these species, along with considerable dietary breadth (Bay-Jouliá *et al.* 2024).

Morphological convergence, specifically comparable body weights, minimizes intraguild conflict a conclusion consistent with the Donadio and Buskirk (2006) framework, which links similar body size ratios among carnivores to reduced intraguild killing (Di Bitetti *et al.* 2022). This effect is complemented by significant ecological partitioning, evidenced by divergent niches and distinct habitat preferences (Di Bitetti *et al.* 2009). Further evidence comes from Romero *et al.* (2025), who reported mean densities of 0.27 individuals/km^2 for *L. gymnocercus* and 0.50 individuals/km^2 for *C. thous* in Mburucuyá National Park. Their density model revealed that greater plant cover positively influenced *C. thous* but negatively affected *L. gymnocercus*, confirming a differentiated habitat use that sustains local coexistence.

In this study, we assess the diet, resource availability, and the selection of resources by *C. thous* and *L. gymnocercus* to understand the potential partitioning or overlap of their trophic niches. The research was conducted on protected populations in the Iberá Region, within Mburucuyá National Park (Corrientes, Argentina). Given the diversity of habitats and food resources within the park, and building upon empirical observations from previous ecological studies, we formulated three main hypotheses: the dietary composition of both species is similar, which will be evident in shared food items and a high niche overlap index; the consumption of fleshy fruits by both species will adjust to their environmental availability, with the percentage of fruit in their diets increasing when these items are abundant and decreasing when availability is scarce; and finally, the fox species inhabit environments with a greater richness of fruit-bearing plants, indicating that the active foraging behaviour for these resources could be happening.

Materials and methods

Study area. The study was conducted in Mburucuyá National Park (MNP), spanning 17,086 hectares in the central-northwestern part of Corrientes province (27°58'S and 58°08'W), northern Argentina (Figure 1). The park's landscape is characterized by a topography of sandy ridges—relicts of an ancient alluvial megafan of the Paraná River—and slow-draining wetlands, locally known as 'esteros' (Contreras and Contreras 2017). From a phytogeographical perspective, the MNP is in the Iberá

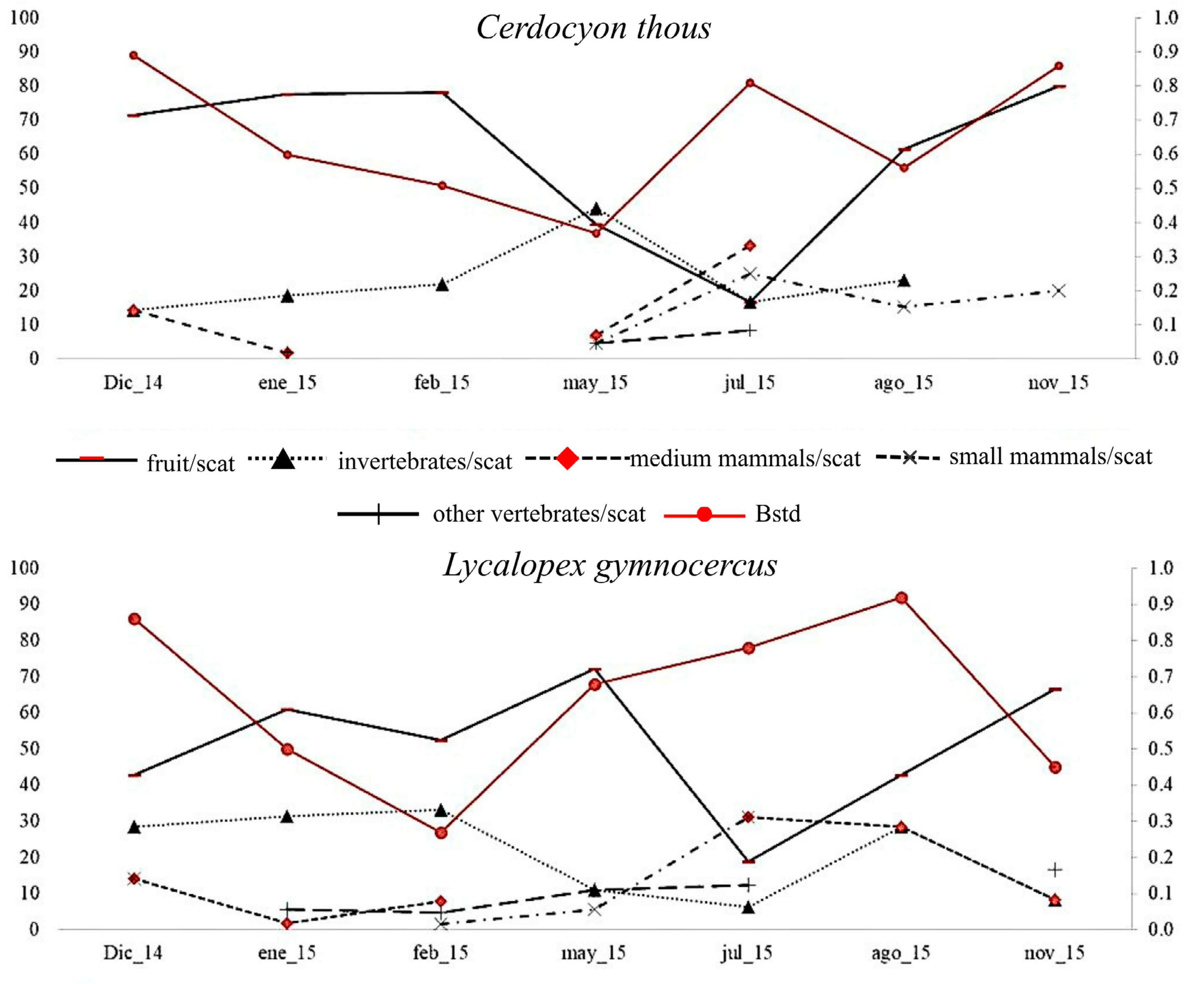

Figure 2: Food items variation (%) in canids *Cerdocyon thous* and *Lycalopex gymnocercus* 2014-2015, measured using the standardized Levins Index, in Mburucuyá National Park (Corrientes, Argentina).

Ecoregion, with a biodiversity that includes plant species from the Eastern Humid Chaco, Paranaense, and Espinal districts (Cabrera 1976; Arbo 2004). Its main habitats consist of tall grasslands, mesophileous forests, and palm groves of *Butia yatay* (Mart.) Becc., where wetlands, including lakes and streams, constitute 64% of the total area, providing crucial ecological functions.

The climate is classified as humid subtropical, with an average annual temperature of 21°C, reaching maximum values above 40°C in summer, but without a defined thermal winter (Contreras *et al.* 2020). Precipitation is rainfall, with an annual average of 1,400 mm, predominantly occurring from spring to autumn (October - May), with peak rainfall in April and May. In contrast, precipitation during winter (June - September) is minimal or absent (Smichowski *et al.* 2022; Smichowski and Contreras 2024).

Field work. Between December 2014 and November 2015, scat samples were collected along twelve transects (1 to 4.5 km in length) located in three MNP habitats: mesophileous forests, grasslands, and *B. yatay* palm groves. Samples were identified in the field by their size, shape, odour, the presence of hair or fruits, location of deposition, and their association with fox tracks (Chame 2003; Pedó *et al.* 2006; Vieira and Port 2007; Varela *et al.* 2008). Scat that could not be attributed with certainty to the species under investigation was discarded, and fragments found within a 0.5 m^2 area were considered a single defecation (Vieira and Port 2007). In the laboratory, samples were assigned to species level by identifying bile acid patterns using thin-layer chromatography (Cazón *et al.* 2009; Casanave *et al.* 2012). Scat analysis was chosen as a reliable, cost-effective, and non-invasive method for

Table 2: Trophic niche overlap. (Pianka Index) and diet composition of canids, *Cerdocyon thous* and *Lycalopex gymnocercus*, in Mburucuyá National Park, Corrientes, Argentina, during winter-summer 2014-2015. References: CT, *C. thous*; LG, *L. gymnocercus*.

	Winter seasonal		Summer seasonal	
	Occurrence percentage (%)			
	CT	LG	CT	LG
Scat samples	49	51	80	113
FLESHY FRUIT PLANTS				
Syagrus romanzoffiana	14.5	19.5	4.7	2.1
Butia yatay	9.7	2.4	22.1	29.7
Bromelia serra	11.3	14.6		
Ocotea acutifolia			22.1	11
Eugenia uniflora			1.6	
Ficus luschnathiana	3.2	2.4	14.2	5.5
Citrus	4.8	7.3		
Chrysophyllum gonocarpum			1.6	
Chrysophyllum marginatum			0.8	4.8
Psidium guajava			1.6	0.7
Solanaceae			1.6	1.4
ANIMAL CATEGORIES				
Invertebrates	35.5	12.2	21.3	31
Fish	1.6			0.7
Reptiles	1.6		1.6	2.1
Birds		9.8	0.8	3.5
Small mammals	11.3	14.6	0.8	2.1
Medium mammals	6.5	17.1	5.5	5.5
PIANKA INDEX	0.75		0.90	

estimating the diet of carnivores, a technique widely used in this type of study (Vieira and Port 2007; Marucco *et al.* 2008; Bay-Jouliá *et al.* 2024)

Fleshy-fruit Availability. The phenology and abundance of 11 species of fleshy-fruited plants—previously detected in the diets of the two fox species under study (Bueno and Motta-Junior 2004; De Almeida Jácomo *et al.* 2004; Pedó *et al.* 2006; Varela *et al.* 2008; Vieira and Port 2007)—were monitored monthly from January to November 2015 at the MNP. For this purpose, 20 sampling sites (100 m x 20 m) were established, distributed equitably and strategically across three vegetation strata: seven in mesophileous forests, seven in grasslands, and six in palm groves, following the methodology proposed by Ganzhorn *et al.* (2011). At each site, the number of individuals per species and their phenological data (flowering, fruit ripening, and percentage of fruit/flower) were recorded. To calculate the biomass of consumed fruits, samples of fruiting plants were obtained to determine the mean mass of their fruits.

Laboratory Analysis. In the laboratory, scat samples were dried in an oven at a temperature of 60°C until they reached a constant weight. Subsequently, samples were disaggregated under water using a 0.5 mm mesh sieve and examined under a stereoscopic binocular microscope (4–40X). Each food item was classified into one of seven main categories: fruits; invertebrates (which included crustaceans, mollusks, arachnids, and insects); fish; amphibians; reptiles; birds; and mammals (small and medium-sized species). The classification of each item was conducted at the most specific taxonomic level possible (species, genus, family, or order), based on the identification of undigested macroscopic structures such as seeds, exoskeletons, hair, bones, and dental remains. The presence of guard hairs in the scats was identified as an important tool in the identification of mammal species, as proposed by Quadros and Monteiro-Filho (2006a, b). The identification of fruits was achieved through a comparison of ingested seeds with the morphological characteristics of seeds from the main plant species in the MNP. The identification of both animal remains and fruits was carried out with the assistance of literature on regional flora and fauna and with the help of specialists in the field (Giraudo *et al.* 2006; Casco *et al.* 2008; Cano *et al.* 2011; Fontana 2017).

Dietary and Statistical Analyses. The diet of *C. thous* and *L. gymnocercus* were analyzed based on three key parameters: occurrence, percentage of occurrence, and consumed biomass. These methods were utilized to ascertain the significance of each food item and to facilitate direct comparisons with other dietary studies on these species and other carnivores (Pia *et al.* 2003; Bueno and Motta-Junior 2004, 2006; Rodrigues *et al.* 2007). Occurrence was defined as the frequency of a particular item relative to the total number of occurrences (Queirolo and Motta-Junior 2007), while percentage of occurrence was the proportion of a given item relative to the total number of items consumed (Pia *et al.* 2003; Bianchi *et al.* 2014).

Furthermore, for the animal items, the numerical frequency percentage (PF) for each item was calculated by determining the ratio between the minimum number of individuals of each category recorded in all scats and the sum of all individuals recorded across all prey categories, multiplied by 100 (Farias and Kittlein 2008). The relative biomass contributed by each animal item was estimated by multiplying its biomass by the PF, and was expressed as the total percentage of consumed biomass (BC) (Farias and Kittlein 2008). In the case of small mammals and birds, the consumption of biomass was calculated using correction factors that had previously been estimated for *Vulpes vulpes* (Linnaeus, 1758) (Ferreras and Fernández-de-Simón 2019). The correction factor is a number that, when multiplied by the total weight of indigestible matter, yields the original weight of the prey ensuring an accurate estimation of the ingested biomass from scat remnants. The biomass of consumed fruits was estimated by multiplying the pulp weight in grams of the found species by the number of records of each item found in the diet (Rodrigues *et al.* 2007), and it was assumed that each fruit was ingested whole. The body mass of animal prey was obtained from extant literature (Canevari and Vaccaro 2007), whereas the biomass of fruit was measured *in situ*.

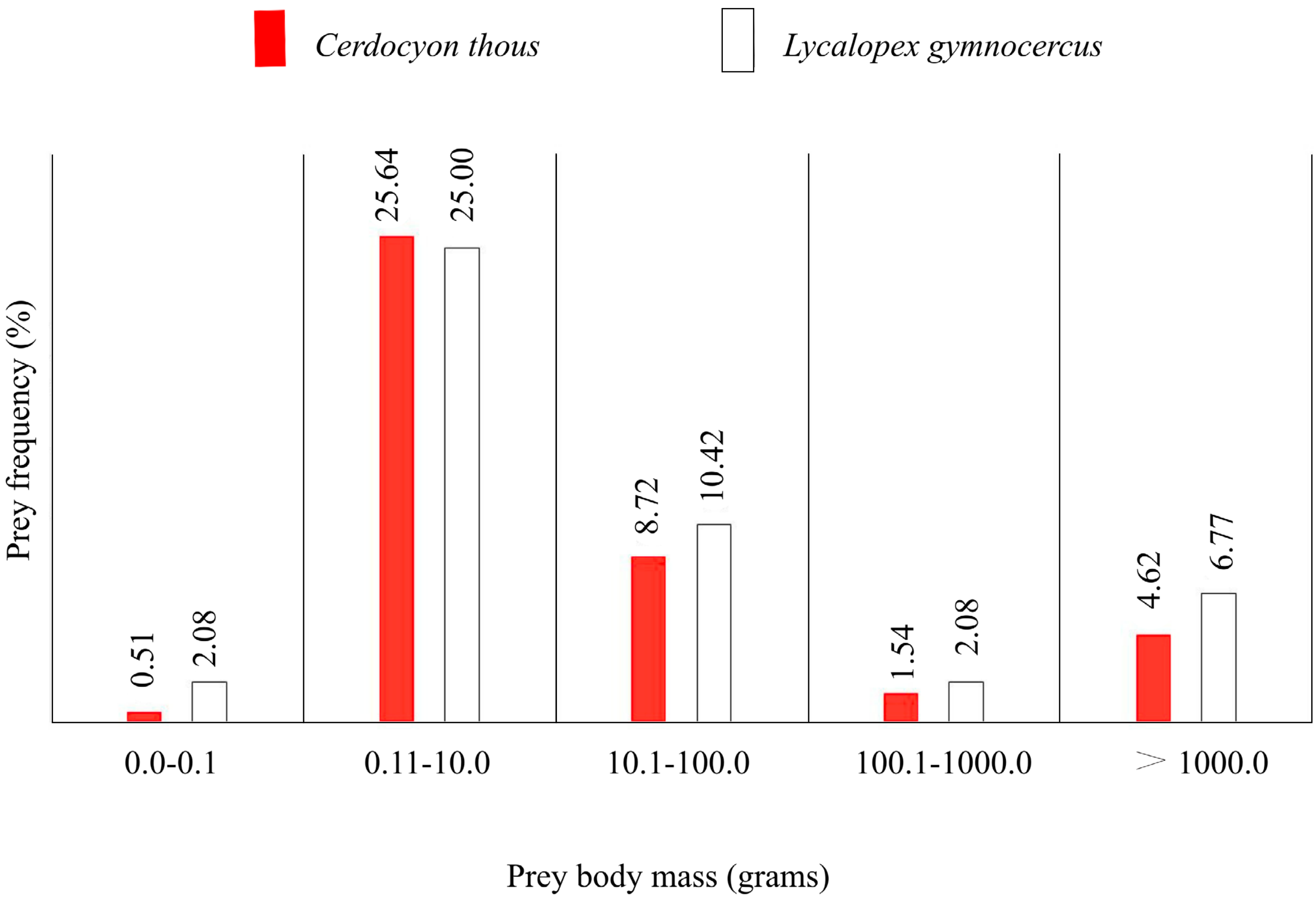

Figure 3. Frequency of consumption (%) of prey of different sizes, in grams, in the diet of canids *Cerdocyon thous* and *Lycalopex gymnocercus* in Mburucuyá National Park, Corrientes, Argentina (2014–2015).

The statistical analysis involved the assessment of dietary similarity. We evaluated diet similarity for each season using Pianka's index: Ojk =∑ *pij* p*ik*/(∑ *pij*2 *pik*2)1/2, where pi is the frequency of occurrence of prey item i in the diet of species j and k (Pianka 1973). Pianka's index (O) varies between 0 (total separation) and 1 (total overlap). This approach facilitates comparisons with other studies (Juarez and Marinho-Filho 2002; De Almeida Jácomo *et al.* 2004; Vieira and Port 2007; Bay-Jouliá *et al.* 2024). The trophic niche breadth was determined using the standardized Levins index (*Bstd*), which is based on the frequency of each food item and ranges from 0 (minimum breadth) to 1 (maximum breadth). In order to establish seasonal variations in the diet of the canids, the percentage of occurrence of plant and animal items found in the scats were compared using a Chi-squared test (Silva and Talamoni 2003). For fruit consumption, a Chi-squared test was utilized to evaluate selectivity (Martínez *et al.* 1993), and the Spearman's correlation coefficient (*rs*) was utilized to ascertain the selection of resources to the seasonal variation in the percentage of occurrence of fruiting species (Silva and Talamoni 2003; Bueno and Motta-Junior 2006). These statistical tests were selected based on similar studies conducted on the diets of canid species from the region, such as *Chrysocyon brachyurus* (Illiger, 1815) in Brazil and *Lycalopex griseus* (Gray, 1837) in Chile (Silva and Talamoni 2003; Bueno and Motta-Junior 2006).

Results

We analyzed a total of 293 scat samples, comprising 129 from *C. thous* and 164 from *L. gymnocercus*. The analysis of these samples revealed a total of 38 food item types, including 11 of plant origin and 27 of animal origin. Animal prey constitutes 41% of the total food intake for *C. thous* and 49% for *L. gymnocercus*, with the remaining percentage composed of fruit. The animal origin categories for both fox species included invertebrates (crustaceans, mollusks, arachnids, and insects) and vertebrates (fish, amphibians, reptiles, birds, and small and medium-sized mammals) (Table 1). Overall, fruits from a total of nine species, one genus, and one family of plants were identified (Table 1).

The dietary overlap between *C. thous* and *L. gymnocercus* was consistently high throughout the year. For instance, the Pianka index showed a high value of 0.90 in summer, which decreased slightly to 0.75 in winter (Table 2). However, the breadth of their respective trophic

Table 3. Animal and vegetal estimated biomass consumed by canids, *Cerdocyon thous* and *Lycalopex gymnocercus*, Mburucuyá National Park, Corrientes, Argentina (2014-2015). References: n, number of records; NFP, Numerical Frequency Percentage; g, mass in gram; EB, Estimated biomass (g); CF, Conversion factors: passeriforme (CF = 45), *Cavia aperea* (CF = 44), Small mammals (CF = 23).

	Cerdocyon thous				*Lycalopex gymnocercus*			
FLESHY FRUIT PLANTS	**n**	**NFP (%)**	**Mass (g)**	**EB**	**n**	**NFP (%)**	**Mass (g)**	**EB**
Syagrus romanzoffiana	108		9.43	1018.4	36		9.4	339.5
Butia yatay	161		6.4	1030.4	239		6.4	1529.6
Bromelia serra	15		5.7	86.1	14		5.7	80.4
Ocotea acutifolia	885		1.2	1044.3	370		1.2	436.6
Eugenia uniflora	38		0.5	18.6				
Ficus luschnathiana	818		1.08	883.4	320		1.1	345.6
Citrus	5		230.7	1153.5	4		230.7	922.8
Chrysophyllum gonocarpum	22		10.2	225.3				
Chrysophyllum marginatum	200		0.1	28	975		0.1	136.5
Psidium guajava	15		23.4	351.3				
Solanaceae	35		7	244	80		7	557.6
Subtotal				6083.3				4348.5
ANIMAL CATEGORIES								
Gasteropoda (*Pomacea canaliculata*)					11	4.6	0.1	0.5
Crustacea (*Trichodactylus kensleyi*)	4	5.3	20	105.3	3	4.6	20	90.9
Ixodidae	3	15.8	0.1	1.6	1	4.6	0.1	0.5
Scorpionidae	3	5.3	0.6	3.2	1	4.6	0.6	2.7
Aranidae					1	4.6	0.6	2.7
Mantidae	1	5.3	0.6	3.2	1	4.6	0.6	2.8
Acrididae	96	5.3	0.7	3.7	63	4.6	0.7	3.2
Gryllidae					1	4.6	0.6	2.7
Tettigonidae					2	4.6	1	4.4
Lepidoptera	3	15.8	0.6	9.5				
Formicidae					1	4.6	0.2	1.
Scarabeidae	6	5.3	1	5.3	14	4.6	1	4.6
Cicindelinae	2	5.3	0.2	1				
Carabidae	1	5.3	1	5.3				
Coleoptera not identified	3	5.3	0.6	3.2				
Insecta not identified	61	5.3	0.6	3.2				
Subtotal				144.2				115.9
Fish not identified	1	5.3	100	526.3	1	4.6	100	454.6
Reptilia not identified	2	5.3	22	115.8	2	4.6	22	100
Culibridae	1	5.3	22	115.8	1	4.6	22	100
Lacertilia	2	5.3	22	115.8				
Egg	1	5.3	10	52.63				
Birds not identified	1	5.3	20	105.3		4.6	20	90.9
Passeriforme					8	4.6	20	4090.9
Cavia aperea	1	5.3	300	69473.7	2	4.55	300	60000
Hydrochoerus hydrochaeris	2	5.3	800.1	4210.5	2	4.55	800	3636.4
Small mammals not identified	7	5.3	20	2421.1	7	4.55	20	2090.9
Medium mammals	9	5.3	2000	10526.3	13	4.55	2000	9090.9
Subtotal				87663.2				79654.6
Total				93890.7				84119

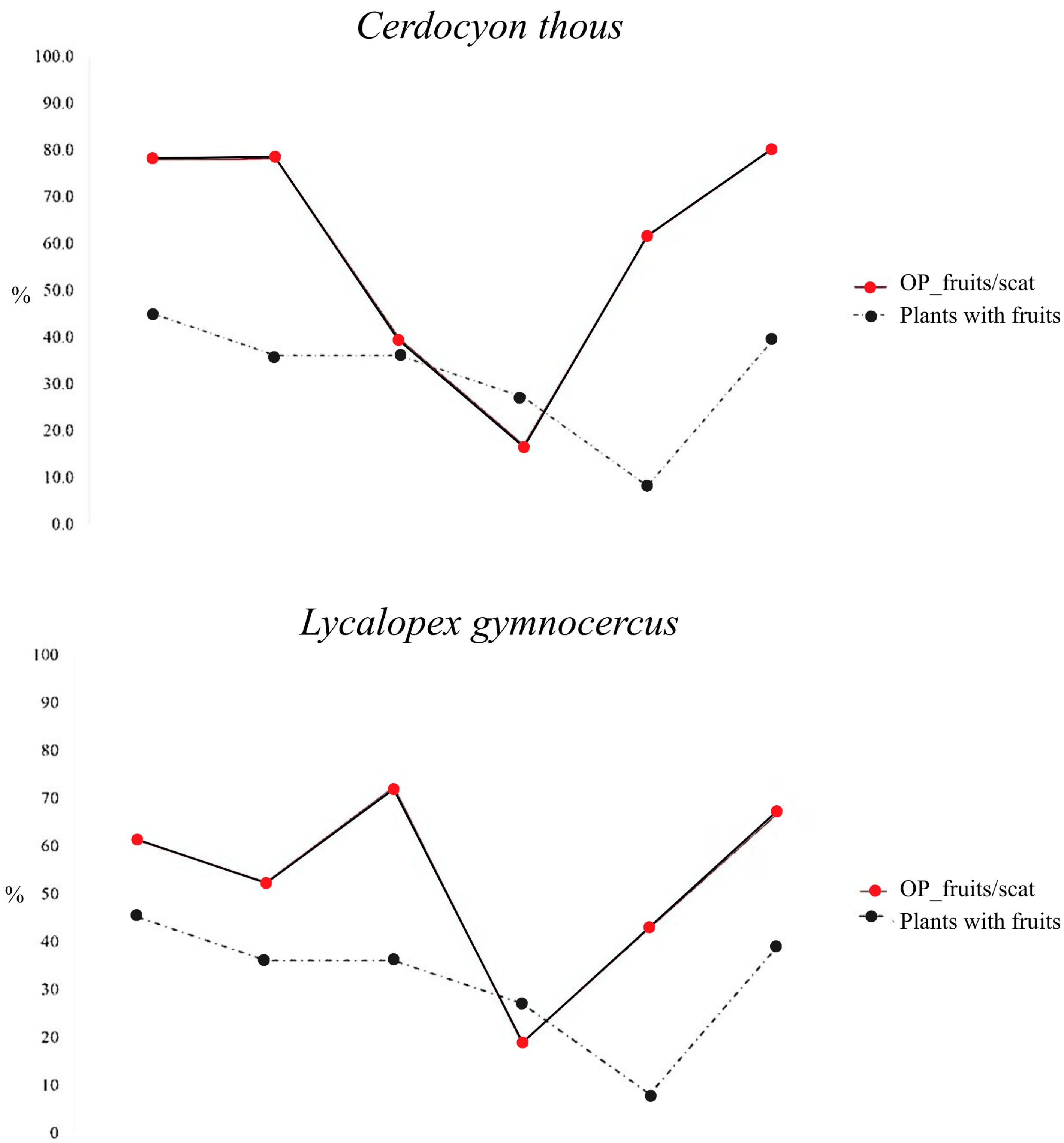

Figure 4. Percentage of plant species in scat samples of canids, *Cerdocyon thous* and *Lycalopex gymnocercus,* and percentage of plants with fruit in Mburucuyá National Park (2015).

niches fluctuated monthly (*C. thous*: *Bstd* = 0.37 to 0.89; *L. gymnocercus*: *Bstd* = 0.3 to 0.9), suggesting differences in food consumption despite the overall dietary overlap (Figure 2). Regarding the diet composition across seasons (Table 2), *C. thous* showed a higher consumption of fruits during the summer, primarily from *B. yatay* (22.1%), *Ocotea acutifolia* (Nees) Mez (22.1%), and *Ficus luschnathiana* (Miq.) Miq. (14.2%). This seasonal variation, which included a higher consumption of invertebrates and small mammals throughout the study, was statistically significant ($\chi 2 = 12.4$, $P = 0.0004$). In contrast, the diet of *L. gymnocercus* did not exhibit significant seasonal fluctuations ($\chi 2 = 1$, $P = 0.32$), maintaining a consistent consumption of *B. yatay* fruits (29.7%) and invertebrates (31%) in summer, and shifting

Table 4: Fleshy fruits consumed (%) monthly in the diet of canids, *Cerdocyon thous* and *Lycalopex gymnocercus*, Mburucuyá National Park, Corrientes, Argentina (2015). References: CT, *C. thous*; LG, *L. gymnocercus*.

	January		February		May		July		August		November	
	CT	LG	CT	LG	CT	LG	CT	LG	CT	LG	CT	LG
Scat samples	37	25	23	40	26	15	12	32	10	8	4	13
Syagrus romanzofianum				1.6		16.7	16.7	18.8	53.8	28.6	20	16.7
Butia yatay	24.1	27.8	40.6	41.3	11.6				7.7	14.3		
Bromelia serra					16.3	33.3						
Ocotea acutifolia	35.2	25.9	25	3.2								
Eugenia uniflora											40	
Ficus luschnathiana	18.5	7.4	3.1	1.6	4.7	5.6						
Citrus					7	16.7						
Chrysophyllum gonocarpum											1.6	
Chrysophyllum marginatum											20	50
Psidium guajava			6.3	1.6								
Solanaceae			3.1	3.2								

slightly to mammals (31.7% of small and medium-sized mammals) and *Syagrus romanzoffiana* (Cham.) Glassman fruits (19.5%) in winter (Table 2). The size of prey consumed by both fox species ranged from 0.10 to 2000g (Figure 3), with no significant differences between prey size categories ($\chi 2$ =1.28, df = 4, P = 0.87) for either species. In relation to consumption frequency, invertebrates were the most common food items (27.5% for *C. thous* and 29.5% for *L. gymnocercus*). However, when considering the contribution to the biomass consumed (Table 3), the diets of these foxes were predominantly composed of small mammals, which represented 78% to 81% of the total.

The selection of resources such as fleshy-fruited species was similar for both fox species when comparing the percentage of occurrence in scat samples with fruit availability in the environment (Figure 4). Specifically, between January and February 2015, the percentage of consumed fruits exceeded the proportion of fruiting species by 25% to 30%. In this period, a high consumption of fruits from *B. yatay*, *O. acutifolia*, and *F. luschnathiana* was observed in both species (Table 3). Notably, *C. thous* also consumed fruits from *Psidium guajava* L. and Solanaceae. This pattern shifted in the first months of winter, with a lower consumption of fruits by *C. thous*. Conversely, *L. gymnocercus* showed a significant peak in consumption of fruits from *Bromelia serra* Griseb., *S. romanzoffiana*, *Citrus* L., and *F. luschnathiana* (Table 4).

The selection of resources by *C. thous* and *L. gymnocercus* was evaluated by analysing the correlation between the percentage of fruit occurrence in their diet and its availability in different habitats during the summer and winter seasons. During summer, no significant correlation was observed for *C. thous* (rs = 0.47, P = 0.27). However, a significant correlation was found between the diet of *L. gymnocercus* and fruit availability (rs = 0.64, P = 0.04).

In summer, an association was observed between the consumption of both foxes' species and the availability of fruits from specific plants, including *S. romanzoffiana*, *O. acutifolia*, and *F. luschnathiana* in mesophileous forests, and *B. yatay* in palm groves. In contrast, during the winter season, the effect of fruits availability on their occurrence percentage in the diet of *C. thous* ($\chi 2$ = 33.52, P = 0.03) and *L. gymnocercus* ($\chi 2$ = 27.24, P = 0.04) was significant. Our dietary analysis identified fruits from *S. romanzoffiana* and *B. yatay*, even though these had not been detected in the field during vegetation surveys, while the highly available.

Eugenia uniflora L., *Chrysophyllum gonocarpum* (Hook. & Arn.) Radlk., *P. guajava*, *Citrus*, and *B. serra* were either minimally represented or completely absent from the diets of *C. thous* and *L. gymnocercus*.

Discussion

This study analyzed the diet, trophic niche overlap, and resource selection of two sympatric foxes, *C. thous* and *L. gymnocercus*, in Mburucuyá National Park (MNP), a protected area within the Iberá Ecoregion, Argentina. The objective was to compare their feeding strategies and assess the potential niche overlap and/or partitioning between these species. The dietary composition of *C. thous* and *L. gymnocercus* in the MNP confirms their classification as hypocarnivorous and omnivorous canids, an ecological trend established by several studies across the Neotropics (Varela *et al.* 2008; Vieira and Port 2007; Rocha *et al.* 2008; Bay-Jouliá *et al.* 2024). However, biomass analysis reveals a crucial trophic dynamic governing coexistence within our study area (MNP): whilst arthropods and insects exhibited the highest frequency of occurrence (the most common, yet lowest energy-yielding outcome), approximately 90% of the total consumed biomass for both species was contributed by small and medium-sized mammals (e.g., *Cavia aperea*, *Hydrochoerus hydrochaeris*). This finding shows that, despite the broad resource base explored, the foraging strategy in the MNP is orientated towards maximizing energy gain from specific animal items.

In the diet of *C. thous*, a higher proportion of fruit was found, which is similar to a study conducted in the Emas National Park (Goiás State, Brazil, 18°19′ S, 52°45′ W), where vegetable items had a 60% occurrence (De Almeida Jácomo *et al.* 2004). However, when compared with the MNP, the Emas National Park has an area of 132,000 ha, with a grassland predominance of 97% and a small presence of Cerrado shrubs and riparian forests (3%). These differences in vegetation are reflected in the differences in the plant species consumed *by C. thous* in our study area. The diet of *L. gymnocercus* in the MNP exhibited equal proportions between plant and animal food categories throughout the year. While this proportion is highly variable by location, other studies report different trends. Varela *et al.* (2008), for instance, discovered that fruits were predominant over animal items in the wet and dry seasons (frequency of occurrence: 69%) at the Los Colorados and Campo Grande Biological Station (Salta, Argentina, 24°43′ S, 63°17′ W). In that analysis, *Sarcomphalus mistol* (Griseb.) Hauenschild was the predominant plant food source, followed by arthropods and vertebrates. Similarly, at the Peruvian site of Lambayeque, *Lycalopex sechurae* (Thomas, 1900), a congeneric species, exhibited a highly hypocarnivorous diet with a high occurrence (84.2%) of vegetable items, dominated by *Neltuma* L. (70.5%), a protein and carbohydrate-rich legume (Prokopiuk *et al.* 2000).

These variations in diet composition show that the tendency towards hypocarnivorous or hypercarnivorous diets is influenced by food resource availability. The diet composition of *C. thous* and *L. gymnocercus* varies according to the study site, ranging from strictly hypercarnivorous diets (Farias and Kittlein 2008) to mixed diets and diets that tend towards hypocarnivory, such as the percentages of plant food occurrence above 50% determined in the present study in the MNP and other protected areas of the Iberá Ecoregion (Bay-Jouliá *et al.* 2024) and other sites in Argentina (Varela *et al.* 2008) and Brazil (De Almeida Jácomo *et al.* 2004). Consequently, the availability of trophic resources, climate, and—potentially—social organisation (Eisenberg and Redford 1999; Courtenay and Maffei 2004) are influential factors in the diet of these canids.

Most of the consumed biomass by *C. thous* and *L. gymnocercus* in the MNP consisted of mesomammals and small mammals (90%), with *Cavia aperea* (Erxleben, 1777) contributing the most significant amount (over 70%). However, when the frequency of prey size was analyzed, the most prevalent were those measuring between 0.10 and 10 grams (i.e. insects and arachnids). These results were consistent with the diet of *C. thous* at the Itapetininga Experimental Station in São Paulo (Brazil), which exhibited a high consumption of insects (Acrididae), with some individuals demonstrating hunting and capture behavior towards small prey (Bueno and Motta-Junior 2004). With regard to the consumption of *C. aperea*, evidence has been documented of its consumption by *C. thous* in Brazil (Bueno and Motta-Junior 2004; Pedó *et al.* 2006; Rocha *et al.* 2008), and by *L. gymnocercus* in Argentina (Farias and Kittlein 2008).

In relation to other prey species, two species of snakes *Helicops leopardinus* (Schlegel, 1837) and *Philodryas olfersii latirostris* (Cope, 1862) have been documented as components of the diet of *C. thous* in the MNP and the San Nicolás Portal of the Iberá National Park (Corrientes province) in Argentina (Ruiz-Garcia *et al.* 2020). The present study also makes a novel contribution by documenting, for the first time, the presence of the gastropod *Pomacea canaliculata* (Lamarck, 1828), *Phrynops hilarii* (Duméril and Bibron, 1835) eggs, and the freshwater crustaceans *Trichodactylus kensleyi* (Rodríguez, 1992) in the diet of *L. gymnocercus*, in addition to scorpions of the genus *Bothriurus* sp. (Peters, 1861).

The Pianka index indicated a high dietary overlap between *C. thous* and *L. gymnocercus* in the study area, with results analogous to those observed in Aparados da Serra National Park in Brazil (Vieira and Port 2007). According to these authors, this high overlap could be attributed to the consumption of small mammals throughout the year, a situation similar to the diet obtained for these species in the MNP, where small mammals contributed the highest with the consumed biomass. However, Vieira and Port (2007) observed a lower percentage of fruit occurrences in their diet, a phenomenon attributed, in part, to the prevalence of grasslands and a limited variety of plant species that produce fleshy fruits in the Aparados da Serra National Park (Brazil).

In the diet of *C. thous* and *L. gymnocercus*, the ingestion of fleshy fruits varied seasonally, characterising an opportunistic behaviour that was linked with MNP peak fruiting. A distinctive finding of our research is the clear manifestation of seasonal trophic plasticity in both foxes and its relationship to the selective consumption of palms (*Butia yatay* and *Syagrus romanzoffiana*). The consumption of *S. romanzoffiana* during the winter should not be regarded as a random trophic event, but rather an essential adaptive strategy. We demonstrate that when the general availability of fleshy fruits decreases drastically during the cold season, both species switch to active foraging behaviour specifically targeting this palm. This critical resource allows both canids to maintain a fundamental energetic contribution when other plant resources are scarce. This temporal partitioning of key resources is the mechanism that likely permits coexistence and mitigates intra-guild conflict, as the exploitation of these key resources during periods of scarcity reduces competitive pressure within the shared ecological niche. The capacity to modify their dietary breadth in this way evidences that, whilst trophic overlap is high, seasonal flexibility mediated by local resources maintains the stability of the predator community in the MNP.

The dietary records of these foxes revealed the presence of fruits from *B. yatay*, *O. acutifolia*, and *F. luschnathiana* during the summer months, while in winter, fruits from *S. romanzoffiana*, *B. serra*, *F. luschnathiana*, and *Citrus* were documented. The evidence of the opportunistic behaviour of *L. gymnocercus* was the correlation between the consumption of fleshy fruits and its availability in summer, a behaviour also observed for the species in the province of Salta (Varela *et al.* 2008). During winter, when fruit availability was scarce, both foxes exhibited active foraging behaviour in search of certain plant species. This has been considered key to the diet of frugivorous mammals in the Paranaense rainforest of Misiones province (Argentina), with *S. romanzoffiana* being a species that fructified more than once and asynchronously (Giombini 2013). This foraging behaviour has also been reported for *Lycalopex vetulus* (Lund, 1842) in the Cerrado of Mato Grosso (Brazil), where it consumed the fruits of *Hancornia speciosa* Gomes during times of scarcity of other plant species, replacing its consumption with fruits of *Solanum lycocarpum* A. St.-Hil. when other species were abundant (Dalponde and De Souza Lima 1999). However, the presence of fruit from certain plant species (*P. guajava*) in the MNP does not necessarily ensure their consumption by *C. thous* and *L. gymnocercus*. A comparable behaviour was observed in *L. vetulus*, whose diet exhibited minimal consumption of bromeliad fruits, despite the presence of fruiting plants in a context of a scarce supply of other edible plant species (Dalponde and De Souza Lima 1999).

The implications of these findings for the conservation of both species and the knowledge of their biology are significant. The high niche overlap and remarkable dietary plasticity of *C. thous* and *L. gymnocercus* confirm their capacity as generalist and opportunistic predators. This dietary flexibility provides them with high adaptability to resource availability, a key trait for their survival in complex, dynamic environments such as the Mburucuyá National Park, as well as in habitats that may be altered by human activities. The confirmation of an active foraging behavior, especially for key resources like palm fruits during periods of scarcity, underscores the importance of conserving these specific plant species and their habitats to ensure the foxes' food security. Finally, this study not only contributes new records of trophic relationships but also validates and expands knowledge on the mechanisms of coexistence between these foxes, which is fundamental for formulating effective management and conservation strategies in the Iberá region and in other areas where these species are sympatric.

Conclusions

In this study, we assessed the diet, overlap, and the selection of resources by *C. thous* and *L. gymnocercus* in a comparative context within the MNP. The research aimed to investigate the dimensions of their ecological niche, evaluating potential overlaps in trophic resource utilization and the mechanisms that facilitate their coexistence. The results confirm the high dietary similarity between the two species, both of which function as generalist predators. Their diet is highly variable, composed of common items such as fleshy fruits, invertebrates, and small mammals, which contributed over 90% of the consumed biomass. The composition of food categories exhibited seasonal variations, suggesting that foraging patterns are influenced by changes in the availability of resources throughout the year.

The study also confirmed a strong opportunistic behavior by the foxes in response to the availability of certain fruits, particularly during summer. However, their diet was not solely dependent on resource abundance; for example, they actively foraged for palm fruits (*S. romanzoffiana*) in the winter when other options were scarce, but they avoided abundant fruits like *P. guajava*. These findings highlight that coexistence between the two species is not maintained through strict dietary partitioning but rather through their flexible feeding strategies, which respond to the dynamic availability of resources in a complex, multi-habitat environment.

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