

Comparative trophic ecology of two sympatric canids in the Brazilian Pampa

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Keywords

Cerdocyon thous; *Lycalopex gymnocercus*; niche breadth; dietary overlap; southern Brazil; sympatric carnivores.

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Editor: Matthew Hayward

Received 20 June 2018; revised 8 October 2018; accepted 24 October 2018

doi:10.1111/jzo.12636

Abstract

Studies on resource utilization by carnivores are essential to assess the role of the species in the ecosystem. These studies help us to understand the mechanisms that influence vertebrate community structure and the relationships between predators and prey. The aims of this study were to compare and describe the food habits of the sympatric Pampas fox (*Lycalopex gymnocercus*) and crab-eating fox (*Cerdocyon thous*) in the Brazilian Pampa, and to evaluate the food niche overlap between them, and infer aspects of habitat preferences on the basis of their prey. For the diet analyses, 25 stomach contents of Pampas foxes and 33 of crab-eating foxes were collected. We identified 80 prey items (49 for the Pampas fox and 63 for the crab-eating fox) and grouped them into eight main categories. Mammals and invertebrates were the most frequent items in the diets of both canids, followed by fruits. The trophic niche breadth of the Pampas fox ($Bsta = 0.56$) was larger than that of the crab-eating fox ($Bsta = 0.47$). The diet overlap between them was $Ojk = 0.58$. However, a PERMANOVA test showed that diets did not differ between species or season. Our results showed that both *L. gymnocercus* and *C. thous* had generalist diets, with a great diversity of prey, but based on similar main food items. Items that contributed the most to the diet of the Pampas fox were insects (Gryllotalpidae and Scarabaeidae) and cavies (*Cavia apereia*) and those that contributed the most to the diet of the crab-eating fox were fruits of *Syagrus romanzoffiana*, beetles (Scarabaeidae), amphibians (*Leptodactylus* spp.) and cavies. This is the first study to describe and compare the food habits of these two species, occurring in sympatry in the Brazilian Pampa.

Introduction

There has been much debate on the mechanisms that allow coexistence between sympatric canids. Interspecific competition for food is a critical factor that determines species coexistence in carnivores (Davies *et al.*, 2007). Habitat and temporal segregation and complementarity in the use of trophic and spatial resources are some mechanisms that promote this coexistence (Novaro, Funes & Jiménez, 2004) compensating for the high niche overlap among similar species (Schoener, 1974). However, the conditions for coexistence may depend on the local balance of processes such as food availability, predation by larger carnivores, and trophic causes as well as habitat complexity (Novaro *et al.*, 2004).

Among the sympatric canids in the Neotropics, the crab-eating fox (*Cerdocyon thous* Linnaeus, 1766) and the Pampas fox (*Lycalopex gymnocercus* Fisher 1814) are two widespread species whose geographic ranges overlap in southern Brazil, northern Argentina and Paraguay (Wilson & Mittermeier, 2009). They are closely related medium-sized canids with a high overlap in body size, with Pampas fox (adult weight:

4.0–5.6 kg) being slightly smaller than crab-eating fox (adult weight: 4.5–8.5 kg) (Perini, Russo & Schrago, 2010; Trigo, Rodrigues & Kasper, 2013). Although they are common species, few studies have compared the ecological aspects of these two canids in regions of sympatry (Vieira & Port, 2007; Di Bitetti *et al.*, 2009; Faria-Corrêa *et al.*, 2009; Abreu *et al.*, 2010). Both species are considered dietary generalists, feeding on small vertebrates, insects and fruits. The Pampas fox is associated with open habitats, whereas the habitat generalist crab-eating fox occurs in all habitats, including open ones. Because the crab-eating fox and Pampas fox are common in the grassland habitats of southern Brazil, they may compete for resources (Vieira & Port, 2007). This fact provides the opportunity to compare their ecology and understand what factors facilitate their coexistence.

Investigations of resource utilization by carnivores are essential to assess the role of the species in the ecosystem, allowing us to understand the mechanisms that influence vertebrate community structure and the relationship between predators and prey (Klare, Kamler & Macdonald, 2011; Nilsen *et al.*, 2012). Therefore, the aims of this study were to compare and describe

the food habits of the sympatric crab-eating fox and Pampas fox in the Brazilian Pampa, and to evaluate the food niche overlap between them, and infer their habitat use on the basis of their prey.

Materials and methods

Study area

Between October 2013 and September 2016, we collected 33 stomach contents of the crab-eating fox and 25 of the Pampas fox along the roads, especially BR-290, one of the main highways in Rio Grande do Sul state, in the extreme south of Brazil. This region is located in the Brazilian Pampa, an ecological formation that represents about 2% of the Brazilian territory and 63% of the Rio Grande do Sul state (Pillar *et al.*, 2009) (Figure 1). This formation displays habitat continuity with the grasslands of Uruguay, composing together the Uruguayan Savanna ecoregion. It is composed of tropical and subtropical grasslands, savannahs and scrublands known as Pampas that extends to the northeast of Argentina (WWF, 2017). Grass-dominated vegetation types prevail in the study area, with sparse shrub and tree formations that co-occur within the grassland matrix (Olson *et al.*, 2001). Riparian forests are present along rivers, which allow the occurrence of species associated with the forests in the region. Over time, this region has been profoundly modified by human activities, such agriculture for rice, soybean and primarily by livestock, particularly cattle ranching (Pillar *et al.*, 2009; Roesch *et al.*, 2009). According to Pillar *et al.* (2009), the anthropogenic impact on this environment promotes the mischaracterization of c. 51% of natural pastures of this region.

Sample identification

The stomach contents were collected from road-killed foxes and stored in 70% alcohol. The contents were washed in running water over a 0.5-mm mesh. Macroscopic materials such

as hair, bones, teeth, beaks, fruits and invertebrate remains were analyzed and identified to the lowest possible taxonomic level by comparison with a reference collection and general literature and consultation with specialists. Mammals were identified on the basis of guard hairs by using an identification key proposed specifically for the Brazilian Pampa region (Migliorini *et al.*, 2017).

Diet analysis

Food items were quantified in terms of frequency of occurrence (FO) expressed by the proportion of samples containing each item and percentage of occurrence (PO) expressed by the proportion of a food item in relation to the sum of all food items in the diet.

To evaluate trophic niche breadth, we used the Levins index: $B = 1/(\sum p_j^2)$, where p_j is the percentage of occurrence of a prey type (Levins, 1968). This index was standardized on a scale ranging from 0 (which indicates a generalist habit), when all prey items are consumed in equal proportions, to 1, (which indicates a specialized diet), when very few prey items are eaten in greater frequency: $B_{sta} = (B-1)/(n-1)$, where B is the Levins index and n is the total number of prey types consumed (Colwell & Futuyma, 1971).

The diet overlap between canids was calculated using the Pianka index (Pianka, 1973): $O_{jk} = \sum P_{ij}P_{ik}/\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}$, where P_i is the proportion of prey item i in the diet of species j and k . The results range from 0 (no prey in common) to 1 (total overlap). The proportion of each prey type was calculated through the relative volume estimated visually: 0 (absence), 1 (<1%), 2 (1–5%), 3 (6–10%), 4 (11–25%), 5 (26–50%), 6 (51–75%), 7 (76–98%) and 8 (>98%). For diet overlap, the scores were converted to the midpoint of each percentage interval (1 = 0.5%, 2 = 3%, 3 = 8%, 4 = 18%, 5 = 38%, 6 = 63%, 7 = 87% and 8 = 99%) (Kruuk & Parish, 1981).

We also applied the index of relative importance (IRI) combining frequency, number of individuals and volume

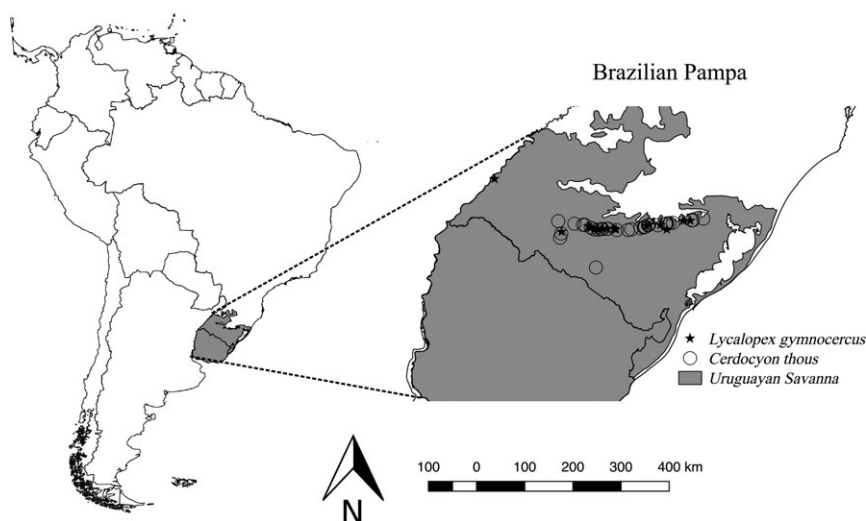


Figure 1 Distribution of the crab-eating fox and Pampas fox collected for diet analysis in the Brazilian Pampa region.

measurements into a single index (Pinkas, Oliphant & Iverson, 1971): $IRI = F(N + V)$, where F is the frequency of occurrence, N is the percentage of occurrence and V is the volumetric percentage. The volumetric percentage was calculated on the basis of prey biomass. The body masses of mammalian, avian, fish and fruit prey were obtained from the literature. The reptilian and amphibian prey body masses were obtained from reference collections. For invertebrates, we assigned a biomass value of 0.5 g per individual, following García & Kittlein (2005). The average body masses of the items not identified to the species level were obtained from the families distributed in the Brazilian Pampa on the basis of literature and scientific collections. Domestic cat and sheep were assumed to have been scavenged and were excluded from the calculations.

There is no information available on the daily ingested biomass for the crab-eating fox and Pampas fox. Therefore, we considered the value of 210 g day^{-1} , described for culpeo fox, *Lycalopex culpaeus* (Silva, Jaksic & Bozinovic, 2005), as a parameter for both species once it is similar in size, being just slightly larger (adult weight: 6–8 kg) than them (Di Bitetti *et al.*, 2009). This value was used as the estimated ingested biomass of prey too large to be consumed entirely. For prey types with biomass below this value, the ingested biomass was estimated by multiplying their average body mass with the minimum number of individuals consumed.

We used a two-way PERMANOVA to test for differences between diet of two species and to test for possible seasonal differences in food habits. Seasonality of diets was tested considering cold and hot periods (May to October and November to April, respectively). Tests were performed with PAST 2.17c software Hammer, Harper & Ryan (2001) considering just the main items, that represented more than 3% of biomass ingested for one of the species. For this analysis, we used a matrix of 25 individuals of each species, and arcsine square root transformed the data considering the similarity index of Bray-Curtis (Hammer & Harper, 2006).

Results

We identified 80 prey items (63 for the crab-eating fox and 49 for the Pampas fox) grouped into eight main categories (Table 1). Mammals and invertebrates were the most frequent items in the diets of both canids, followed by fruits. The frequency of occurrence of grass was high in the diets of both species (52% for the Pampas fox and 78% for the crab-eating fox). However, we did not include this item in any analysis because it does not represent a considerable part of the ingested biomass in their diets.

The trophic niche breadth of the Pampas fox ($B_{sta} = 0.56$) was larger than that of the crab-eating fox ($B_{sta} = 0.47$). The diet overlap between them was $O_{jk} = 0.58$. The two-way PERMANOVA showed that there were no significant differences in the diets of the crab-eating fox and Pampas fox. In addition, there were no seasonal differences in the diet or 'interactions' between the factors 'ssp' and 'seasonality' (Table 2).

On the basis of IRI, most of the prey items had relatively low importance, and only some were highly consumed

(Table 1). For the crab-eating fox, items that contributed the most to the diet included fruits of *Syagrus romanzoffiana*, beetles (Scarabaeidae), amphibians (*Leptodactylus* spp.), and caviés (*Cavia aperea*); for the Pampas fox, insects (especially Gryllotalpidae and Scarabaeidae) and caviés were most important.

Discussion

Crab-eating fox and Pampas fox presented similar diets, consuming similar proportions of items of animal origin (77.4% for crab-eating fox and 76.9% for Pampas fox) and fruits (19.6% for crab-eating fox and 15.2% for Pampas fox). Our results showed that these two species had generalist diets, consuming a wide range of items that were relatively well-distributed in terms of frequency of consumption. However, of the 80 food items found, only 32 were the same for both foxes, resulting in a niche overlap of 58%. This value is quite different from that found by Vieira & Port (2007) and Kasper *et al.* (2016), probably because of the differences in taxonomic identification, because different levels of prey identification have a strong influence on this type of analysis (Greene & Jaksic, 1983).

Vertebrates comprised 56 and 49.7% of the diets of the crab-eating fox and Pampas fox, respectively, with mammals (especially rodents) being the most consumed prey. Caviés, which are widely distributed and tolerant to environmental disturbances (González & Martínez-Lanfranco, 2012), were the mammals with the highest relative importance for both foxes (especially for the Pampas fox). Their crepuscular activity and occurrence in open fields, swamps edges and roadside habitats may favor their predation by these canids. It is important to note that these two canids live in a state of 'mesopredator release' (Crooks & Soulé, 1999) because the absence of puma (*Puma concolor*) and maned wolf (*Chrysocyon brachyurus*) in the region of Brazilian Pampa (Trigo *et al.*, 2013). Because of the higher abundance expected for medium-sized carnivores in the absence of top predators (Crooks & Soulé, 1999), it is possible that these foxes are using habitats with high abundance of prey (especially caviés) as road-sides, despite the noise and vehicle occurrence.

Amphibians were an important part of the diet of the crab-eating fox, which differed from the results of previous studies (Juarez & Marinho-Filho, 2002; Jácomo, Silveira & Diniz-Filho, 2004; Rocha, dos Reis & Sekiama, 2004; Pedó *et al.*, 2006; Vieira & Port, 2007; Raíces & Bergallo, 2010). Only Bianchi *et al.* (2013) recorded frogs as an important food item for this species during the dry season in Pantanal. The butter frog, *Leptodactylus latrans*, is one of the biggest amphibians in southern Brazil, and it occupies either preserved or disturbed habitats (Josende *et al.*, 2015) and seems to represent an important food resource for the crab-eating fox.

Birds are usually considered to have low importance in the diet of the Pampas fox (García & Kittlein, 2005; Varela *et al.*, 2008) even where this prey category had a diverse assemblage and was abundant (Farias & Kittlein, 2008). However, they were an important item in the present study, where Gruiformes had a relatively high importance in the diet of the Pampas fox, with an important biomass intake for the species.

Fishes and reptiles were consumed in small proportions. However, it is interesting to note the consumption of

Table 1 Frequency of occurrence (FO), percentage of occurrence (PO), relative volume (Vol%), minimum number of individuals (MNI) and average adult body mass of the food items found in the stomach contents of two sympatric canids in the Brazilian Pampa. Contribution to the diets is estimated using the index of relative importance (IRI)

Food items	Mass (g)	<i>Cercopithecus thous</i> (n = 33)					<i>Lycalopex gymnocercus</i> (n = 25)				
		FO	PO	Vol%	MNI	IRI	FO	PO	Vol%	MNI	IRI
Mammals		69.7	21.7				60.0	22.7			
<i>Cavia aperea</i>	549.0 ¹	15.2	3.4	9.5	6	224.70	16.0	4.2	12.9	4	330.12
<i>Akodon azarae</i>	24.0 ¹	3.0	0.7	1.9	4	4.83	–	–	–	–	–
<i>Akodon reigi</i>	40.0 ¹	6.1	1.4	3.8	6	31.92	–	–	–	–	–
<i>Calomys laucha</i>	19.0 ¹	9.1	2.1	1.3	4	50.55	–	–	–	–	–
<i>Deltamys kempii</i>	26.0 ¹	9.1	2.1	4.9	4	39.91	4.0	1.1	2.5	1	6.59
<i>Oligoryzomys</i> sp.	22.5 ^{a1}	6.1	1.4	2.5	1	5.96	4.0	1.1	1.5	3	8.80
<i>Lundomys molitor</i>	280.0 ¹	–	–	–	–	–	4.0	1.1	2.5	1	13.11
<i>Nectomys squamipes</i>	250.0 ¹	3.0	0.7	1.2	2	6.67	4.0	1.1	1.5	1	21.90
<i>Holochilus vulpinus</i>	210.0 ¹	6.1	1.4	3.8	3	35.59	8.0	2.1	7.9	2	88.66
<i>Wilfredomys oenax</i>	75.0 ¹	6.1	1.4	0.2	1	3.58	4.0	1.1	0.3	1	7.33
<i>Cuniculus paca</i>	9300.0 ¹	3.0	0.7	1.9	1	8.80	8.0	2.1	4.0	2	56.44
Dasypodidae	4525.0 ^b	3.0	0.7	2.6	1	6.88	–	–	–	–	–
<i>Euphractus sexcinctus</i>	5400.0 ¹	3.0	0.7	1.2	1	11.20	–	–	–	–	–
<i>Dasypus novemcinctus</i>	3650.0 ¹	3.0	0.7	1.2	1	5.27	–	–	–	–	–
<i>Lepus europaeus</i>	4750.0 ¹	3.0	0.7	0.1	1	5.27	4.0	1.1	2.5	1	20.30
<i>Felis catus</i>		3.0	0.7	0.5	1		–	–	–	–	–
<i>Ovis aries</i>		–	–	–	–	–	8.0	2.1	4.1	2	
Birds		30.3	9.4				20.0	7.5			
Tinamiformes	624.5 ^{a2,3}	6.1	1.4	0.2	2	26.04	–	–	–	–	–
<i>Rhynchotus rufescens</i>	927.5 ²	6.1	1.4	1.7	2	25.32	4.0	1.1	4.0	1	22.16
<i>Gallus gallus</i>	1300.0 ³	12.1	2.7	2.0	4	119.35	–	–	–	–	–
Gruiformes	423.20 ^c	–	–	–	–	–	12.0	3.2	7.8	3	166.21
Passeriformes	52.25 ^{a4}	6.1	1.4	0.6	2	15.36	4.0	1.1	1.5	1	15.36
Reptiles		27.3	7.5				20.0	7.5			
<i>Trachemys dorbignii</i>	1127.04 ⁵	3.0	0.7	1.2	1	5.27	8.0	2.1	0.1	2	61.55
Dipsadidae	180.7 ^b	–	–	–	–	–	8.0	2.1	1.6	2	47.51
<i>Boiruna maculata</i>	477.8 ^c	3.0	0.7	1.2	1	5.15	–	–	–	–	–
<i>Erythrolamprus poecilogyrus</i>	73.21 ^c	3.0	0.7	1.2	1	14.27	–	–	–	–	–
<i>Thamnodynastes hypoconia</i>	22.0 ^c	6.1	1.4	0.2	1	2.96	–	–	–	–	–
<i>Philodryas olfersii</i>	149.7 ^c	3.0	0.7	1.9	1	8.86	–	–	–	–	–
<i>Bothrops alternatus</i>	631.0 ^c	3.0	0.7	1.2	1	6.80	–	–	–	–	–
Snake moult		3.0	0.7	0.1	1		4.0	1.1	0.7	1	
<i>Amphisbaena</i> sp.	15.0 ^c	6.1	1.4	0.5	1	2.79	–	–	–	–	–
Amphibians		42.4	13.2				20.0	7.5			
Leptodactylidae	46.0 ^b	3.0	0.7	0.1	1	3.71	–	–	–	–	–
<i>Leptodactylus chaquensis</i>	49.0 ^c	6.1	1.4	0.3	2	16.05	–	–	–	–	–
<i>Leptodactylus latinasus</i>	32.57 ^c	9.1	2.1	0.8	3	16.93	4.0	1.1	0.1	1	6.13
<i>Leptodactylus latrans</i>	75.32 ^c	15.2	3.4	4.0	8	154.46	–	–	–	–	–
<i>Leptodactylus gr. latrans</i>	32.4 ⁶	24.2	5.5	5.9	10	245.50	4.0	1.1	1.5	2	9.84
<i>Leptodactylus gracilis</i>	40.95 ^c	–	–	–	–	–	4.0	1.1	1.5	2	13.92
<i>Physalaemus biligonigerus</i>	32.66 ^c	3.0	0.7	0.2	1	2.82	4.0	1.1	1.5	5	9.69
<i>Odontophrynus americanus</i>	40.13 ^c	3.0	0.7	1.2	2	3.61	–	–	–	–	–
Bufonidae	20.5 ^c	6.1	1.4	2.3	2	12.01	–	–	–	–	–
<i>Rhinella</i> gr. <i>granulosa</i>	15.2 ^c	3.0	0.7	0.5	1	2.71	4.0	1.1	0.1	1	5.87
Fishes		12.1	3.8				12.0	4.5			
Cichlidae	18.9 ^c	–	–	–	–	–	4.0	1.1	0.1	1	5.95
<i>Hoplias malabaricus</i>	456.7 ⁷	6.1	1.4	3.2	2	30.32	4.0	1.1	1.0	1	12.93
<i>Synbranchus marmoratus</i>	148.3 ^c	3.0	0.7	2.6	1	11.40	–	–	–	–	–
Callichthyidae	207.5 ^c	3.0	0.7	0.5	1	6.82	–	–	–	–	–
<i>Callichthys callichthys</i>	80.0 ⁷	–	–	–	–	–	4.0	1.1	0.3	1	7.50
Invertebrates		69.7	21.7				72.0	27.2			
Caelifera	0.5 ⁸	–	–	–	–	–	12.0	3.2	0.4	3	56.91
Blattodea	0.5 ⁸	–	–	–	–	–	4.0	1.1	0.1	1	4.86

Table 1 Continued.

Food items	Mass (g)	<i>Cercocyon thous</i> (n = 33)					<i>Lycalopex gymnocercus</i> (n = 25)				
		FO	PO	Vol%	MNI	IRI	FO	PO	Vol%	MNI	IRI
Belostomatidae	0.5 ⁸	3.0	0.7	0.1	1	2.29	–	–	–	–	–
Cicadoidea	0.5 ⁸	3.0	0.7	0.1	1	2.30	–	–	–	–	–
Scarabaeidae	0.5 ⁸	39.4	8.9	6.3	178	535.37	28.0	7.4	0.8	16	241.34
Lepidoptera	0.5 ⁸	–	–	–	–	–	4.0	1.1	0.1	1	4.95
Lepidoptera larvae	0.5 ⁸	12.1	2.7	1.7	101	35.08	20.0	5.3	0.7	13	125.68
Diptera larvae	0.5 ⁸	15.2	3.4	0.5	46	85.97	16.0	4.2	1.0	57	107.60
Hymenoptera	0.5 ⁸	3.0	0.7	0.1	1	2.34	8.0	2.1	0.2	2	19.57
Formicidae	0.5 ⁸	9.1	2.1	0.3	28	21.20	8.0	2.1	0.2	3	19.85
Grylloidea	0.5 ⁸	12.1	2.7	0.4	4	37.16	16.0	4.2	0.4	6	81.87
Gryllotalpidae	0.5 ⁸	9.1	2	0.3	3	20.60	36.0	9.5	1.7	37	584.35
Gryllotalpidae nymph	0.5 ⁸	–	–	–	–	–	4.0	1.1	0.7	49	9.78
<i>Coprophaneus</i> sp.	0.5 ⁸	3.0	0.7	0.5	4	2.36	–	–	–	–	–
Insects not identified	0.5 ⁸	3.0	0.7	0.1	1	–	4.0	1.1	2.6	1	–
Scorpiones	0.5 ⁸	9.1	2.1	0.3	4	20.68	4.0	1.1	0.3	2	13.53
Palaemonidae	0.5 ⁸	–	–	–	–	–	4.0	1.1	0.3	7	5.55
Brachyura	0.5 ⁸	–	–	–	–	–	4.0	1.1	0.1	2	5.05
Stylommatophora	0.5 ⁸	3.0	0.7	0.1	1	2.30	–	–	–	–	–
Pulmonata	0.5 ⁸	3.0	0.7	0.1	1	2.30	4.0	1.1	0.1	1	4.89
Fruits		63.6	19.8				40.0	15.2			
<i>Citrus</i> sp.	160.2 ⁹	3.0	0.7	0.1	1	10.16	–	–	–	–	–
Fabaceae	66.20 ¹⁰	–	–	–	–	–	4.0	1.1	0.7	1	12.18
<i>Hovenia dulcis</i>	7.36 ^c	9.1	2.1	3.6	3	49.51	4.0	1.1	4.0	1	22.21
<i>Psidium</i> sp.	8.0 ³	3.0	0.7	0.1	1	2.62	–	–	–	–	–
<i>Physalis pubescens</i>	3.71 ¹¹	6.1	1.4	0.6	40	18.60	16	4.2	4.1	15	128.99
<i>Phytolacca dioica</i>	0.3 ¹²	–	–	–	–	–	4.0	1.1	1.5	1	4.85
<i>Solanum lycopersicum</i>	55.96 ¹³	–	–	–	–	–	4.0	1.1	1.5	1	7.00
<i>Solanum tuberosum</i>	113.46 ^c	–	–	–	–	–	4.0	1.1	1.5	1	10.93
<i>Syagrus romanzoffiana</i>	5.61 ¹⁴	39.4	8.9	9.3	152	697.78	12	3.2	4.2	21	97.02
<i>Zea mays</i>	12.4 ¹⁵	6.1	1.4	1.2	2	13.99	–	–	–	–	–
Not identified		3.0	0.7	0.5	1	–	–	–	–	–	–
Others		9.1	2.8				20	7.6			
Plants not identified		3.0	0.7	0.1	1	–	–	–	–	–	–
Garbage		6.1	1.4	0.2	2	–	12	3.2	2.7	3	–
Carrion		3.0	0.7	0.1	1	–	8.0	2.1	5.0	2	–

1. Paglia *et al.* (2012); 2. Blake (1977); 3. Rodrigues *et al.* (2007); 4. Sick (1997); 5. Bujes, Molina & Verrastro (2011); 6. Josende *et al.* (2015); 7. Costa Lima *et al.* (2017); 8. García & Kittlein (2005); 9. Gallo *et al.* (1977); 10. Dutra *et al.* (2017); 11. El Sheikh *et al.* (2008); 12. Galetti, Pizo & Morellato (2011); 13. Mohamed, Ali & Mohamed (2012); 14. Goudel *et al.* (2013); 15. Farnia, Mansouri & Branch (2014).

^aAverage body mass calculated on the basis of average adult body mass of the species in the taxon occurring in the Brazilian Pampa.

^bAverage body mass of species belonging to the taxon and found in this study.

^cAverage body mass obtained from the reference collection.

Table 2 Results of two-way PERMANOVA analyzing possible differences in the diet of crab-eating fox and Pampas fox, and seasonality in Brazilian Pampa region

Two-way PERMANOVA	Pseudo F	P	SS
Species	0.90	0.50	3674.2
Seasons	1.74	0.08	7069.5
Species versus Seasons	1.12	0.32	4565.2

poisonous animals, such snakes belonging to the genus *Bothrops* Wagler, 1824 by the crab-eating fox. The consumption of snakes belonging to this genus has been reported by other authors such as Rocha *et al.* (2004); Gatti *et al.* (2006); and Rocha *et al.* (2008). We suggest that this canid consumes

dead specimens or may have some strategy for catching this type of prey. However, further studies need to be performed to demonstrate whether it is resistant to the toxins.

The consumption of invertebrates may be especially important during periods of low availability of vertebrate prey, when both foxes must eat whatever is available for survival. Invertebrate items do not perhaps satisfy all the nutritional requirements of these canids; however, they probably represent an important source of nutritional compounds (Silva *et al.*, 2005). For *L. gymnocercus*, insects were frequent in the diet, but usually represent small contributions in biomass intake, as observed in Varela *et al.* (2008) for Argentinean Chaco or Canel *et al.* (2016) in Argentinean grasslands. However in some cases, insects can be important in terms of biomass as

described by Castillo *et al.* (2011) in Argentinean Pampas, comparing diet of adults and cubs.

The most important item in the diet of the crab-eating fox was the fruits of *Syagrus romanzoffiana*. This fruit can be found throughout the year (Carvalho, 2006), and this could be the reason for the lack of seasonality in the diet of the crab-eating fox. In southern Brazil, this fruit is common in forest formations, except at high altitudes (more than 800 m above sea level), and it is particularly abundant in primary vegetation on very humid and swampy soils (Sobral, 2006). Previous studies conducted in different habitats have reported fruits as an important resource throughout the year (Varela *et al.*, 2008) or seasonally (Motta-Junior, Lombardi & Talamoni, 1994; Facure, Giaretta & Monteiro-Filho, 2003; Bianchi *et al.*, 2013). According to Varela & Bucher (2006), both crab-eating fox and Pampas fox are legitimate seed dispersers, enhancing seed germination and increasing dispersal distance for several fruit species. Although the Pampas fox consumes fruits to a lesser extent than the crab-eating fox, we found a higher diversity of fruits in its diet, and *Physalis pubescens* and *S. romanzoffiana* were the main species consumed. The first is a shrubby species with ruderal behavior (Soares *et al.*, 2009), which explains its presence in the diets of both foxes (especially for the Pampas fox).

Both species are considered of Least Concern by IUCN (Lucherini, 2015, 2016) and nationally (Beisiegel *et al.*, 2013; Queirolo, Kasper & Beisiegel, 2013). However these canids are threatened by practices, such as retaliation/prevention of alleged predation of domestic animals, and they are frequent victims of shootings and poisoning (Beisiegel *et al.*, 2013; Queirolo *et al.*, 2013). Although foxes have been reported to attack lambs, sheep remains were absent in the diet of the crab-eating fox and comprised only 2.1% of the items consumed by the Pampas fox. This consumption may be related to their scavenger habits (Farias & Kittlein, 2008), because carrion has been found in the diets of both foxes. We also observed low predation of poultry, which comprised only 2.7% of the diet of the crab-eating fox. Previous studies have recorded poultry in the diet, but it usually represents <10% of the diet (Facure *et al.*, 2003). Despite this low index, landowners tend to be intolerant of these potential predations. This attitude, which is also unethical, does not consider the benefits of the canids' predation pressure on the populations of plague species such as the introduced hare and rodents (García & Kittlein, 2005; Farias & Kittlein, 2008).

This was the first study to describe the diets of the crab-eating fox and Pampas fox to the species level in the Brazilian Pampa region. Our results confirm the omnivorous-generalist habits of these species, which has been described in other regions (García & Kittlein, 2005; Farias & Kittlein, 2008; Rocha *et al.*, 2008; Varela *et al.*, 2008) with a great diversity of prey, but based on similar main food items. The foraging strategies of these canids could be associated with the exploration of different microhabitats and thus they do not differ only with respect to their periods of activity (Vieira & Port, 2007; Di Bitetti *et al.*, 2009; Abreu *et al.*, 2010). This plasticity may be important for the survival of these species under the constant loss of their natural environments, persecution and other sources of mortality.

Acknowledgements

We thank João Luiz Cavaleiro Dias Ucha for the samples provided. We offer special thanks to José Paulo Souto Dias for helping to identify the birds and Gabriel Martini Lemos for identifying the plant species. We also thank two anonymous reviewers that improved substantial issues in the final version of this paper.

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