Diet and habitat use by two sympatric canids in the Pampas of South America

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Abstract
The crab-eating fox (Cerdocyon thous) and the Pampas fox (Lycalopex gymnocercus) are two canids with very similar food and habitat requirements, which live in sympatry across parts of their distributions. Here we describe the diet and habitat use of both canids in the Pampas biome. The study took place in southern Brazil from December 2012 to December 2013. Diet and habitat use analyses were based on fecal samples, footprints and direct visualizations. Diet overlap was measured using Pianka’s index, while habitat use was measured using presence records from three different environments; forests, edges and open areas. Both canids feed on invertebrates and vertebrates but have preferences for fruits, especially Syagrus romanzoffiana. Pianka’s index showed a high overlap of their diets throughout the year, with the exception of autumn. Regarding habitat use, C. thous preferred to inhabit forested areas while L. gymnocercus was more active in open areas. Our results showed that fruits were the most consumed food item in the Pampas biome. Our findings suggest that habitat use by these two canids is affected by seasonal variation in fruit abundance, but other factors, such as parental care, should be taken into account when explaining how they behave throughout the year.

Keywords
Canidae, Cerdocyon thous, feeding habits, foxes, fruit consumption, Lycalopex gymnocercus
Introduction

Mammals have different types of feeding behaviors and are adapted to fill a wide variety of ecological niches (Pough et al., 1993). Based on the variability of their diets, mammals are characterized as specialists or generalists (Jedrzejewska and Jedrzejewski, 1998). Generalist species consume a wide range of resources, whereas specialists tend to show a more restricted diet that is based on a certain type of resource (Elmhagen et al., 2000; Kaneko et al., 2006).

The Canidae family is a widely distributed group (Kleiman, 1967) with the capacity to adapt to a range of different environments (from forests to open areas) and to obtain resources using different strategies (Berta, 1982). In South America, the crab-eating fox (Cerdocyon thous) (Linnaeus 1766) and the Pampas fox (Lycalopex gymnocercus) (Fischer 1814) coexist over a large part of their distributions and have both similar body sizes and generalist diets (Emmons and Feer, 1997; Sillero-Zubiri et al., 2004). The distribution of C. thous extends from southern Colombia to Venezuela, through Paraguay and Uruguay to northern Argentina. Lycalopex gymnocercus presents a more restricted distribution, extending from southeastern Bolivia to southern Brazil and western Paraguay, Uruguay and northern Argentina (Berta, 1982; Redford and Eisenberg, 1992; Sillero-Zubiri et al., 2004; Lucherini and Vidal, 2008).

Although several studies have described the ecology of C. thous and L. gymnocercus separately, or have studied them as part of a group of sympatric canids (Juarez and Marinho-Filho, 2002; Bueno and Motta-Junior, 2004; Jácomo et al., 2004; Pedó et al., 2006; Vieira and Port, 2007; Varela et al., 2008; Castillo et al., 2011; Di Bitetti et al., 2009), only Vieira and Port (2007) and Di Bitetti et al. (2009) have conducted comparative studies of these two species. While these studies analyzed the canids in similar environments, including grasslands and forests, neither of them assessed the situation where both canids live in sympatry in the Pampas of South America. We quantified and compared C. thous and L. gymnocercus diets in the Pampas biome in southern Brazil and described their relative patterns of habitat use, testing if a large overlap in the diet of the species resulted in a differential use of the environment.

Material and methods

The study was conducted in the Pampas of southern Brazil, in the Horto Botânico Irmão Teodoro Luis (31°48’50”S, 52°25’55”W), which is a permanent federal conservation unit under the responsibility of the Universidade Federal de Pelotas (UF-Pel). It has an area of 100 ha and is situated in the municipality of Capão do Leão (Figure 1). The study area belongs to the geomorphological region of the Coastal Plain, in the state of Rio Grande do Sul, southern Brazil. The area is a mosaic landscape composed of fragments of Restinga forest, native fields, wetlands and an agricultural system mainly consisting of rice crops, pastures and Eucalyptus plantations. The region has a humid, temperate climate with a hot summer, corresponding to
Köppen’s Cfa climate zone (Köppen, 1948). During the study period the annual rainfall was 1,391 mm and the average temperature was 16.9°C. The mean temperature and precipitation of each season (calendar-based seasons) were 22.9°C and 421 mm, respectively, in summer, 17.6°C and 259 mm in autumn, 9.4°C and 227 mm in winter and 17.9°C and 483 mm in spring (Estação Agroclimatológica de Pelotas, 2015).

Data collection was performed for 12 months (December 2012 to December 2013) (52 weeks/year and 13 weeks/season). The total sampling effort was 352 hours/year and 88 hours/season. Transects were taken within the Restinga forest, grasslands and at the interface between the forest and grassland environments, which allowed us to evaluate the environment used by both species at a refined scale. To identify habitat use by *C. thous* and *L. gymnocercus*, we recorded the habitat type where fecal samples, direct visualizations and footprints of both canids were found during the surveys. The fecal samples were collected individually in labeled plastic bags for later evaluation. A total of 9 km of transects, corresponding to the sum of the transects depicted in Figure 1, were surveyed every week, always in the morning. Within the 9 kilometers of trails sampled 3 km were located within open areas, 3 km in forest areas and 3 km in edge areas. The distance of the trails was...
measured with a GPS at the beginning of the field work. The 9 kilometer trail was sampled on two consecutive days each week. On the first day the trails referring to the forest areas (3 km) were sampled, while on the second day the trails referring to the open and border areas (3 + 3 km) were sampled. Every week we walked exactly the same sections of these transects.

Fecal samples were examined under a stereomicroscope in the laboratory. The food items collected from the samples were separated, washed in running water and dried at 40°C in an oven for 24 hours. The food items were identified to the lowest possible taxonomic category with the help of specialists. We followed the studies of Martins (2005) and Quadros and Monteiro-Filho (2006) to identify the canid species using the microstructure and cuticle patterns of the hairs that were found inside the fecal samples due to the self-grooming behavior of the canids. Fecal samples that could not be identified due to lack of hair were discarded.

For each species, the relative frequency of each food item in the diet was calculated by dividing the number of fecal samples that contained a particular food item by the total number of feces (Dietz, 1984). This method was used to avoid an overestimation of small items, such as fruits with a large amount of seeds. In this scenario, only the presence of the item is accounted for in the feces, and its biomass is not considered.

We evaluated the diet similarity between the two canids using Pianka’s index, \( O_{jk} = \sum P_{ij} \sum P_{ik} / (\sum P_{ij}^2 \sum P_{ik}^2)^{1/2} \), which presents values ranging from zero (total niche separation) to one (total niche overlap). In this index, \( P_i \) corresponds to the frequency of occurrence of the item \( i \) for the species \( j \) and \( k \) (Pianka, 1973). The food niche breadth of each species was calculated, both per season and for the entire year, using Levins’ index: \( B = 1/\sum P_i^2 \), where \( P_i \) is the proportion of a specific food item found in the diet of a specimen (Levins, 1968). The Levins’ index was standardized according to Hurlbert (1978): \( B' = B - 1/(n-1) \), where \( B \) is the niche breadth value of the Levins’ index and \( n \) is the total number of food items consumed by the individual. Thus, values closer to 1 correspond to a generalist diet while values nearer to 0 indicate a specialist diet.

Footprints of both canids were identified using the guide called “Manual de rastros da fauna paranaense” (IAP, 2008). Each record indicates the presence of one individual and the habitat type where it was found. We classified the localities where the records were found as one of three different environments: forest, when the records were located in trails surrounded by arboreal vegetation which were at least 10m from the border of the fragment; forest edge, when records were found in trails bordering the forest fragment (<10m from the forests’ boarder); and grassland, when records were located in open areas at least 10m from the boarder of the forest fragment. The frequency of use of the three habitats by both species both throughout the year and between seasons was evaluated through the Pearson’s Chi-squared test. All indexes and statistical tests were calculated in the software R (R Development Core Team, 2008), using the \textit{spaa} package (Zhang, 2010).
Table 1. Number of samples and relative frequency of food items in the diet of *Cerdocyon thous* (C) and *Lycalopex gymnocercus* (L) in the Pampas of southern Brazil. Standard deviations and *P* values are from Pianka's index.

<table>
<thead>
<tr>
<th>Seasons</th>
<th>Food items</th>
<th>Summer</th>
<th>Autumn</th>
<th>Winter</th>
<th>Spring</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>C(37)</td>
<td>L(18)</td>
<td>C(28)</td>
<td>L(28)</td>
<td>C(16)</td>
</tr>
<tr>
<td>Fruits</td>
<td>Syagrus <em>romanzoffiana</em></td>
<td>2.7</td>
<td>5.6</td>
<td>35.7</td>
<td>14.3</td>
<td>56.2</td>
</tr>
<tr>
<td></td>
<td><em>Hovenia dulcis</em></td>
<td>-</td>
<td>-</td>
<td>14.3</td>
<td>3.6</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td><em>Ficus organensis</em></td>
<td>16.2</td>
<td>22.2</td>
<td>64.3</td>
<td>39.3</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td><em>Syzygium cumini</em></td>
<td>-</td>
<td>5.6</td>
<td>7.1</td>
<td>42.9</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td><em>Vitex montevizensis</em></td>
<td>37.8</td>
<td>27.8</td>
<td>-</td>
<td>3.6</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td><em>Eugenia uniflora</em></td>
<td>5.4</td>
<td>16.7</td>
<td>7.1</td>
<td>21.4</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Unidentified (n=8)</td>
<td>29.7</td>
<td>22.2</td>
<td>-</td>
<td>10.7</td>
<td>18.8</td>
</tr>
<tr>
<td>Animal items</td>
<td>Invertebrates</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Coleoptera</td>
<td>56.7</td>
<td>55.6</td>
<td>10.7</td>
<td>7.1</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>Orthoptera - Gryllidae</td>
<td>5.4</td>
<td>11.1</td>
<td>-</td>
<td>7.1</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Crustacea</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>Gastropoda - Pomacea</td>
<td>2.7</td>
<td>11.1</td>
<td>-</td>
<td>-</td>
<td>6.3</td>
</tr>
<tr>
<td>Vertebrates</td>
<td>Osteichthyces - Fish</td>
<td>8.1</td>
<td>-</td>
<td>3.6</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Amphibia - Anura</td>
<td>2.7</td>
<td>5.6</td>
<td>-</td>
<td>-</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Reptilia - Snakes</td>
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<td>5.6</td>
<td>-</td>
<td>3.6</td>
<td>12.5</td>
</tr>
<tr>
<td></td>
<td>Aves</td>
<td>-</td>
<td>-</td>
<td>3.6</td>
<td>-</td>
<td>6.3</td>
</tr>
<tr>
<td></td>
<td>Mammalia - Rodentia</td>
<td>10.8</td>
<td>-</td>
<td>7.1</td>
<td>3.6</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>Unidentified (n=1)</td>
<td>-</td>
<td>-</td>
<td>7.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Indexes</td>
<td>Levin</td>
<td>0.275</td>
<td>0.347</td>
<td>0.210</td>
<td>0.301</td>
<td>0.340</td>
</tr>
<tr>
<td></td>
<td>Pianka</td>
<td>0.943</td>
<td>0.719</td>
<td>0.942</td>
<td>0.987</td>
<td>0.938</td>
</tr>
<tr>
<td></td>
<td>Standard deviation</td>
<td>0.068</td>
<td>0.155</td>
<td>0.077</td>
<td>0.071</td>
<td>0.058</td>
</tr>
<tr>
<td></td>
<td><em>P</em></td>
<td>&lt; 0.05</td>
<td>&lt; 0.05</td>
<td>&lt; 0.05</td>
<td>&lt; 0.05</td>
<td>&lt; 0.05</td>
</tr>
</tbody>
</table>
Results

A total of 169 fecal samples were collected. Hundred were found to belong to *C. thous* and 69 were found to belong to *L. gymnocercus*. The fecal contents demonstrate that both species feed on fruits, invertebrates and vertebrates (Table 1). *Cerdocyon thous* presented a diet composed of fruits from 14 different species, of which *Syagrus romanzoffiana* (CHAM.) Glassman, *Ficus organensis* (Miq.) Miq. and *Vitex montevidensis* CHAM. were dominant. Coleoptera, Rodentia and Anura were the most consumed animal items. The diet of *L. gymnocercus* was composed of fruits from 13 species, with a dominance of *S. romanzoffiana*, *Ficus organensis* and *Syzygium cumini* (L.) Skeels (Table 1). Coleoptera, Rodentia and Anura remains were also found. The Levins’ index was similar for both species, showing a moderate niche breadth value for *C. thous* and *L. gymnocercus* throughout the entire year. However, when we analyzed seasonal variation the index showed that both *C. thous* and *L. gymnocercus* were fruit consumption specialists, but their frequency of item consumption changed among the seasons (Table 1). Pianka’s index showed high overlap between the diets of the two canids throughout the year (*O* = 0.938), as well as in the summer, winter and spring seasons. In the autumn the diets were distinct due to the preference of *F. organensis* and *S. romanzoffiana* by *C. thous*, while *L. gymnocercus* consumed *S. cumini*, *F. organensis* and *Eugenia uniflora* L. In addition, during the autumn *C. thous* consumed animal items at a higher frequency than *L. gymnocercus* did (Table 1).

We obtained 113 presence records of *C. thous* in the study area (45 records in the forest environment, 44 in the forest edge environment and 24 in the grassland

![Figure 2](image-url).

**Figure 2.** Habitat use by *Cerdocyon thous* and *Lycalopex gymnocercus* across the three types of vegetation, in the Pampas of southern Brazil, shown for the entire year. The value of the Y axis is a percentage of the total number of records.
environment). Of these records of *C. thous*, 100 were obtained from fecal samples, two came from direct visualizations of the canid and 11 were from footprints. For *L. gymnocercus*, we obtained 83 records (17 in the forest environment, 32 in the forest edge environment and 34 in the grassland environment; Figure 2). Of these, 69 were from fecal samples, one came from direct visualization of the canid and 13 were from footprints. *Cerdocyon thous* used forest areas with a high frequency, while *L. gymnocercus* was more active in grasslands ($X^2 = 13.92$, $df = 6$, $P = 0.001$; Figure 2). Our results show that both species use forest edge environments similarly.

Our results also indicated a seasonal variation in habitat use. *Cerdocyon thous* used forest areas more frequently in summer and spring, while in autumn and winter it was more active in the forest edge environment ($X^2 = 24.23$, $df = 6$, $P < 0.001$; Figure 3). We did not find evidence for a seasonal change in the pattern of habitat type use for *L. gymnocercus* ($X^2 = 8.59$, $df = 6$, $P = 0.198$; Figure 4).

**Discussion**

The diets of *C. thous* and *L. gymnocercus* presented a great overlap, with both species consuming a wide variety of food items. While other authors have emphasized the importance of fruits in the diets of these foxes (Facure and Giaretta, 1996; Facure and Monteiro-Filho, 1996; Facure et al., 2003; Rocha et al., 2008), our study shows that this importance is maintained throughout the whole year. A probable explanation for this behavior is that there is a constant source of fruits available throughout the year in the forested areas. This situation occurs because of the different life cycles of the plant species, since for example *S. romanzoffiana* produces a large quan-

![Figure 3](image)

**Figure 3.** Seasonal variation in habitat use by *Cerdocyon thous* across the three types of vegetation in the Pampas of southern Brazil. The value of the Y axis is a percentage of the total number of records.
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quantity of fruit during winter and spring. Therefore, fruits end up being an attractive and abundant resource for both canids throughout the entire year.

Levins’ index demonstrated that both species present opportunistic behaviors. *Cerdocyon thous* and *L. gymnocercus* exhibited very similar food behaviors in each season. During the summer the high diversity of consumed items was probably due to the lack of their main food resource, *S. romanzoffiana*, which does not fruit during this period. However, during the other seasons the consumption of *S. romanzoffiana* was high while the proportion of other resources in the canids’ diet varied. In autumn *C. thous* and *L. gymnocercus* exhibited different diets, which resulted in a decrease in overlap of their food niches. It is clear that *S. romanzoffiana* is a very important resource for both canids due its high consumption. Due the great amount of its seeds found in good condition in the fecal samples, it is likely that *C. thous* and *L. gymnocercus* are dispersers of the plant in this area. Similar results already demonstrated the high consumption of *S. romanzoffiana* in the diet of canids (Rocha *et al*., 2008), confirming how important this resource is for both species.

The habitat use of *C. thous* has always been associated with forest environments in the literature, but it is noted that it also exhibits flexibility due to its use of open areas. On the other hand, *Lycalopex gymnocercus* is more strongly associated with open areas (Langguth, 1975; Redford and Eisenberg, 1992; Sánchez-Lalinde and Pérez-Torres, 2008). Our results showed that both canids used the three habitat types...
differentially, supporting the information in the literature. Similar results where demonstrated by Vieira and Port (2007) and Di Bitetti et al. (2009).

Considering the premise that feeding behavior influences habitat use, one plausible explanation for the high use of forest areas by *C. thous* in the summer is the abundant quantity of mature fruits within the forest fragments. In addition, there were no trees of *S. romanzoffiana* (one of their main diet constituents) fruiting in the area during the summer, suggesting the need for *C. thous* to spend more time inside forest areas foraging for available resources. On the other hand, *L. gymnocercus* preferred forest edges and open areas during the same season. By contrast, in autumn and winter there was a scarcity of fruits across the whole study site. However, *S. romanzoffiana* began to fruit and thus became a very attractive resource. In addition to this, there was a great concentration of *S. romanzoffiana* trees in the forest edges, which makes this environment very important for both foxes during these seasons. These ideas originated from phenological observations made during the study period, but the lack of a phenological monitoring in other studies that address the diet of canids unfortunately does not allow us to compare our observations with data from other localities.

Habitat utilization showed that *C. thous* and *L. gymnocercus* exhibited the highest number of records in forest and open areas, respectively, during spring. This situation probably occurred because during this season both species produce offspring (Macdonald, 1983; Eisenberg and Redford, 1999). Therefore, it is plausible that both species spend more time caring for their pups in their dens, which are located in their preferential environments; forest areas for *C. thous* and open areas for *L. gymnocercus*. In fact, this behavior was observed in the records, as two *C. thous* dens containing pups were located in the forest area while a female *L. gymnocercus* and her offspring were recorded in the open area.

Our results suggest that both canids present omnivorous diets, with a high consumption of fruits and small animals. We also discovered a higher relative frequency of fruits in the diets of both species than previously recorded in other studies. In addition, we demonstrated that both canids use the habitat types in the study area to different degrees.

**Acknowledgments**

We thank E. Zefa, J. E. F. Dornelles and C. J. Drehmer for their help in the identification of animal remains. We thank R. Lüdtke for her help in the identification of plant items and for helping us find references. We thank the two anonymous reviewers who helped to improve this work. We also thank F. D. Kober and L. Nunes for their help during field work. We thank EMBRAPA Clima Temperado for authorizing the study in the area and finally, we would like to thank FAPERGS for the scholarship given to L. M. V. Porto during this research.
References


**Resumo**

Fatores ambientais modulando a distribuição batimétrica dos grupos demográficos de *Achelous spinimanus* (Crustacea)

O graxaim-do-mato (*Cerdocyon thous*) e o graxaim-do-campo (*Lycalopex gymnocercus*) são dois canídeos com exigências ecológicas similares, vivendo em simpatria em parte de suas distribuições. Aqui descrevemos a dieta e o uso de habitat das duas espécies no bioma Pampa. O estudo foi conduzido no sul do Brasil, entre dezembro de 2012 e dezembro de 2013. As análises de dieta e habitat foram baseadas em amostras fecais, pegadas e visualizações das espécies. A sobreposição das dietas foi medida usando o índice de Pianka, enquanto que a utilização dos habitats foi medida usando registros de presença das espécies nas três diferentes áreas, floresta, borda e áreas abertas. Ambas as espécies se alimentam de invertebrados e vertebrados, mas têm preferência por frutos. O índice de Pianka demonstrou uma alta sobreposição das dietas ao longo do ano. *Cerdocyon thous* prefere utilizar áreas florestais, enquanto *L. gymnocercus* prefere áreas abertas. Verificamos que, no bioma Pampa, frutos são os itens mais consumidos. Além disso, a utilização de habitat por ambas as espécies é influenciada pela variação da abundância de frutos, mas outros fatores como cuidados parentais devem ser levados em consideração para explicar o comportamento das espécies ao longo do ano.

**Palavras-chave**