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Trophic relationships of sympatric small carnivores in fragmented landscapes of southern Brazil: niche overlap and potential for competition

Abstract: Between 2000 and 2010, digestive tracts collected from carnivore carcasses found in southern Brazil were analyzed to determine the frequency and proportion of items constituting the diets of each species. Material was collected and analyzed from 194 animals of 10 species: *Cerdocyon thous*, *Lycalopex gymnocercus* (Canidae), *Procyon cancrivorus* (Procyonidae), *Galictis cuja* (Mustelidae), *Conepatus chinga* (Mephitidae), *Leopardus colocolo*, *Leopardus geoffroyi*, *Leopardus guttulus*, *Leopardus wiedii*, and *Puma yagouaroundi* (Felidae). Most of these species are sympatric, which makes them potential competitors when sharing, to a greater or lesser degree, the same resources. The food niche breadth was relatively narrow, demonstrating that even generalist species, such as the crab-eating raccoon, used food resources rather unequally. An extensive overlap (>90%) in food niches was found among the cat species, the grison, and the Pampas fox, which had diets based on rodents. Crab-eating raccoons occupied a different food niche, based on aquatic or semiaquatic prey and fruits. *Conepatus chinga* was unique in exploiting arthropods and insect larvae as basic dietary items.

Keywords: food habits; Neotropical region; niche breadth; niche overlap, sympatric species.

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Introduction

Southern Brazil is composed of a mosaic of Pampas grasslands in the south and Atlantic Forest formations in the north. The eastern, coastal part of Rio Grande do Sul State is covered by pioneer vegetation in association with a series of coastal lagoons [Instituto Brasileiro de Geografia e Estatística (IBGE) 1986]. This mixture of influences from tropical and temperate regions makes southern Brazil a distinctive environment, representing the southern limit of several species and the only known location in the country for others. However, this region is also one of the most fragmented parts of Brazil, with the few protected areas comprising only 2.6% of the total area of the state of Rio Grande do Sul (Backes 2012).

Animal communities in southern Brazil suffer practically no influences from top predators. The jaguar *Panthera onca* (Linnaeus, 1758) is restricted to one protected area, while the maned wolf *Chrysocyon brachyurus* (Illigier, 1815) was only recently rediscovered (Pinto and Duarte 2013) and is probably very close to extinction. The giant river otter *Pteuronura brasiliensis* (Gmelin, 1788) disappeared from this region in the 1950s, as has the bush dog *Speothos venaticus* (Lund, 1842), which probably occurred in southern Brazil and northeastern Argentina in the past (Fontana et al. 2003). Mountain lions *Puma concolor* (Linnaeus, 1771) persist in some parts of the region, although probably in very low abundance (Mazzolli 1993, Castilho et al. 2010). Thus, this assemblage of carnivores probably lives in a state of “mesopredator release” (Crooks and Soulé 1999), most likely without the effect of predators regulating their populations. This theory predicts that top predators can regulate the abundance of mesopredators, affecting the prey base as well. The absence of top predators in the environment, then, can lead to an explosion in the numbers of smaller predators, placing increased pressure on their prey. Another possible consequence of mesopredator release, usually not taken into account, is the potential for increased competition caused by an increase in predator abundance and the reduction of prey numbers.

Sympatry of carnivores is mediated by several ecological factors that allow related species to coexist. Several studies have indicated that one of the most important features in ecological separation is related to dietary differences (Konecny 1989, Ray and Sunquist 2001, Juarez and Marinho-Filho 2002). These differences may not be specifically associated with how items are consumed, but with what frequency, and with the energy content of each item. Among sympatric carnivores, differences in size predators are usually correlated to size of their prey (Rosenzweig 1966). However, similar predators may coexist due to differential predation of different preys (Powell and Zielinski 1983). Other features, such as the differential use of microhabitats and time partitioning, also have great importance in allowing the coexistence of sympatric species (Vieira and Port 2007, Di Bitetti et al. 2009, Faria-Corrêa et al. 2009). However, knowledge of niche breadth and the degree of overlap of food habitats among sympatric species is one of the first steps in understanding the ecological structures of communities (Zapata et al. 2007).

The concept of guild was created to define groups of species that use the same resources in a similar way (Terborgh and Robinson 1986). This procedure simplifies the analysis of food webs, grouping species according to similarities in feeding habit. These similarities can be interpreted as potential for competition, but never as a synonym, as many other factors are involved in the competition theory. One way to identify the existence of guilds is by analyzing the niche overlap among sympatric species (Pianka 1980).

In this study, we describe the general food habits of 10 carnivores, analyze the niche breadth and niche overlap between sympatric species, determine the guild structure pattern, and discuss the potential for competition among these species. Our hypothesis is that different carnivore species are using different food sources, to avoid competition, and we will observe moderate diet overlap.

Materials and methods

Study area

Southern Brazil comprises three states, of which Rio Grande do Sul is the southernmost; the region is limited to the west by Argentina, the south by Uruguay, and the east by the Atlantic Ocean. Its position confers unique characteristics on the region, which represents the southern limit of the Atlantic Forest and the northeastern limit of the Pampas grassland. The coastal region is a strip ca. 50 km wide that contains a succession of lagoons, with typical vegetation called Pioneer Formations. Finally, in the northeastern portion of the state are open fields in the highlands of the Atlantic Forest, at altitudes of 800–1200 above sea level. All these environments, including the transition zones, occur in an area of <300,000 km^2. The vegetation of Rio Grande do Sul State comprises two main vegetation categories: the grassland formations that predominate in the southern half of the state and the forested vegetation covering the northern half. The grassland formations include two specific regions: steppe and steppical savanna. The forested formations included the ecoregions of dense and mixed ombrophilous forests, and deciduous and semideciduous seasonal forests, all associated to Atlantic Forest Biome (IBGE 1986).

Diet analysis

Between 2000 and 2010, we collected the digestive tracts from road-killed carnivores along highways of Rio Grande do Sul. Stomachs and intestines were collected only from fresh carcasses (<48 h), and stored in 70% ethanol. At the laboratory, digestive tracts were opened to remove all contents, which were washed in running water over mesh with openings of about 0.1 mm diameter in order to remove soluble parts. The macroscopic residue was analyzed and identified to order level, comparing it to a reference collection and general literature.

For diet analysis, we grouped trophic items into 11 main groups, which were then subdivided into 33 groups corresponding to main orders found into each group: mollusks, insect larvae, adult insects and chelicerates, crustaceans, fish, amphibians, reptiles, birds, mammals, fruits, and vegetal material (basically grass leaves). The representation of each food type in the diet was expressed as frequency of occurrence, FO (the percentage of stomachs that contained that item in relation to the total number of examined stomachs×100); and percentage of occurrence, PO (the frequency of each food item divided by the sum of the frequency of all items×100). The FO% indicates how common an item was in the diet, while the PO% indicates the relative importance of an item in the diet. We also estimated the relative biomass of each item present in the diet. The percent volume of each prey type in a particular stomach was estimated by eye [following Kruuk and Parish (1981) and Ray and Sunquist (2001)] and scored on a nine-point scale: 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 calculations, 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%, 8=99%). This analysis was done to prevent some possible biases in the interpretation of the other indices (FO and PO), such as the constant presence of a small item with insignificant contribution in terms of biomass.

Food niche breadth was calculated using Levins' (1968) index. The measurement of food niche breadth was standardized on a scale ranging from 0 to 1 (Cowell and Futuyama 1971). A value close to 1 indicates a generalist habit, meaning a more equally distributed diet (i.e., prey items are consumed in more equal proportions to one another). A value close to 0 means that a very few prey categories are eaten in greater frequency, while most of the prey categories are eaten in lower frequency, suggesting a specialized diet. The overlap, or similarity of food habits between pairs of species, was calculated using the Pianka index (Pianka 1973), defining values ranging from 0 (total differentiation of food habits) to 1 (total overlap of food niches). The raw data for these analyses consist of the proportion in the diet of each food eaten, calculated from volumetric measurements for the 33 prey items. This is because quantification methods based on the biomass of prey are more appropriate to estimate trophic relationships among vertebrate predators when prey sizes are variable (Fedriani and Travaini 2000). We compared the niche overlap only for species with at least 10 stomach samples.

The matrix of biomass percentage of the 11 main food groups of all species was clustered by the unweighted pair group method with arithmetic mean (UPGMA) technique, using the Morisita index, to identify which groups of species were similar in terms of food habits. We adopted a similarity of 50% as a cutoff point in order to determine a guild; this is the same value adopted by Fedriani and Travaini (2000), and similar to the value adopted by Zapata et al. (2007). We also identified the major axes of dietary variation based on 11 main groups of prey items among carnivore species, using correspondence analysis (following Ray and Sunquist 2001).

Results

We collected 198 digestive tracts of 10 carnivore species: two Canidae, *Cerdocyon thous* (Linnaeus, 1766) and *Lycalopex gymnocercus* (G. Fischer, 1814); one Procyonidae, *Procyon cancrivorus* (G. Cuvier, 1798); one Mustelidae, *Galictis cuja* (Molina, 1782); one Mephitidae, *Conepatus chinga* (Molina, 1782); and five Felidae, *Leopardus colocolo* (Molina 1782), *Leopardus geoffroyi* (d'Orbigny and Gervais, 1844), *Leopardus guttulus* (Schreber, 1775), *Leopardus wiedii* (Shinz, 1821), and *Puma yagouaroundi* (E. Geoffroy, 1803). We found 16 digestive tracts that were totally empty. Another 17 contained vestiges of food items, such as a few hairs or small fragments of bones and exoskeleton. We therefore restricted our analyses to 165 digestive contents, which contained enough residues to allow identification of the prey (to order level), and to estimate the proportion of biomass ingested. The number of stomachs from each species was variable, as well as the proportions of items that composed each diet. In these digestive tracts, we identified 520 items divided into 33 groups, summarized in Table 1.

Only four main groups of food items were present in all diets: insects, birds, mammals, and plant material. Insects, although they were present in the stomach contents of all carnivores analyzed, were important in terms of biomass only for *Conepatus chinga*. For other species, insects were eaten by few individuals, contributing only a small amount to biomass ingested (Table 1). Birds were present in intermediate (or low) proportions, usually representing <15% of biomass ingested. Mammals, on the other hand, were highly important in the diets of most species, except *C. chinga* and *Procyon cancrivorus*, representing a mean of 75% biomass ingested by the other eight species (Table 1). Grass was found in all diets, occurring at frequencies of 30–77% of the stomachs, but comprised <1% of biomass intake for all species.

The niche breadths of all species were relatively narrow (Table 2), indicating a non-equivalent use of food resources. The broadest niche was found for *Procyon cancrivorus*, followed by *Cerdocyon thous*, *Conepatus chinga*, and *Lycalopex gymnocercus* with intermediate values. The narrowest niche was found for the cat species and for *Galictis cuja*. There was a small niche overlap between *C. chinga* and all species, suggesting a different food source. The same occurred with *P. cancrivorus*, which showed the smallest mean overlap (0.18±0.18). Overlap in the feeding habit of *P. cancrivorus* was just as intermediate when paired with *C. thous* and *L. gymnocercus*. The feeding habits of *C. thous* and *L. gymnocercus* overlapped extensively with each other, as well as with *G. cuja*. The cat species showed the largest overlap in food habits of all pairs of species, with values of >90% similarity, as well with *L. gymnocercus*.

These 10 carnivore species can be combined into three groups with similar food habits (Figure 1), which can be interpreted as guilds. These divisions also become clear in the correspondence analysis (Figure 2): *Conepatus chinga* is associated with insects; *Procyon cancrivorus* is associated with fruits, mollusks, crustaceans and fish; cats and *Galictis cuja* are associated with mammals. Foxes are grouped in the cats/grison group, but in an

Table 1: Frequency of occurrence (FO), percentage of occurrence (PO), and proportional volume (% vol; all values expressed in%) of 11 prey classes in diets of eight carnivore species in southern Brazil.

Prey class		*Leopardus colocolo* (2)	*Leopardus geoffroyi* (14)	*Leopardus guttulus* (10)	*Leopardus wiedii* (3)	*Puma yagouaroundi* (10)	*Cerdocyon thous* (26)	*Lycalopex gymnocercus* (18)	*Galictis cuja* (38)	*Conepatus chinga* (27)	*Procyon cancrivorus* (17)
Mollusks	FO	–	–	–	–	–	–	–	–	–	41.2
	PO	–	–	–	–	–	–	–	–	–	12.5
	% vol	–	–	–	–	–	–	–	–	–	7.1
Insect larvae	FO	–	–	10.0	–	–	11.5	16.7	2.6	81.5	5.9
	PO	–	–	4.8	–	–	3.0	5.4	1.5	29.7	1.8
	% vol	–	–	0.1	–	–	0.7	1.1	0.1	44.7	0.1
Insects and Chelicerates	FO	–	21.4	20.0	–	10.0	69.2	55.6	2.6	81.5	47.1
	PO	–	11.1	9.5	–	4.3	18.2	17.9	1.5	29.7	14.3
	% vol	–	0.1	10.2	–	0.1	3.4	12.6	0.1	27.2	5.0
Crustaceans	FO	–	–	–	–	–	3.8	–	–	–	52.9
	PO	–	–	–	–	–	1.0	–	–	–	16.1
	% vol	–	–	–	–	–	0.1	–	–	–	12.8
Fish	FO	–	–	–	–	–	7.7	–	2.6	–	29.4
	PO	–	–	–	–	–	2.0	–	1.5	–	8.9
	% vol	–	–	–	–	–	0.8	–	1.0	–	11.6
Amphibians	FO	–	7.1	–	–	–	53.8	22.2	18.4	37.0	52.9
	PO	–	3.7	–	–	–	14.1	7.1	10.8	13.5	16.1
	% vol	–	7.1	–	–	–	12.2	5.1	6.1	10.5	23.6
Reptiles	FO	–	7.1	–	–	10.0	19.2	11.1	13.2	11.1	–
	PO	–	3.7	–	–	4.3	5.1	3.6	7.7	4.1	–
	% vol	–	0.6	–	–	6.3	6.2	2.6	8.3	2.4	–
Birds	FO	–	21.4	10.0	–	40.0	26.9	16.7	15.8	3.7	17.6
	PO	–	11.1	4.8	–	17.4	7.1	5.4	9.2	1.4	5.4
	% vol	–	6.8	3.8	–	22.2	8.8	7.7	13.7	0.1	6.6
Mammals	FO	100	92.9	90.0	100	90.0	76.9	77.8	78.9	18.5	17.6
	PO	66.7	48.1	42.9	50.0	39.1	20.2	25.0	46.2	6.8	5.4
	% vol	99.0	83.7	84.3	99.0	68.3	46.0	53.2	69.9	14.2	6.5
Fruits	FO	–	–	–	–	–	42.3	38.9	–	–	41.2
	PO	–	–	–	–	–	11.1	12.5	–	–	12.5
	% vol	–	–	–	–	–	24.3	12.5	–	–	28.7
Plant material	FO	50.0	42.9	50.0	100	80.0	69.2	72.2	36.8	40.7	23.5
	PO	33.3	22.2	23.8	50.0	34.8	18.2	23.2	21.5	14.9	7.1
	% vol	0.5	0.4	0.5	0.5	0.4	0.5	0.5	0.2	0.2	0.3

Table 2: Niche breadths,[a] standardized niche breadths (Bsta),[b] food niche overlap, and results of Mantel test (p-Values) between pairs of eight carnivores in southern Brazil.

Carnivores species	*Leopardus geoffroyi* (14)	*Leopardus guttulus* (10)	*Puma yagouaroundi* (10)	*Cerdocyon thous* (26)	*Lycalopex gymnocercus* (18)	*Galictis cuja* (38)	*Conepatus chinga* (27)	*Procyon cancrivorus* (17)	Mean food niche overlap (±SD)	Niche breadth (B)	Standardized niche breadth (Bsta)
Leopardus geoffroyi	×								0.69±0.35	1.39	0.04
Leopardus guttulus	–	×							0.63±0.38	1.50	0.04
Puma yagouaroundi	0.94	0.92	×						0.69±0.35	2.46	0.09
Cerdocyon thous	0.79	0.76	0.79	×					0.71±0.21	4.58	0.25
Lycalopex gymnocercus	0.93	0.92	0.92	0.97	×				0.75±0.29	4.06	0.19
Galictis cuja	0.98	0.96	0.97	0.81	0.94	×			0.71±0.35	2.69	0.09
Conepatus chinga	0.23	0.21	0.21	0.26	0.29	0.23	×		0.23±0.04	4.23	0.23
Procyon cancrivorus	0.06	0.01	0.08	0.56	0.30	0.10	0.16	×	0.18±0.18	6.01	0.45

[a]Niche breadth (*B*) was calculated for 34 prey types, ranging from 1 (the narrowest niche) to 34 (the broadest niche); [b]*Bsta* was calculated for the 11 main groups of prey. –, do not occur in sympatry.

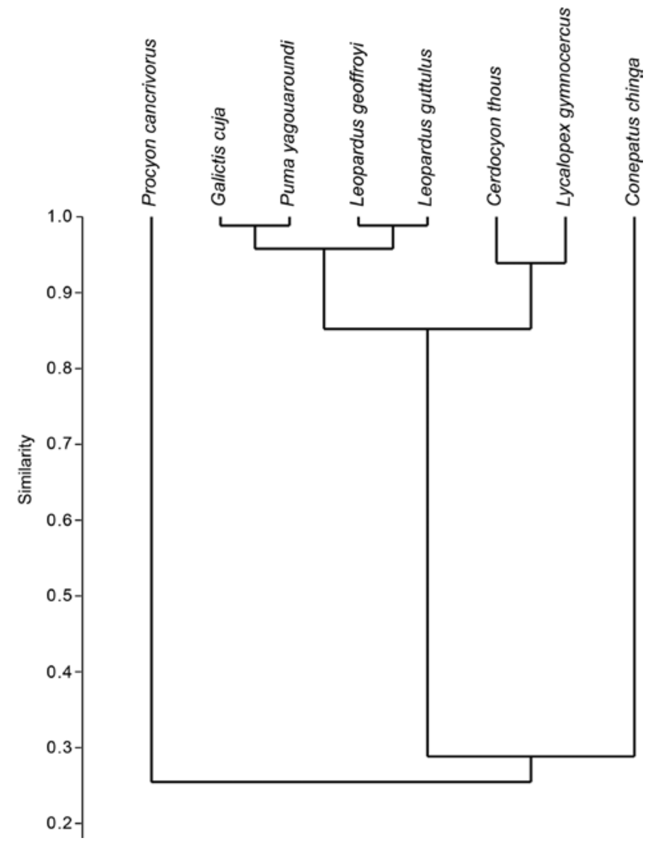

Figure 1: Analysis of similarity (Morisita index) in the diets of eight carnivore species of southern Brazil, calculated by the biomass percentage of 11 main food groups.

intermediate position, influenced by the consumption of fruits, amphibians, and mammals. Therefore, three basic guilds have been determined: insectivores, omnivores, and carnivores/frugivores.

Discussion

The trophic guild relationships analyzed here showed an interesting pattern, with several species using very similar food resources. This result was contrary to our expectations, and shows that small carnivores present high potential to competition. The great overlap in food habits observed among cat species, grison, and canid species occur because of the high dependence of rodent consumption.

The cat species (*Leopardus geoffroyi*, *Leopardus guttulus*, and *Puma yagouaroundi*) fed almost exclusively on rodents, as did *Galictis cuja* and *Lycalopex gymnocercus*. As a result, niche overlaps among these species were very high, with a 94.3% mean similarity. The Pampas

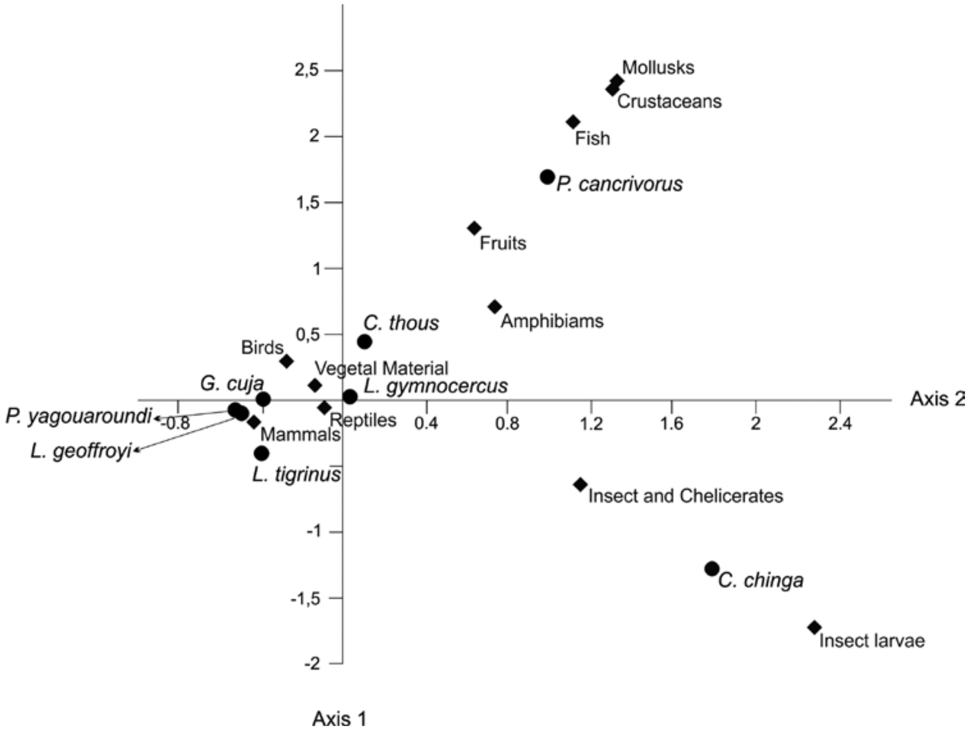

Figure 2: Correspondence analysis of the main food groups (lozenges) in the diets of eight carnivores (circles) of southern Brazil. The first axis accounts for 44.9% of the total variation (84.4%); the second axis accounts for 39.5%.

fox (*L. gymnocercus*) showed a high overlap (97%) in its feeding habits with the related species *Cerdocyon thous*. Altogether, these six species form a large guild (dependent on the large-scale rodent consumption) that can be considered here as "truly carnivorous." The degree of similarity found in this study shows the need for deeper analysis, probably to species level, as an attempt at understanding how these animals share food resources. Obviously, other ecological and behavioral factors play important roles in the coexistence of these species, such as time partitioning and the use of microhabitats (for living or foraging) on the landscape scale. However, this large group had at least one important subdivision, which is the grouping of foxes in a separate clade. This division was clearly associated with the consumption of fruits and amphibians by these fox species, differing from the grison and the cat species. Therefore, it is possible to identify two guilds: strictly carnivorous (composed of *G. cuja* and the cat species), and carnivorous/frugivorous (composed of the fox species). The consumption of mammals, especially rodents, by small cats follows the general pattern observed in several studies (see Kruuk 1986) and is in accordance with the suggestion of Van Valkenburgh (1989) that cats specialize in the predation of mammals. However, very few studies have addressed the diets of small cats living in sympatry and their relationships to each other, such as Silva-Pereira et al. (2011).

Leopardus geoffroyi is probably the best known among the small cats studied here. Studies in Argentina have reported diets based on small mammals, the most frequent item preyed upon by three groups, although "large mammals" and "large birds" are the most important categories in terms of biomass (Manfredi et al. 2004), as also observed in coastal southern Brazil (Souza and Bager 2007). In accordance with our data, both these studies reported the consumption of fish, amphibians, reptiles, and insects in low proportions. Therefore, Geoffroy's cat seems to have a diet based on small rodents, the most common item in practically all areas where it has been studied (Bisceglia et al. 2011). This species shows some association with wetlands, such as marshes, riparian forests, and even rice fields (personal observation), which explains the occurrence of several aquatic and semiaquatic prey, including fish, amphibians, water snakes, aquatic birds, and mammals associated with marshes. The use of this specific habitat can help explain its coexistence with other carnivores that show high niche overlap.

The jaguarondi diet described in this study is very similar to previous reports (Manzani and Monteiro-Filho 1989, Oliveira 1994, Cheida et al. 2006, Silva-Pereira et al.

2011), including the preferential consumption of small mammals, birds, and reptiles. As in Belize (Konecny 1989), mammals were the most important item, representing almost 70% of biomass ingested, followed by birds, corresponding to >20% of biomass. The frequency of mammals is also similar to that described by Silva-Pereira et al. (2011) in Brazil.

Other cats, all members of genus *Leopardus* (*L. guttulus*, *L. wiedii*, and *L. colocolo*) had diets based almost exclusively on rodents. The dominance of rodents in the cat diet differs from the study by Wang (2002), who reported diets with a conspicuous presence of marsupials, but is congruent with the studies by Silva-Pereira et al. (2011). Although we collected few samples of the margay and the Pampas cat, only *L. guttulus* included birds in its diet, although in a low proportion. This is remarkable, as all previous studies cited birds as an important food resource for small cats. Interestingly, the contents of one sample from *L. guttulus* consisted exclusively of butterflies (Lepidoptera). The consumption of insects by the little spotted cat, which is presently considered two species, *L. guttulus* in the south and *L. tigrinus* in the north (Trigo et al. 2013), was also reported by Olmos (1993) from the Caatinga. However, as noted by Oliveira (1994), insects probably contribute little in terms of energy.

In southern Brazil, our data suggest that *Galictis cuja* bases its diet on rodents, although it includes other small vertebrates such as amphibians, reptiles, and birds, as well as insects in low proportions. Studies from Argentina describe the grison's diet as being based on rodents and introduced lagomorphs, which comprise >95% of the biomass intake (Delibes et al. 2003). Similarly, Zapata et al. (2005) found a diet based on rodents (56% of biomass) and lagomorphs (34.5%) from the southern limit of the species' distribution, while Ebensperger et al. (1991) described *G. cuja* as preying on rabbits, rodents, and small marsupials in central Chile. However, in our study, we found no evidence that the grison consumed lagomorphs, despite the high abundance of *Lepus europaeus* (Pallas, 1778) in some parts of Rio Grande do Sul (Kasper et al. 2012a).

The overlap of food niches between *Galictis cuja* and the small cats found here is remarkable, with indices of up to 95% similarity. However, these species probably use different foraging strategies. While cats in general are known for ambushing their prey, grisons are known locally for their behavior of tirelessly following *Cavia* spp. (Pallas, 1766), sometimes for hours (personal observations). Surprisingly, the majority of rodents found in the stomach contents were members of Cricetidae, mostly nocturnal rodents. This is interesting because in southern Brazil, *G. cuja* is mainly diurnal (personal observations). These facts suggest that the foraging strategies of this species are associated with locating and attacking den sites and nests of its prey. This hypothesis, also suggested by Delibes et al. (2003), is supported by some stomach contents that included rat pups only a few days old.

The dependence on mammal consumption extended to the foxes, especially *Lycalopex gymnocercus*. About 50% of the biomass intake of this species consisted of mammals, in contrast to the other species, which were more dependent on rodents (mean of 84%). As a result, we have interpreted foxes to be separate from the strict carnivores, as their diets included large amounts of other food sources. The crab-eating fox showed a slightly wider niche than *L. gymnocercus*, including more items, which were consumed more equitably. The Pampas fox took more insects/chelicerates than *Cerdocyon thous*, as well as rodents and carcasses. On the other hand, *C. thous* consumed more amphibians and reptiles, and much larger amounts of fruit than *L. gymnocercus*. We classified the foxes as carnivorous/frugivorous in southern Brazil, because their diet was dominated by rodents (although not as exclusively as cats and the grison), and included fruits, which were very important in some areas. We did not classify foxes as omnivorous because the proportions of food items consumed were very unequal, indicating a much narrower niche than the crab-eating raccoon. The proportion of insects eaten by the Pampas fox was larger than all other carnivores in our data, except for *Conepatus chinga*, which specialized in this item, as discussed below. Amphibians are rarely cited in the diet of this species (Schalk and Morales 2012), but occurred in intermediate frequency in our study. This may be associated with the relatively dry and cold habitats where most studies on *L. gymnocercus* have been conducted. Fruits were frequent in the diet of the Pampas fox, but comprised only a small proportion of the biomass. Fruits are sometimes the most important component in the diet of this species, as observed by Varela et al. (2008), but in our study are less frequent than observed in the diets of *C. thous* and *Procyon cancrivorus*.

In the diet of the crab-eating fox, fruits are an important resource as cited by many investigators throughout the species' range, although there is a wide variation in the consumption rate (Facure et al. 2003, Rocha et al. 2004, Pedó et al. 2006). This species is an opportunistic predator with a diet that varies according to availability, seasonality, and social aspects (Courtney and Maffei 2004). Some studies from southern and southeastern Brazil exemplify the plasticity of food habits of this fox. In our study, only *Procyon cancrivorus* ate fruits in a higher frequency than *Cerdocyon thous*.

Analysis of diet similarity and niche breadth revealed that *Procyon cancrivorus* had the widest niche breadth among the species studied here. The crab-eating raccoon had a diet very different from the other species, with the lowest consumption of mammals, as also found elsewhere (Santos and Hartz 1999, Gatti et al. 2006, Pellanda et al. 2010). For this reason, the species is alone in a guild with the smallest mean overlap in feeding habits. The crab-eating fox showed a diet relatively similar (0.56%) to the crab-eating raccoon, but much less so than previously reported by Gatti et al. (2006), who found 96% similarity between the two. Our data showed a higher consumption of amphibians and crustaceans than previously reported. We also found a significant consumption of mollusks, which is probably even more important than estimated. This prey group was identified only by the operculum, and contributed little biomass using the method adopted here. Therefore, the crab-eating raccoon can be considered omnivorous, as it consumes a wide variety of food resources. This diet is associated with wetland habitats, as aquatic animals, such as mollusks, crustaceans, fish, and amphibians, represented >55% of the biomass intake.

Another guild is represented by *Conepatus chinga*, which has a diet based on insect larvae and other arthropods. Many investigators combine these two items under the grouping of insects; however, we prefer to separate them into larvae and insects (adults), as they represent two different ways of foraging. The foraging behavior of Molina's hog-nosed skunk in southern Brazil seems to be based on active searching for insect larvae. The skunk continually moves through open fields, stopping every few meters to dig small holes to catch larvae and insects buried underground (personal observations). The consumption of insects and insect larvae was reported in all previous studies (Travaini et al. 1998, Donadio et al. 2004, Medina et al. 2009, Peters et al. 2011), with frequencies of occurrence >80%. However, the importance of insect larvae estimated in these studies varies from insignificant (Travaini et al. 1998) to being the main prey (Medina et al. 2009). In southern Brazil, insect larvae represent the main food item of the skunk's diet, responsible for almost 50% of biomass intake. Our data are congruent with the study of Peters et al. (2011) on the feeding habits of *C. chinga* in southern Brazil, which also cited insects (mostly Coleoptera and Orthoptera) as the most important item of the skunk diet.

Although they forage for insects and larvae, skunks are clearly opportunistic predators, and several other food items may be included in the diet, such as mammals, reptiles, and amphibians. Vertebrate prey occurs mainly in low frequency compared to arthropods, but probably has great importance in terms of biomass and energy gain. The foraging for vertebrates may not cost more energy than is usually spent in the search for arthropods, as it probably does not involve the pursuit of prey, but only locating it in burrows or discovering inactive prey (in the case of reptiles and amphibians). Skunks also take advantage of some temporarily available resources, such as eggs of freshwater turtles and ground-nesting birds. We found no evidence of consumption of eggs, but they probably represent an important energy source in some regions, such as the coastal regions of southern Brazil and Uruguay, where Gonçalves et al. (2007) reported the predation of 98% of turtle nests, 31% of them by *Conepatus chinga*. In a study of the spatial ecology of *C. chinga*, Kasper et al. (2012b) recorded several instances of skunks preying on turtle and bird nests to eat eggs, mainly in summer.

Several species based their diets on the same specific item, rodents. This was not expected, as it would be assumed that specialist species specialize in different food resources to avoid competition. The coincident use of the same resources may be associated with high availability, although we did not test this hypothesis. In any case, it seems clear that the small carnivores evaluated in this study show a high potential for resource competition, especially among cats, the grison, and the Pampas fox and between the Pampas fox and the crab-eating fox. The means by which these species exploit available resources and how they avoid competition should be studied in more depth. This study represents a step toward understanding how carnivore assemblages are structured.

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