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Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic Forest remnants, Southern Brazil

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Abstract: The diet of some sympatric carnivore species in three Atlantic Forest remnants of Southern Brazil was studied in order to assess their food niche. We conducted monthly field trips between February 2003 and January 2004 to collect fecal samples that were subsequently examined together with others collected sporadically between November 1994 and January 2003. Of the 416 samples analysed, 198 had the "author" species identified through microscopic analysis guard hairs, which revealed the presence of 10 carnivores and some information about their diet. *Puma yagouaroundi* had the largest dietary niche breadth, whereas *Leopardus tigrinus* and *Nasua nasua* showed the lowest values. Extensive niche overlap was observed between *L. tigrinus* and *N. nasua*, *L. tigrinus* and *L. wiedii*, and between *L. tigrinus* and *L. pardalis*. Data presented here not only increases the understanding of carnivore feeding ecology, but also contributes towards their conservation in the study region and other fragmented landscapes in Brazil and neighboring countries.
Keywords: *carnivores, diet, endangered species, Atlantic Forest, forest fragments, neotropics, niche overlap.*

ROCHA-MENDES, F., MIKICH, S.B., QUADROS, J. & PEDRO, W.A. **Ecologia alimentar de carnívoros (Mammalia, Carnivora) em fragmentos de Floresta Atlântica do Sul do Brasil**. Biota Neotrop. 10(4): http://www.biotaneotropica.org.br/v10n4/pt/abstract?article+bn00210042010.

Resumo: Este trabalho apresenta informações sobre a dieta, a amplitude e a sobreposição de nicho alimentar de algumas espécies simpátricas de carnívoros em três fragmentos de Floresta Atlântica do Sul do Brasil. A coleta de material fecal foi realizada com periodicidade mensal de fevereiro de 2003 a janeiro de 2004. No entanto, amostras obtidas esporadicamente entre novembro de 1994 e janeiro de 2003 também foram incluídas nas análises. Das 416 amostras analisadas, 198 possibilitaram a identificação de 10 espécies "autoras" por meio da análise microscópica de pelos-guarda, bem como informações sobre sua dieta. *Puma yagouaroundi* teve a maior amplitude de nicho, enquanto *Leopardus tigrinus* e *Nasua nasua* apresentaram os menores valores. Maiores sobreposições de nicho foram observadas entre *L. tigrinus* e outras espécies: *N. nasua*, *L. wiedii* e *L. pardalis*. Espera-se que estes dados, além de contribuírem para incrementar o conhecimento sobre a ecologia alimentar de carnívoros neotropicais, possam auxiliar de forma efetiva na conservação das espécies encontradas na região de estudo e em outras paisagens fragmentadas do território brasileiro e países limítrofes.
Palavras-chave: *carnívoros, dieta, espécies ameaçadas, Floresta Atlântica, fragmentos florestais, neotrópico, sobreposição de nicho.*

Introduction

The stability of animal communities is related, in varying degrees, to how different species share the available resources (MacArthur & Levins 1967, Gordon 2000). Consequently, interspecific competition is one of the mechanisms that determine the "stability" of species coexistence, through the use of different parts of the available niche (Schoener 1974). Competition can influence the coexistence of terrestrial mammal carnivores that live in the same area and have strong morphological and behavioral similarities, especially when related to hunting strategies (Rosenzweig 1966, Bothman et al. 1984, Konecny 1989, Sunquist et al. 1989). Ecological partitioning for these sympatric species can involve habitat use, activity patterns or diet (e.g.: Durant 1998, Fedriani et al. 1999, Karanth & Sunquist 2000, Wang 2002, Scognamillo et al. 2003, Jácomo et al. 2004), with species interactions (or their avoidance) becoming more complex as these variables are combined (v. Schoener 1974). However, some authors (e.g.: Sunquist et al. 1989, Wang 2002) have found that spatial and temporal differences seem to be less important than diet to segregate carnivores.

Analysis on the use of resources can help to identify factors responsible for the stability of interspecific relationships or to diagnose the effects of disturbances in the structure of communities. Such analyses are still scarce for neotropical carnivores, with current knowledge limited to a few species and regions. This limits its application in conservation programs. The available literature rarely focuses on the whole carnivore community. However, in analyzing the diet of some species, researchers have contributed to a better understanding of some of the ecological processes relevant to these issues (e.g.: Konecny 1989, Bisbal 1986, Olmos 1993, Facure & Giaretta 1996, Juarez & Marinho-Filho 2002, Bueno & Motta-Junior 2004, Jácomo et al. 2004).

Here we present data on the diet of ten Brazilian carnivores that live in remnants of the Atlantic Forest, as well as information on niche breadth and overlap. Such knowledge will provide a better understanding of the mechanisms involved in local community organization and, thus, contribute towards the conservation of carnivores in forest remnants.

Material and Methods

1. Study site

Our study site was located in the municipality of Fênix, mid-west Paraná State, South Brazil (Figure 1). Mean altitude is 650 m a.s.l.; climate is Cfa (Köppen) with mean temperature during the hottest months above 22 °C and in the coldest months below 18 °C; summers are hot and temperatures below 0 °C are rare (Instituto... 1978, Maack 1981). June, July and August are the driest months, while December, January and February are the wettest (Instituto... 1987, Mikich & Oliveira 2003). However, based on data obtained at the nearest meteorological station (Vila Rica, 23º 45' S and 51º 57' W), we identified one rainy season that extends from October to March and one dry season that extends from April to September.

The study site was once completely covered by semideciduous Atlantic Forest (Veloso et al. 1992), but today only a few small fragments (up to 800 ha) remain surrounded by a matrix composed mainly of corn and soybean plantations, although other crops are also present (Mikich & Silva 2001, Mikich & Oliveira 2003). Three forest sites (Figure 1) were selected for the study based on their location, accessibility and previous knowledge of their flora and fauna. The three areas have different sizes, with some slight differences in vegetation structure and composition, history of occupation and soil use (Mikich & Silva 2001), as presented below.

1) Vila Rica do Espírito Santo State Park (VR) (23º 55' S and 51º 57' W) has 354 ha and is bordered by the Ivaí and Corumbataí Rivers, as well as cultivated areas. Most of the area (approximately 75%) is covered by secondary forest more than 375 years old, with the existing vegetation very similar to primary forests of the region. However, some parts (approx. 25%) of the VR were cultivated in the recent past, including an orchard that was abandoned in 1980 (Mikich & Silva 2001, Mikich & Oliveira 2003).

2) Cagibi Farm (FC) (23º 52' S and 51º 58' W) has 325 ha divided into two irregular, unconnected fragments bordered by monocultures and the Ivaí River. The area exhibits some signs of

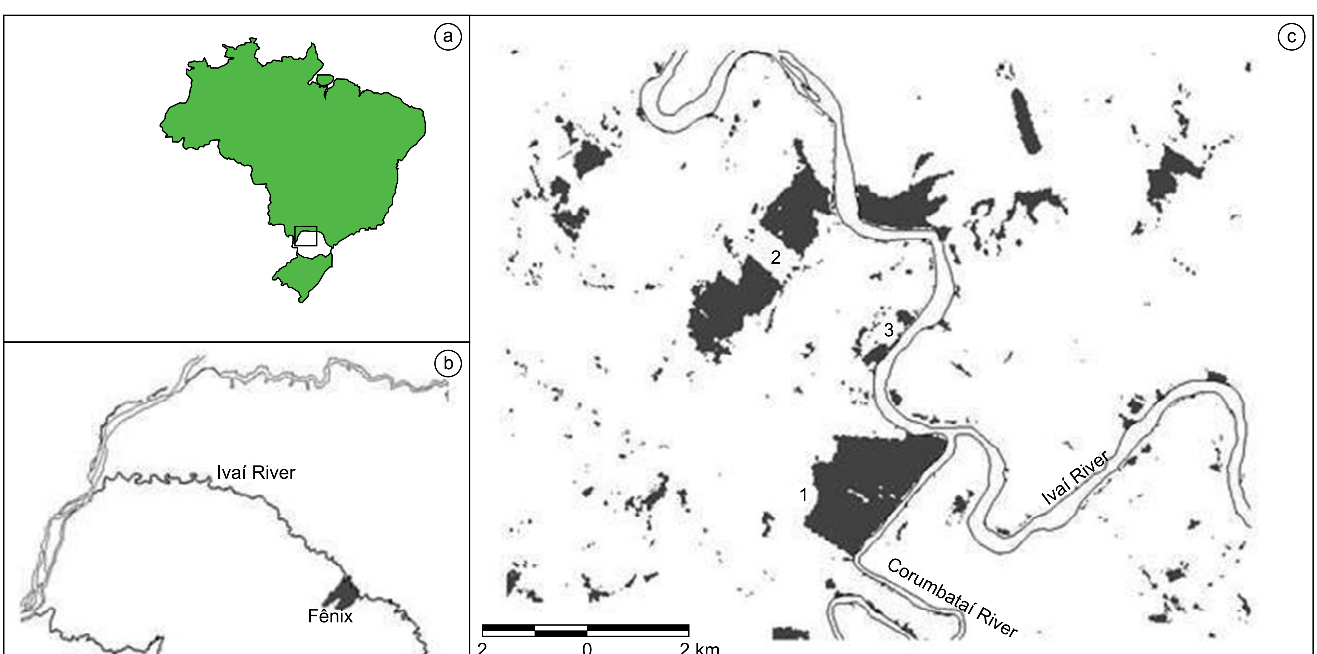

Figure 1. a) Location of Paraná State in Southern Brazil, b) location of the municipality of Fênix in Paraná State, and c) spatial distribution of the forest remnants studied, where: 1) Vila Rica do Espírito Santo State Park, 2) Cagibi Farm, 3) Guajuvira Farm.

human disturbances, such as low levels of timber exploitation, but the less disturbed areas are floristically and structurally similar to VR (Mikich & Silva 2001).

3) Guajuvira Farm (FG) (23° 53' S and 51° 57' W): has 24 ha and is located between the two previous areas. It is divided into two fragments, with similar sizes but different shapes, bordered by cultivated areas and the Ivaí River. Most of this area is covered by riparian secondary forest (Mikich & Silva 2001).

2. Feces collection and identification

Between February 2003 and January 2004, we conducted monthly field trips to collect carnivore fecal samples. Surveys were conducted along trails, forest borders and roads in and between the three forest sites. During four trips (September 2002; March, June and October 2003) we also surveyed the Ivaí and Corumbataí Rivers along the limits of the VR by boat. We also included in the analysis fecal samples sporadically collected between November 1994 and January 2003.

Fecal samples were dried in the sun and stored for later processing and identification of food items. We grouped food remains as: fur from prey; mammalian bones; bird, reptile or fish remains; invertebrates; egg shells; plant material; and fur from the predator, which we used to identify the species that produced the sample. The only exception were samples of the Neotropical River Otter (*Lontra longicaudis*) whose characteristic shape, size, smell and deposition site allowed us to identify the species without having to analyse the fur.

To identify carnivore species, we prepared cuticular and medullar slides of hair obtained from the fecal samples (cf. Quadros & Monteiro-Filho 2006) and identified them based on Quadros (2002) or by comparison with a reference collection constituted of fur collected from mammalian specimens held at the Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Paraná State, Brazil. We also followed the same procedure to identify mammalian prey in scats. We sent the rest of the food items to specialists in order to identify them to the lowest taxonomic level possible.

3. Diet analysis

To determine the importance of each food item in the diet of carnivore species, we calculated the Percentage of Occurrence (PO) by dividing the total frequency of a particular item by the sum of the frequencies of all items (Maehr & Brandy 1986). To quantify how common a particular item is in the diet we calculated the Frequency of Occurrence (FO), which is the percentage of samples that contained that item (Konecny 1989). The degree of specialization of the diet of a particular species was estimated based on the Levins' standard index of niche breadth (B_{sta}) that ranges from 0 to 1, so that values close to 1 indicate a generalist diet and those close to 0 indicate a specialized diet. We calculated niche overlap using the Morisita's index, for which values close to 0 indicate low overlap and values close to 1 indicate high overlap (Krebs 1999). In order to visualize the similarity among the diets of different carnivore species we constructed a dendogram (cluster analysis) based on the frequency of occurrence of food items, given by Morisita's index, using the Past program (Hammer et al. 2001). We analysed niche breadth only for some species particularly those that have less information on diet. We excluded the leaves of Cyperales (grasses) and the seeds of Poaceae from analysis since they were probably consumed to help in the digestive process and not to obtain nutrients as suggested by Dietz (1984) and Motta-Junior et al. (1994) for canids.

We constructed a cumulative curve for the number of food items found in the diet of *Leopardus tigrinus* (Oncilla), which had the largest number of fecal samples collected, in order to analyse the sampling effort.

Results

1. Diet

We collected 416 feces, of which 198 (47.6%) could be assigned to a carnivore species based on the ingested hairs from the predator (n = 184) or distinguishing characteristics of *Lontra longicaudis* (n = 14). Most samples were from *Leopardus tigrinus* (n = 102; 51.5% of the identified samples), followed by *Nasua nasua* (South American Coati - 38 samples; 19.2%), and *Puma yagouaroundi* (Jaguarundi) and *Lontra longicaudis* (14 each; 7%) (Table 1). A total of 56 food items were recorded, 28 mammalian prey (50.0%), eight invertebrates (14.3%), seven plants (12.5%), five birds (8.8%), four fish (7.1%), three reptiles (5.6%) and eggs (1.7%). Next, we present the items found in the diet of each of the ten carnivores sampled.

Leopardus pardalis (Linnaeus, 1758), Ocelot: we found ten food items, all representing animal material. Mammals were represented in 80% of the samples from this felid and birds in 20%. Leaves of Cyperales were found in 44% of the samples and seeds of Poaceae in 67%.

Leopardus tigrinus (Schreber, 1775), Oncilla: we identified 37 food items, mostly small mammals (rodents and marsupials), birds, reptiles and invertebrates. In 40% of the samples from this species we found leaves of Cyperales and in only 2% we found seeds of Poaceae. The cumulative curve of food items per number of samples of *L. tigrinus* (the only species for which this analysis was possible) did not reach an asymptote, but rather increased until the end of the study period (Figure 2).

Leopardus wiedii (Schinz, 1821), Margay: we identified seven food items for this cat, with small mammals (rodents and marsupials) and birds representing the majority, although reptiles, invertebrates and seeds were also found.

Puma concolor (Linnaeus, 1771), Puma: we identified eight food items for this large felid, including small sized mammals and birds that together represented the most frequently found items. We found leaves of Cyperales in 20% of the samples examined.

Puma yagouaroundi (É. Geoffroy Saint-Hilare, 1803), Jaguarundi: we found 19 food items in this cats's samples, 89% of which were mammals (58% small rodents, 21% marsupials and 10% medium sized mammalian species), including *Cuniculus paca* (Paca) and the *Mazama nana* (Pygmy Brocket). The rest of the diet was composed of invertebrates (11% of the items). We also observed leaves of Cyperales in 28% of the samples and seeds of Poaceae in 7%.

Cerdocyon thous (Linnaeus, 1766), Crab-eating Fox: we found six food items, mostly plant material, although leaves of Cyperales were found in only one fecal sample.

Lontra longicaudis (Olfers, 1818), Neotropical River Otter: we also found six food items for this species, including fish and invertebrates, mostly Crustacea.

Galictis cuja (Molina, 1782), Lesser Grison: only one fecal sample of this species was found, which contained five different food items, including the fur of a large rodent, the Capybara *Hydrochoerus hydrochaeris*.

Nasua nasua (Linnaeus, 1766), South American Coati: we identified 35 food items in the diet of this species. Vertebrates were the most common prey, followed by invertebrates and plant material. In 34.2% of the fecal samples we found leaves of Cyperales and in 5% seeds of Poaceae.

Procyon cancrivorus (G. [Baron] Cuvier, 1795), Crab-eating Raccoon: we recorded only one food item for this species, the marsupial *Didelphis* sp.

Table 1. Food items recorded for the diet of 10 carnivore species of the municipality of Fênix, Paraná State, Brazil. n = number of samples; N = number of occurrences of each item; FO = Frequency of Occurrence (%); PO = Percentage of Occurrence (%).

Plant and animal items	*L. pardalis* (n = 9)			*L. tigrinus* (n = 102)			*L. wiedii* (n = 5)			*P. concolor* (n = 10)			*P. yagouaroundi* (n = 14)			*C. thous* (n = 4)			*L. longicaudis* (n = 14)			*G. cuja* (n = 1)			*N. nasua* (n = 38)			*P. cancrivorus* (n = 1)		
	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO
MAMMALS																														
Not identified	-	-	-	3	2.9	1.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	3	7.9	3.1	-	-	-
Didelphimorphia																														
Caluromys lanatus (Olfers, 1818)	-	-	-	2	2.0	1.0	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Didelphis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100	100
Didelphis aurita (Wied-Neuwied, 1826)	1	11.1	5.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marmosops sp.	-	-	-	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Micoureus paraguayanus (Tate, 1931)	-	-	-	2	2.0	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Monodelphis sp.	1	11.1	5.6	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Philander frenatus (Olfers, 1818)	-	-	-	1	1.0	0.5	2	40.0	18.2	1	10.0	5.9	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Not identified	1	11.1	5.6	5	4.9	2.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Primates																														
Cebus nigritus (Goldfuss, 1809)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Rodentia																														
Akodon sp.	1	11.1	5.6	16	15.7	8.2	1	20.0	9.1	2	20.0	11.8	3	21.4	13.0	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Holochilus brasiliensis (Desmarest, 1819)	1	11.1	5.6	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juliomys sp.	-	-	-	-	-	-	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Necromys lasiurus (Lund, 1841)	-	-	-	2	2.0	1.0	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nectomys squamipes (Brants, 1827)	-	-	-	2	2.0	1.0	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Oligoryzomys flavescens (Waterhouse, 1837)	-	-	-	4	3.9	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Hylaeamys megacephalus (Fischer, 1814)	-	-	-	5	4.9	2.6	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxymycterus sp.	-	-	-	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Thaptomys nigrita (Lichtenstein, 1829)	-	-	-	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Mus musculus Linnaeus, 1758	-	-	-	10	9.8	5.1	1	20.0	9.1	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Rattus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Hydrochoerus hydrochaeris (Linnaeus, 1766)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100	20.0	-	-	-	-	-	-
Cuniculus paca (Linnaeus, 1758)	-	-	-	2	2.0	1.0	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Myocastor coypus (Molina, 1782)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Not identified	7	77.8	38.9	30	29.4	15.3	-	-	-	7	70.0	41.2	4	28.6	17.4	-	-	-	-	-	-	1	100	20.0	3	7.9	3.1	-	-	-
Lagomorpha																														

Table 1. Continued...

Plant and animal items	*L. pardalis* (n = 9)			*L. tigrinus* (n = 102)			*L. wiedii* (n = 5)			*P. concolor* (n = 10)			*P. yagouaroundi* (n = 14)			*C. thous* (n = 4)			*L. longicaudis* (n = 14)			*G. cuja* (n = 1)			*N. nasua* (n = 38)			*P. cancrivorus* (n = 1)		
	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO	N	FO	PO
Sylvilagus brasiliensis (Linnaeus, 1758)	1	11.1	5.6	3	2.9	1.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Carnivora																														
Nasua nasua (Linnaeus, 1766)	1	11.1	5.6	2	2.0	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Artiodactyla																														
Mazama nana (Hensel, 1872)	-	-	-	-	-	-	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-		1	2.6	1.0	-	-	-
BIRDS																														
Pteroglossus aracari (Linnaeus, 1758)	-	-	-	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zenaida auriculata (Des Murs, 1847)	-	-	-	-	-	-	-	-	-	1	10.0	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Picumnus cirratus Temminck, 1825	1	11.1	5.6	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thraupinae	-	-	-	-	-	-	-	-	-	1	10.0	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Not identified	3	33.3	16.7	56	54.9	28.6	4	80.0	36.4	3	30.0	17.6	-	-	-	2	50.0	28.5	-	-	-	1	100	20.0	25	65.8	25.8	-	-	-
REPTILES																														
Colubroidea	-	-	-	1	1.0	0.5	1	20.0	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	5.3	2.1	-	-	-
Small Colubridae	-	-	-	2	2.0	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Medium/Large Colubridae	-	-	-	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
FISHES																														
Hoplias sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	14.3	10.5	-	-	-	-	-	-	-	-	-
Hypostomus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	64.3	47.4	-	-	-	-	-	-	-	-	-
Pimelodus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	14.3	10.5	-	-	-	-	-	-	-	-	-
Not identified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	7.1	5.3	-	-	-	-	-	-	-	-	-
INVERTEBRATES																														
Crustacea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	14.3	10.5	-	-	-	-	-	-	-	-	-
Hymenoptera	-	-	-	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	-	-	-	3	7.9	3.1	-	-	-
Coleoptera	-	-	-	10	9.8	5.1	-	-	-	-	-	-				1	25.0	14.3	-	-	-	1	100	20.0	6	15.8	6.2	-	-	-
Hemiptera	-	-	-	1	1.0	0.5	-	-	-	-	-	-	1	7.1	4.3	-	-	-	-	-	-	1	100	20.0	1	2.6	1.0	-	-	-
Odonata	-	-	-	-	-	-	1	20.0	9.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orthoptera	-	-	-	13	12.7	6.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	7.9	3.1	-	-	-
Diplopoda	-	-	-	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Not identified	-	-	-	8	7.8	4.1	-	-	-	1	10.0	5.9	-	-	-	1	25.0	14.3	3	21.4	15.8	-	-	-	11	28.9	11.3	-	-	-
PLANTS																														
Oryza sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	10.5	4.1	-	-	-
Zea mays L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Syagrus romanzoffiana (Cham.)	-	-	-	5	4.9	2.6	1	20.0	9.1	1	10.0	5.9	-	-	-	1	25.0	14.3	-	-	-	-	-	-	7	18.4	7.2	-	-	-
Hovenia dulcis Thunb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	25.0	14.3	-	-	-	-	-	-	-	-	-	-	-	-
Solanum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	25.0	14.3	-	-	-	-	-	-	-	-	-	-	-	-
Maclura tinctoria (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
Psidium guajava (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2.6	1.0	-	-	-
OTHERS																														
Eggs	-	-	-	1	1.0	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	7.9	3.1	-	-	-
TOTAL	18	-	100	196	-	100	11	-	100	17	-	100	23	-	100	7	-	100	19	-	100	5	-	100	97	-	100	1	-	100

2. Niche breadth

This analysis revealed that *P. yagouaroundi* was the most generalist of the ten carnivores, and did not show high levels of consumption of any particular item, whereas *L. tigrinus* and *N. nasua* showed smaller niche breadth as they preyed more frequently on only a few items (Table 2).

3. Niche overlap

We found higher niche overlap between *L. tigrinus* and *N. nasua* (0.835), *L. tigrinus* and *L. wiedii* (0.717), *L. tigrinus* and *L. pardalis* (0.697), and between *L. wiedii* and *N. nasua* (0.686) (Table 2). The similarity dendogram is presented in Figure 3.

Discussion

1. Diet

Few studies have focused on evaluating the diet of carnivores based on the microscopic analysis of the predators' hair. Quadros (2002) had an identification success rate of only 21.6% from 719 feces analyzed using this method, while Wang (2002) reported an exceptional success of 92.6% (n = 64). Thus, the 44.2% of fecal samples identified to species level in our study can be considered satisfactory, especially when we take into account the fact it would be otherwise impossible to identify predators from most of the fecal samples obtained during our surveys.

Table 2. Niche breadth (Levins' index = B_{sta}) and niche overlap between (Morisita's index) six carnivores of the municipality of Fênix, Paraná State, Brazil. Where: Lp = *Leopardus pardalis*; Lt = *Leopardus tigrinus*; Lw = *Leopardus wiedii*; Py = *Puma yagouaroundi*; Ll = *Lontra longicaudis*; Nn = *Nasua nasua*; N = number of fecal samples for each species.

	Lp	Lt	Lw	Py	Ll	Nn
B_{sta}	0.43	0.15	0.64	0.70	0.50	0.29
Lp	*	0.697	0.319	0.568	0.000	0.377
Lt	0.697	*	0.717	0.437	0.031	0.835
Lw	0.319	0.717	*	0.166	0.000	0.686
Py	0.568	0.437	0.166	*	0.000	0.161
Ll	0.000	0.031	0.000	0.000	*	0.092
Nn	0.377	0.835	0.686	0.161	0.092	*
N	9	102	5	14	14	38

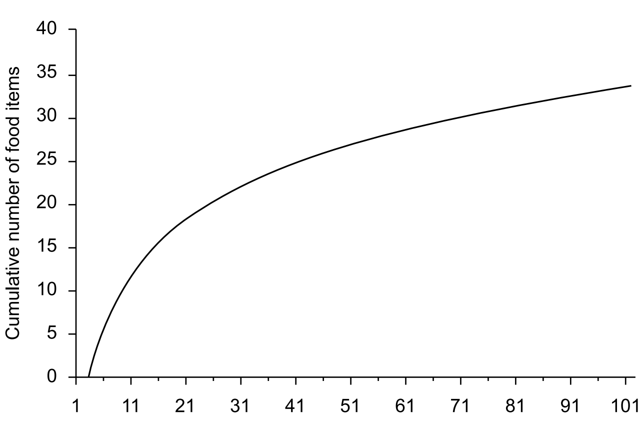

Figure 2. Cumulative number of food items in the diet of *Leopardus tigrinus*, based on 102 fecal samples collected between November 1994 and January 2004 in the municipality of Fênix, Paraná State, Brazil.

Differences in the success of finding the hair of the species responsible for a collected sample can be related to the experience of the researcher, or to particular characteristics of the study areas. Nevertheless, it is imperative to stress the importance of hair analysis as a tool in studying the diet of small and medium sized carnivores. Feces characteristics (e.g.: volume, weight, shape) are frequently the same, making it impossible to tell them apart at the species level (Quadros 2002).

Leopardus pardalis: data of Ocelot diet agreed with information available elsewhere (e.g.: Bisbal 1986, Emmons 1987, Ludlow & Sunquist 1987, Konecny 1989, Sunquist et al. 1989, Chinchilla 1997, Murray & Gardner 1997, Meza et al. 2002, Wang 2002), which indicated the frequent consumption of small mammals. In our study area, besides those groups, we recorded the consumption of *N. nasua* and *Sylvilagus brasiliensis* (Tapeti), both prey previously cited for *L. pardalis* (v. Murray & Gardner 1997), as well as birds and leaves (e.g.: Bisbal 1986, Konecny 1989, Sunquist et al. 1989, Emmons 1987). According to Oliveira et al. (2010), small mammals are the most frequent prey of the Ocelot, although larger animals contribute more in terms of overall biomass consumed.

Leopardus tigrinus: the large number of fecal samples obtained for the Oncilla (n = 102) is unusual if compared to similar studies elsewhere (e.g.: Olmos 1993 - 17 samples; Facure & Giaretta 1996 - 7; Wang 2002 - 24). However, this apparently large number of samples was not enough for the cumulative curve of food items to reach an asymptote (Figure 2). The main prey items found were similar to those of other areas (e.g.: Garder 1971, Ximenez 1982, Moldolfi 1986, Olmos 1993, Facure & Giaretta 1996, Wang 2002). However, unexpectedly, there were also larger species found in the diet, suggesting possible opportunistic / scavenging behavior. New records of prey consumption include: *N. nasua*, *S. brasiliensis* and *C. paca*. It is important to emphasize that the South American Coati is abundant in our study area and the other two species are also relatively common

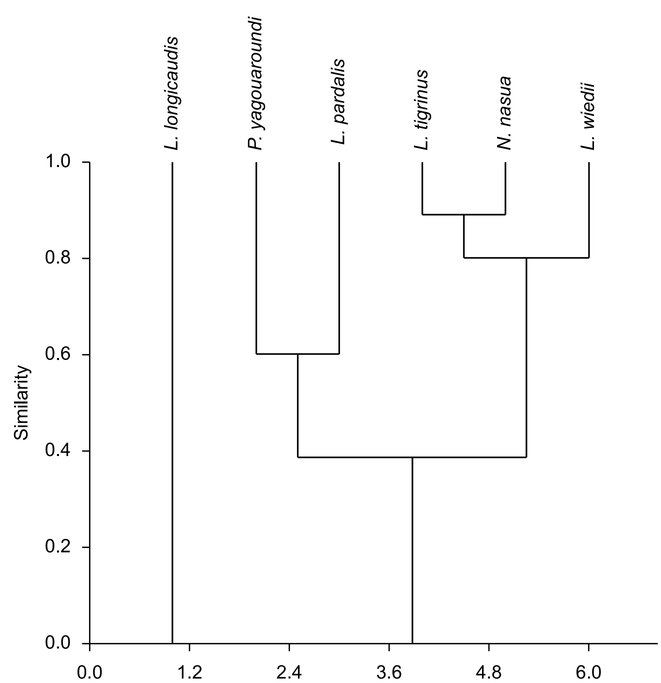

Figure 3. Similarity (Morisita's index) based on the frequencies of occurence of the items in the diet of carnivores of the municipality of Fênix, Paraná State, Brazil.: *L. pardalis = Leopardus pardalis; L. tigrinus = Leopardus tigrinus; L. wiedii = Leopardus wiedii; P. yagouaroundi = Puma yagouaroundi; L. longicaudis = Lontra longicaudis; N nasua = Nasua nasua.*

(Mikich & Oliveira 2003), which could explain their consumption. The diet of this felid in Brazil shows some variation in the frequency of the consumed items. Only in the Brazilian semi-arid Caatinga results differed considerably, as reptiles were by far the most important item (Olmos 1993). Most studies agree that small mammals, birds and reptiles are the main items (Facure & Giaretta 1996, Wang 2002, the present study). The ingestion of grass and invertebrates was also reported by Olmos (1993) and Facure & Giaretta (1996). However, according to Oliveira (1994), the inclusion of these items in the diet of the Oncilla it is probably not related to energy input.

Leopardus wiedii: it has been reported that the diet of Margay is composed mainly by arboreal mammals (Guggisberg 1975, Konecny 1989, Oliveira 1994) and birds (Leyhausen 1990) – which could be related to its morphological traits adapted to arboreal habits (Oliveira 1994). However, the limited data available on Margay diet suggests that this felid takes predominatly small terrestrial mammalian prey, and also to a lesser degree birds (e.g.: Moldolfi 1986, Ximenez 1982, Azevedo 1996, Facure & Giaretta 1996, Wang 2002, the present study).

Puma concolor: the diet of Puma in the neotropics is composed mainly of medium to large sized mammals, including: Peccaries, Deers, Pacas, Coatis and Capybaras (Emmons 1987, Olmos 1993, Aranda & Sánchez-Coedero 1996, Facure & Giaretta 1996, Guix 1997, Taber et al. 1997, Nuñez et al. 2000, Crawshaw & Quigley 2002, Leite & Galvão 2002), although smaller prey, like small mammals, birds, reptiles, fish, invertebrates and fruits are also consumed (e.g.: Emmons 1987, Olmos 1993, Aranda & Sánchez-Coedero 1996, Facure & Giaretta 1996, Nuñez et al. 2000, Crawshaw & Quigley 2002, Leite & Galvão 2002). In our study small mammals were most commonly found in the diet of the Puma compared with other items. Indeed the largest species identified was the marsupial *Philander frenatus,* that weighs approximately 360 g (s. Fonseca et al. 1996). Such a result does not mean that *P. concolor* feeds only on small prey in our study area, rather it highlights that its diet in the area needs further investigation.

Puma yagouaroundi: according to the available literature (e.g.: Konecny 1989, Guerrero et al. 2002), the diet of Jaguarundi is composed mainly of small rodents (Cricetidae). Although this felid does hunt and kill prey > 1 kg, it is unusual to find large mammals (> 5 kg) in its diet, such as Pygmy Brocket (*Mazama nana* – ca. 10-15 kg) and Paca (*Cuniculus paca* – ca. 8 kg) in VR. This large rodent had been previously recorded in the diet of this felid by Wang (2002). Cabrera & Yepes (1960) considered the predation of a small sized deer, like the Pygmy Brocket, by *P. yagouaroundi* a possibility. However, Oliveira (1998) believes that remains like this indicate the consumption of carcasses or, alternatively, could represent a young individual. Invertebrates are commonly listed for the diet of *P. yagouaroundi* (e.g.: Konecny 1989, Olmos 1993, Guerrero et al. 2002) but according to Konecny (1989) they should be of little significance in terms of energy. The consumption of leaves by this cat has been also reported by Bisbal (1986) and Facure & Giaretta (1996).

Cerdocyon thous: previous studies described the diet of Crab-eating Fox in Brazil as omnivorous (e.g.: Motta-Junior et al. 1994, Facure & Monteiro-Filho 1996, Facure & Giaretta 1996, Juarez & Marinho-Filho 2002, Facure et al. 2003, Jácomo et al. 2004, Bueno & Motta-Junior 2004, Rocha et al. 2004), even though the frequency of the consumed items varied among the study areas. Facure & Monteiro-Filho (1996) reported that fruits were the main items in the diet of this canid in São Paulo State. These authors recorded the presence of *Hovenia dulcis*, *Syagrus romanzoffiana* and *Solanum* sp. – plants also found in the diet of this species in our study area.

Lontra longicaudis: the diet of the Neotropical River Otter in our study area was composed predominantly of fish, as previously reported by some Brazilian studies, like Passamani & Camargo (1995) in Minas Gerais; José & Andrade (1997) in Espírito Santo; Pardini (1998) in São Paulo; and Quadros & Monteiro-Filho (2001) in Santa Catarina. According to José & Andrade (1997) the fish that are more likely to be preyed upon by *L. longicaudis* are abundant and easy to catch. Even though fish availability was not directly measured, the genera we found in the fecal samples of the Neotropical River Otter (*Hoplias* sp. – Trahira, *Hypostomus* sp. - Catfish and *Pimelodus* sp. - Catfish) can all be considered common in the rivers of the study region (V. Abilhoa pers. com.). The second most frequent prey items were crustaceans, which agrees with available information from Southern and Southwestern Brazil (Passamani & Camargo 1995, José & Andrade 1997, Pardini 1998, Quadros & Monteiro-Filho 2001).

Galictis cuja: information about the diet of the Lesser Grison's is rare throughout its range. In Chile, Ebensperger et al. (1991) studied the trophic niche of this species based on 21 fecal samples and found 34 vertebrate preys, mainly small mammals, followed by reptiles. Other authors described *G. cuja* as an important consumer of small and medium sized vertebrates, especially rodents, rabbits, birds, frogs, lizards, snakes and their eggs (Mann 1945, Silva 1994, Jiménz 1996, Quintana et al. 2000, Yensen & Tarifa 2003). Diuk-Wasser & Cassini (1998) found a preference for mammals (Lagomorpha and Cricetidae), followed by birds and reptiles. Additionally, they observed that the Grison ate almost exclusively leporids when they occur at a high population density. Even though most food items identified for *G. cuja* in our study area do agree with previous studies, with only a single fecal sample we cannot make any inference on the feeding ecology of this species. However, it is worth mentioning that among the identified items found in that sample there were remains (fur) of Capybara (*Hydrochoerus hydrochaeris*), probably due to the consumption of a carcass of this huge rodent.

Nasua nasua: Gompper & Decker (1998) found a diet consisting mainly of invertebrates (e.g.: insects, myriapods and spiders) and fruits, although vertebrates and their carcasses can also be consumed. Costa-Alves et al. (2004), analysing the diet of *N. nasua* in Minas Gerais State, Brazil, reported that invertebrates are commonly consumed, followed by plant parts and vertebrates. However, for the 38 fecal samples of Coatis identified in our study area, vertebrates were the most common components, followed by invertebrates, and finally by plant parts. When Mikich (2001) analysed the frugivorous diet of this species in the same locality that we studied, she listed 56 plant species consumed during six years of collection. In the present study, the records of plants were limited to five species and *Oryza* sp. was the only one not cited by Mikich (2001). Previously unrecorded large prey items, such as the Capuchin Monkey (*Cebus nigritus*), *Cuniculus paca*, Nutria (*Myocastor coypus*), and especially *Mazama nana*, constitute an important contribution to the feeding ecology of *N. nasua.* The consumption of these animals may suggest a necrophagous diet (Gompper & Decker 1998) or a highly predatory behavior.

Procyon cancrivorus: like the South American Coati, there is little information available on this species, especially with regard to its diet. In our study only one food item was identified for *P. cancrivorus* (n = 1 fecal sample) based on the microscopic analysis of the hair of the prey, an Opossum (*Didelphis*), which constitutes a first time record. As the hair was incomplete the specific determination could not be done.

2. Niche breadth

Leopardus pardalis: In spite of the small sample size for this species, niche breadth showed similar values to other areas (B_{sta} = 0.50), including Southwestern Brazil (Wang 2002; 0.50), Belize (Konecny 1989; 0.46) and Venezuela (Bisbal 1986; 0.45). But some authors found lower values, for example Ludlow & Sunquist (1987) in Venezuela (0.19) and Emmons (1987) in Peru (0.23). Such information suggests that the species may have an opportunistic behavior, preying on abundant species, however further samples are required to confirm this.

Leopardus tigrinus: The small niche breadth (B_{sta} = 0.15) observed for the Oncilla in our study area was caused by the large amount of unidentified birds and rodents in the fecal samples. However, the large amount of small rodents and birds in the diet of this species may indicate an opportunistic behavior if those are the most common prey in the study area. In the study of Wang (2002), the value obtained for this index (B_{sta} = 0.44), based on 24 samples, indicates a less specialized diet, with an elevated consumption of a few items, such as marsupials and passerines.

Leopardus wiedii: In spite of the small number of feces analyzed, the value we obtained for B_{sta} (0.64) was similar to that found in the State of São Paulo, Brazil (Wang 2002 – 0.63), Belize (Konecny 1989 – 0.63) and Venezuela (Moldolfi 1986 – 0.63), indicating an evenly distributed diet.

Puma yagouaroundi: The niche breadth index indicates a lack of high consumption of items at our study area. In Venezuela, Moldolfi (1986) and Bisbal (1986) also found high values for this index (0.85 and 0.68, respectively). In spite of that, Konecny (1989), suggested that the diet of *P. yagouaroundi* in Belize was basically composed of a specific group of prey, resulting in low niche breadth (0.37).

Lontra longicaudis: In Santa Catarina State, Brazil, Quadros & Monteiro-Filho (2001) classified *L. longicaudis* as a generalist species with a piscivorous-cancrivorous diet, the same as observed in our study site. Taken into account that the species of fish that were consumed are common in the region, the Neotropical River Otter can be considered as both a generalist and an opportunist.

Nasua nasua is omnivorous, and there are previous records of consumption of eggs, snakes, fish and carcasses (Schaller 1983, Bisbal 1986, Redford & Stearman 1993, Gompper & Decker 1998, Costa-Alves et al. 2004). In spite of this, its niche breadth in our study area (B_{sta} = 0.29) indicates that a few items (especially unidentified birds and invertebrates) are mainly consumed. However, if these items are common in our study area, the species would be considered opportunist.

3. Niche overlap

Felids, in general, tend to be more carnivorous (Olmos 1993, Facure & Giaretta 1996), while procyonids tend to be omnivorous (Schaller 1983, Redford & Stearman 1993). The high overlap found between *L. tigrinus* and *N. nasua* (0.835) is unexpected but could be explained by the large amount of unidentified birds in their feces. This is probably related to the high availability of birds; especially doves that use agricultural fields as feeding grounds and/or dormitories and by doing so become easy prey for these predators.

Carnivores with taxonomic, ecological and behavioral affinities usually exhibit high niche overlap, like the congeners *L. tigrinus* and *L. wiedii* (0.717) or *L. tigrinus* and *L. pardalis* (0.697). A similar study conducted by Wang (2002) in the State of São Paulo, Brazil, found even higher overlaps (0.824 and 0.800 respectively) for the same species. It seems that the small niche overlap between *P. yagouaroundi* and other species found in our study area should be related to the lack of birds in the diet of this wild cat.

Final Considerations

Niche partitioning in terrestrial carnivores can involve several dimensions, such as habitat use, activity patterns and food (Karanth & Sunquist 2000, Scognamillo et al. 2003). However, some authors believe that even for sympatric species, with different morphological traits and hunting strategies, spatial and temporal dimensions assume less importance than diet itself (Sunquist et al. 1989, Wang 2002). In spite of the large variation found in the diet of the ten carnivore species presented here, the small number of fecal samples for some species does not allow us to consider feeding as the main mechanism that facilitates coexistence in forest fragments.

Regarding this, it is important to stress that the forest remnants sampled were small and relatively isolated (VR = 3.5 km^2; FC = 3.2 km^2; FG = 0.2 km^2). If we consider that the home range of most carnivores is greater than 10 km^2 (*s.* Crawshaw 1995) (e.g.: *P. yagouaroundi*: 7 - 19.6 km^2; *L. pardalis*: 15.6 – 50.9 km^2), we suggest that the natural habitat left is not sufficient to maintain stable populations of several species. The inclusion of exotic rodents (*Mus musculus* and *Rattus* sp.) and birds (*Zenaida auriculata*) that live in the plantations and other non-forested areas of our study site in the diet of the carnivores we studied, suggest that at least some of them use all available habitat types found in the landscape to hunt.

The present study is unique due to the number of sympatric carnivores studied. The information presented here is important for a better understanding of carnivore ecology and how this community partitions food resources in fragmented landscapes of the highly threatened Atlantic Forest. This information is useful for the management of such areas and shows that despite fragmentation, small forest patches are in fact important for maintaining carnivore diversity in this critical biome.

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