

# Intraspecific, interspecific, and seasonal differences in the diet of three mid-sized carnivores in a large neotropical wetland

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**Abstract** The diet and partitioning of food resources among mid-sized mammalian carnivores is poorly known, especially in the tropics. We evaluated the resource partitioning between *Leopardus pardalis* (ocelot), *Cerdocyon thous* (crab-eating fox), and *Nasua nasua* (brown-nosed coati) in the Pantanal of Brazil. Between December 2005 and February 2008, we collected data necessary to better understand interspecific, intra-specific, and seasonal variability in diet. Food habits were

assessed by analysis of feces ( $n=293$ ) collected from known individuals ( $n=128$ ), and differences in dietary composition were evaluated through nonmetric dimensional scaling using the Jaccard similarity index. The main diet differences were observed between the specialist ocelot and the more generalist crab-eating fox and brown-nosed coati. Crab-eating foxes and brown-nosed coatis preyed on arthropods, fruits, and vertebrates whereas ocelots preyed almost entirely on vertebrates, mainly rodents and snakes. Ocelots' consumption of snakes was the highest ever recorded, as was the extent of carnivory by brown-nosed coatis. For the crab-eating fox and the brown-nosed coati, there were large differences between the use of fruits and animal foods in the wet and dry season. Yet for both species there were no significant differences in the diets of males and females. Despite the conspicuous sexual dimorphism and spatial segregation that are typical of brown-nosed coatis, the results do not support the hypothesis that size dimorphism is primarily an adaptation to reduce intersexual competition for food. Rather, dimorphisms and patterns of space use may be more related to competition among males for access to females.

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## Introduction

Identifying and quantifying the resources required for species to exist, and to coexist with similar species, are fundamental foci of animal ecology. This information is essential for understanding interspecific and intraspecific competition (Litvaitis 2000), which are a major force determining species dynamics (Tilman 2007). Among the resources that can be partitioned by co-occurring species and individuals, food is perhaps the most important (Schoener 1974).

The dietary overlap between sympatric species of similar size can be indicative of the extent of exploitation or interference competition (Caro and Stoner 2003; Moreno et al. 2006; Hayward and Kerley 2008). These negative interspecific interactions may influence the distribution and abundance of less dominant species, suggesting that selection may favor behavioral and morphological attributes that minimize competition and the likelihood of aggressive encounters (Van Valkenburgh 1985, 1988, 1999; Dayan and Simberloff 1996). Among carnivores, for example, variation in interspecific geographic range overlap is associated with morphological divergence in dentition (Davies et al. 2007). Habitat and diet are often complementary niche dimensions, suggesting that to co-exist, species compensate for similarities in habitat use by differing in food resource utilization (Schoener 1974; Fuentes 1976; Rautenbach and Nel 1978; Kiltie 1984, 1988; Iriarte et al. 1990).

Mesocarnivorous mammals can drive community structure and function in ways that are similar to, or altogether different from, their larger counterparts. Theoretical and empirical evidence suggest that mesocarnivores may be fundamentally important drivers of ecosystem function and structure by occupying unique roles that cannot be filled by larger bodied carnivores, such as when they are direct dispersers of seeds or predators of important seed dispersers (Roemer et al. 2009). Yet despite these important roles, the diet and mechanisms of resource partitioning of the vast majority of mid-sized carnivores (more than 90 % of species in the order Carnivora; Gittleman and Gompper 2005) is poorly known, especially in the tropics. Thus, there is a pressing need to increase the knowledge of their feeding ecology.

As part of a broader study of population, community, and disease ecology of carnivores of the Pantanal of Brazil (Bianchi 2009; Olifiers 2010), we examined the feeding ecology of ocelots (*Leopardus pardalis*, ~10 kg), brown-nosed coatis (*Nasua nasua*, ~3–6 kg), and crab-eating foxes (*Cerdocyon thous*, ~8 kg). These three species are widely distributed in the Neotropics, and are abundant in many parts of their geographic ranges. This is particularly true in the Brazilian Pantanal (Schaller 1983; Robinson and Redford 1986; Alho et al. 1987) where even the ocelot, a species designated as threatened in Brazil (Oliveira and Bianchi 2008), is abundant (Bianchi 2009). The ocelot is considered an opportunistic carnivore, mainly consuming small mammals (<1 kg), (Ludlow and Sunquist 1987; Wang 2002; Bianchi and Mendes 2007), although it can also consume larger prey, such as deer, agoutis, and armadillos (Crawshaw Jr 1995; Moreno et al. 2006; Bianchi et al. 2010). In contrast, crab-eating foxes and brown-nosed coatis are thought to be generalist omnivores. Yet despite having a wide distribution and being abundant even in disturbed

habitats, the diets of these species are still poorly known. In Brazil, the few studies of the diet of crab-eating fox have reported the consumption of fruits, arthropods, and small vertebrates (Pedó et al. 2006; Gatti et al. 2006). Likewise, the feeding ecology of the brown-nosed coati is principally known from studies conducted in peri-urban areas (Costa 2003; Alves-Costa et al. 2004; Santos and Beisiegel 2006, but see Hirsch 2009) where they primarily feed on fruits and ground-litter invertebrates.

Our goals for this study were threefold: (1) to document the diet of these three species in an environment where they are abundant and the broader carnivore community is intact, (2) to assess the extent of sex- and season-related intraspecific variability in the diet of these species at a locality that has marked wet and dry seasons, and (3) to quantify dietary diversity and overlap for these three species. The issue of sex-related differences was of particular interest for the brown-nosed coati, a species with extensive sexual dimorphism (Olifiers et al. 2010), as work on the closely-related white-nosed coati (*N. narica*) has observed differences in feeding behavior of males and females (Gompper 1996). For ocelots, we also (1) evaluated whether larger-vertebrate prey are consumed according to their availability in the environment and (2) examined the range-wide inclusion of reptile biomass in their diet. Villa Meza et al. (2002) have hypothesized that a latitudinal cline in reptile body size and abundance may underpin the inclusion of reptiles in ocelot diets. However, this hypothesis has yet to be closely examined.

## Materials and methods

### Study area

The study was conducted in and around Nhumirim Ranch (18°59' S, 56°39' W), a 43-km<sup>2</sup> research station of The Brazilian Agricultural Research Corporation (Embrapa) located in the Pantanal of Brazil. The Pantanal is a large Neotropical floodplain located in the centre of South America. The climate is tropical, with two marked seasons: a wet season (October to March) and a dry season (April to September). Human density is low (<2 people/km<sup>2</sup>) and the main economic activity is cattle ranching. The study area is characterized by sandy soil with a mosaic vegetation of semi-deciduous forest, dispersed shrub vegetation, and seasonally flooded fields (Rodela 2006). Permanent and temporary fresh water ponds and alkaline ponds occur throughout the area.

### Sample collection and analyses

Diet was determined by analysis of fecal samples collected primarily from individuals live-captured in wire box traps.

Therefore some recaptured individuals were the source of more than one scat. Scats were also collected opportunistically when tracking radio-collared animals or when animals associating with radio-collared animals were observed to defecate.

Once collected, the fecal samples were placed in paper bags and oven-dried for  $\geq 24$  h at 60 °C. Dried scats were washed on a sieve and the screened material (e.g., hair, teeth, and scales) was identified to lowest taxonomic level possible by comparison with reference specimens deposited in collections at Embrapa Pantanal and at Federal University of Mato Grosso do Sul. Guard-hair preparation and identification was done as described by Quadros and Monteiro-Filho (2006a, b). These results were quantified as frequency of occurrence (frequency of a particular item in the total number of collected scats) and as percentage of occurrence (percentage of a given item in the total items consumed).

To verify whether diet composition varied with gender, season, or species, we used nonmetric dimensional scaling (NMDS) to ordinate the diet composition in two or three axes (Clarke 1993). To maximize the independence of data, we merge the results from fecal samples originated from the same individuals in a same season. In cases in which we had fecal samples of the same individual from the two seasons, we exclude one of them. We used the Jaccard similarity coefficient, which relates variables that may represent the presence or absence of an attribute. We then graphically analyzed the configuration of points in the resulting two- or three-dimensional space and graphed the Pearson correlations of the axes resulting from the NMDS analyses with dietary items. The obtained ellipses represent a standard deviation of a bivariate normal distribution and are centered on the average of the samples X and Y. We calculated the dietary diversity for all species using the Levins' standardized niche breadth index and Shannon index (Krebs 1999), and dietary overlap between species using Pianka's index (Krebs 1999). We used EcoSim 7 software (Gotelli and Entsminger 2006) to test for significance of niche overlap by comparing observed values with values obtained from 10,000 random iterations of the original matrices. For estimating the number of vertebrate taxa used in the diet, we used a Jackknife procedure (Colwell and Coddington 1994), which corrects for sub-sampling bias, allowing estimation of confidence intervals, and hypothesis testing. We conducted the Jackknife analyses using program EstimateS (Colwell 1997), which also produced a collector curve from the output of the Jackknife analyses.

We investigated whether ocelots consumed vertebrate prey proportionally to their availability in the environment, using the Spearman rank correlation. The density of mammals in the study area was determined by other studies carried out in the same area (Desbiez et al. 2010 for

medium- to large-sized mammals), as was the availability of frogs, snakes, and lizards (Vanda Lúcia Ferreira, unpublished data collected using pitfall traps). We first ranked the density of mammals separately from the remaining species (because their sampling methods were distinct) and subsequently assigned a general rank for the whole dataset based on the premise that the density of medium- to large-sized endotherms is smaller than the density of small ectotherms (that is, the density of frogs, snakes, and lizards is expected to be larger than any of the medium- to large-sized mammals in the dataset). We also tested for food preferences using the Manly's  $\alpha$  (Krebs 1999) on mammalian prey items (density of mammals with  $>1$  kg) (Desbiez et al. 2010). The index is compared with a threshold estimated as  $1/m$  ( $m$ =total number of prey types). If  $\alpha_i$  is greater than  $1/m$ , then prey species  $i$  is preferred in the diet (Krebs 1999).

Finally, we looked for a possible correlation between the percentage of reptiles present in ocelot's feces and the latitude, using data compiled from the literature.

All animal procedures were approved by the Brazilian Government Institute for Wildlife and Natural Resources Care (IBAMA, first license 183/2005—CGFAU/LIC; last license 11772-2).

## Results

### Ocelot

We collected 46 scat samples, including 22 scats from nine individuals (6 males and 16 females) during capture–recapture events, and 24 scats that were attributed to ocelots due to the presence of footprints around the scats or guard-hairs in the samples. Ocelots primarily consumed mammals, which occurred in 96 % of the samples and comprised almost half the identified dietary taxa (Table 1). Rodents occurred in 56 % of the scats and represented 30 % of the total items consumed. The broad-headed spiny rat (*Clyomys laticeps*) was the species most frequently found in the scats (30 % of the samples). Reptiles occurred in 63 % of scats, with snakes (46 %) being the most important group, followed by lizards (21 %) (Table 1). Larger-bodied prey species (body mass,  $>1$  kg) occurred in almost 40 % of scats and represented 14 % of the total items consumed.

The NMDS ordination of samples from individuals of known sex resulted in a stress=0.11 with an  $R^2=0.95$ , indicating that the ordination was able to recover the main patterns of diet (Clarke 1993). The resulting ordination axes indicate that the diet of males and females were similar (Fig. 1)

Overall, ocelots consumed some vertebrates according to their availability in the environment ( $R_s=0.71$ ;  $p=0.02$ ), but

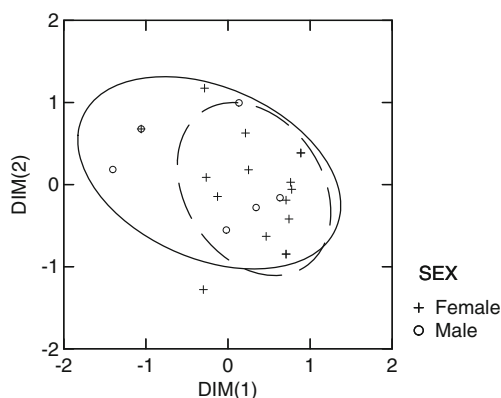
**Table 1** Food items found in 294 fecal samples of mid-size carnivores collected from Nhimirim Ranch in the Central Pantanal, Brazil, during December 2005 to February 2008. Individual items grouped by higher taxa are in bold

	Ocelot (46 scats; 121 items)		Crab-eating fox (164 scats; 673 items)		Brown-nosed coati (84 scats; 276 items)	
	% scats	% items	% scats	% items	% scats	% items
<b>Vertebrata</b>	<b>100</b>	<b>94</b>	<b>79.9</b>	<b>32.8</b>	<b>39.3</b>	<b>14.3</b>
<b>Mammalia</b>	<b>95.7</b>	<b>46.4</b>	<b>25</b>	<b>6.4</b>	<b>4.8</b>	<b>1.5</b>
<b>Rodentia</b>	<b>56.5</b>	<b>30.6</b>	<b>18.9</b>	<b>4.6</b>	<b>0</b>	<b>0.8</b>
<i>Clyomys laticeps</i>	30.4	11.6	6.1	1.5	0	0
<i>Thrichomys pachyurus</i>	17.4	6.6	3	0.7	0	0
Muridae n.i.	17.4	6.6	2.4	0.6	1.2	0.4
<i>Dasyprocta azarae</i>	15.2	5.8	7.3	1.8	1.2	0.4
<b>Didelphimorphia</b>	<b>19.6</b>	<b>7.4</b>	<b>2.4</b>	<b>0.6</b>	<b>2.4</b>	<b>0.7</b>
Didelphidae	19.6	7.4	2.4	0.6	2.4	0.7
<b>Artiodactyla</b>	<b>10.9</b>	<b>4.2</b>	<b>4.9</b>	<b>1.1</b>	<b>0</b>	<b>0</b>
<i>Mazama</i> sp.	6.5	2.5	0.6	0.1	0	0
<i>Ozotocerus bezoarticus</i>	2.2	0.8	0	0	0	0
<i>Sus scrofa</i>	2.2	0.8	4.3	1.0	0	0
<b>Pilosa</b>	<b>6.5</b>	<b>2.5</b>	<b>0.6</b>	<b>0.1</b>	<b>0</b>	<b>0</b>
<i>Tamandua tetradactyla</i>	6.5	2.5	0.6	0.1	0	0
<b>Carnivora</b>	<b>4.3</b>	<b>1.7</b>	<b>0</b>	<b>0.0</b>	<b>0</b>	<b>0</b>
<i>Nasua nasua</i>	4.3	1.7	0	0.0	0	0
<b>Aves</b>	<b>39.1</b>	<b>14.9</b>	<b>14.6</b>	<b>3.6</b>	<b>0</b>	<b>0</b>
Aves	39.1	14.9	14.6	3.6	0	0
<b>Squamata</b>	<b>63</b>	<b>28.1</b>	<b>37.2</b>	<b>10.5</b>	<b>21.4</b>	<b>6.6</b>
Lacertilia	26.1	9.9	21.3	5.2	18.1	5.4
Teiidae	2.2	0.8	1.2	0.2	1.2	0.4
Colubridae	41.3	15.7	18.3	4.5	1.2	0.4
<i>Bothrops matogrossensis</i>	4.3	1.7	2.4	0.6	1.2	0.4
<b>Amphibia</b>	<b>10.9</b>	<b>4.1</b>	<b>50</b>	<b>12.2</b>	<b>20.2</b>	<b>6.2</b>
Amphibia	10.9	4.1	50	12.2	20.1	6.2
<b>Pisces</b>	<b>0</b>	<b>0</b>	<b>0.6</b>	<b>0.1</b>	<b>0</b>	<b>0</b>
Pisces	0	0	0.6	0.1	0	0
<b>Arthropoda</b>	<b>15.2</b>	<b>6.7</b>	<b>87.8</b>	<b>33.4</b>	<b>82.1</b>	<b>46.6</b>
Coleoptera	13	5.0	56.7	13.8	65.5	19.9
Orthoptera	4.3	1.7	47	11.4	47.6	14.5
Crustacea	0	0	20.7	5.1	3.6	1.1
Blattaria	0	0	3	0.7	4.8	1.4
Diplopoda	0	0	1.8	0.4	21.4	6.5
Chilopoda	0	0	1.8	0.4	0	0
Aranae	0	0	0.6	0.1	4.8	1.4
Diptera	0	0	0.6	0.1	2.4	0.7
Hemiptera	0	0	0.6	0.1	0	0
Isoptera	0	0	0.6	0.1	0	0
Odonata	0	0	0.6	0.1	0	0
Scorpinae	0	0	0.6	0.1	1.2	0.4
Arthropoda n.i.	0	0	2.4	0.6	2.4	0.7
<b>Gastropoda</b>	<b>0</b>	<b>0</b>	<b>1.8</b>	<b>0.4</b>	<b>1.2</b>	<b>0.4</b>
Gastropoda	0	0	1.8	0.4	1.2	0.4
<b>Fruits</b>	<b>0</b>	<b>0</b>	<b>77.4</b>	<b>33.1</b>	<b>81</b>	<b>38.6</b>
<i>Annona dioica</i>	0	0	24.4	5.9	11.9	3.6

**Table 1** (continued)

	Ocelot (46 scats; 121 items)		Crab-eating fox (164 scats; 673 items)		Brown-nosed coati (84 scats; 276 items)	
	% scats	% items	% scats	% items	% scats	% items
<i>Guazuma ulmifolia</i>	0	0	21.3	5.2	7.1	2.2
<i>Byrsonima orbignyana</i>	0	0	19.5	4.8	11.9	3.6
<i>Mouriri elliptica</i>	0	0	10.4	2.5	2.4	0.7
<i>Bromelia balansae</i>	0	0	9.8	2.4	8.3	2.5
<i>Acrocomia aculeata</i>	0	0	9.1	2.2	14.3	4.3
<i>Vitex cymosa</i>	0	0	7.9	1.9	9.5	2.9
<i>Copernicia alba</i>	0	0	4.9	1.2	2.4	0.7
<i>Diospyrus hispida</i>	0	0	4.3	1.0	14.3	4.3
<i>Harrisia bonplandii</i>	0	0	4.3	1.0	21.4	6.5
<i>Hancornia speciosa</i>	0	0	3	0.7	1.2	0.4
<i>Ficus</i> sp.	0	0	1.8	0.4	2.4	0.7
<i>Hymenaea stigonocarpa</i>	0	0	1.2	0.3	0	0.0
<i>Psidium</i> sp.	0	0	1.2	0.3	1.2	0.4
<i>Genipa americana</i>	0	0	0.6	0.1	2.4	0.7
<i>Annona cornifolia</i>	0	0	0.6	0.1	0	0
<i>Protium heptaphyllum</i>	0	0	0	0.0	3.6	1.1
<i>Allagoptera leucocalyx</i>	0	0	0	0.0	1.2	0.4
Other fruits	0	0	11.6	2.8	11.9	3.6
Total		100		100		100

the anteater (*Tamandua tetradactyla*) was consumed more than expected based on its density in the study area (Table 2). The correlation between latitude and reptiles consumption by ocelot is not significant when tested by absolute decimal latitude ( $r=-0.06$ ) or when considering south decimal latitude as negative values ( $r=0.12$ ) (Table 3).



**Fig. 1** Dimensions 1 and 2 from the NMDS ordination of items identified in 22 fecal samples from ocelots (*L. pardalis*) captured at the Nhimirim Ranch, Brazil, from December 2005 to February 2008. Ellipses for males (solid line) and females (dashed line) are centered on the averages of each group and comprise about 1 standard deviation. Stress value=0.11

#### Crab-eating fox

We collected a total of 164 fecal samples from crab-eating foxes from 64 captured individuals and four from non-identified foxes that were seen defecating. The main items consumed by this species were arthropods, vertebrates and fruits (Table 1). Each of these groups occurred in >77 % of scats and represented approximately one third of the items consumed. The composition of samples merged by individuals resulted in an NMDS ordination in three dimensions with a stress=0.164 ( $R^2=0.86$ ). The resulted configuration did not indicate differences in diets between sex (Fig. 2a), but suggests that diet composition differed between the dry and wet seasons (Fig. 2b). The most important items during the dry season ( $n=36$ ) were frogs, coleopterans, and fruits of *Guazuma ulmifolia* and *Hancornia speciosa*. During the wet season ( $n=30$ ), the most important food items were orthopterans and fruits of *Byrsonima orbignyana* and *Annona dioica* (Fig. 2c).

#### Brown-nosed coati

We collected 83 fecal samples of brown-nosed coati: 76 were collected from 55 known individuals and 7 from animals observed defecating. The main items consumed by brown-nosed coatis were arthropods (82 % of samples comprising 47 % of food items) and fruits (81 % of samples



**Table 2** Mid-sized and large prey species consumed by ocelot, the density of these species in the study area, and Manly's  $\alpha$  preference index

Species	Consumed (% scats)	Density <sup>a</sup>	Manly's $\alpha$
<i>Dasyprocta azarae</i>	15	17	0.095
<i>Tamandua tetradactyla</i> <sup>b</sup>	7	1	0.757
<i>Mazama</i> sp.	7	8	0.095
<i>Nasua nasua</i>	4	36	0.012
<i>Ozotocerus bezoarticus</i>	2	8	0.027
<i>Sus scrofa</i>	2	16	0.014
<i>Dasypus novemcinctus</i>	0	0.3	0.000

<sup>a</sup>Desbiez et al. (2010)<sup>b</sup>If feeding is selective, Manly's  $\alpha$  should be  $\geq 0.143$ 

comprising 39 % of items) (Table 1). Vertebrates, primarily lizards and frogs, occurred in 39 % of scats but comprised just 14 % of food items. The samples from individuals of known sex ( $n=82$ ) resulted in an NMDS ordination that did not indicate differences in diet composition between males and females (Fig. 3a). The NMDS ordination resulted in a stress=0.15, with an  $R^2=0.92$ . The graph of the resulting ordination axes indicated that diet composition differed between the dry and wet seasons (Fig. 3b): the most important items in the dry season ( $n=41$ ) were coleopterans, diplopods and fruits of *Diospyrus hispida*, while in the wet season ( $n=42$ ), fruits of *Harrisia bonplandii*, *A. dioica*, and *B. orbignyana* were common (Fig. 3c).

#### Interspecific comparisons

The niche breadth of the brown-nosed coati (0.40) was larger than that of the crab-eating fox (0.28) and ocelot

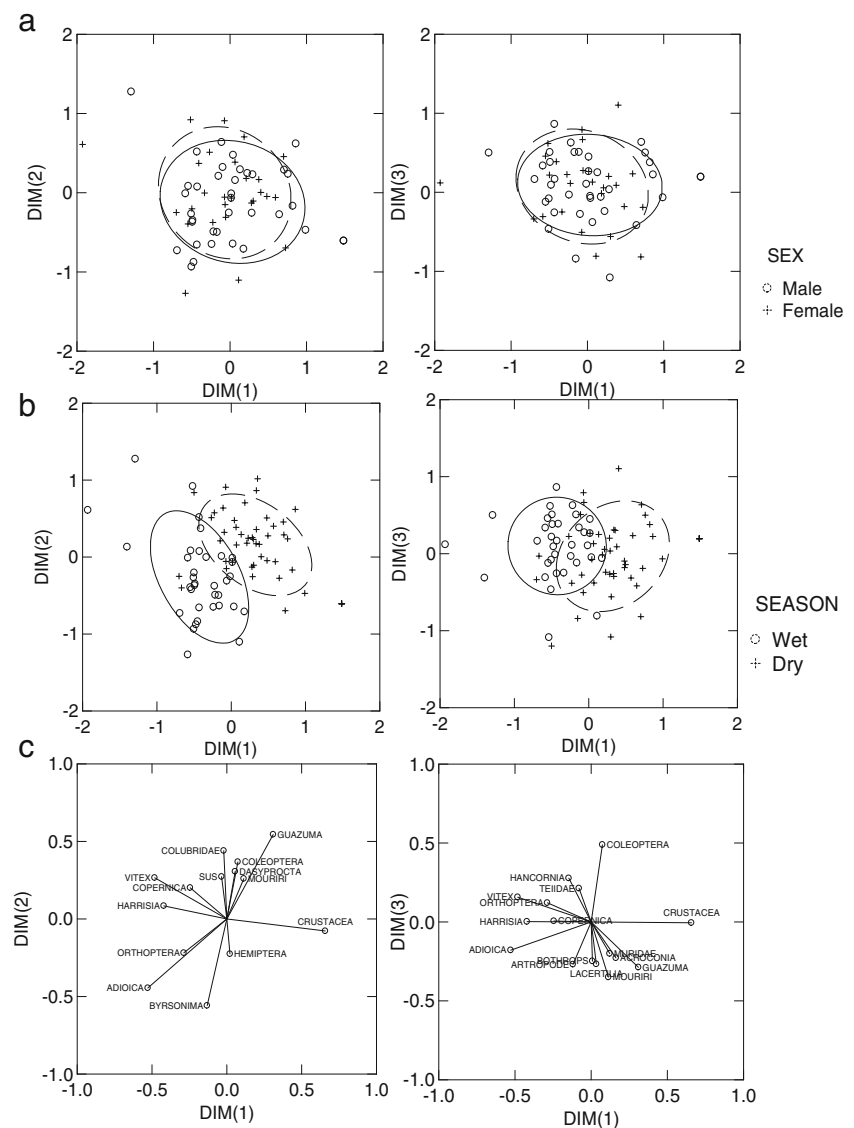
(0.19), but the number of items per scat and the Shannon–Wiener diversity was higher for the crab-eating fox ( $673/164=4.10$ ;  $H=3.07$ ) than for the brown-nosed coati ( $276/83=3.32$ ;  $H=2.87$ ) and the ocelot ( $121/46=2.63$ ;  $H=2.55$ ). The overlap between brown-nosed coatis and crab-eating foxes was larger ( $0.85$ ;  $\bar{x}=0.25$ , variance=0.010,  $P_{\text{obs}>\text{exp}}<0.01$ ) than between brown-nosed coatis and ocelots ( $0.24$ ;  $\bar{x}=0.20$ , variance=0.012,  $P_{\text{obs}>\text{exp}}=0.28$ ) or crab-eating foxes and ocelots ( $0.44$ ;  $\bar{x}=0.23$ , variance=0.012,  $P_{\text{obs}>\text{exp}}=0.05$ ). The number of taxa occurring in fox scats, as assessed by the Jackknife procedure ( $48\pm 2.51$ ), was more than twice that occurring in ocelot scats ( $20\pm 2.7$ ) and almost 1.5 times larger than in brown-nosed coati scats ( $36\pm 1.61$ ). The species (food items) accumulation curve (Fig. 4) also indicates that sample sizes were adequate to describe the dietary diversity of each species.

The NMDS ordination for the three species resulted in a stress=0.17 and  $R^2=0.86$ . The graphic analysis suggests

**Table 3** Percentage of occurrence of reptiles (percentage of reptiles to total items) consumed by *Leopardus pardalis* from published data in different latitudes ( $r=-0.0565$ )

Region	Latitude	% reptiles	Source
México	19°29' N	32.1	Villa Meza et al. (2002)
Belize	17°32' N	0	Konecny (1989)
Panama	9°05' N	10.1	Moreno et al. (2006)
Panama	9°09' N	14.3	Moreno et al. (2006)
Venezuela	8°34' N	14.7	Sunquist et al. (1989)
Venezuela	8°34' N	11.3	Ludlow and Sunquist (1987)
Costa Rica	8°26' N	6.2	Chinchilla (1997)
Peru	11°10' S	11.9	Emmons (1987)
Brazil, North Pantanal	16°50' S	19.2	Bachega (2004)
Brazil, Central Pantanal	18°59' S	28.1	This study
Brazil, Southeast	19°06' S	21	Bianchi et al. (2010)
Brazil, Southeast	19°50' S	7.3	Bianchi and Mendes (2007)
Brazil, South Pantanal	20°05' S	1.9	Concone (2004)
Brazil, Southeast	23°07' S	0	Facure-Giaretta (2002)
Brazil, Southeast	23°17' S	13.6	Wang (2002)
Brazil, Southeast	24°18' S	18.5	Martins et al. (2008)
Brazil, South	25°29' S	5	Abreu et al. (2008)
Brazil, South	25°40' S	6.7	Crawshaw, Jr (1995)

**Fig. 2** **a** Dimensions 1 and 2 and 1 and 3 from the NMDS ordination of items identified in fecal samples of 64 crab-eating foxes (*C. thous*) males (solid line) and females (dashed line). **b** Dimensions 1 and 2 and 1 and 3 from the NMDS ordination of the main items consumed during the dry ( $n=46$ ; solid line) and wet seasons ( $n=35$ ; dashed line), in Nhimirim Ranch, Brazil, from December 2005 to February 2008. Ellipses for males and females and dry and wet season are centered on the averages of each group and comprise about 1 standard deviation. Stress value=0.164. **c** Pearson correlation between the axes of the NMDS ordination and the frequency of items found in fecal samples



that there was extensive overlap in the diets of the crab-eating fox and brown-nosed coati but relatively little overlap between the diets of these species and that of the ocelot (Fig. 5a). The items explaining most of the variation were rodents (*C. laticeps* and *T. pachyurus*), birds, and snakes, which were collectively more often consumed by ocelot than by the two omnivorous carnivores (Fig. 5b).

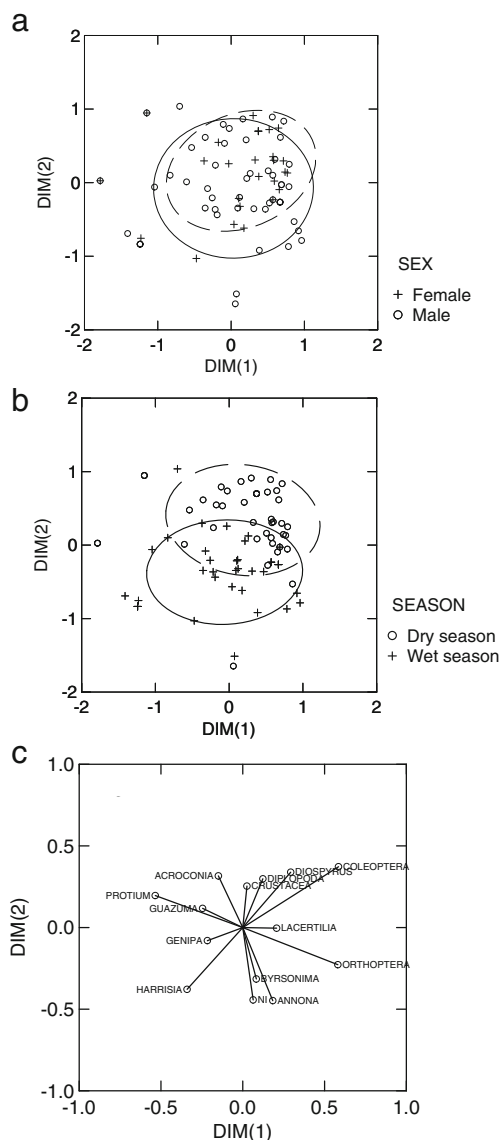
## Discussion

### General dietary patterns

In the Brazilian Pantanal, ocelots prey on both small vertebrates (especially small rodents, snakes, and lizards) as well as medium-sized animals. This differs from the Pantanal sub-region of Miranda, where small mammals represented

83 % of the prey items consumed (Concone 2004). Indeed, the ocelot is sometimes regarded as a specialist consumer of small vertebrates (Emmons 1987; Ludlow and Sunquist 1987). However, several studies have shown that ocelots can eat more mid-sized mammals than expected by chance (Crawshaw Jr 1995; Moreno et al. 2006; Bianchi and Mendes 2007; Bianchi et al. 2010; Oliveira et al. 2010).

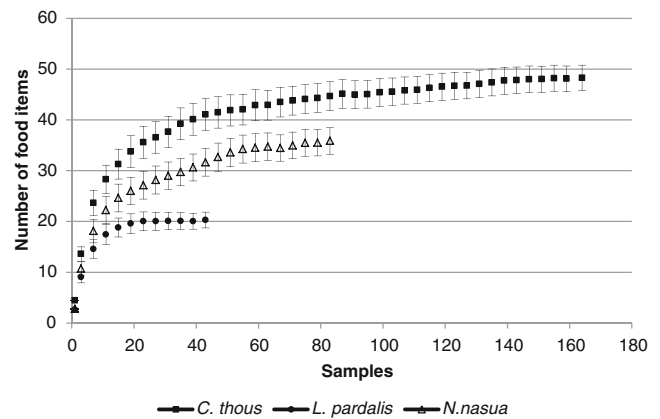
Two observations of ocelot feeding habits are particularly striking. First, the low consumption of armadillos is somewhat surprising not only due to the absence of jaguars—for which armadillos are a common prey (Moreno et al. 2006) but also because armadillos occur in high densities in the Nhimirim Ranch (Desbiez et al. 2010). In two Atlantic Forest areas, for instance, armadillos were very important prey of ocelots (Crawshaw Jr 1995; Bianchi et al. 2010). Moreover, anteaters were frequently consumed in the



**Fig. 3** **a** Dimensions 1 and 2 from the NMDS ordination of items identified in 82 fecal samples from male (solid line) and female (dashed line) brown-nosed coatis (*N. nasua*) and **b** 83 fecal samples from dry and wet season in Nhumirim Ranch, Brazil, from December 2005 to February 2008. Ellipses are centered on the averages of each group and comprise about 1 standard deviation. Stress value=0.15. **c** Pearson correlation between the axes of the NMDS and frequencies of items found in fecal samples

Nhumirim Ranch whereas consumption was rare in other areas (Martins et al. 2008).

Second, the proportion of snakes in the ocelot scats, in turn, was among the highest ever registered. Villa Meza et al. (2002) suggested that there would be positive relationship between the consumption of reptiles and latitude due to latitudinal clines in reptile diversity and biomass. However Villa Meza et al. (2002) did not attempt to test this hypothesis. Using data from 18 studies on the food habits of ocelots across a latitude gradient of 25° S to 18° N, we failed to observe any such clinal relationship (Table 2).



**Fig. 4** Accumulation rates of new prey with sampling ( $\pm$ SD) of carnivores scats in Nhumirim Ranch, Brazil, from December 2005 to February 2008, evaluated by Jackknife procedure

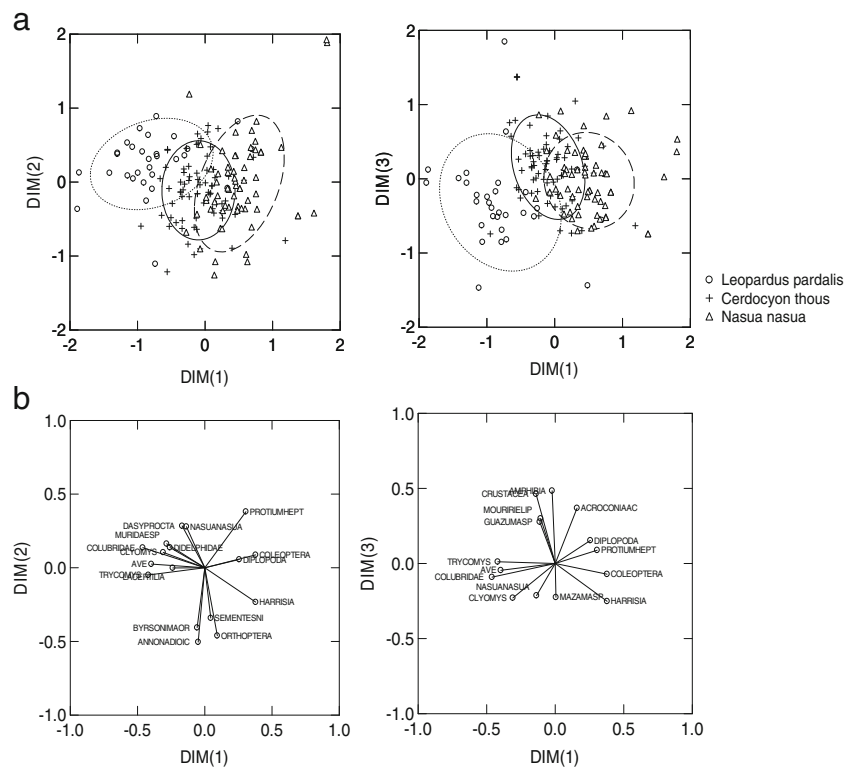
Consumption of fruits, arthropods, and vertebrates by crab-eating foxes has been reported in many studies (e.g., Macdonald and Courtenay 1996; Gatti et al. 2006), and in the Nhumirim Ranch, crab-eating foxes ate similar proportions of each of these three groups (30 % of each item consumed). There was no difference between the diet composition of male and female crab-eating foxes in the study area. Given that males and females are similar in size, and usually travel and forage in pairs, this finding was not unexpected (Bianchi 2009).

The little available information on the diet of the brown-nosed coati is mainly derived from studies conducted in areas near or within large urban centers (Costa 2003; Alves-Costa et al. 2004; Santos and Beisiegel 2006), except for the study conducted by Hirsch (2009) in Foz Iguaçu Park, a protected area as well-preserved as the Pantanal study area, and in all areas, brown-nosed coatis had a primarily insectivorous-frugivorous diet. In central Pantanal, brown-nosed coatis also showed an insectivorous-frugivorous diet, but with a high frequency of frogs, lizards, and snakes (39 % of scats; 12 % of items). Fruits were more important in the wet season (*H. bonplandii*, *A. dioica*, and *B. orbignyana*) and coleopterans and diplopods were more consumed in the dry season. In southeastern Brazil, fruits were an important resource during periods of arthropod scarcity (Alves-Costa et al. 2004) and in other peri-urban areas, fruits seem important year round (Costa 2009).

There was no difference between the diet composition of male and female brown-nosed coatis in the study area, even though there are morphological and ecological differences between sexes. Body size dimorphism of coatis is prominent. In the Pantanal, differences between sexes vary from 8 (tail and head length) to 62 (body mass) and 103 % (lower canine height) (Olfifiers et al. 2010). Adult male and female brown-nosed coatis are also usually spatially segregated during most of the year. While females and immature



**Fig. 5** **a** Dimensions 1 and 2 and dimensions 1 and 3 from the NMDS ordination of the diets of ocelot ( $n=31$ ; dotted line), crab-eating fox ( $n=73$ ; solid line), and brown-nosed coati ( $n=63$ ; dashed line) analyzed from fecal samples collected at Nhumirim Ranch, Pantanal, Brazil from December 2005 to February 2008. The ellipses are centered on the averages of each group and comprise about 1 standard deviation. Stress value=0.170. **b** Pearson correlation between the axes of the NMDS ordination and the frequency of items found in fecal samples



individuals live in social groups (termed bands), males are usually solitary except during the breeding season (Bianchi 2009). Collectively, these differences would suggest different foraging strategies between sexes. However, we observed that the same items were consumed at similar frequencies. Thus, despite the sexual dimorphism, there is no evidence from this population of sexual differences in diet. This differs from *N. narica*; in Panama males and females were observed to differ in their feeding rates (Gompper 1996). If dietary differences are not associated with sexual dimorphism then differences in feeding patterns observed at sites such as Panama may be a consequence rather than a selective cause of dimorphism. In carnivores, dimorphism in body size and dentition size and shape is related with mating systems, with more polygynous species exhibiting greater dimorphism (Gittleman and VanValkenburgh 1997). In fact, several male brown-nosed coatis captured during the study showed wounds or scars. Therefore we suggest that the conspicuous differences in body size and canine morphology are probably related to competition among males for access to females.

#### Dietary segregation between species

Dietary overlap between mid-sized carnivores in Pantanal was high, particularly for the crab-eating foxes and brown-nosed coatis; the overlap between these taxa was larger than between each of these species and the ocelot. Although crab-eating foxes and brown-nosed coatis consume great

amounts of fruits and insects, they also extensively consumed vertebrates in the studied area. Indeed, the greatest overlap among the three species was in the consumption of vertebrates, even though ocelots consumed larger prey than coatis or foxes.

Competitive relationships between predators of different sizes are asymmetric because larger animals can feed on items unavailable to smaller competitors (Sinclair et al. 2003), but the reverse is less likely (Wilson 1975). While such observations break down when species become too large (ca. 21.5 kg) and can no longer sustain their energetic needs on smaller prey (Carbone et al. 1999), ocelots are small enough that they should be able to gain their energetic needs from small prey if necessary, and consume prey typical of the other mesocarnivores with which they spatially overlap. However, as a larger mesocarnivore they can also gain access to species not usually consumed by the smaller predators. Therefore, body size can be used to explain differences in diet in sympatric mesocarnivores. The ocelot can be a competitor and an important predator of mid-size carnivores (Moreno et al. 2006; Bianchi et al. 2010; Oliveira et al. 2010), but its small body size in the Pantanal (8–10 kg; Bianchi 2009) may preclude it as an important predator of mid-sized carnivores. For instance, during our 4-year-monitoring of carnivores, we did not find crab-eating foxes in ocelot scats, and only one ocelot scat had coati hair despite the high density of foxes and coatis in the study area (Desbiez et al. 2010).

Despite of the large diet overlap between coatis and foxes, foraging strategies, habitat use, and activity patterns may minimize competition for resources between these two omnivores. Some fruits are available to crab-eating fox only when they fall while coatis can access them easily on trees. Also, coatis used more forested areas than crab-eating foxes and are active throughout the day while foxes show crepuscular habits (Bianchi 2009). Collectively, the difference in dietary composition among these species implies that crab-eating foxes and brown-nosed coatis have a more diversified diet than ocelots, with separation of the ocelots' diet depending not only on the limited contribution of fruits and invertebrates, but also on the availability and contribution of larger prey. This may partially underpin the degree of resilience of these species. While crab-eating foxes and the brown-nosed coatis are among the most abundant Neotropical carnivores and are commonly found in disturbed environments, ocelots are limited only to environments where those specific preys remain available (Bianchi and Mendes 2007; Oliveira et al. 2010).

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