Feeding of small Neotropical felids (Felidae: Carnivora) and trophic niche overlap in anthropized mosaic landscape of South Brazil

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Resumo

Alimentação de pequenos felídeos neotropicais (Felidae: Carnivora) e sobreposição de nicho trófico na paisagem mosaico antropizada no sul do Brasil. Conhecer a diversidade de uma comunidade e compreender sua dinâmica é especialmente importante em um habitat alterado onde estas informações podem ajudar a melhorar programas de conservação da biodiversidade. Na paisagem alterada de Mata Atlântica de Interior, no oeste do estado do Paraná (25º41' a 25º20'S e 53º56' a 54º35'W), foram coletadas amostras (310) de fezes de felídeos neotropicais, das quais 110 foram identificadas, sendo 39 para *Leopardus guttulus* (gato-do-mato-pequeno), 38 para *Leopardus wiedii* (gato-maracajá) e 33 para *Puma yagouaroundi* (gato-mourisco). As amostras identificadas continham espécies de presas sinantrópicas, como o roedor *Mus musculus* em 44% (*L. guttulus*), 32% (*L. wiedii*) e 15% (P. *yagouaroundi*). Esta observação e a coleta destas amostras na paisagem de uso agrícola sugerem que estes pequenos felinos utilizam esta paisagem antropizada mosaica. Os pequenos mamíferos (< 100 g) foram mais comuns na dieta dessas espécies, sendo *Akondontini* e *Monodelphis* spp. os grupos de presas com maior ocorrência. Além disto, a elaboração do fator de correção de biomassa para estas espécies mostrou ser significativamente eficaz na correção de biomassa consumida de duas das três espécies de felinos estudadas, e por esta razão, é recomendado em futuros estudos destas espécies.

Palavras-chave: Floresta Atlântica de Interior; *Leopardus guttulus*; *Leopardus wiedii*; Matriz agrícola; *Puma yagouaroundi*

Abstract

Understanding the diversity of a community and its dynamics is especially important in altered habitats such as agricultural fields, where this information can help biodiversity conservation programs. In an altered landscape of the interior Atlantic Forest, western Paraná State, Brazil (25º41' to 25º20'S and 53º56' to 54º35'W), samples (310) were collected and a total of 110 samples could be determined for some small Neotropical felids, including 39 *Leopardus guttulus* (oncilla), 38 *L. wiedii* (margay) and 33 *Puma yagouaroundi* (jaguarondi). The diets of these felids contained typical synanthropic prey such as *Mus musculus* in 44% (*L. guttulus*), 32% (*L. wiedii*) and 15% (*P. yagouaroundi*) of the total samples. This observation and the sample collection in agricultural places demonstrate that felids can use this anthropized landscape. The small mammals (<100 g) were more common in the diet of these species. Nevertheless, the correction factor was shown to have significant efficiency in correcting estimates of biomass ingested for two of the three species of felids, and we therefore recommend that these species be used in future studies. Even with this observed coexistence, the food niche of the three species showed a large overlap.

Key words: Agricultural matrix; Interior Atlantic Forest; *Leopardus guttulus*; *Leopardus wiedii*; *Puma yagouaroundi*

Introduction

Knowing how a species uses and shares resources is essential for understanding the mechanisms that allow the coexistence of species (e.g., guild of small Neotropical felids), since differences in resource use may be a key factor in a competitive scenery (SCHOENER 1974) and may determine the diversity in a community (PULLIAM, 2000; DAVIES et al., 2007; DI BITETTI et al., 2010).

Competition for resources may be expected in guilds if morphological and behavioral similarity exists between species, when competitive exclusion of subordinate species may be a consequence (DONADIO; BUSKIRK, 2006; MEACHEN-SAMUELS; VALKENBURGH, 2009; MORIN, 2011). However, resource partition or displacement character can reduce competition and facilitate coexistence among species (MACARTHUR; LEVINS, 1964; MORIN, 2011). Among the resource partition factors, there can be a partition in horizontal (type) and vertical (forest stratum) habitat, time and diet (AUGUST, 1983; DAYAN; SIMBERLOFF, 1998; DI BITETTI et al., 2010). In the food dimension, the use of abundant resources or segregation in prey size can minimize competition, allowing the coexistence of species (ROSENZWEIG, 1966; MOTTA-JUNIOR, 2006). The feeding habit permeates every aspect of the life history of an animal, where it is essential to understand the ecology of a species (CRAWSHAW; QUIGLEY, 2002).

Leopardus guttulus (oncilla), *L. wiedii* (margay) and *Puma yagouaroundi* (jaguarondi) are among the smallest Neotropical felids, with discrete body-weight distribution: *L. guttulus* 1.9 - 2.4 kg (NASCIMENTO, 2010), *L. wiedii* 2.6 - 4.0 kg, *P. yagouaroundi* 3.8 - 6.5 kg (SUNQUIST; SUNQUIST, 2002). *Leopardus guttulus* was recently separated from *L. tigrinus* on the basis of molecular and morphological data that demonstrated that populations of *L. tigrinus* in southern Brazil support a formal recognition as a species (NASCIMENTO, 2010; TRIGO et al., 2013). Thus, in this study we considered all specimens of oncilla as *L. guttulus*.

Two of these species (*L. wiedii* and *P. yagouaroundi*) have a wide geographical distribution, from southern Mexico to southern Brazil (NOWELL; JACKSON, 1996). *Leopardus guttulus* has a smaller distribution area, which includes only the southern distribution area of the old denomination *L. tigrinus* (NASCIMENTO, 2010; TRIGO et al., 2013). This distribution area includes Southeast, South and West-Central regions of Brazil, and northeastern Argentina and Paraguay (NASCIMENTO, 2010). Although these three small Neotropical felids are considered threatened, little ecology information is available about them *in situ* (CALLEIA et al., 2009; DI BITETTI et al., 2010; IUCN, 2014). For example, only four dietary studies are available for *L. wiedii* (KONECNY, 1989; WANG, 2002; ROCHA-MENDES et al., 2010; BIANCHI et al., 2011), and these do not include data in agricultural landscapes and in sympatry

with two other species, *L. guttulus* and *P. yagouaroundi*. For the latter two species, there is also little information about their feeding in a sympatry context (TÓFOLI et al., 2009; SILVA-PEREIRA et al., 2011).

These three small Neotropical felids occur in disturbed places (DI BITETTI et al., 2010; KOSYDAR et al., 2014) and their known feeding repertoire includes insects, amphibians, reptiles, birds and mammals, mostly small species (KONECNY, 1989; WANG, 2002; TÓFOLI et al.. 2009; ROCHA-MENDES et al., 2010; BIANCHI et al., 2011; SILVA-PEREIRA et al., 2011). On the other hand, medium-sized mammals are also reported in the feeding of these small Neotropical felids (WANG, 2002; TÓFOLI et al., 2009). Thus, to compensate for a possible overestimation of the biomass of medium-sized species and a consequent undervaluation of small-sized species, it is important to use correction factors of biomass consumed (OLIVEIRA, 2002). A correction factor is not available for the Neotropical felids, except for *P. concolor* (ACKERMAN et al., 1984), and a bobcat correction factor has been used for smaller species such as *L. pardalis* (VILLA MEZA et al., 2002).

Since *L. guttulus*, *L. wiedii* and *P. yagouaroundi* are known in the interior Atlantic Forest, a region that has undergone great disturbance in natural habitat, and since the information on feeding habitat for these small wildcat species is anecdotal, the objectives of this study were: (1) to provide information on the diet breadth and food niche overlap for these three species when in sympatry; and (2) to develop and test correction factors for the biomass consumed by *L. guttulus* and *L. wiedii*.

Materials and Methods

The extreme west of Paraná State, in southern Brazil (25º41' to 25º20'S and 53º56' to 54º35'W), is located between 120 and 540 m a.s.l. (SANTOS et al., 2006), and has an annual rainfall between 1,500 and 2,200 mm and mean temperature between 16 and 22 ºC (DE ANGELO et al., 2011). The study locality belongs to the ecoregion of the Upper Paraná Atlantic Forest or interior Atlantic Forest (DE ANGELO et al., 2011), which up to the middle of the last century consisted of submontane semi-deciduous forest and alluvial forest

(SALAMUNI et al., 1999). After the human occupation that occurred in the 1950s and the extensive conversion of forest to agricultural areas, only 6% of original forest remains in formations of the Upper Paraná Atlantic Forest (GIRAUDO et al., 2005). However, these remaining forests are fragmented and form, along with the agricultural matrix, a mosaic landscape where annual crops such as soybean (*Glycine max*) and corn (*Zea mays*) predominate. In this region, the National Park of Iguaçu (Brazil) is a major conservation unit and connects to the National Park of Iguazú (Argentina) to form a continuous native forest of over 2,500 km^2 (DI BITETTI et al., 2003).

Carnivore feces were collected between 2007 and 2009, covering foot edges, trails, paths and roads in the small forest fragments, in the agricultural matrix and in the interior of Iguaçu National Park (ParNa Iguaçu). The areas of this study (Figure 1) were selected due proximity and easy accessibility and are presented below.

1) Iguaçu National Park (ParNa Iguaçu) (25º05' to 25º41'S and 53º40' to 54º38'W) is the largest conservation unit in the interior Atlantic Forest, covering 185,256 ha (AZEVEDO, 2008). This conservation unit is bordered to the south by the Iguaçu River, which is the frontier with Iguazu National Park, Argentina. There, sampling was carried out next to Iguaçu Falls (Cataratas do Iguaçu), an area of approximately 3,300 ha, which is tourist site. The samples were collected in Poço-preto secondary road and Bananeiras, Hidrômetro and Macuco trails.

2) Santa Maria corridor located between Iguaçu National Park and Itaipu Binacional Dam reservoir (details in MARCON et al., 2013). The samples were collected in the Santa Maria Conservation Unit (SMCU), a private reserve of natural patrimony with 242 ha (25°49'S and 54°36'W), on a road at Santa Maria farm and in the riparian forest of the Apepú River next to SMCU.

3) Três Pinheiros farm (25°38'S and 54°11'W) is 12 km from São Miguel do Iguaçu city and 9 km from Iguaçu Nacional Park. The legal reserve of secondary forest this farm

FIGURE 1: Location of sampling areas in western Paraná State, southern Brazil. (A) The study (black) area in South America, and; (B) in the triple frontier: Argentina, Brazil and Paraguay. (C) Forest remnants and watercourses in study area.
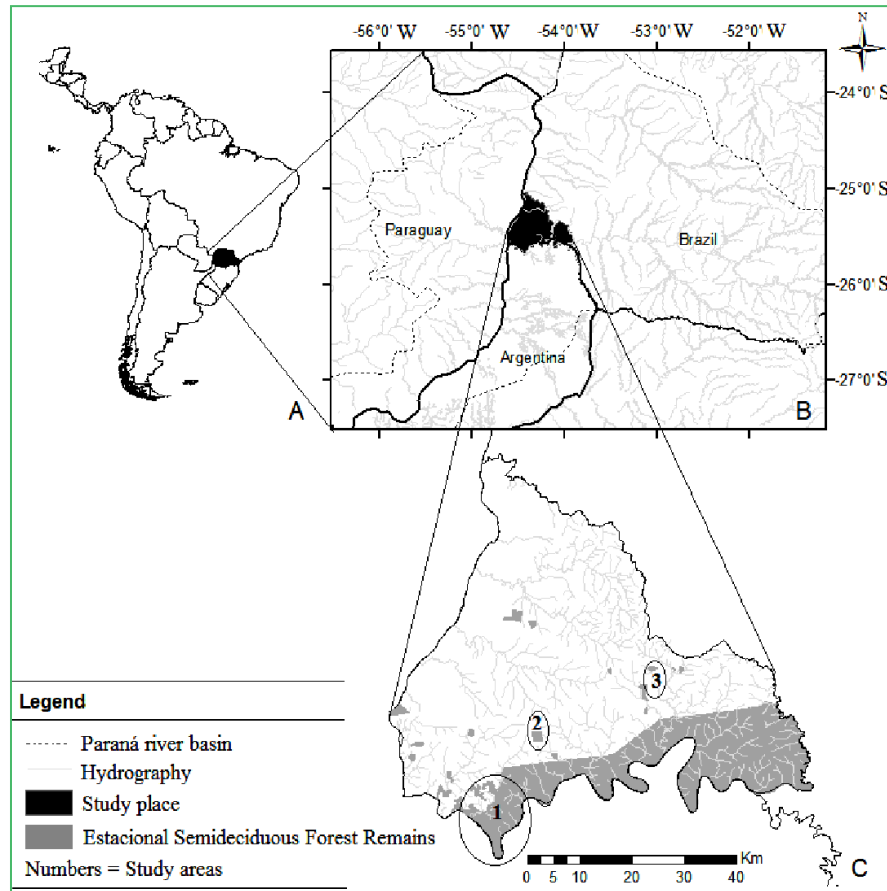
is connected to the secondary riparian forest of the Represo River and together covers 70 ha. On this farm, samples were collected on secondary roads in agricultural places, trails in the interior of secondary forests and edges of these forest fragments.

In addition, samples sporadically collected next to ParNa Iguaçu and gastrointestinal samples of roadkill of small Neotropical felids were also included in this analysis.

A total of 310 samples were collected. Of these, 298 were fecal samples and twelve were gastrointestinal samples directly removed from dead felids found on the road. All these samples were collected under authorizations 025-2007, 18,347 and 12,200, provided by IBAMA (Environment Institute of Brazil) and ICMBio (Biodiversity Conservation Institute of Brazil),

and 224/10 IAP, provided by IAP (Environment Institute of Paraná State – Brazil).

After being collected, the samples were stored in plastic bags, identified and further processed by washing in 0.02 mm filtering mesh cones and drying at 60 ºC for 24 h. During sample screening (fecal or gastrointestinal samples), we separated and stored the contents that allowed the identification of animal species by assessing the microstructure of the guard hairs. The current identification method used for these three species follows three procedures: identification of the medullary pattern, cuticular pattern, and width to length ratio of the cuticular scales of the hair shaft (QUADROS; MONTEIRO-FILHO, 2010). The medullary pattern, called trabecular with fringed margins, is similar in all small Brazilian Neotropical felids (VANSTREELS et al., 2010). The cuticular character, however, divides

them into two pairs of species: the losangic pattern clusters *L. guttulus* with *P. yagouaroundi*, and *L. wiedii* shows the foliaceous pattern (QUADROS; MONTEIRO-FILHO, 2010). Each small Neotropical Brazilian felid can be identified using the width to length ratio of the scales (Figure 2) on the shaft of the guard hairs (QUADROS; MONTEIRO-FILHO, 2006; 2010). The hairs of predators and prey were identified using reference data (QUADROS, 2002; subsequently published as QUADROS; MONTEIRO-FILHO, 2010; and MIRANDA et al., 2014). Samples were identified to the species level using the guard hairs, which enter the gastrointestinal system by ingestion during self-cleaning behavior (ECKSTEIN; HARTS, 2000). Other items (prey hairs, teeth, exoskeleton, feathers, seeds) were identified by comparative analysis (see table results for details) with museum pieces (Collection of Zoology Department, Mammology Section at Paraná Federal University (DZUP-CCMZ-UFPR)) or pieces obtained in the study area (*e.g.*, *Zea mays*, *Triticum aestivum* and *Glycine max*).

The occurrence frequency of food items were calculated by dividing the number of samples in which a given item was found by the total number of samples (resulting in a percentage), and the percentage of occurrence of each item was calculated by dividing the number of samples in which a given item was found by the total number of all items (resulting in a percentage). Frequency of occurrence indicates whether an item is frequent in the diet (KONECNY, 1989; MARTINS et al., 2008), whereas percentage of occurrence indicates the relative importance between items (MAEHR; BRADY, 1986; MARTINS et al., 2008).

The niche breadths of the species were determined using the standardized Levins index and Smith´s measure (KREBS, 1999). The standardized Levins (B_{sta}) is widely used and was calculated as a comparative measurement with other works. This index is expressed on a scale of zero to one, where values close to zero represent a narrow niche and those close to one a broad niche. Smith's measures (FT) were calculated to measure the confidence interval and to determine if niche breadth differs between felid species. This index varies like the standardized Levins with zero representing a narrow niche and one a broad niche. The Pianka index (KREBS, 1999) was used to assess the degree of overlap between feeding niches, which is also expressed on a scale from zero to one, where values close to zero represent little overlap and those close to one extensive overlap. The prey records observed were randomized, and the overlap

FIGURE 2: Hair patterns of the three species of Neotropical felids. (A) Medullary pattern, trabecular with fringed margins; losangic pattern for (B) *Leopardus guttulus* and (D) *Puma yagouaroundi*; and imbricate foliaceous for (C) *L. wiedii*.
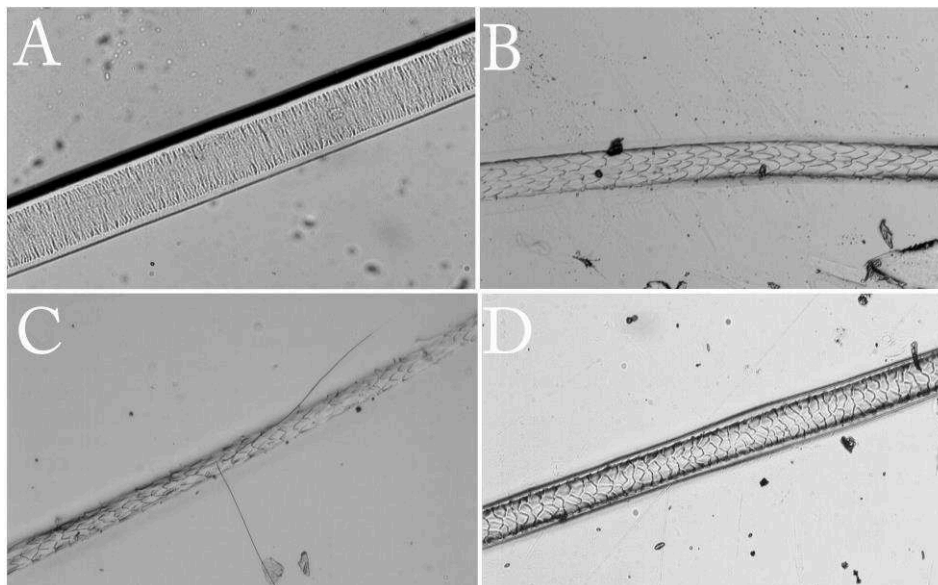
niches were recalculated 1000 times. We did not consider that the observed overlap was equal to the expected overlap when the occurrence was equal or less than 5% of randomized values ($\alpha \leq 0.05$).

To calculate the consumed biomass, we used the information on the live weights of prey (PAGLIA et al., 2012). The estimates of biomass consumed by predators were calculated as the product of the weight of the prey and the frequency of occurrence observed in stool samples. These values were corrected by a linear factor (ACKERMAN et al., 1984). For this, whole carcasses of rat (*Rattus novergicus*) and quail (*Coturnix* sp.) were offered to adult captive *L. guttulus* (n = 21) and *L. wiedii* (n = 14) maintained at the ITAIPU Binacional Wildlife Breeding Center. Carcasses were offered to all specimens of *L. guttulus* and *L. wiedii* simultaneously at 6:00 p.m. for eight days, with four consecutive days for quail and for rat. On average, we offered 384 ± 42 (SD) g of quail and 355 ± 50 g of rat to *L. guttulus*, and 412 ± 86 g of quail and 385 ± 32 g of rat to *L. wiedii*. On the next morning of each day, the remnants of offered carcass were measured for each individual and the weight consumed calculated. All offered and consumed biomass values were used to calculate a linear regression for *L. guttulus* and for *L. wiedii*, and to obtain a linear correction factor.

A total of 168 measurements for *L. guttulus* and 112 for *L. wiedii* were utilized in the linear regression. Normality of the data was tested prior to regression analysis. The linear equation obtained ($\hat{y} = a - b.X$) was used as a correction factor for the biomass consumed, in which $\hat{y}$ is the value of consumed biomass corrected, *a* is the constant representing the intercept of the line with the vertical axis, *b* is the constant representing the slope of the line and *X* is the observed biomass or the live weight of the prey. Difference hypothesis between uncorrected (expected) and corrected biomass (observed) was tested with a Wilcoxon signed-rank test (T) considering $\alpha = 0.05$. This test was used because number of prey for all felids was less than 20 and observed and expected data were considered paired. Due to the small number of specimens of *P. yagouaroundi* in captivity, the correction of biomass for this felid was calculated with the correction factor of *L. wiedii*, because this felid has

a similar body weight as *P. yagouaroundi* (NOWELL; JACKSON, 1996). Regarding the correction factor of consumed biomass, the linear regression between the values of biomass supplied and consumed provided the following linear equations: *L. guttulus* $\hat{y} = 197.9 + 0.19 * X$, and $r^2 = 0.006$; *L. wiedii* $\hat{y} = 154.6 + 0.35 * X$, and $r^2 = 0.03$. According to the behavior of biomass correction by the linear equations obtained, biomass consumption values were corrected beginning at 245 g for *L. guttulus* and 238 g for *L. wiedii*.

To evaluate the importance of prey size, we adapted the method developed by Emmons (1987) that organizes prey size into biomass classes and calculates the percentage occurrence of biomass prey considering the total sum of prey biomass consumed and its frequency. Here, we considered the followings biomass classes: weight less than 100 g, between 100 and 1000 g and more than 1000 g.

Results

Of the 310 samples, 157 (51%) were identified as being from wild felids, most of which (110 or 35%) were one of the three species of small Neotropical felids under study. Of these, 98 were identified from stool samples and 12 from gastrointestinal contents of felids that were dead on the roads. Only one sample was found in the stomach of *L. wiedii* and contained two specimens of *Didelphis* sp. Other hair samples were collected in the distal intestine.

All dead felids were found at the intersection between river and road. Among the other identified samples, six were from *L. pardalis* (ocelot), 33 from *P. concolor* (puma) and eight from *Panthera onca* (jaguar), all of which were collected inside Iguaçu National Park.

A total of 39 samples were assigned to *L. guttulus* (Table 1), 38 to *L. wiedii* (Table 2) and 33 to *P. yagouaroundi* (Table 3). On average, mammals represented 79% of the items consumed by the three species. *L. guttulus* (80%, n = 50) and *P. yagouaroundi* (82.2%, n = 37) consumed more mammalian prey than did *L. wiedii* (74.1%, n = 46).

TABLE 1: Relative frequency and biomass of prey consumed by oncilla (*Leopardus guttulus*), collected in Southwest Paraná State, Atlantic Forest domain, Brazil.

Species weight	ID[1]	N[2]	PO%[3]	FO%[4]	BP (kg)[5]	FC (kg)[6]	BC (kg)[7]	BR (%)[8]
Less than 100 g								
Monodelphis spp.	H,T	08	12.9	20.5	0.05	0.05	0.40	11.8
Akodontini	T	13	20.9	33.3	0.05	0.05	0.65	19.2
Oligoryzomys spp.	H	03	4.8	7.6	0.03	0.03	0.09	2.6
Mus musculus	T	17	27.4	43.5	0.02	0.02	0.34	10.0
100-1000 g								
Caluromys lanatus	H	02	3.2	5.1	0.35	0.26	0.52	15.3
Didelphis spp.	H	02	3.2	5.1	0.80	0.34	0.68	20.1
Nectomys squamipes	H,T	02	3.2	5.1	0.10	0.10	0.20	5.9
Rattus spp.	H,T	02	3.2	5.1	0.10	0.10	0.20	5.9
Cavia sp.	H	01	1.6	2.5	0.10	0.30	0.30	8.8
Serpentes NI	SD	04	6.4	10.2	0.55	–	–	–
Ave NI	F	08	12.9	20.5	–	–	–	–
Subtotal		**62**	**100**	**–**	**–**	**–**	**3.30**	**100**
Other items								
Grass (NI)	S	07	–	–	–	–	–	–
Coleoptera	C	02	–	–	–	–	–	–

1 Identification method: H = microscopic pattern of hair, T = tooth or bone structure, SD = scale and/or ectoderm, F = feather, S = grass, C = comparison of exoskeleton portion; 2 Total identified items; 3 Number of records for this prey species ÷ total records for all prey species; 4 Number of records for this prey species ÷ total number of fecal samples; 5 Approximate weight of adult prey; 6 Corrected biomass; 7 Total consumed biomass; 8 Frequency of occurrence of biomass = values of BC (kg) x100 ÷ total sum of BC (kg).

The frequency of occurrence of all prey species in their respective live-weight ranges revealed that small prey were the most important for the three carnivores (less than 100 g). On the other hand, when the biomass consumed was analyzed, prey between 100 and 1000 g were more important to *L. guttulus* and *P. yagouaroundi*, and prey greater than 1000 g for *L. wiedii* (Tables 1, 2, 3). Prey heavier than 1000 g were not detected in the diet of *L. guttulus*. In these samples, insect exoskeletons (Blattaria, Hymenoptera, Lepidoptera and Orthoptera) and grasses (Poaceae) were less important in biomass. However, these were found respectively in 29 (26%) and 19 (17%) samples for all three species. The Akondontini rodents and Monodelphis marsupials were the most important food items for the three small Neotropical felids.

TABLE 2: Relative frequency and biomass of prey consumed by margay (*Leopardus wiedii*), collected in Southwest Paraná State, Atlantic Forest domain, Brazil.

Species weight	ID[1]	N[2]	PO%[3]	FO%[4]	BP (kg)[5]	FC (kg)[6]	BC (kg)[7]	BR(%)[8]
Less than 100 g								
Monodelphis spp.	H,T	04	6.4	10.5	0.05	0.05	0.20	2.1
Akodontini	T	15	24.1	39.4	0.05	0.05	0.75	8.4
Mus musculus	T	12	19.3	31.5	0.02	0.02	0.24	2.6
100-1000 g								
Marmosa paraguayanus	H	01	1.6	2.6	0.13	0.13	0.13	1.4
Caluromys lanatus	H	03	4.8	7.8	0.35	0.27	0.81	8.9
Philander frenatus	H	02	3.2	5.2	0.16	0.16	0.32	3.5
Didelphis spp.	H	03	4.8	7.8	0.80	0.43	1.29	14.1
Salvator merianae	SD	04	6.4	10.2	0.50	0.32	1.28	14.0
Ave NI	F	12	19.3	20.5	–	–	–	–
More than 1000 g								
Coendou spinosus	H	01	1.6	2.6	1.20	0.57	0.57	6.2
Galicts cuja	H	01	1.6	2.6	1.50	0.67	0.67	7.3
Sapajus nigritus	H	02	3.2	5.2	2.00	0.85	1.70	18.6
Sylvilagus brasiliensis	H	02	3.2	5.2	1.20	0.57	1.14	12.5
Subtotal		**62**	**100**				**09**	**100**
Other items								
Grass (NI)		06	–	–	–	–	–	–
Zea mays (seed)		01	–	–	–	–	–	–
Triticum aestivum (seed)		01	–	–	–	–	–	–
Glycine max (seed)		01	–	–	–	–	–	–
Blattaria		01	–	–	–	–	–	–
Coleoptera		05	–	–	–	–	–	–
Hymenoptera		05	–	–	–	–	–	–
Lepidoptera		01	–	–	–	–	–	–
Orthoptera		02	–	–	–	–	–	–

1 Prey identification method: H = microscopic pattern of hair, T = tooth or bone structure, SD = Scale and/or ectoderm, F = Feather, S = grass, E = exoskeleton portion, SE = seed; 2 Total identified items; 3 Number of records for this prey species ÷ total records for all prey species; 4 Number of records for this prey species ÷ total number of fecal samples; 5 Approximate weight of adult prey; 6 Corrected biomass; 7 Total consumed biomass; 8 Frequency of occurrence of biomass = values of BC (kg) x100 ÷ total sum of BC (kg).

TABLE 3: Relative frequency and biomass of prey consumed by jaguarondi (*Puma yagouaroundi*), collected in Southwest Paraná State, Atlantic Forest domain, Brazil.

Species weight	ID[1]	N[2]	PO%[3]	FO%[4]	BP (kg)[5]	FC (kg)[6]	BC (kg)[7]	BR(%)[8]
Less than 100 g								
Monodelphis spp.	H,T	10	22.7	30.3	0.05	0.05	0.50	8.7
Akodontini	T	10	22.7	30.3	0.05	0.05	0.50	8.7
Oligoryzomys spp.	H	01	2.2	03	0.03	0.03	0.03	0.5
Mus musculus	T	05	11.3	15.1	0.02	0.02	0.10	1.7
100-1000 g								
Didelphis spp.	H	04	09	12.1	0.80	0.43	1.72	30
Nectomys squamipes	H,T	01	2.2	03	0.10	0.10	0.10	1.7
Rattus spp.	H,T	01	2.2	03	0.10	0.10	0.10	1.7
Cavia sp.	H	01	2.2	03	0.55	0.34	0.34	5.9
Serpentes NI	SD	01	2.2	03	–	–	–	–
Ave NI	F	07	15.9	21.2	–	–	–	–
More than 1000 g								
Dasyprocta azarae	H	01	2.2	03	3.00	1.20	1.20	20.9
Coendou spinosus	H	01	2.2	03	1.20	0.57	0.57	9.9
Sylvilagus brasiliensis	H	01	2.5	03	1.20	0.57	0.57	9.9
Subtotal		**44**	**100**				**5.73**	**100**
Other items								
Grass (NI)		05	15.1	–	–	–	–	–
Coleoptera		03	09	–	–	–	–	–
Hymenoptera		01	03	–	–	–	–	–
Lepidoptera		01	03	–	–	–	–	–
Orthoptera		01	03	–	–	–	–	–

1 Prey identification method: H = microscopic pattern of hair, T = tooth or bone structure, SD = scale and/or ectoderm, F = feather, S = grass, C = exoskeleton portion; 2 Total identified items; 3 Number of records for this prey species ÷ total records for all prey species; 4 Number of records for this prey species ÷ total number of fecal samples; 5 Approximate weight of adult prey; 6 Corrected biomass; 7 Total consumed biomass; 8 Frequency of occurrence of biomass = values of BC (kg) x100 ÷ total sum of BC (kg).

The trophic niche breadth of the three species was similar (see Smith's measure in Table 4). However, *L. guttulus* was the broadest, followed by the niches of *L. wiedii* and *P. yagouaroundi*. All three species had high levels of trophic niche overlap (average ≈ 90%). For *L. guttulus* and *L. wiedii*, this overlap was larger than that for *L. guttulus* and *P. yagouaroundi* or *P. yagouaroundi* and *L. wiedii* (Table 4). All observed niche values were higher than expected (α<0.05).

Regarding the correction factor for consumed biomass, five items for three prey were corrected for *L. guttulus*, 16 items for seven prey for *L. wiedii*, and eight items for five prey for *P. yagouaroundi*. Differences

between observed and corrected biomass were detected for *L. wiedii* (T = 0.00, Z=2.20, p < 0.05) and *P. yagouaroundi* (T = 0.00, Z=2.02, p < 0.05), but not for *L. guttulus* (T = 0.00, Z=1.60, p > 0.05).

Discussion

The success in identification of fecal samples for wild felids (51%) can be considered a satisfactory result since results above 40% are considered efficient (ROCHA-MENDES et al., 2010). Even with this good result, this technique can provide better results if considered as part of a tool set that includes footprints

TABLE 4: Amplitude and overlap of trophic niches among oncilla (*Leopardus guttulus*), margay (*Leopardus wiedii*) and jaguarondi (*Puma yagouaroundi*) in an agricultural mosaic in Southwest Paraná State, Atlantic Forest domain, Brazil.

Predator	B_{sta}[1]	FT[2]	Pianka's overlap index		
			L. guttulus	*L. wiedii*	*P. yagouaroundi*
L. guttulus	0.51	0.91 (0.85-0.95)	1.00	–	–
L. wiedii	0.47	0.89 (0.83-0.94)	0.89[3]	1.00	–
P. yagouaroundi	0.43	0.87 (0.80-0.94)	0.85[3]	0.84[3]	1.00

[1] Standardized Levins index for niche breadth; [2] Smith's measure for niche breadth and minimum and maximum 95% confidence interval; [3] |Overlap larger than expected by chance α ≤ 0.05 in 1000 randomizations.

and biomolecular techniques (VANSTREELS et al., 2010).

Few identified samples of small Neotropical felids were collected inside Iguaçu National Park (n = 27). In this region, a camtrap study detected more *L. guttulus* and *L. wiedii* in the least-protected sites where the big felids were less associated (DI BITETTI et al., 2010). This pattern of small Neotropical felids in degraded areas was related to released ocelot and puma populations, which are possibly caused by a decline in jaguar populations (see also MORENO et al., 2006; PAVIOLO et al., 2008) and also explains that observed in this study. The other samples (n = 83) were collected in the buffer zone of Iguaçu National Park (10 km of the edge this conservation unit). These samples were collected at the edge of small forest fragments or the forests that surround small rivers. In both cases the sampling sites were transition areas between forest fragment and corn or soybean fields.

The noted predominance of mammals lighter than 1000 g in the diets of *L. guttulus*, *L. wiedii* and *P. yagouaroundi* (KONECNY, 1989; FACURE; GIARETTA, 1996; WANG, 2002; TÓFOLI et al., 2009; ROCHA-MENDES et al., 2010; SILVA-PEREIRA et al., 2011) may be related to the fact that these are the most abundant mammals in the Neotropical region (ROBISON; REDFORD, 1986; SOLARI; RODRIGUES, 1997; ABREU et al., 2008), and tend to increase in abundance in regions of altered forest habitat (LAURANCE et al., 2002). This is especially supported by the low occurrence of rodents in the diet of small Neotropical felids in landscapes where they are

less abundant, with the highest occurrence of potentially more abundant items in the landscape, such as lizards (OLMOS, 1993). Furthermore, medium- and large-sized species (>1000 g) are less abundant and less diverse in altered landscapes (CHIARELLO, 1999). Thus, the predominance of small mammals in the diets of small Neotropical felids points to their possible opportunistic character, since they do not seem to maximize their energy input by selecting prey by size and consuming small items, which are potentially more abundant in the altered landscape (SILVA-PEREIRA et al., 2011). Sharing abundant resources is one of the factors that may explain the broad food niche overlap between these three species and their coexistence (see also WANG, 2002; MOTTA-JUNIOR, 2006; SILVA-PEREIRA et al., 2011; DI BITETTI et al., 2010). This is corroborated by the data of abundance of non-volant small mammals in the interior Atlantic Forest, where Akodontini is more abundant group (DE LA SANCHA, 2014). On the other hand, the consumption of large prey (>1000 g), for example, *Dasyprocta azarae* and *Sapajus nigritus*, by *L. wiedii* and *P. yagouaroundi* (WANG, 2002; TÓFOLI et al., 2009; ROCHA-MENDES et al., 2010; SILVA-PEREIRA et al., 2011), but not observed for *L. guttulus* (SILVA-PEREIRA et al., 2011), is other factor that may contribute to reducing the competition between these species (ROSENZWEIG, 1966).

These observations of large prey consuming small Neotropical felids are related to the use of carcasses (WANG, 2002; TÓFOLI et al., 2009). However, there is no evidence of such behavior in small Neotropical felids (SILVA-PEREIRA et al., 2011). The fact that these animals consume prey heavier than 1000 g highlights

the importance of using correction factors of biomass in studies of the feeding ecology of small Neotropical felids, since their capacity to consume biomass is less than the live weight of the species included in their food. The difference between the observed and corrected biomass was significant only for *L. wiedii* and *P. yagouaroundi*, illustrating that estimates are not corrected and are overestimated. Because of the correlation between the densities of the prey biomass available in the landscape and population density of carnivores (CARBONE; GITTLEMAN, 2002; HETHERINGTON; GORMAN, 2007), the accuracy of such information is important for the proper planning of the conservation of this group of species *in situ*.

Furthermore, it is important to note that the partition of circadian activity of these three species may be another niche dimension that facilitates their coexistence. Diurnal-crepuscular prey, e.g., *Sapajus nigritus*, *Galicts cuja* and *Dasyprocta azarae* (CULLEN et al., 2000; DI BITETTI et al., 2000; YENSEN; RARIFA, 2003), were consumed only by *L. wiedii* and *P. yagouaroundi* and not *L. guttulus*. In a circadian rhythm study conducted in this same area (DI BITETTI et al., 2010), the circadian activity of *L. wiedii* and *P. yagouaroundi* was nocturnal with small percentage at twilight.

It is also important to highlight the consumption of cursorial and arboreal prey by the *L. wiedii*, a felid considered adapted to arboreal life (OLIVEIRA, 1998). This information indicates that this species makes use of food resources on both forest strata (PASSAMANI, 1995; AZEVEDO, 1996; SOLORZÁNO-FILHO, 2006; CALLEIA et al., 2009). Another work has indicated that the margay moves on the ground (KONECNY, 1989), and eats mostly arboreal rodents (FACURE; GIARETTA, 1996), but this is based on few observations. On the other hand, reports on *L. wiedii* using the upper stratum of forests and consuming arboreal prey or birds are frequent (XIMENEZ, 1982; MONDOLFI, 1986; PASSAMANI, 1995; AZEVEDO, 1996; OLIVEIRA, 1998; SOLORZÁNO-FILHO, 2006; BIANCHI et al., 2011). In this fragmented place, arboreal species were found in stool samples of the three small Neotropical felids collected in the agricultural matrix,

e.g., *Caluromys lanatus*, *Sapajus nigritus*, *Marmosa paraguayanus* (DI BITETTI et al., 2000; GRELLE, 2003). This consumption of arboreal prey also suggests that the maintenance of forest fragments is an important factor for these small Neotropical felids in this landscape with agricultural use.

Finally these results emphasize that these three felids use small prey as important food items, such as Akodontini rodents and *Mus musculus*. Nevertheless, we found that *L. wiedii* and *P. yagouaroundi* consumed medium-sized mammals. For this, the correction factor improved efficiency in estimates of consumed biomass, and it is important to use it in future studies. For this reason, we point out the need for correction factors for biomass in *L. pardalis* and *P. yagouaroundi*, which must be determined and tested in the future. The results of their broad feeding niche overlap indicate that the coexistence of these small wildcats may be facilitated by the consumption of abundant prey such as Akondontini rodents, beyond subtle stratification in circadian activity, verticalization of habitat and body size of these felids.

Acknowledgements

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