



Original investigation

## Temporal and dietary segregation in a neotropical small-felid assemblage and its relation to prey activity

Mariana B. Nagy-Reis <sup>\*</sup>,<sup>1</sup>, Victor H.S. Iwakami, Cesar A. Estevo <sup>1</sup>, Eleonore Z.F. Setz

Universidade Estadual de Campinas, UNICAMP, Biology Institute, Bertrand Russel, 01505, Mailbox: 6109, Campinas, 13083-970, Brazil

### ARTICLE INFO

#### Article history:

Received 7 January 2018

Accepted 16 December 2018

Available online 17 December 2018

Handled by Mauro Lucherini

#### Keywords:

Ocelot  
Margay  
Oncilla  
Jaguarundi  
Niche segregation

### ABSTRACT

Mechanisms that decrease niche overlap in at least one of its dimensions (i.e., spatial, temporal, or dietary) tend to facilitate coexistence of similar, sympatric species. We investigated whether temporal or dietary segregation plays a significant role in the coexistence of Neotropical small felids. In addition, we examined the role of prey activity in shaping their time use. We compared the activity and diet of four felids (oncilla - *Leopardus guttulus*, margay - *L. wiedii*, jaguarundi - *Puma yagouaroundi*, and ocelot - *L. pardalis*) using camera trapping and scat surveys (45 sampling sites) in an Atlantic Forest remnant (35,000 ha) in Brazil. Ocelot, margay, and oncilla seem to be generalists and, overall, they consumed mammalian prey species of distinct sizes. As a consequence, we found moderate dietary overlap between all pairs of felids and low between ocelot and the other species. Oncilla and margay seem to be cathemeral, jaguarundi diurnal, and ocelot nocturnal, which resulted in low to moderate temporal overlap between them, potentially decreasing interspecific encounters. Predator-prey temporal overlap seems to be moderate for oncilla, margay, and jaguarundi, but high for ocelot. Our results suggest that time partitioning associated with dietary differences contribute to the coexistence of this Neotropical small-felid assemblage, and that prey activity is a factor shaping their activity pattern, especially for ocelot.

© 2018 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

### Introduction

Morphologically similar and closely related species usually have high niche overlap, which leads to competitive interactions when in sympatry (Schoener, 1974). Such competitive interactions can influence the presence, abundance, behavior, and distribution of sympatric carnivores (Macdonald et al., 2011), and mechanisms that decrease niche overlap in at least one of its dimensions (i.e., spatial, temporal, or dietary) are usually selected.

Although segregation in habitat and space are typical mechanisms to alleviate niche overlap across several taxa, time partitioning is expected to be common among predators, since their food (prey) display peaks of activity throughout the day (Schoener, 1974). Therefore, prey activity may also play an important role in shaping how predators use their time (e.g., Delibes-Mateo et al., 2014; Foster et al., 2013; Harmsen et al., 2011; Roth and Lima, 2007; Weckel et al., 2006).

Felids present similar morphologies due to relatively recent divergence and constraints imposed by foraging and diet (Johnson et al., 2006; Kitchener et al., 2011). Therefore, they are a good model for understanding how closely related and morphologically similar species can coexist. In the Neotropical rainforests, four small felids are found living in sympatry: ocelot (*Leopardus pardalis*), jaguarundi (*Puma yagouaroundi*), margay (*L. wiedii*), and oncilla (*L. guttulus*) or northern oncilla (*L. tigrinus*; formerly the same species as *L. guttulus* - Trigo et al., 2013a). These species have limited differences in body sizes (8–15 kg, 4.5–9 kg, 3–9 kg, and 1.5–3 kg, respectively; Emmons and Feer, 1997), which typically lead to high exploitative competition (Donadio and Buskirk, 2006; Rosenzweig, 1966). At the same time, as ocelot is 2–4 times larger than the other three species, the chances of interference competition (i.e., harassment and killing) are also high (Donadio and Buskirk, 2006).

Considering that Neotropical small felids seem to co-occur independently and do not seem to avoid each other spatially (Massara et al., 2016; Nagy-Reis et al., 2017), here we investigated whether dietary or temporal segregation plays an important role in their coexistence. In addition, we also examined the importance of prey activity in shaping their time use. If species segregate in diet, we would expect them to have low dietary overlap by consuming prey of distinct species/sizes. If they segregate in time, we would expect them to have low temporal overlap by being active in different time

\* Corresponding author.

E-mail address: [nagy.reis@ualberta.com](mailto:nagy.reis@ualberta.com) (M.B. Nagy-Reis).

<sup>1</sup> Current address: Department of Biological Sciences, University of Alberta, 116 St. and 85 Ave, Edmonton, T6G 2R3, Canada.

of day. Lastly, if prey activity is a key factor shaping their use of time, we would expect to find a high temporal overlap between these predators and their main prey.

## Methods

### Study area

Serra do Japi is a protected area located in southeast Brazil (47°03'40"W to 46°52'20"W and 23°22'30"S to 23°11'35"S). Although it represents one of the few large remnants of Atlantic Forest (35,000 ha), as most of this ecoregion, it suffers several anthropogenic pressures, including poaching, real state pressure, and productive activities. The study site is characterized by semideciduous mesophilic forest with mountainous terrain and a seasonal climate (Morellato, 1992). The mean temperature is 19.7°C, and the mean annual rainfall is 1422 mm, with a dry and cold season occurring from April to September and a wet and warm season from October to March (Morellato, 1992).

### Data collection

We surveyed 45 sampling sites distributed in a regular grid and spaced approx. 1.5 km apart (Fig. 1). Data were collected from April 2013 to September 2014 using camera trapping (passive infrared camera traps; Bushnell Trophy Cam; N = 5198 trap days) and scat sampling (see Nagy-Reis et al., 2017 for details; our paper is intended to complement their study). We collected data on four species of Neotropical small felids: oncilla (*Leopardus guttulus*), margay (*L. wiedii*), jaguarundi (*Puma yagouaroundi*), and ocelot (*L. pardalis*), in addition to data on their main prey. We visited each sampling site six times to collect scats (three in the dry season and three in the rainy season). We collected all scats found along a 1-km segment in the dirt road closest to each site (total sampling effort = 207 km).

### Diet

We identified felid scats using trichology (analyzing the cuticle patterns of the guard hairs; following Quadros and Monteiro-Filho, 2006) and validated our identification using molecular analysis (using mini-barcoding and comparing two markers from mitochondrial DNA; see Nagy-Reis et al., 2017 for details). We washed scats in two sieves (0.5 mm and 1.0 mm) under running water and then separated food items macroscopically (according to Reynolds and Aebischer, 1991), into the following categories: mammal bones, bird bones, reptile bones, hair, feathers, scales, insect parts, plant parts, and inorganic materials (e.g., sediments and rock fragments). We identified the items at the lowest taxonomic level possible (e.g., species, genus, family, order) with the help of specialists (see acknowledgements) and literature (Sakane, 2015). Items that we were unable to classify but were morphologically similar were grouped into morphotypes. We then determined the number of occurrence (i.e., number of items,  $n$ ), percentage of occurrence (i.e., proportion of item in diet, PO), and frequency of occurrence (i.e., proportion of scats with item, FO). Additionally, we calculated the geometric mean body weight of mammalian prey, which considers the number of occurrence ( $n$ ) of each prey species and their respective body weight from the literature. The number of taxa found in the diet of each felid was assumed to be the minimum number of taxa, as some items were not successfully identified.

### Activity pattern

Activity patterns were obtained from the time printed in the photos of the four small felids and their main prey. We used

only one photo every 60-minute interval to avoid auto-correlation (similarly to Porfirio et al., 2016). We used our diet results and literature review (Bianchi et al., 2010, 2011; Meza et al., 2002; Moreno et al., 2006; Silva-Pereira et al., 2011; Tófoli et al., 2009; Trigo et al., 2013b; Wang, 2002) to determine the main potential prey of each felid species. We considered small mammals (<1 kg; mainly small rodents and marsupials) and small birds (<0.2 kg; mainly passerines and doves) as the main prey for margay, oncilla, and jaguarundi, and small and medium-sized mammals (between 1 and 13 kg; mainly opossums – *Didelphis* sp., Brazilian rabbit – *Sylvilagus brasiliensis*, paca – *Cuniculus paca*, armadillos – *Dasypodidae*, and porcupine – *Coendou spinosus*) as well as small and medium-sized birds (at a smaller degree; <0.5 kg; passerines, doves, and tinamous) for ocelot. Although cameras are more commonly used to survey medium- and large-sized mammals, they can also be used to collect data on birds (O'Brien and Kinnaird, 2008), as well as on small mammals, particularly when activity pattern is the main objective of the survey (Torre et al., 2005).

### Data analysis

#### Diet

We investigated the niche breadth of each species using the standardized Levins index ( $B_a$ ; its values range from 0 = generalist to 1 = specialist; Krebs, 1998). Niche overlap was estimated using Pianka Index ( $O$ ; its values range from 0 = total segregation to 1 = equal use of resources; Pianka, 1974).

#### Activity pattern

We performed a Rayleigh test of uniformity to each felid species to verify the significance of the mean direction of their activity in the 24-hour cycle. This test informs if the activity records are uniformly distributed throughout the day or randomly distributed (Lund and Agostinelli, 2015), indicating, therefore, whether the species is cathemeral or not.

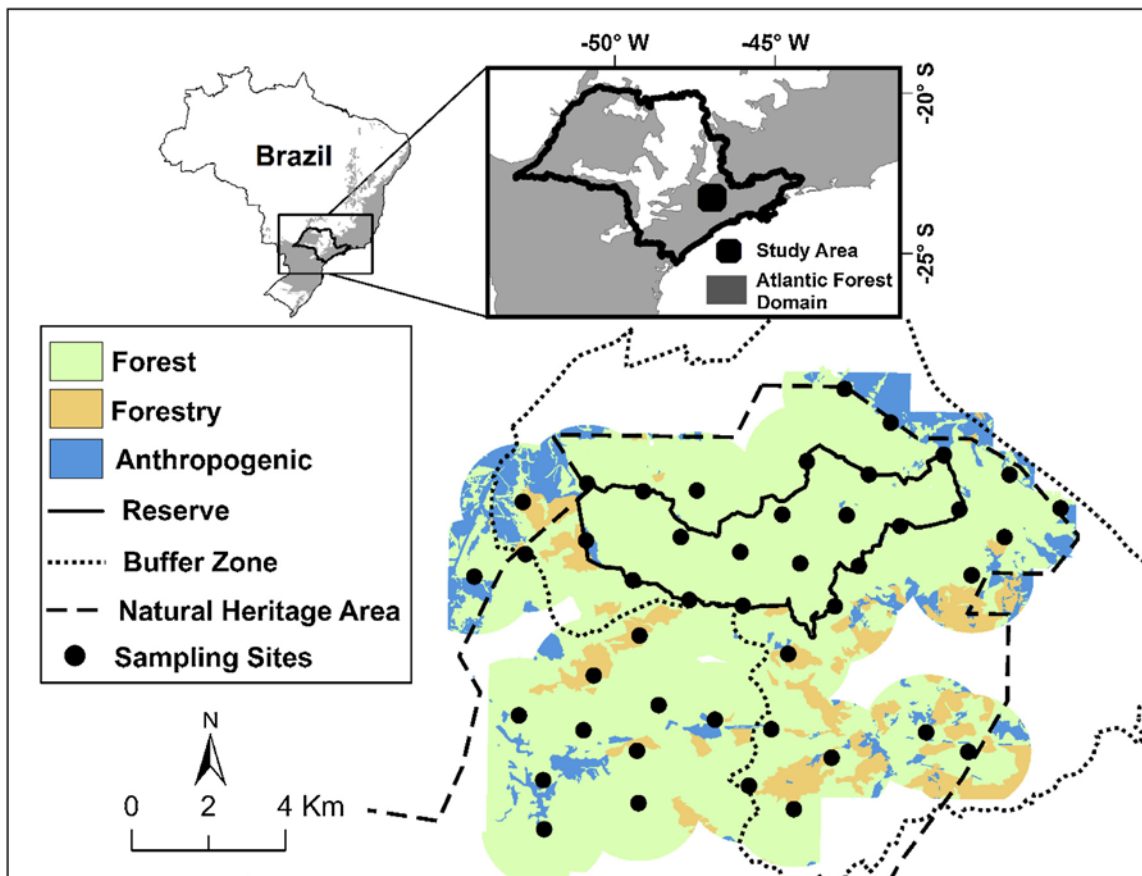
Time use and temporal overlap were estimated using kernel density estimation (Linkie and Ridout, 2011; Ridout and Linkie, 2009) and a coefficient of overlapping ( $\Delta$ ) that ranges from 0 (no overlap) to 1 (complete overlap). We used the estimator  $\hat{\Delta}_1$ , which is recommended for small sample sizes (Ridout and Linkie, 2009). Standard errors were obtained from the confidence intervals estimated from 1000 bootstrap samples. Analyses were performed using the packages 'circular' (Lund and Agostinelli, 2015) and 'overlap' (Meredith and Ridout, 2016) in R (R Development Core Team, 2014).

## Results

### Diet

We collected 71 scat samples of small felids ( $N_{\text{oncilla}} = 31$ ,  $N_{\text{margay}} = 27$ ,  $N_{\text{jaguarundi}} = 5$ ,  $N_{\text{ocelot}} = 8$ ). Oncilla's diet was mostly composed of small mammals (43% of items), reptiles (25%), and birds (18%; Table 1). Margay's diet was mainly composed of birds (38%) and small mammals (36%), and ocelot's diet mostly included small mammals (39%), reptiles (17%), and medium-sized mammals (11%). We found mainly bird items in jaguarundi's scats (67%), however, we had not only a low number of scats but also an extremely low number of food items for this species. Therefore, we have excluded it from our dietary analysis.

None of the small felids seems to be a specialist (niche breadth of  $B_{a, \text{oncilla}} = 0.68$ ,  $B_{a, \text{margay}} = 0.50$ , and  $B_{a, \text{ocelot}} = 0.55$ ). Dietary niche overlap was moderate between all pairs of small felids, being highest between oncilla and margay ( $O = 0.69$ ) and intermediate between ocelot and oncilla ( $O = 0.54$ ) and ocelot and margay ( $O = 0.53$ ). In addition, the three felids consumed mammalian prey



**Fig. 1.** Map of the study area (Serra do Japi; 35,000 ha) where data on oncilla (*Leopardus guttulus*), margay (*L. wiedii*), jaguarundi (*Puma yagouaroundi*), ocelot (*L. pardalis*), and their main prey were collected using camera trap and scat sampling. Adapted from Nagy-Reis et al., 2017.

species of distinct sizes: the geometric mean body weight of mammalian prey for ocelot was 57 g, whereas it was 32 g for margay, and 23 g for oncilla.

#### Activity pattern

We obtained 66 photos of small felids ( $N_{\text{oncilla}} = 29$ ,  $N_{\text{margay}} = 12$ ,  $N_{\text{jaguarundi}} = 9$ , and  $N_{\text{ocelot}} = 16$ ) and 4382 photos of their prey ( $N_{\text{small birds}} = 1,472$ ,  $N_{\text{small and medium birds}} = 1,936$ ,  $N_{\text{small mammals}} = 77$ , and  $N_{\text{medium-sized mammals}} = 897$ ). Oncilla and margay appeared to be active throughout the entire 24-hour cycle (Rayleigh,  $r = 0.15$ ,  $p = 0.76$ ,  $N = 29$ ;  $r = 0.18$ ,  $p = 0.38$ ,  $N = 12$ , respectively), presenting cathemeral activity patterns (Fig. 2). Contrarily, the records of jaguarundi and ocelot were not homogeneously distributed throughout the hours of the day (Rayleigh,  $r = 0.63$ ,  $p < 0.05$ ,  $N = 9$ ;  $r = 0.64$ ,  $p < 0.001$ ,  $N = 16$ ; respectively). Jaguarundi was recorded both in the day and at dusk, and ocelot was mainly nocturnal (Fig. 2). In general, we found a moderate overlap in the time use of the four small felids ( $\hat{\Delta}_1$  between pairs of species ranged from 0.29 to 0.73; Fig. 2).

The activity of their main prey was the following: birds were diurnal, small mammals were mostly nocturnal but had some activity during the day, and medium-sized mammals were primarily nocturnal (Fig. 3). Temporal overlap ( $\hat{\Delta}_1$ ) between predators and prey ranged from 0.17 to 0.81, being highest between ocelot and its prey (Fig. 3).

#### Discussion

Morphologically similar sympatric species typically select mechanisms that decrease niche overlap in at least one of its dimensions (i.e., spatial, temporal, or dietary; Estevo et al., 2017; Foster et al., 2013; Harmsen et al., 2009; Sunarto et al., 2015). Here, by investigating the time use and diet of four similar sympatric Neotropical small felids (oncilla, margay, jaguarundi, and ocelot) in a large Atlantic forest remnant, we found some evidence that both, temporal and dietary segregation, are important mechanisms facilitating their coexistence and that prey activity potentially affects their temporal use.

Ocelot, margay, and oncilla seem to be generalists (similarly to Migliorini et al., 2018; Silva-Pereira et al., 2011; Wang, 2002), whereas jaguarundi has been previously reported as generalist in an Atlantic Forest mosaic (Tófoli et al., 2009) and specialist in the Brazilian pampa (Migliorini et al., 2018). Although these small felids have discrete differences in body sizes and may occasionally show high dietary overlap (Silva-Pereira et al., 2011; Wang, 2002), our results suggest that they share only a moderate portion of their food sources in our study area (similarly to Kasper et al., 2016; Rocha-Mendes et al., 2010), and that they would feed on prey of different sizes. This is especially more suggestive when we compare the ocelot's diet with those of the other species. This is possibly because ocelot has craniodental adaptations to feed on small as well as larger prey (Meachen-Samuels and Van Valkenburgh, 2009) and has a larger body size, which make it a mixed-sized prey feeder

**Table 1**

Diet of four sympatric Neotropical small felids in a large remnant of Atlantic Forest in Brazil. N = number of scat samples; n = number of occurrence; PO = percentage of occurrence; FO = frequency of occurrence.

Item	Oncilla (N=31)			Margay (N=27)			Jaguarundi (N=5)			Ocelot (N=8)			Prey weight (g)
	n	PO	FO	n	PO	FO	n	PO	FO	n	PO	FO	
<b>Small mammals</b>													
Rodentia													
Sigmodontinae	1	2.5	3.2	-	-	-	-	-	-	-	-	-	-
<i>Oligoryzomys cf. nigripes</i>	4	10.0	12.9	1	2.4	3.7	-	-	-	1	5.6	12.5	17.5 <sup>a</sup>
<i>Brucepattersonius</i>	1	2.5	3.2	2	4.8	7.4	-	-	-	-	-	-	32.4 <sup>a</sup>
<i>Blarinomys cf. breviceps</i>	1	2.5	3.2	-	-	-	-	-	-	-	-	-	23.0 <sup>a</sup>
<i>Akodon</i>	2	5.0	6.5	6	14.3	22.2	-	-	-	1	5.6	12.5	29.8 <sup>a</sup>
<i>Thaptomys cf. nigrita</i>	1	2.5	3.2	1	2.4	3.7	-	-	-	4	22.2	50.0	20.5 <sup>a</sup>
<i>Delomys cf. sublineatus</i>	-	-	-	-	-	-	-	-	-	1	5.6	12.5	41.8 <sup>a</sup>
Murinae													
<i>Rattus rattus</i>	-	-	-	1	2.4	3.7	-	-	-	-	-	-	200.0 <sup>b</sup>
Unidentified small rodent	5	12.5	16.1	-	-	-	-	-	-	-	-	-	-
Didelphimorphia													
<i>Gracilinanus microtarsus</i>	1	2.5	3.2	2	4.8	7.4	-	-	-	-	-	-	29.5 <sup>a</sup>
<i>Monodelphis scalops</i>	1	2.5	3.2	2	4.8	7.4	-	-	-	-	-	-	31.1 <sup>a</sup>
<b>Medium mammals</b>													
Rodentia													
<i>Coendou spinosus</i>	-	-	-	-	-	-	-	-	-	1	5.6	12.5	1700.0 <sup>c</sup>
Lagomorpha													
<i>Sylvilagus brasiliensis</i>	-	-	-	-	-	-	-	-	-	1	5.6	12.5	934.0 <sup>b</sup>
<b>Reptiles</b>													
Lacertilia													
Gymnophthalmidae	1	2.5	3.2	-	-	-	-	-	-	2	11.1	25	-
<i>Heterodactylus cf. imbricatus</i>	2	5.0	6.5	-	-	-	-	-	-	-	-	-	-
Serpentes													
Crotalinae	2	5.0	6.5	-	-	-	-	-	-	-	-	-	-
<i>Bothrops cf. jararaca</i>	5	12.5	16.1	-	-	-	-	-	-	-	-	-	-
Dipsadidae													
<i>Xenodon cf. newwiedii</i>	-	-	-	1	2.4	3.7	-	-	-	-	-	-	-
Unidentified reptile	-	-	-	1	2.4	3.7	-	-	-	1	5.6	12.5	-
<b>Birds</b>													
Morphotype 1	3	7.5	9.7	5	11.9	18.5	-	-	-	1	5.6	12.5	-
Morphotype 2	0	-	-	-	-	-	1	33.3	20.0	-	-	-	-
Unidentified bird	4	10.0	12.9	11	26.2	40.7	1	33.3	20.0	-	-	-	-
<b>Invertebrates</b>													
Plants	25	-	80.6	23	-	85.2	4	-	80.0	4	-	50.0	-
Unidentified	6	15.0	19.4	9	21.4	33.3	1	33.3	20.0	5	27.8	62.5	-
<b>Total items*</b>	40	100		42	100		3	100		18	100		
<b>Minimum number of taxa*</b>	17			13			2			11			

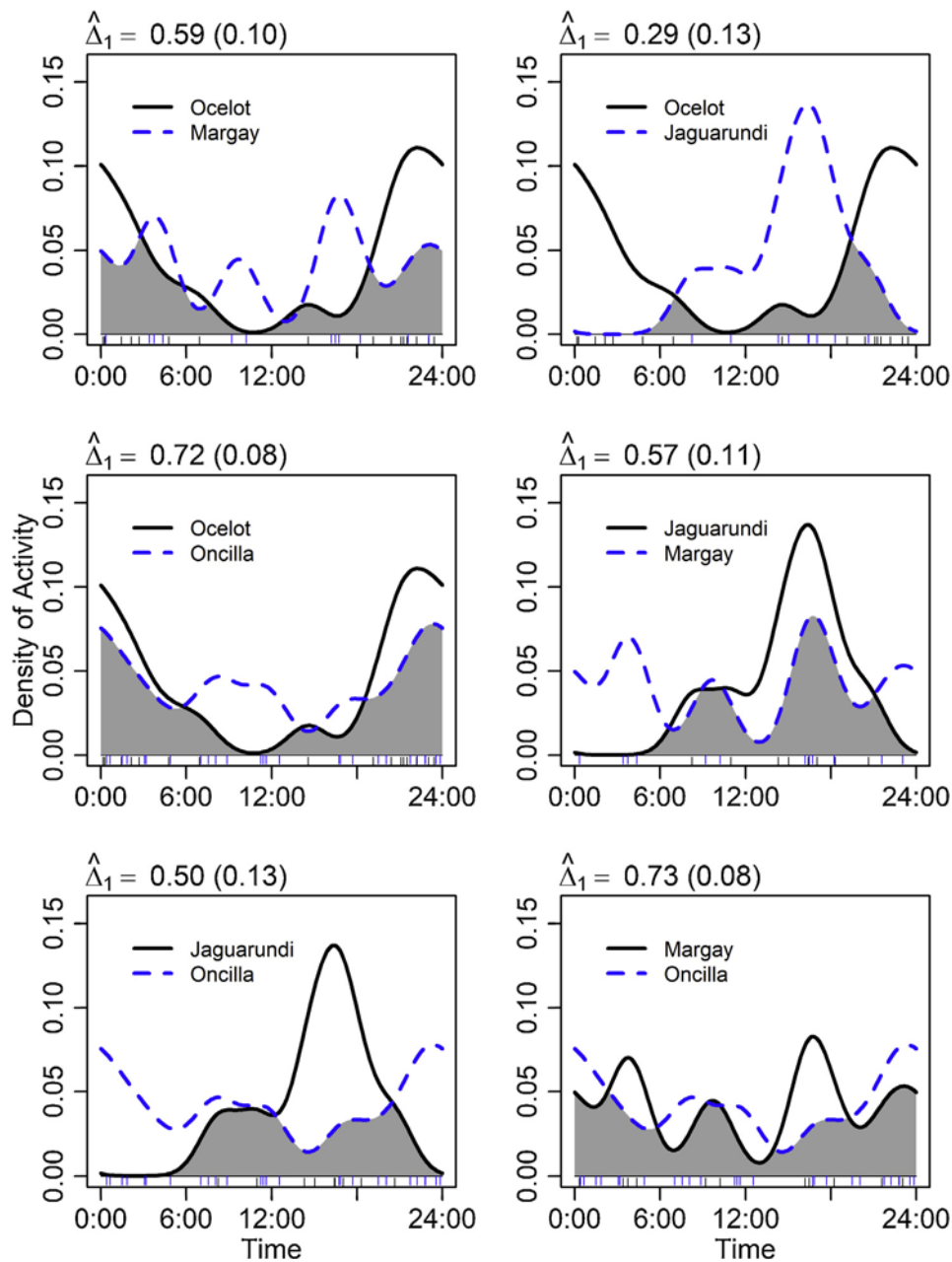
\*Without plant parts and invertebrates. Prey weight obtained from: <sup>a</sup>Rossi, 2011; <sup>b</sup>Eisenberg and Redford, 1989; <sup>c</sup>Passamani, 2010.

(Bianchi et al., 2010; Silva-Pereira et al., 2011; Wang, 2002). It has been suggested, however, that interactions between ocelot and larger felids limit the niche of ocelot as it shifts its diet to smaller prey in the presence of pumas (*Puma concolor*) and jaguars (*Panthera onca*) (Moreno et al., 2006). Consequently, the presence of larger felids may also play a role in the degree of dietary overlap between small felids, and future studies should investigate this aspect.

Habitat partitioning has often been suggested as the main mechanism allowing the coexistence of Neotropical large felids (Foster et al., 2013; Harmsen et al., 2011; Scognamiglio et al., 2003). Neotropical small felids, however, seem to co-occur independently and do not seem to have habitat segregation, at least in protected Atlantic Forest remnants (Massara et al., 2016; Nagy-Reis et al., 2017). We cannot discard, however, the possibility of vertical habitat segregation (e.g., in forest strata) between margay and the other felids, since it has morphological adaptation to climbing and can use more the canopy than the other species (Leyhausen, 1963). Here, we found some evidence that the four Neotropical small felids may segregate in time: the two smaller cats (margay and oncilla) seem to be cathemeral, while jaguarundi seems to be diurnal, and ocelot nocturnal. Similar results were found for oncilla and ocelot in other protected areas of Atlantic Forest (Massara et al., 2016), but not for northern oncilla (*Leopardus tigrinus*) and ocelot (*L. pardalis*) in the semiarid Caatinga, where the harsh environment may apply

constraints to their activity patterns and northern oncilla is more nocturnal (Penido et al., 2017). Previous studies have suggested that oncilla, the smallest of our study species, changes its behavior in response to the presence and/or detection of margay and ocelot (Nagy-Reis et al., 2017), and may present activity flexibility to avoid direct conflict with ocelot, being cathemeral when they co-occur and nocturnal otherwise (Massara et al., 2016; Oliveira et al., 2011; Oliveira-Santos et al., 2012). These previous findings, along with our results, highlight the importance of behavioral mechanisms in mediating the coexistence of Neotropical small felids. In addition, because we do not have data on the population abundance of these cats and the previous studies on their habitat segregation did not investigate potential effects of density (Massara et al., 2016; Nagy-Reis et al., 2017), it is still unclear if one species affects the abundance of the other rather than its habitat and/or time uses. This alternative effect is supported by the finding that oncilla abundance is higher in the absence of other felids (Oliveira-Santos et al., 2012).

We also found some evidence that the activity of the four Neotropical small felids overlaps with those of their main prey, at least to some extent, even though none of these felids seems to be a specialist and despite the fact that we have grouped prey by their type. Hunting when prey is active tends to facilitate detection and optimize the outcomes as felids rely on auditory and visual cues to successfully hunt (Kitchener et al., 2011). Predator-prey time use synchronism has been previously found in a few other carnivores,

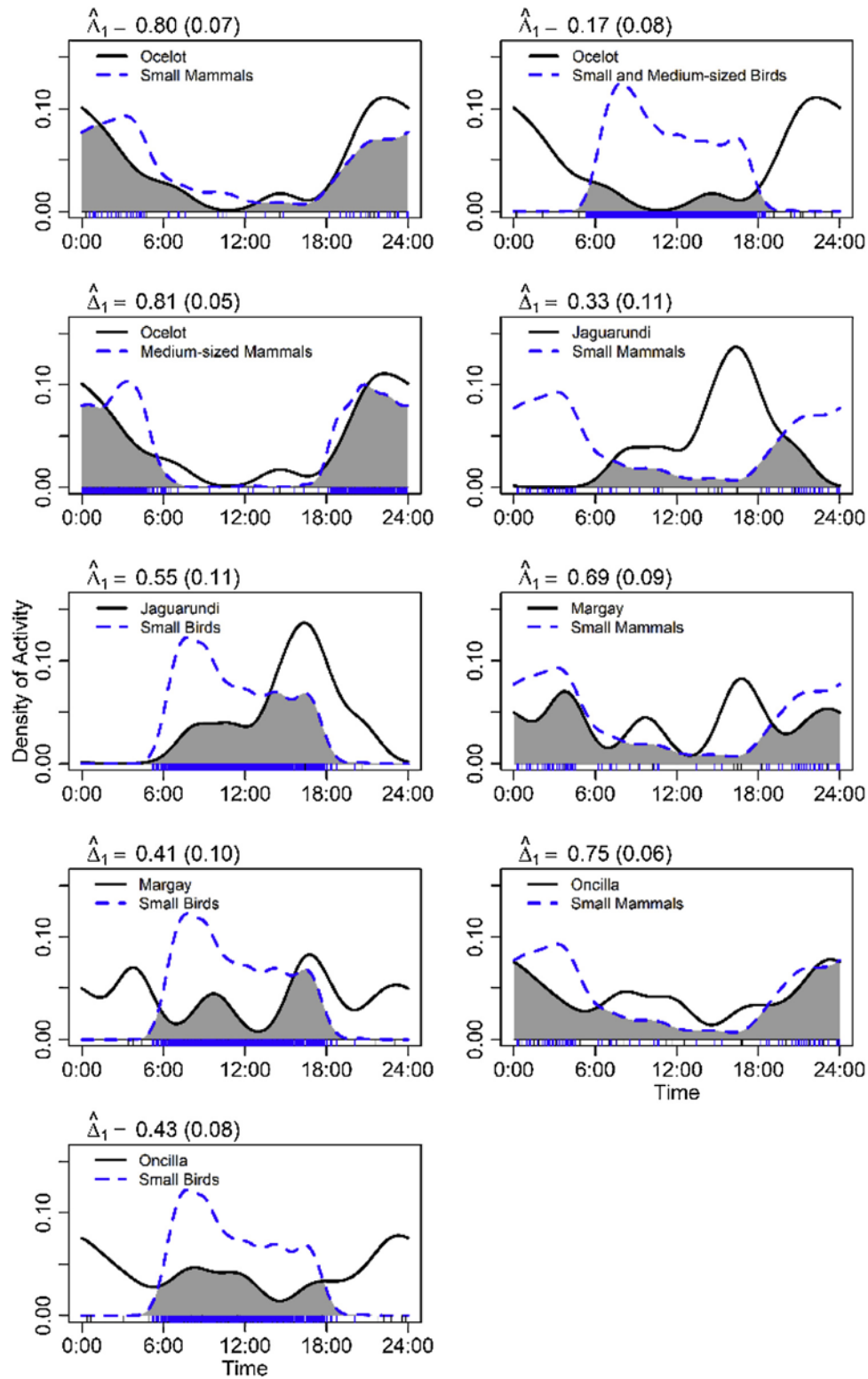


**Fig. 2.** Time use and temporal overlap ( $\Delta_1 \pm SE$ , in parenthesis) of four sympatric Neotropical small felids in a large Atlantic Forest remnant in Brazil. Lines are kernel-density estimates of activity patterns based on the time of each photo (indicated by short vertical lines above the x-axis). Shaded area represents the temporal overlap between pair of species.

especially in felids (ocelot, Porfirio et al., 2016; northern oncilla, Marinho et al., 2018; Sumatran tiger (*Panthera tigris sumatrae*), Linkie and Ridout, 2011; guiña (*Leopardus guigna*), Delibes-Mateo et al., 2014; hawks (*Accipiter* spp.), Roth and Lima, 2007; puma and jaguar, Weckel et al., 2006; Harmsen et al., 2011; Foster et al., 2013). Although predator-prey time use synchronism is mostly reported at species level, for more generalist predators such as the four small felids analyzed here, the synchronism may also occur at a more general level (i.e., with the overall activity of main prey type, not species; e.g., Marinho et al., 2018). Ocelot, the largest and possibly the dominant felid of the assemblage we studied, appeared to have the highest temporal overlap with prey, except with birds, which are not considered a main food source for ocelots (present study; Meza et al., 2002). Oncilla and margay had the second highest overlap with their prey activity, and oncilla-prey overlap (0.75) was

identical to what has been previously found for northern oncilla (*Leopardus tigrinus*; Marinho et al., 2018).

Possibly because of the difficulty in obtaining data for these cryptic and elusive species, basic information on their biology and ecology are still scarce (Macdonald et al., 2011; Nowell and Jackson, 1996). Although we had a small sample size, it is interesting to notice that the few previous studies with Neotropical small felids revealed similar general diets (Bianchi et al., 2010, 2011; Migliorini et al., 2018; Silva-Pereira et al., 2011; Tófoli et al., 2009; Wang, 2002) and activity patterns (Di Bitetti et al., 2010; Maffei et al., 2007; Massara et al., 2016; Oliveira et al., 2011; Oliveira-Santos et al., 2012; Porfirio et al., 2016), and many of our results were congruent with findings from other ecoregions of the Neotropics (Kasper et al., 2016; Migliorini et al., 2018; Rocha-Mendes et al., 2010; Silva-Pereira et al., 2011; Wang, 2002). However, the results



**Fig. 3.** Time use and temporal overlap ( $\Delta_1 \pm SE$ , in parenthesis) of four Neotropical small felids in relation to their main prey in a large Atlantic Forest remnant in Brazil. Lines are kernel-density estimates of activity patterns based on the time of each photo (indicated by short vertical lines above the x-axis). Small mammals (<1 kg) are mainly small rodents and marsupials; medium-sized mammals (1–13 kg) are mostly opossums, Brazilian rabbit, paca, armadillos, and porcupine; small birds (<0.2 kg) are predominantly passerines and doves; and small and medium-sized birds (<0.5 kg) are mainly passerines, doves, and tinamous.

presented here should be taken carefully and more studies should investigate the patterns suggested by our data. In conclusion, we suggest that small differences in diet associated to time partitioning contribute to the coexistence of Neotropical small felids, and that prey activity is a factor potentially shaping their activity pattern, especially for ocelot.

## Acknowledgements

We are thankful to Jundiá City Hall and all private owners for permission to conduct this project at Serra do Japi. This work was supported by the Coordination for the Improvement of Higher Education Personnel (CAPES); São Paulo Research Foundation (FAPESP); and Idea Wild. We are also grateful to M. J. F. Penteadó for confirming species photo identification; P. R. Manzani (UNICAMP), A. R. Percequillo (ESALQ), and A. P. Carmignotto (UFSCar) for helping identifying prey species in scats; M. F. Rossi and M. C. S. Canhoto for facilitating scat sampling and trichology; and M. Lucherini and three anonymous reviewers whose comments helped to improve this article.

## References

- Bianchi, R.D., Mendes, S.L., Júnior, P.M., 2010. Food habits of the ocelot, *Leopardus pardalis*, in two areas in southeast Brazil. *Stud. Neot. Fauna Environ.* 45 (3), 111–119.
- Bianchi, R.D.C., Rosa, A.F., Gatti, A., Mendes, S.L., 2011. Diet of margay, *Leopardus wiedii*, and jaguarundi, *Puma yagouaroundi*, (Carnivora: Felidae) in Atlantic Rainforest, Brazil. *Zoologia (Curitiba)* 28, 127–132.
- Delibes-Mateo, M., Díaz-Ruiz, F., Caro, J., Ferreras, P., 2014. Activity patterns of vulnerable guña (*Leopardus guigna*) and its main prey in the Valdivian rainforest of southern Chile. *Mamm. Biol.* 79, 393–397.
- Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E., Paviolo, A., 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. *Acta Oecol.* 36, 403–412.
- Donadio, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in Carnivora. *Am. Nat.* 167 (4), 524–536.
- Eisenberg, J.F., Redford, K.H., 1989. *Mammals of the Neotropics, Volume 3: Ecuador, Bolivia, Brazil*. University of Chicago Press, Chicago.
- Emmons, L.H., Feer, F., 1997. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago.
- Estevo, C.A., Nagy-Reis, M.N., Nichols, J.D., 2017. When habitat matters: habitat preferences can modulate co-occurrence patterns of similar sympatric species. *PLoS One* 12 (7), e0179489.
- Foster, V.C., Sarmento, P., Sollmann, R., Tôres, N., Jácomo, A.T., Negrões, N., Fonseca, C., Silveira, L., 2013. Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* 45, 373–379.
- Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E., Doncaster, C.P., 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca*) and pumas (*Puma concolor*) in a Neotropical forest. *J. Mamm.* 90, 612–620.
- Harmsen, B.J., Foster, R.J., Silver, S.C., Ostro, L.E.T., Doncaster, C.P., 2011. Jaguar and puma activity patterns in relation to their main prey. *Mamm. Biol.* 76, 320–324.
- Johnson, W.E., Eizirik, E., Pecon-Slattey, J., Murphy, W.J., Antunes, A., Teeling, E., O'Brien, S.J., 2006. The late Miocene radiation of modern Felidae: a genetic assessment. *Science* 311, 73–77.
- Kasper, C.B., Peters, F.B., Christoff, A.U., Freitas, T.R.O., 2016. Trophic relationships of sympatric small carnivores in fragmented landscapes of southern Brazil: niche overlap and potential for competition. *Mammalia* 80 (2), 143–152.
- Kitchener, A.C., Valkenburgh, B.V., Yamaguchi, N., 2011. Felid form and function. In: Macdonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, New York, pp. 83–106.
- Krebs, C.J., 1998. *Ecological Methodology*, second ed. Benjamin Cummings, Menlo Park.
- Leyhausen, V.P., 1963. Über südamerikanische Pardelkatzen. *Ethology* 20, 627–640.
- Linkie, M., Ridout, M.S., 2011. Assessing tiger-prey interactions in Sumatran rainforests. *J. Zool.* 284, 224–229.
- Lund, U., Agostinelli, C., URL 2015. Circular Statistics: The 'Circular' Package (Accessed 10.05.15) <https://cran.r-project.org/web/packages/circular/circular.pdf>.
- Macdonald, D.W., Loveridge, A.J., Nowell, K., 2011. *Dramatis personae: an introduction to the wild felids*. In: Macdonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, New York, pp. 3–58.
- Maffei, L., Noss, A., Fiorello, C., 2007. The jaguarundi (*Puma yagouaroundi*) in the kaaiya del gran Chaco National Park, Santa Cruz, Bolivia. *Mastozool. Neotrop.* 14, 263–266.
- Marinho, P.H., Bezerra, D., Antongiavanni, M., Fonseca, C.R., Venticinqu, E.M., 2018. Activity patterns of the threatened northern tiger cat *Leopardus tigrinus* and its potential prey in a Brazilian dry tropical forest. *Mamm. Biol.* 89, 30–36.
- Massara, R.L., Paschoal, A.M.O., Bailey, L.L., Doherty, P.F., Chiarello, A.G., 2016. Ecological interactions between ocelots and sympatric mesocarnivores in protected areas of the Atlantic Forest, southeastern Brazil. *J. Mammal.* 97 (6), 1634–1644.
- Meachen-Samuels, J., Van Valkenburgh, B., 2009. Craniodental indicators of prey size preference in the Felidae. *Biol. J. Linn. Soc. Lond.* 96, 784–799.
- Meredith, M., Ridout, M., URL 2016. Package 'overlap' (accessed 05.10.17) <https://cran.r-project.org/web/packages/overlap/overlap.pdf>.
- Meza, A.V., Meyer, E.M., González, C.A.L., 2002. Ocelot (*Leopardus pardalis*) food habits in a tropical deciduous forest of Jalisco, Mexico. *Am. Midl. Nat.* 148, 146–154.
- Migliorini, R.P., Peters, F.B., Favarini, M.O., Kasper, C.B., 2018. Trophic ecology of sympatric small cats in the Brazilian Pampa. *PLoS One* 13 (7), e0201257.
- Morellato, L.P.C., 1992. *História natural da Serra do Japi: Ecologia e preservação de uma área florestal no Sudeste do Brasil*, first ed. Editora da Unicamp, Campinas.
- Moreno, R.S., Kays, R.W., Samudio Jr, R., 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *J. Mamm.* 87, 808–816.
- Nagy-Reis, M.B., Nichols, J.D., Chiarello, A.G., Ribeiro, M.C., Setz, E.Z.F., 2017. Landscape use and co-occurrence patterns of Neotropical spotted cats. *PLoS One* 12 (1), e0168441.
- Nowell, K., Jackson, P., 1996. *Wild Cats: Status Survey and Conservation Action Plan*. IUCN/SSC Cat Specialist Group. IUCN, Switzerland.
- O'Brien, T.G., Kinnaird, M.F., 2008. A picture is worth a thousand words: the application of camera trapping to the study of birds. *Bird Conserv. Int.* 18, 144–162.
- Oliveira, T.G., Tortato, M.A., Silveira, L., Kasper, C.B., Mazim, F.D., Lucherini, M., Jácomo, A.T., Soares, J.B.G., Marques, R.V., Sunquist, M., 2011. Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. In: Macdonald, D.W., Loveridge, A.J. (Eds.), *Biology and Conservation of Wild Felids*. Oxford University Press, New York, pp. 559–580.
- Oliveira-Santos, L.G.R., Graipel, M.E., Tortato, M.A., Zucco, C.A., Cáceres, N.C., Goulart, F.V.B., 2012. Abundance changes and activity flexibility of the ocella, *Leopardus tigrinus* (Carnivora: felidae), appear to reflect avoidance of conflict. *Zoologia* 29, 115–120.
- Passamani, M., 2010. Use of space and activity pattern of *Sphiggurus villosus* (F. Cuvier, 1823) from Brazil (Rodentia: erethizontidae). *Mamm. Biol.* 75, 455–458.
- Penido, G., Astete, S., Jácomo, A.T.A., Sollmann, R., Tôres, N., Silveira, L., Marinho-Filho, J., 2017. Mesocarnivore activity patterns in the semiárid Caatinga: limited by harsh environment or affected by interspecific interactions? *J. Mammal.* 98 (6), 1732–1740.
- Pianka, E.R., 1974. Niche overlap and diffuse competition. *Proc. Natl. Acad. Sci. U. S. A.* 71, 2141–2145.
- Porfírio, G., Foster, V.C., Fonseca, C., Sarmento, P., 2016. Activity patterns of ocelots and their potential prey in the Brazilian Pantanal. *Mamm. Biol.* 81, 511–517.
- Quadros, J., Monteiro-Filho, E.D.A., 2006. Coleta e preparação de pêlos de mamíferos para identificação em microscopia óptica. *Rev. Bras. Zool.* 23, 274–278.
- R Development Core Team, 2014. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reynolds, J., Aebischer, N.J., 1991. Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the Fox *Vulpes vulpes*. *Mamm. Rev.* 3, 97–122.
- Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14, 322–337.
- Rocha-Mendes, F., Mikich, S.B., Quadros, J., Pedro, W.A., 2010. Feeding ecology of carnivores (Mammalia, Carnivora) in Atlantic Forest remnants, Southern Brazil. *Biota Neotrop.* 10 (4), 21–30.
- Rosenzweig, M.L., 1966. Community structure in sympatric Carnivora. *J. Mamm.* 47, 602–612.
- Rossi, N.F., 2011. *Pequenos mamíferos na o-voadores do Planalto Atlântico de São Paulo: Identificação, história natural e ameaças*. Master's dissertation. Universidade de São Paulo.
- Roth II, T.C., Lima, S.L., 2007. The predatory behavior of wintering Accipiter hawks: temporal patterns in activity of predators and prey. *Oecologia* 152, 169–178.
- Sakane, K.K., 2015. *Pequenos mamíferos da Serra do Japi, município de Jundiá-SP: diferenças altitudinais*. Master's dissertation. Universidade Estadual de Campinas.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185, 27–39.
- Scognamiglio, D., Maxit, I.E., Sunquist, M., Polisar, J., 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J. Zool.* 259, 269–279.
- Silva-Pereira, J.E., Moro-Rios, R.F., Bilski, D.R., Passos, F.C., 2011. Diets of three sympatric Neotropical small cats: food niche overlap and interspecies differences in prey consumption. *Mamm. Biol.* 76, 308–312.
- Sunarto, S., Kelly, M.J., Parakkasi, K., Hutajulu, M.B., 2015. Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. *J. Zool.* 296, 1–12.

- Tófoli, C.F., Rohe, F., Setz, E.Z.F., 2009. Jaguarundi (*Puma yagouaroundi*) (Geoffroy, 1803) (Carnivora, Felidae) food habits in a mosaic of Atlantic Rainforest and eucalypt plantations of southeastern Brazil. *Braz. J. Biol.* 69, 871–877.
- Torre, I., Peris, A., Tena, L., 2005. Estimating the relative abundance and temporal activity patterns of wood mice (*Apodemus sylvaticus*) by remote photography in Mediterranean post-fire habitats. *Galemys* 17, 41–52.
- Trigo, T.C., Schneider, A., Oliveira, T.G., Lehugeur, L.M., Silveira, L., Freitas, T.R.O., et al., 2013a. Molecular data reveal complex hybridization and cryptic species of Neotropical wild cat. *Curr. Biol.* 23, 2528–2533.
- Trigo, T.C., Tirelli, F.P., Machado, L.F., Peters, F.B., Indrusiak, C.B., Mazim, F.D., Sana, D., Eizirik, E., Freitas, T.R.O., 2013b. Geographic distribution and food habits of *Leopardus tigrinus* and *L. Geoffroyi* (Carnivora, Felidae) at their geographic contact zone in southern Brazil. *Stud. Neotrop. Fauna Environ.* 48, 56–67.
- Wang, E., 2002. Diets of ocelots (*Leopardus pardalis*), margays (*L. wiedii*), and oncillas (*L. tigrinus*) in the Atlantic rainforest in southeast Brazil. *Stud. Neotrop. Fauna Environ.* 37, 207–212.
- Weckel, M., Giuliano, W., Silver, S., 2006. Jaguar (*Panthera onca*) feeding ecology: distribution of predator and prey through time and space. *J. Zool.* 270, 25–30.