Journal of Zoology

ZSL LET'S WORK FOR WILDLIFE

Journal of Zoology. Print ISSN 0952-8369

Feline predator–prey relationships in a semi-arid biome in Brazil

D. M. Dias[1], R. L. Massara[2,3], C. B. de Campos[4] & F. H. G. Rodrigues[1]

1 Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
2 Laboratório de Ecologia e Conservação, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
3 Instituto SerraDiCal de Pesquisa e Conservação, Belo Horizonte, Brazil
4 Instituto para a Conservação dos Carnívoros Neotropicais – Pró-Carnívoros, Atibaia, Brazil

Keywords
neotropics; mesocarnivores; species interactions; spatiotemporal distribution; spatial segregation; temporal segregation.

Correspondence
Douglas de Matos Dias, Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Avenida Antônio Carlos, 6627, Pampulha, Belo Horizonte, MG 3127-901, Brazil.
Email: diasdm.bio@gmail.com

Editor: Matthew Hayward

Received 2 July 2018; revised 18 October 2018; accepted 22 November 2018

doi:10.1111/jzo.12647

Abstract

The spatiotemporal distribution of a predator within an environment tends to be synchronized with that of its prey, to maximize the efficiency of its hunting behavior. However, small predators may also be obliged to avoid potentially agonistic encounters with larger predators due to interspecific competition and intraguild predation. We used occupancy models and indices of temporal overlap to evaluate whether the occurrence of prey species, ocelots and top predators (puma and jaguar) influenced the habitat use and activity patterns of the northern tiger cat and jaguarundi in a region of the semi-arid Caatinga biome in Bahia, northeastern Brazil. The occurrence of prey had a positive influence on the use of habitat by the small felids. The northern tiger cat was nocturnal-crepuscular and presented a high degree of temporal overlap with Spix's cavy and the rock cavy. The jaguarundi was diurnal, by contrast and overlapped temporally with the agouti. The occurrence of the ocelot did not influence the habitat or daily activity pattern of the jaguarundi, but presented a high degree of temporal overlap with the northern tiger cat, which adopted a strategy of spatial segregation to avoid direct contact with this dominant competitor. The top predators did not influence the spatiotemporal distribution of the small felids, indicating that their niches are segregated by dietary parameters related to differences in body size. Our results indicate that the availability of prey has a more profound influence on the spatiotemporal ecology of the small felids than the occurrence of the top predators, although the presence of the northern tiger cat appeared to be correlated negatively with that of the ocelot. We believe that environmental factors, such as the conservation status, size and isolation of native habitats, may have a fundamental influence on the strategies adopted by the northern tiger cat to mediate its coexistence with the ocelot.

Introduction

Habitat selectivity permits species coexistence and is an important factor maintaining biological diversity (Orians & Wittenberg, 1991). Variation in biotic and abiotic conditions may affect the competitive capacity of the different species in a community (Tilman, 2004), given that the spatial distribution of animals is related to their biological and ecological requirements, such as escape routes, refuges, breeding sites and foraging areas (Tews *et al.*, 2004). The selection of habitats by a predator, for example, may be determined by its hunting success in different types of environment (Gorini *et al.*, 2012). Predators should use space in such a way as to maximize their foraging success and they would be expected to prefer habitats in which their prey are more common or vulnerable (Luttbeg & Sih, 2004; Gorini *et al.*, 2012). In fact, a number of studies have shown that the presence of predators tends to be correlated positively with prey density (Milakovic *et al.*, 2011; Zanin *et al.*, 2015). Even so, predator–prey interactions are complex and include a series of behavioral mediators, such as social organization, diet, ranging and temporal segregation (Berger, 2010; Dias, Campos & Rodrigues, 2018).

Amply distributed opportunist predators typically exploit a large variety of prey and tend to adjust their behavioral patterns in response to the principal prey species found in different regions (Foster *et al.*, 2013). The leopard (*Panthera pardus*), for example is a nocturnal predator throughout most of its distribution in the African savanna, but is diurnal in West Africa, where the majority of its prey are active during the day (Jenny & Zuberbühler, 2005). Despite these relationships with prey, the behavior exhibited by a carnivore may be a response to the presence of larger predators. Carnivorous mammals may even kill and sometimes feed on other members of the same guild, behaviors known as interspecific killing and intraguild predation, respectively (Palomares & Caro, 1999). These interactions are considered to be extreme forms of competition and have profound effects on the ecology of the species (Polis, Myers & Holt, 1989).

Smaller carnivores have to resolve a trade-off between adapting their behavior to the activity patterns of their prey and the avoidance of contact with larger predators (Caro & Stoner, 2003). Cheetahs (*Acinonyx jubatus*) avoid lions (*Panthera leo*) by moving to areas of low prey density, where lions are less abundant (Durant, 2000). In this case, active avoidance by habitat displacement allows the dominant competitor to exploit preferred resources, while the subordinate is restricted to habitats of lower quality (Carothers & Jaksic, 1984). Spatial partitioning, however, is not always the main strategy of species to mitigate competition or the risk of predation. There is considerable evidence that temporal segregation plays a fundamental role in the facilitation of species coexistence in many carnivore communities (Di Bitetti *et al.*, 2010).

The carnivore guild that contains the jaguar (*Panthera onca*, 61–158 kg), puma (*Puma concolor*, 22–70 kg) and ocelot (*Leopardus pardalis*, 8–15 kg) plays a significant role in the structuring of Neotropical communities (Oliveira & Pereira, 2014). As it is less vulnerable to interference from the larger predators in relation to habitat use and activity pattern (Massara *et al.*, 2015, 2018*a*), the ocelot appears to have a greater influence on the smaller felids, such as the northern tiger cat (*Leopardus tigrinus*, 1.5–3 kg) and the jaguarundi, *Herpailurus yagouaroundi* (3–6 kg) (Oliveira *et al.*, 2010). While some data are available on the interspecific interactions among these small felids, the larger predators (Di Bitetti *et al.*, 2010; Massara *et al.*, 2016) and their potential prey (Penido *et al.*, 2017; Marinho *et al.*, 2018*a*), no previous study has focused on the simultaneous influence of prey availability, the ocelot and the top predators (puma and jaguar) on the probability of occupancy and temporal activity of the small felids. Data of this type can provide important insights into the ecological interactions of these carnivore communities, in particular in semi-arid ecosystems, where research on this group is still incipient.

We used occupancy models to evaluate the occurrence of prey species, the ocelot and top predators (puma and jaguar) and how could influence the occupancy and detection probabilities of the small Neotropical felids, the northern tiger cat and the jaguarundi. Considering that the presence of predators may be correlated positively with that of their prey (Luttbeg & Sih, 2004), we evaluated the hypothesis that the occupancy and detection probabilities of the small felids are influenced positively by the occurrence of their potential prey. However, given the largest body size of the ocelot and the top predators, we expected these carnivores to have a negative influence on the probability of occupancy and detection of both the northern tiger cat and the jaguarundi. We also describe the activity patterns of the species and evaluate the temporal overlap between the small felids, prey species, the ocelot and the top predators. We expected a high degree of temporal overlap between the small felids and their potential prey, but a high degree of temporal segregation between the northern tiger cat and the ocelot and top predators. As the jaguarundi is a diurnal species, we did not expect to find any evidence of the influence of larger predators on its activity patterns.

Materials and methods

Study area

The study area was a region known as Boqueirão da Onça, in the northern extreme of the Brazilian state of Bahia (Fig. 1). The Boqueirão da Onça is inserted in the Seasonally Dry Tropical Forest (Caatinga biome). In this region, the rainy season is short and unpredictable, but typically extends between October and December. The mean annual precipitation and temperature was 563.6 mm and 27°C, respectively (INMET, 2018). The arboreal-shrubby caatinga and the arboreal caatinga are the predominant vegetation types in this ecoregion (Velloso, Sampaio & Pareyn, 2002), although a mosaic of phytophysiognomies can be found, including open areas of shrubby caatinga, rock fields, plateau forests and stands of palms, known as veredas (Roos *et al.*, 2012). Tracts of denser vegetation, with emergent trees, can be found on escarpments and in deep valleys.

Data collection

We established a 20 km × 30 km grid (600 km^2) on the study area, which we subdivided into 150 plots of 4 km^2. As 60 camera traps were available, we randomized 60 sampling points. We installed a camera trap at each point to record mammals, with a mean distance of 2 km (range: 1.50–3.30 km) between traps. The traps were regulated to operate during 24 h and were installed primarily on tracks and unpaved roads, which are the typical travel routes of the local carnivorous mammals. We did not use bait to avoid biasing the frequency of records of the focal species. The study covered 200 days of the dry season period, between January and July, 2017, with a total sampling effort of 8678 trap-days (not including two stolen traps and the days on which the traps had malfunctioned). In the case of malfunction, the trap was assumed to have been working up until the date of the last record for the calculation of sampling effort.

Both the northern tiger cat and the jaguarundi are known to feed basically on small vertebrates (<1 kg), although they may also prey on larger mammals (Oliveira, 1998; Oliveira *et al.*, 2013). Based on the available records (Olmos, 1993; Dias & Bocchiglieri, 2015; Rinaldi *et al.*, 2015), we selected three species, Spix's cavy, *Galea spixii* (Wagler, 1831) [140–560 g], the rock cavy, *Kerodon rupestris* (Wied-Neuwied, 1820) [750–900 g] and the agouti, *Dasyprocta nigriclunis* (Osgood, 1916) [1400–3000 g], as the potential prey of the northern tiger cat and jaguarundi for the present study. Data on body mass were obtained from Bonvicino, Oliveira & D'Andrea (2008). As we believe that the influence of puma and jaguar (top predators) on the smaller felids is effectively the same, we grouped these two felids together for analysis in a single 'top predator' category.

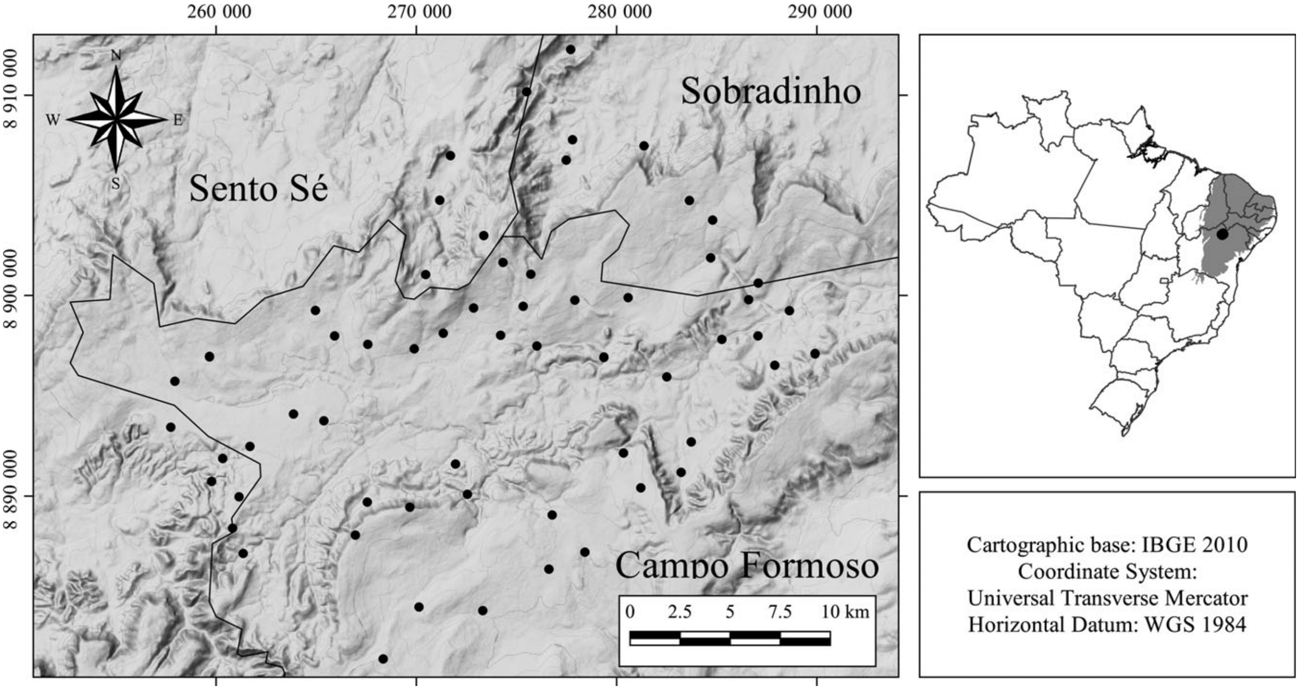

Figure 1 Distribution of the camera traps (black dots) in the Boqueirão da Onça, Bahia, Brazil. The gray lines represent the limits of the three municipalities Sento Sé, Sobradinho and Campo Formoso. The insert (top right) shows the study site (black dot) within the Caatinga biome (gray shading) in northeastern Brazil.

Modeling the occupancy and detection probabilities of the study species

To investigate the direct influence of the prey species, ocelots and top predators on the occupancy probability of the northern tiger cat and jaguarundi, we estimated separately the conditional occupancy probability ($\Psi_{\text{conditional}}$; Mackenzie *et al.*, 2006) of each potential prey (Spix's cavy, rock cavy and agouti), the ocelot and the top predators for each site using the 'single-season' occupancy model in the PRESENCE program (Hines, 2006). The conditional occupancy probability is defined as the probability that one of the species (prey species, ocelot or top predators) is present at a site, given it was never detected. If a species is detected at a site, $\Psi_{\text{conditional}} = 1$ (Mackenzie *et al.*, 2006). The estimates of $\Psi_{\text{conditional}}$ were used as covariates in the analysis (Table 1). We then used the detection of each species (prey, ocelot or top predator) as 'sampling covariates', to evaluate their influence on the detection probability of the northern tiger cat and jaguarundi. Specifically, each of these covariates will be related to the detection (1) or not (0) of the species at each site in each sampling period (Table 1). The detection probability may vary spatially due to habitat characteristics, or temporarily due to seasonal fluctuations in animal behavior patterns and environmental conditions (Bailey, Simons & Pollock, 2004). These factors may influence the habitat use by mammals and, therefore, the detectability of the species (Cassano, Barlow & Pardini, 2014). In this context, we interpreted the detection probability as the frequency (or intensity) of use of a location (e.g. Cassano *et al.*, 2014; Massara *et al.*, 2018*a*). We also considered the number of days on which each camera trap was operational at each point and during each sampling period to evaluate the potential effect of this covariate ('camera operation', Table 1) on the detection probability of the northern tiger cat and jaguarundi.

We used the 'single-season' occupancy model (Mackenzie *et al.*, 2002) in the Mark program (White & Burnham, 1999) to analyze the influence of these covariates on the probability of occupancy and detection of the northern tiger cat and jaguarundi. The 200 sampling days were divided into 20 sampling periods of 10 days, to compile the detection history of each species at each sampling point. As the objective of the present study was to identify the predictor covariates that had the greatest influence on the probability of occupancy and detection of the northern tiger cat and jaguarundi, we selected the model based on all the possible combinations that would satisfy our *a priori* hypothesis. Specifically, we constructed 563 models (Data S1) based on all the possible combinations of covariates that may influence the probability of occupancy (Ψ) and detection (p) of the northern tiger cat and jaguarundi. This approach resulted in a set of balanced models (Doherty, White & Burnham, 2012) that permitted the calculation of the cumulative AICc (w_+) weight of each covariate (Burnham & Anderson, 2002) and identify which were most likely ($w_+ \geq 0.50$) to influence the probability of occupancy and detection of the northern tiger cat and jaguarundi. We also tested the data for a possible lack of independence (overdispersion) among the sites using the goodness-of-fit test developed

Table 1 Covariates used to model the probabilities of occupancy (Ψ) and detection (*p*) of the northern tiger cat and jaguarundi in the Boqueirão da Onça, Bahia, Brazil. The mean and range (minimum–maximum) of each covariate are presented. The values for the detection of prey (Spix's cavy, rock cavy and agouti), ocelots and top predators are the proportions of sampling period ($n = 20$) during which each species or group was detected, averaged across sites. See Materials and methods for details

Covariates	Mean and range (minimum–maximum)
$\Psi_{\text{conditional}}$ of Spixi's cavy	0.72 (0.00–1.00)
$\Psi_{\text{conditional}}$ of rock cavy	0.15 (0.00–1.00)
$\Psi_{\text{conditional}}$ of agouti	0.33 (0.00–1.00)
$\Psi_{\text{conditional}}$ of ocelot	0.69 (0.00–1.00)
$\Psi_{\text{conditional}}$ of top predators	0.36 (0.01–1.00)
Detection of Spixi's cavy	0.21 (0.03–0.42)
Detection of rock cavy	0.06 (0.00–0.12)
Detection of agoutis	0.10 (0.05–0.15)
Detection of ocelots	0.09 (0.03–0.15)
Detection of top predators	0.02 (0.00–0.08)
Days of camera operation	144.6 (30–200)

specifically for the analysis of 'single-season' occupancy (Mackenzie & Bailey, 2004), in the PRESENCE program (Hines, 2006).

Activity patterns and temporal overlap

To minimize the nonindependence of consecutive photographs, we considered only the records of a species obtained at a given site separated by an interval of at least one hour (Goulart *et al.*, 2009). To assess whether the occurrence of prey, ocelots or top predators influenced the activity patterns of the northern tiger cat and jaguarundi, we converted the activity records of each species to solar time to adjust the actual time to the circadian cycle of the species (Linkie & Ridout, 2011). These adjustments were based on the sunrise and sunset times for the study area, extracted from Tropsolar 5.0 (Cabús, 2015). We defined an animal as being predominantly diurnal when more than 60% of the photographic records were obtained between one hour after sunrise and one hour before sunset. We defined an animal as being predominantly nocturnal when more than 60% of the photographic records were taken between one hour after sunset and one hour before sunrise. Animals were defined as crepuscular when at least 50% of activity was recorded within one hour (before or after) sunrise and sunset (see e.g. Massara *et al.*, 2018*b*). Strictly diurnal or nocturnal species were those recorded exclusively during either the day or night, respectively (Dias *et al.*, 2018) and cathemeral species were those which were active throughout the circadian cycle.

We used the photographs to determine the general activity pattern of each focal mammal species in the study area. We determined the nychthemeral distribution of the camera trap records of each species using a circular statistic, which tests whether the set of angles (i.e. the number of records per hour of the day) is distributed uniformly (Zar, 2010). We assessed the uniformity of the circular distribution of the records collected during the study period using Rayleigh's uniformity test (*Z*), run in Oriana 4.01 (Kovach Computing Services, Anglesey, UK).

Using the Overlap package (Meredith & Ridout, 2018), we estimated the density of the activity of each species using the kernel density, a nonparametric approach that evaluates the probability function of the density of a random variable (Worton, 1989). We then calculated the most adequate overlap coefficient (Δ), which varies from 0 (no overlap) to 1 (complete overlap) of each pair of species (Meredith & Ridout, 2018). We used the Δ_1 estimator, which is recommended when the smaller sample has <75 observations (see Meredith & Ridout, 2018) and calculated 95% confidence intervals of Δ_1, based on 10 000 bootstrap replicates. We considered Δ_1 values of <0.50 to represent a low level of overlap, values of between 0.50 and 0.60 to reflect moderate overlap and values of over 0.60 to represent a high level of overlap (Massara *et al.*, 2018*a,b*). We ran these analyses in the R software (R Core Team, 2017). To complement this analysis, we compared the 24-h cycles between species using the Mardia-Watson-Wheeler test (W), run in Oriana 4.01 (Kovach Computing Services, Anglesey, UK).

Results

We obtained a total of 1764 independent records of the focal species, including 161 of ocelot, 63 of northern tiger cat, 35 of the top predators and 33 of the jaguarundi. The most common prey species was Spix's cavy (n = 828 records), followed by the rock cavy (n = 347) and the agouti (n = 297). The occupancy probability of the northern tiger cat correlated positively with the presence of Spix's cavy ($w_+ = 0.91$) and negatively with the presence of the ocelot ($w_+ = 0.75$; Table 2). The occurrence of the rock cavy was an important predictor of the detection of the northern tiger cat ($w_+ = 0.50$; Table 2). The occurrence of Spix's cavy was the only covariate that influenced the occupancy of the jaguarundi, with a very strong, positive relationship ($w_+ = 1.00$; Table 2). The probability of detection of this feline was also correlated positively with the occurrence of the top predators ($w_+ = 0.50$). The number of days on which the camera traps were operational also had a positive influence on the probability of detection of both small felids ($w_+ > 0.50$; Table 2).

The results of Rayleigh's uniformity test (Table 3) indicated that the daily activity of the study species did not have a uniform distribution. The species presented clear preferences for a specific portion of the circadian cycle, with most being predominantly nocturnal (more than 60% of records obtained at night). Despite the predominantly nocturnal pattern (46%), northern tiger cat presented a considerable crepuscular activity with 35% of the records in this period. By contrast, the jaguarundi (67% of records) and the agouti (60.3%) were predominantly diurnal.

The coefficient of temporal overlap between the northern tiger cat and the two smaller prey species (the cavies) was high ($\Delta_1 > 0.75$; Fig. 2), declining to moderate ($\Delta_1 = 0.54$) for the agouti. Even so, the *W* test indicated significant differences between the circadian distribution of the northern tiger cat and

Table 2 Cumulative AICc weights for the covariates used to model the probabilities of occupancy (Ψ) and detection (p) of the small felids (northern tiger cat and jaguarundi) in the Boqueirão da Onça, Bahia, Brazil. The estimates of the effects of the covariates (β parameters) are given for the most parsimonious model that included each covariate. The probabilities of occupancy were modeled as a function of the $\Psi_{\text{conditional}}$ of Spix's cavy, the $\Psi_{\text{conditional}}$ of rock cavy, the $\Psi_{\text{conditional}}$ of agoutis, the $\Psi_{\text{conditional}}$ of ocelots and the $\Psi_{\text{conditional}}$ of top predators. The detection probabilities were modeled as a function of the detection of the species and according to the number of days on which the cameras operated. The mean values of occupancy (Ψ) and detection (p) of the species were obtained from the most parsimonious models, which included the covariates with the highest cumulative weight ($w_+ \geq 0.50$)

		β parameters			Real parameters		
Covariates	Cumulative AICc weights	Estimate	Lower 95% CI	Upper 95% CI	Estimate	Lower 95% CI	Upper 95% CI
Northern tiger cat occupancy (Ψ)							
Cavy$_{\text{cond}}$	0.91	6.79	−1.12	14.71	–	–	–
Ocelot$_{\text{cond}}$	0.75	−9.99	−24.13	4.14	–	–	–
Rock$_{\text{cond}}$	0.05	−1.00	−3.48	1.47	–	–	–
Agouti$_{\text{cond}}$	0.02	0.13	−1.91	2.18	–	–	–
Predators$_{\text{cond}}$	0.02	0.10	−2.14	2.36	–	–	–
$\widehat{\Psi}$	–	–	–	–	0.64	0.47	0.82
Northern tiger cat detection (p)							
Camera operation	0.98	0.40	0.11	0.68	–	–	–
Detection of rock cavy	0.50	1.25	0.40	2.10	–	–	–
Detection of Spix's cavy	0.40	0.73	0.17	1.29	–	–	–
Detection of top predators	0.12	−19.0	−18.94	−19.10	–	–	–
Detection of ocelot	0.06	0.71	−0.12	1.54	–	–	–
Detection of agouti	0.02	0.10	−0.71	0.88	–	–	–
$\widehat{p}$	–	–	–	–	0.05	0.03	0.06
Jaguarundi occupancy (Ψ)							
Cavy$_{\text{cond}}$	1.00	9.40	−34.8	53.6	–	–	–
Rock$_{\text{cond}}$	0.13	0.42	−3.60	4.41	–	–	–
Agouti$_{\text{cond}}$	0.13	−0.70	−3.40	2.02	–	–	–
Ocelot$_{\text{cond}}$	0.13	−0.12	−2.93	2.70	–	–	–
Predators$_{\text{cond}}$	0.12	−0.29	−3.02	2.43	–	–	–
$\widehat{\Psi}$	–	–	–	–	0.52	0.27	0.77
Jaguarundi detection (p)							
Camera operation	0.83	0.22	0.01	0.44	–	–	–
Detection of top predators	0.50	1.50	0.10	2.82	–	–	–
Detection of agouti	0.18	0.52	−0.56	1.60	–	–	–
Detection of ocelot	0.18	0.33	−0.70	1.34	–	–	–
Detection of rock cavy	0.15	0.45	−0.97	1.90	–	–	–
Detection of Spix's cavy	0.14	−0.14	−1.00	0.71	–	–	–
$\widehat{p}$	–	–	–	–	0.04	0.01	0.08

Table 3 Rayleigh's uniformity test (Z) for temporal activity patterns, with the critical Z value being defined for a significance level of $P = 0.05$, based on the number of independent records (N) collected for each species.

	Z	P	Z_{critical}	N
Northern tiger cat	4.83	0.008	2.98	63
Jaguarundi	6.05	0.002	2.97	33
Spix's cavy	200.46	1×10^{-12}	2.99	828
Rock cavy	60.78	1×10^{-12}	2.99	347
Agouti	63.29	1×10^{-12}	2.99	297
Ocelot	46.16	1×10^{-12}	2.99	161
Top predators	8.60	1×10^{-4}	2.97	35

those of Spix's cavy ($W = 15.1$; d.f = 2; $P < 0.001$), the rock cavy ($W = 13.5$; d.f = 2; $P = 0.001$) and the agouti ($W = 48.3$; d.f = 2; $P < 0.001$). The northern tiger cat also presented a high degree of temporal overlap with the ocelot ($\Delta_1 = 0.74$), although the distribution of the daily records of these two species was dissimilar ($W = 19.9$; d.f = 2; $P = 0.001$). However, while the northern tiger cat also overlapped highly with the top predators ($\Delta_1 = 0.76$; Fig. 2), there was no difference in the distribution of their daily records ($W = 5.1$; d.f = 2; $P = 0.07$).

In the case of the jaguarundi, there was considerable overlap with the agouti ($\Delta_1 = 0.76$) and no difference in the circadian distribution of the records ($W = 1.2$; d.f = 2; $P = 0.53$). However, the predominantly diurnal activity pattern of this feline was reflected in low temporal overlap with the other species, of both prey and predator (Fig. 2), with significant differences between the daily distribution of the records of Spix's cavy ($W = 55.1$; d.f = 2; $P < 0.001$), the rock cavy ($W = 47.1$; d.f = 2; $P < 0.001$), the ocelot ($W = 54.6$; d.f = 2; $P < 0.001$) and the top predators ($W = 32.8$; d.f = 2; $P < 0.001$).

Discussion

The occupancy probabilities of the northern tiger cat and jaguarundi were both correlated positively with the presence of Spix's cavy. This is consistent with the theory that opportunist predators use space according to the availability of their prey (Luttbeg & Sih, 2004). Unfortunately, no reliable estimates of the population density of the three prey species are available for the study area and this requires further investigation by future studies. Even so, Spix's cavy is a small, terrestrial rodent that is very common in both shrubby Caatinga vegetation and plantations (Oliveira & Bonvicino, 2011). The jaguarundi is known to be a feline capable of occupying open areas (Oliveira, 1998). The northern tiger cat, by contrast, appears to prefer areas of denser vegetation in the Caatinga, more isolated from anthropogenic environments (Marinho *et al.*, 2018*b*). In the present study area, however, the spatial distribution of this feline was also correlated negatively with the presence of the ocelot.

The presence of one species may interfere with the occurrence of the other, with the subordinate species being obliged to occupy structurally less complex habitats (Palomares & Caro, 1999). Evidence of a process of this type has been found in forested ecosystems in Argentina, where northern tiger cats were more abundant in less well-preserved areas, thus avoiding competition with the ocelot (Di Bitetti *et al.*, 2010, Cruz *et al.*, 2018). A similar situation may be occurring in our study area, where the ocelot occupies habitats with denser vegetation in comparison with the northern tiger cat, which may be restricted to areas of shrub caatinga. This is consistent with an observation known as 'ocelot effect', where ocelots may have a negative impact on smaller sympatric felids due to the potential for intraguild predation, which may be reflected in an altered distribution of the smaller felids (Oliveira *et al.*, 2010). However, we believe that the spatial segregation of the northern tiger cat and ocelot will only arise in more extensive areas of well-preserved habitat, such as that found in our study area and the mosaic of protected areas surveyed in Argentina (Di Bitetti *et al.* 2010, Cruz *et al.*, 2018). On the contrary, where the landscape was characterized by small and isolated fragments of forest, the northern tiger cat did not segregate spatially from ocelots, but became more active during the day (Massara *et al.*, 2016).

The detection probability of the northern tiger cat correlated positively with the frequency of the rock cavy. These rodents are abundant and gregarious and are typically found in association with rocky outcrops (Dias *et al.*, 2018). We believe that this specific feature of the habitat use of this species makes encounters more predictable, which may enable the northern tiger cat to maximize its foraging efficiency by returning regularly to areas frequented by these rodents.

We found no evidence of a direct influence of the ocelot on the spatial distribution of the jaguarundi, perhaps due to the temporal segregation between these species, given that jaguarundi and ocelot were predominantly diurnal and nocturnal, respectively. In addition, contrary to our predictions, the jaguarundi did not appear to avoid areas used by the top predators. Given the positive relationship between the occurrence of top predators and habitat quality as well as the abundance of preys (Davis, Kelly & Stauffer, 2011), it seems likely that the jaguarundi will visit more intensely the sites most frequented by top predators due to the higher prey intensity in these sites.

Camera traps are an extremely valuable research tool for the systematic collection of data on carnivore communities and activity patterns (Massara *et al.*, 2016; Dias *et al.*, 2018). However, the use of camera traps also has certain limitations, such as malfunctions and theft. This emphasizes the need to maximize the number of sampling days to ensure reliable records. Unreliable data will obviously have a negative effect on modeling and the potential for realistic estimates of occupancy probabilities. This is emphasized by the fact that the operational trap-days was the most important covariate of the probability of detection of the felids in the present study.

The activity patterns recorded in the present study were consistent with those described in Oliveira *et al.* (2013), which have shown the northern tiger cat to be nocturnal and crepuscular and the jaguarundi to be diurnal (Oliveira, 1998). In extreme environments, such as semi-arid ecosystems, carnivores are believed to adopt more nocturnal habits, as a way of avoiding the intense heat of the daytime period (Penido *et al.*,

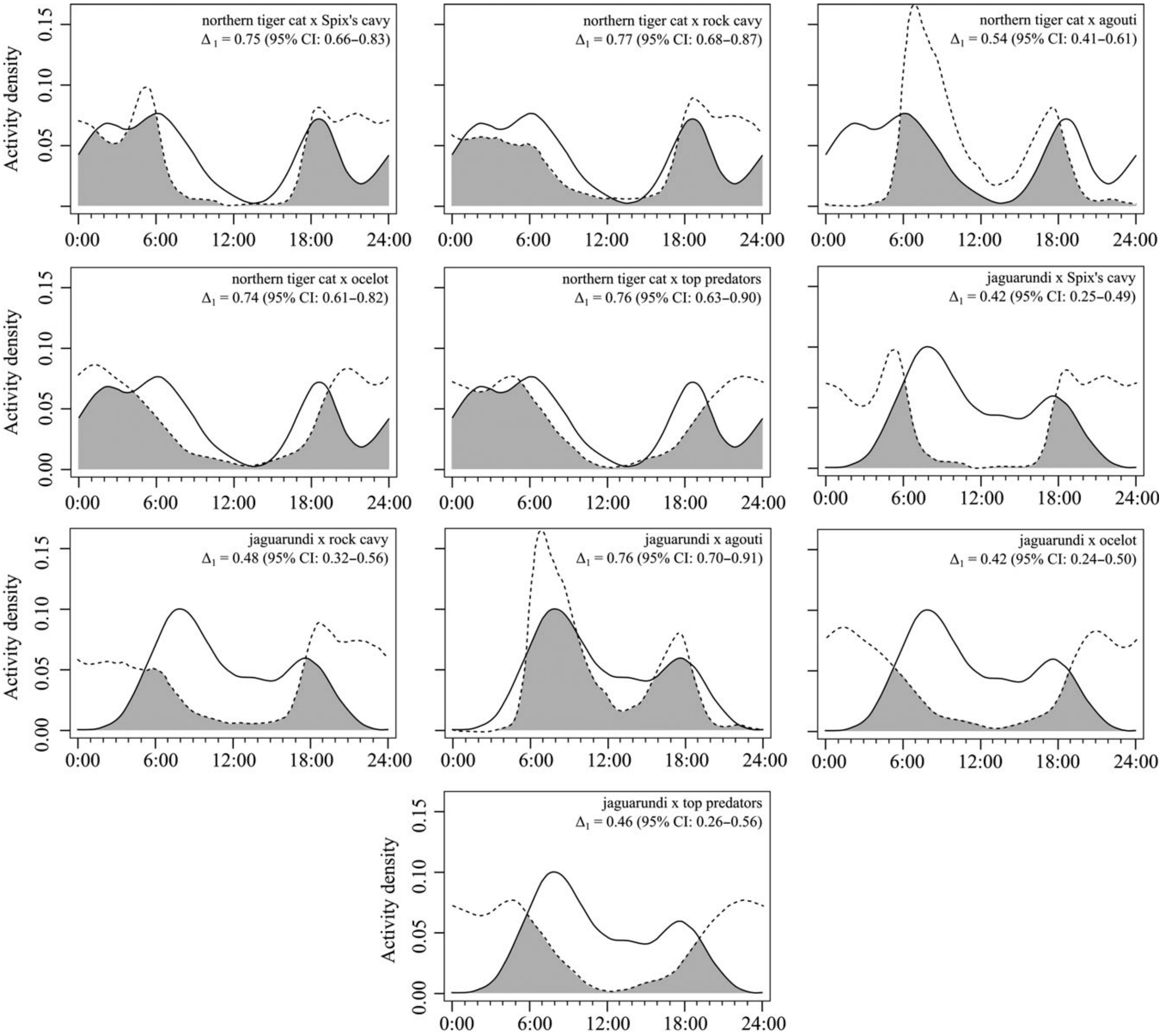

Figure 2 Temporal activity of the small felids (northern tiger cat and jaguarundi), represented by the solid line and the degree of overlap (95% CIs) with the three prey species, the ocelot and the top predators, represented by the dotted lines, in the Boqueirão da Onça, Bahia, Brazil. The overlap between activity periods is represented by the shaded area. The *x* axis represents the time of day, with sunrise occurring at 06:00 h and sunset at 18:00 h.

2017), as in the specific case of the northern tiger cat in the Caatinga, despite the fact that more nocturnal habits increase its temporal overlap with larger felids. In the Atlantic Forest, where temperatures are generally less intense, Massara *et al.* (2016) observed more diurnal behavior in the northern tiger cat, possibly in response to the presence of the larger felids.

We believe that interspecific interactions may have the strongest influence on the activity patterns of the study species. In other Brazilian regions, for example, felids activity patterns are influenced primarily by the availability of preys (Foster *et al.*, 2013; Azevedo *et al.*, 2018). While we found dissimilarities between the distribution of activity in the northern tiger cat and its two potential prey species (the cavies), given the asynchronous peaks in activity, we also found a high degree of temporal overlap between these species. Similar results were obtained in other locations of Caatinga (Marinho *et al.*, 2018*a*). Our temporal overlap results, together with the strong spatial correlation, indicate that the cavies may represent an important feeding resource for the northern tiger cat in the present study area. Despite being predominantly diurnal, the agouti also presented a moderate temporal overlap with the northern tiger cat, although the lack of a spatial correlation between these two species implies that the predation of this rodent by the northern tiger cat will be intermittent.

By contrast, we identified a high temporal overlap between the jaguarundi and the agouti, the only predominantly diurnal prey species analyzed in the present study. However, we found no spatial correlation between these two species, which indicates that the jaguarundi may focus on other groups of prey in the Caatinga, such as birds and lizards (Olmos, 1993; Dias & Bocchiglieri, 2015).

In communities dominated by large carnivores, the behavior of subordinate competitors reflects the trade-off between the need to capture prey and avoid agonistic encounters with dominant competitors (Caro & Stoner, 2003). In this case, trophic and spatial overlap between members of the carnivore guild may support temporal segregation (Oliveira & Pereira, 2014). A number of previous studies have shown that the northern tiger cat may become more diurnal or cathemeral where it coexists with larger felids (Di Bitetti *et al.*, 2010; Oliveira-Santos *et al.*, 2012; Massara *et al.*, 2016). In the Brazilian Atlantic Forest, for example, the ocelot does not influence the spatial distribution of the northern tiger cat, which may nevertheless avoid encounters through temporal segregation (Massara *et al.*, 2016). This contrasts with the pattern observed in the Caatinga (Penido *et al.*, 2017), however and in particular in the area of the present study. While we did find differences in the circadian distributions of the two species, with activity peaking in the northern tiger cat at 06:00 h and 18:30 h and at 01:00 h and 21:00 h in the ocelot, the high temporal overlap observed between these two species indicates that the northern tiger cat is influenced by the availability of its potential prey, adopting a strategy of spatial segregation to avoid contact with the ocelot. As the only diurnal feline in the study area, there was little temporal overlap between the jaguarundi and the larger felids, allowing it to visit the same areas used by the ocelot and top predators with little risk of encounters.

Contrary to our hypothesis, we found no evidence of the influence of the top predators on the activity patterns or distribution of the small felids. Even the northern tiger cat, which had a high degree of temporal overlap, appears to also overlap spatially with the top predators. Davis *et al.* (2011) observed a similar situation in Belize, Central America, where they concluded that the low densities of the larger felids would make encounters with the smaller species relatively rare. While no recent data are available for Boqueirão da Onça, top predators appear to be rare in the Caatinga in general (Paula, Campos & Oliveira, 2012; Azevedo *et al.*, 2013). One other alternative is that the differences in the trophic niches of the species alone are enough to avoid spatial or temporal segregation. In this case, the northern tiger cat and jaguarundi would be too small to be considered potential competitors to the top predators, given that the intraguild predation theory predicts that predation will be most intense when the dominant species is 2.0–5.4 larger than the subordinate one (Donadio & Buskirk, 2006). In this case, the ocelot would have the greater influence on the small felids, as shown in this study.

Overall, the present study provides an important overview of the spatial and temporal interactions found in a community of Neotropical felids. In contrast with previous studies in Brazil, we investigated the simultaneous effects of potential prey and large felids on the occupancy and activity patterns of small felids. The results indicate that the availability of prey and their activity patterns may have a greater influence on the spatiotemporal ecology of the small felids than the top predators. However, the ocelot appears to have a negative effect on the small felids, in particular the northern tiger cat, through either competition or intraguild predation. Our findings also provide new insights into the behavioral response of the northern tiger cat to sympatry with the ocelot. We believe that spatial segregation in the northern tiger cat is more viable in more extensive areas of well-preserved habitat, where the greater availability of space and resources may facilitate divergences in habitat use. In more restricted and fragmented landscapes, however, space may become a limiting factor for the northern tiger cat, forcing it to segregate temporally from the ocelot. Due to the temporal asynchronism, we did not find the influence of the ocelot on the jaguarundi. In this case, the 'ocelot effect' may be operating through other mechanisms, perhaps restricting the abundance of jaguarundi, as suggested by Oliveira *et al.* (2010), this deserves to be investigated through population studies. Further research should also focus on areas with varying degrees of habitat disturbance to better discern to what extent habitat modifications may influence the behavior of these species. More systematic data on trophic ecology would also contribute to a better understanding of the relationships among these predator species.

Acknowledgments

We are grateful to the Neotropical Grassland Conservancy for providing memorial grants and the Rufford Foundation for a small grant (project 18442-1). We also thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing grants to DMD and RLM. We are also grateful to Professor Adriano Paglia of the Federal University of Minas Gerais and the Pró-Carnívoros Institute for logistic support. We also thank the Mariano Neto, Dito and Ananias for assistance in field activities. We also thank A.M. Paschoal, F.C. Azevedo, R. C. de Paula, T.G. de Oliveira and the anonymous reviewers for their valuable suggestions to improving the manuscript.

References

Azevedo, F.C., Lemos, F.G., Almeida, L.B., Campos, C.B., Beisiegel, B.M., Paula, R.C., Crawshaw, P.G. Jr, Ferraz, K.M.M.B. & Oliveira, T.G. (2013). Avaliação do risco de extinção da onça-parda *Puma concolor* (Linnaeus, 1771) no Brasil. *Biodiversidade Brasileira* **2013**, 107–121.

Azevedo, F.C., Lemos, F.G., Freitas-Junior, M.C., Rocha, D.G. & Azevedo, F.C.C. (2018). Puma activity patterns and temporal overlap with prey in a human-modified landscape at Southeastern Brazil. *J. Zool. (Lond.)* **305**, 246–255.

Bailey, L.L., Simons, T.R. & Pollock, K.H. (2004). Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecol. Appl.* **14**, 692–702.

Berger, J. (2010). Fear-mediated food webs. In *Trophic cascades: predators, prey and the changing dynamics of* *nature*: 241–254. Terborgh, J. & Estes, J.A. (Eds). Washington: Island Press.

Bonvicino, C.R., Oliveira, J.A. & D'Andrea, P.S. (2008). *Guia de roedores do Brasil, com chaves para gêneros baseadas em caracteres externos*. Rio de Janeiro: Centro Pan-Americano de Febre Aftosa – OPAS/OMS.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach*. 2nd edn. New York: Springer-Verlag.

Cabús, R. (2015). Tropsolar 5.0. Grupo de Pesquisa em Iluminação (GRILU). Maceió, Brazil. http://www.ctec.ufal.br/grupopesquisa/gril (accessed 4 November 2017).

Caro, T.M. & Stoner, C.J. (2003). The potential for interspecific competition among African carnivores. *Biol. Conserv.* **110**, 67–75.

Carothers, J.H. & Jaksic, F.M. (1984). Time as a niche difference: the role of interference competition. *Oikos* **42**, 403–406.

Cassano, C.R., Barlow, J. & Pardini, R. (2014). Forest loss or management intensification? Identifying causes of mammal decline in cacao agroforests. *Biol. Conserv.* **169**, 14–22.

Cruz, P., Iezzi, M.E., De Angelo, C., Varela, D., Di Bitetti, M.S. & Paviolo, A. (2018). Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. *PLoS ONE* **13**, e0200806.

Davis, M.L., Kelly, M.J. & Stauffer, D.F. (2011). Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve. *Belize. Anim. Conserv.* **14**, 56–65.

Dias, D.M. & Bocchiglieri, A. (2015). Dieta de carnívoros (Mammalia, Carnivora) em um remanescente de Caatinga, Nordeste do Brasil. *Bioikos* **29**, 13–19.

Dias, D.M., Campos, C.B. & Rodrigues, F.H.G. (2018). Behavioural ecology in a predator-prey system. *Mamm. Biol.* **92**, 30–36.

Di Bitetti, M.S., De Angelo, C., Di Blanco, Y.E. & Paviolo, A. (2010). Niche partitioning and species coexistence in a neotropical felid assemblage. *Acta Oecol.* **36**, 403–412.

Doherty, P.F., White, G.C. & Burnham, K.P. (2012). Comparison of model building and selection strategies. *J. Ornithol.* **152**, S317–S323.

Donadio, E. & Buskirk, S.W. (2006). Diet, morphology, and interspecifc killing in carnivora. *Am. Nat.* **167**, 1–13.

Durant, S.M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.* **11**, 624–632.

Foster, V.C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A.T.A., Negrões, N., Fonseca, C. & Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. *Biotropica* **45**, 373–379.

Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. & Nilsen, E.B. (2012). Habitat heterogeneity and mammalian predator-prey interactions. *Mammal. Rev.* **42**, 55–77.

Goulart, F.V.B., Cáceres, N.C., Graipel, M.E., Tortato, M.A., Ghizoni, I.R. Jr & Oliveira-Santos, L.G.R. (2009). Habitat selection by large mammals in a southern Brazilian Atlantic Forest. *Mamm. Biol.* **74**, 182–190.

Hines, J.E. (2006). Presence2- software to estimate patch occupancy and related parameters. Available at http://www.mbr-pwrc.usgs.gov/software/presence.html (accessed January 2018).

INMET – Instituto Nacional de Meteorologia. (2018). Clima. Available at http://www.inmet.gov.br/portal/index.php?r=home2/index (accessed August 2018).

Jenny, D. & Zuberbühler, K. (2005). Hunting behaviour in West African forest leopards. *Afr. J. Ecol.* **43**, 197–200.

Linkie, M. & Ridout, M.S. (2011). Assessing tiger–prey interactions in Sumatran rainforests. *J. Zool. (Lond.)* **284**, 224–229.

Luttbeg, B. & Sih, A. (2004). Predator and prey habitat selection games - the effects of how prey balance foraging and predation risk. *Israel J. Zool.* **50**, 233–254.

Mackenzie, D.I. & Bailey, L.L. (2004). Assessing the fit of site-occupancy models. *J. Agric. Biol. Environ. Stat.* **9**, 300–318.

Mackenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Burlington: Elsevier/Academic Press.

Marinho, P.H., Bezerra, D., Antongiovanni, M., Fonseca, C.R. & Venticinque, E.M. (2018a). 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.

Marinho, P.H., Bezerra, D., Antongiovanni, M., Fonseca, C.R. & Venticinque, E.M. (2018b). Estimating occupancy of the Vulnerable northern tiger cat *Leopardus tigrinus* in Caatinga drylands. *Mamm. Res.* **63**, 33–42.

Massara, R.L., Paschoal, A.M.O., Doherty, P.F. Jr, Hirsch, A. & Chiarello, A.G. (2015). Ocelot population status in protected Brazilian Atlantic Forest. *PLoS ONE* **10**, e0141333.

Massara, R.L., Paschoal, A.M.O., Bailey, L.L., Doherty, P.F. Jr & Chiarello, A.G. (2016). Ecological interactions between ocelots and sympatric mesocarnivores in protected areas of the Atlantic Forest, southeastern Brazil. *J. Mammal.* **97**, 1634–1644.

Massara, R.L., Paschoal, A., Bailey, L.L., Doherty, P.F. Jr, Hirsch, A. & Chiarello, A.G. (2018a). Factors influencing ocelot occupancy in Brazilian Atlantic Forest reserves. *Biotropica* **50**, 125–134.

Massara, R.L., Paschoal, A., Bailey, L.L., Doherty, P.F. Jr, Barreto, M.F. & Chiarello, A.G. (2018b). Effect of humans and pumas on the temporal activity of ocelots in protected areas of Atlantic Forest. *Mamm. Biol.* **92**, 86–93.

Meredith, M. & Ridout, M. (2018). Overview of the overlap package. R Project. 1–9. Available at https://cran.r project.org/web/packages/overlap/vignettes/overlap.pdf (accessed 26 August 2018)

Milakovic, B., Parker, K.L., Gustine, D.D., Lay, R.J., Walker, A.B.D. & Gillingham, M.P. (2011). Habitat selection by a focal predator (*Canis lupus*) in a multiprey ecosystem of the northern Rockies. *J. Mammal.* **92**, 568–582.

Oliveira, T.G. (1998). Herpailurus yagouaroundi. *Mamm. Species* **578**, 1–6.

Oliveira, L.O. & Bonvicino, C.R. (2011). Ordem Rodentia. In *Mamíferos do Brasil*: 358–414. Reis, N.R., Peracchi, A.L., Pedro, W.A. & Lima, I.P. (Eds). Londrina: Edição do Autor.

Oliveira, T.G. & Pereira, J.A. (2014). Intraguild predation and interspecific killing as structuring forces of carnivoran communities in South America. *J. Mammal. Evol.* **21**, 427–436.

Oliveira, T.G., Tortato, M.A., Silveira, L., Kasper, C.B., Mazim, F.D., Lucherini, M., Jácomo, A.T., Soares, J.B.G., Rosane, V.M. & Sunquist, M. (2010). Ocelot ecology and its effects on the small-felid guild in the lowland Neotropics. In *Biology and conservation of wild felids*: 559–580. Macdonald, D.W. & Loveridge, A.J. (Eds). Oxford: Oxford University Press.

Oliveira, T.G., Tortato, M.A., Almeida, L.B., Campos, C.B. & Beisiegel, B.M. (2013). Avaliação do risco de extinção do Gato-do-mato *Leopardus tigrinus* (Schreber, 1775) no Brasil. *Biodiversidade Brasileira* **3**, 56–65.

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 northern tiger cat, *Leopardus tigrinus* (Carnivora: Felidae), appear to reflect avoidance of conflict. *Zoologia* **29**, 115–120.

Olmos, F. (1993). Notes on the food habits of Brazilian caatinga carnivores. *Mammalia* **57**, 126–130.

Orians, G.H. & Wittenberg, J.F. (1991). Spatial and temporal scales in habitat selection. *Am. Naturalist* **137**, 29–49.

Palomares, F. & Caro, T.M. (1999). Interspecific killing among mammalian carnivores. *Am. Naturalist* **153**, 492–508.

Paula, R.C., Campos, C.B. & Oliveira, T.G. (2012). Red list assessment for the jaguar in the Caatinga Biome. *Cat News* **7**, 19–24.

Penido, G., Astete, S., Jácomo, A.T.A., Sollmann, R., Tôrres, N., Silveira, L. & Marinho Filho, J. (2017). Mesocarnivore activity patterns in the semiarid Caatinga: limited by the harsh environment or affected by interspecifc interactions? *J. Mammal.* **98**, 1732–1740.

Polis, G.A., Myers, C.A. & Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**, 297–330.

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org.

Rinaldi, A.R., Rodriguez, R.H., Carvalho, A.L. & Passos, F.C. (2015). Feeding of small neotropical felids and trophic nich overlap in antropized mosaic landscape, South Brazilian. *Biotemas* **28**, 155–168.

Roos, A.L., Souza, E.A., Campos, C.B., Paula, R.C. & Morato, R.G. (2012). Primeiro registro do Jacu-estalo *Neomorphus geoffroyi* Temminck, 1820 para o bioma Caatinga. *Rev. Bras. Ornitol.* **20**, 81–85.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structure. *J. Biogeog.* **31**, 79–92.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl Acad. Sci.* **101**, 10854–10861.

Velloso, A.L., Sampaio, E.V.S.B. & Pareyn, F.G.C. (2002). *Ecorregiões propostas para o bioma Caatinga*. Recife: APNE/The Nature Conservancy.

White, G.C. & Burnham, K.P. (1999). Program mark: survival estimation from populations of marked animals. *Bird Study* **46**, 120–139.

Worton, B.J. (1989). Kernel methods for estimating the utilization distribution in home-range. *Ecology* **70**, 164–168.

Zanin, M., Sollmann, R., Tôrres, N.M., Furtado, M.M., Jácomo, A.T.A., Silveira, L. & De Marco, P. (2015). Landscapes attributes and their consequences on jaguar *Panthera onca* and cattle depredation occurrence. *Eur. J. Wildlife Res.* **61**, 529–537.

Zar, J.H. (2010). *Biostatistical analysis*. 5th edn. Hoboken: Pearson Education Inc..