BRENO CAMPELO LIMA

A REFINED POPULATION AND OCCUPANCY ASSESSMENT OF TWO ENDANGERED FELIDS: NORTHERN TIGER CAT (*Leopardus tigrinus*) AND PAMPAS CAT (*Leopardus colocola*) IN THE NORTHERN SAVANNAS OF BRAZIL

SÃO LUÍS

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Dissertação de Mestrado apresentada ao Programa de Pós-Graduação em Ciência Animal PPGCA/UEMA, como parte dos requisitos para obtenção do título de Mestre em Ciência Animal, área de concentração em Reprodução e Conservação Animal

Orientador: Prof. Dr. Tadeu Gomes de Oliveira

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Aprovada em / /

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“O homem nunca tem o bastante sem ter em demasia”

(James Lovelock)

SUMÁRIO

APRESENTAÇÃO

O Brasil é considerado como um dos países de maior diversidade biológica por abrigar mais de 10% das formas viventes no planeta (MYERS et al., 2000) que estão distribuídas nos mais variados ambientes. Nesse contexto, encontra-se o Cerrado, também chamado de savana brasileira. Esse bioma ocupa o ranking de segundo maior bioma brasileiro, ocupando uma área com mais 2 milhões de km², equivalente a 23% do território brasileiro (EITEN 1972, AB'SABER, 1977).

Também reconhecido como hotspot, o Cerrado padece com um intenso processo de conversão da cobertura vegetal por atividades produtivas, tendo perdido mais de 51% da sua cobertura original. Dentre as regiões apontadas como prioritárias para conservação da biodiversidade do Cerrado, encontra-se a segunda maior Unidade de Conservação (UC) do Cerrado – o "Parque Estadual do Mirador" (PEM).

O PEM apresenta uma importância singular para conservação da biodiversidade. A despeito disso, estudos preliminares apontam uma grande riqueza dos mais variados grupos, especialmente para a mastofauna. Dados pretéritos, sugerem o PEM como uma importante UC na conservação de espécies mundialmente ameaçadas, como os felinos *Leopardus tigrinus* (Schreber, 1775) (gato-do-mato/gato-pintado) e *Leopardus colocola* (Molina, 1782) (gato-palheiro). Diante do exposto, o PEM passou a ser considerado pela IUCN como uma das áreas mais importantes para a conservação ao nível mundial desses felinos ameaçados.

Esta dissertação abordará aspectos ecológicos e conservacionistas de duas espécies de felinos ameaçados *Leopardus tigrinus* e *Leopardus colocola* na porção norte do Cerrado brasileiro. O manuscrito foi dividido em dois capítulos que estarão estruturados de acordo com as normas das revistas de interesse para publicação.

Capítulo I **- A refined population and conservation assessment of the elusive and endangered northern tiger cat (*Leopardus tigrinus*) in its key worldwide conservation area in Brazil**

Neste capítulo é apresentado a primeira estimativa de densidade publicada para *Leopardus tigrinus*. Também foi realizado uma Análise de Viabilidade Populacional (PVA) e avaliado o impacto de cães domésticos na população do gato-do-mato do Parque.

Adicionalmente, extrapolamos as análises de densidade para outras áreas que compõem o corredor na porção norte da Reserva da Biosfera do Cerrado.

As estimativas de densidade de gato-do-mato foram de 0,12 e 0,25 indivíduos / km² (através da análise não-espacial) ou 0,087 e 0,11 indivíduos / km² (na análise espacial), enquanto as abundâncias relativas variaram de 0,124-2,168 indivíduos/100 noites de armadilha. A população foi estimada em 522 indivíduos, o PVA estimou uma probabilidade de extinção de 0% nos próximos 100 e 1.000 anos, em cenários de surtos leves a inexistentes de doença. Ao extrapolar as análises para a Reserva da Biosfera, os resultados indicaram que a população é de aproximadamente 700 indivíduos no complexo de áreas protegidas que compõem a porção norte da Reserva da Biosfera e de 2000 a 3000 indivíduos em todo área considerada habitável pela espécie na Reserva. Artigo publicado na Revista Global Ecology and Conservation em janeiro de 2020 (https://doi.org/10.1016/j.gecco.2020.e00927).

Capítulo II - **Of small cats and dogs: Interspecific relationships of wild and domestic carnivores in the northern savannas of Brazil**

Neste capítulo abordamos a influência de variáveis ambientais e antrópicas nos mecanismos de exploração espaço-temporal dos pequenos felinos *Leopardus tigrinus* e *Leopardus colocola* no Parque Estadual do Mirador. Utilizamos Modelos Lineares Generalizados (GLM) e Modelos de Ocupação (OM) para estimar a influência das covariáveis nos padrões de uso do habitat, também extrapolamos seus efeitos para os locais amostrados. Adicionalmente, analisamos padrões de atividade para ambas as espécies.

Os registros foram obtidos entre maio de 2018 e março de 2019 com 30 armadilhas fotográficas instaladas em duas áreas dentro do parque, totalizando 4.312 armadilhas. Obtivemos uma taxa de ocupação natural de 0,23 e 0,50 para *L. colocola* e *L. tigrinus*, respectivamente. A detectabilidade de ambas as espécies foi afetada diretamente pela estrutura da vegetação, enquanto as análises de seleção de habitat mostraram que *L. tigrinus* evitava áreas próximas a assentamentos humanos e com alta intensidade de uso por cães domésticos; por outro lado, a seleção do habitat de *L. colocola* foi influenciada principalmente pela estrutura da vegetação. As espécies de gatos e os cães domésticos apresentaram um grau moderado de sobreposição temporal, enquanto houve uma segregação temporal significativa entre os dois felídeos; o maior nível de sobreposição de atividades foi observado entre *L. tigrinus* e *Cerdocyon thous*. O artigo foi estruturado de acordo com as normas da Revista de interesse para publicação – Perspectives in Ecology and Conservation.

CAPITULO I

Artigo publicado na Global Ecology and Conservation

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A refined population and conservation assessment of the elusive and endangered northern tiger cat (*Leopardus tigrinus*) in its key worldwide conservation area in Brazil

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Abstract

The northern tiger cat (*Leopardus tigrinus*) is one of Brazil's least studied felids, with no published population density estimates. A potential key conservation unit for the species is Mirador State Park (MSP) in NE Brazil, an area that also hosts humans and domestic dogs. Therefore, we assessed the park's importance in terms of tiger cat conservation and whether domestic dogs present a threat to the survival of this species. We established 52 camera trap stations at three sites and monitored them for a total of 5,030 trap-days. We calculated population densities using spatial and nonspatial methods and relative abundances in MSP and extrapolated these results to the other protected areas and corridor that comprise the northern portion of the Cerrado Biosphere Reserve. We conducted a population viability analysis for tiger cats in the park and assessed the potential impact of domestic dogs. The tiger cat density estimates were 0.12 and 0.25 individuals/km^2 (nonspatial) and 0.087 and 0.11 individuals/km^2 (spatial), whereas the relative abundances ranged from 0.124-2.168 individuals/100 trap-nights. The tiger cat population was estimated at 287 individuals, with 0% extinction probability within the next 100 and 1,000 years, but only in scenarios of mild to no disease outbreaks. Large outbreaks or habitat loss will be detrimental to species survival in the area. Domestic dogs were detected at 80% of the stations where tiger cats were observed. The threat of disease transmission by domestic dogs potentially impacts 65% of the park and seems to be the primary threat for the species there. The northern tiger cat population was estimated at approximately 700 individuals in the entire protected area of the northern savannas, which together with the additional corridor of the Cerrado Biosphere Reserve could yield up to 2,000-3,000 individuals. Our results provide the first published density estimates of tiger cats and confirm the potential threat of domestic dogs to this felid in Mirador, thereby confirming the park's importance as a key area for tiger cat conservation and the need for conservation actions. Given its density and abundance of tiger cats, as well as its area size, compared to other locations in the northern savannas, MSP may be the most important site for the worldwide, long-term conservation of *Leopardus tigrinus.*

Keywords: *Leopardus tigrinus*; northern savannas of Brazil; Northern tiger cat; population and conservation assessments; population viability analysis; spatial and nonspatial density.

Highlights:

- The first density estimates for *Leopardus tigrinus* are reported.
- This is the first PVA analysis conducted for a small cat in tropical America.
- Populations will be viable with mild-disease but nonviable with a large outbreak or habitat loss.
- Disease transmission by domestic dogs in the primary threat for the species in MSP.
- MSP is the most important site for the long-term conservation of *Leopardus tigrinus*.

1. Introduction

Conservation often requires population estimates to improve or identify a proper course of action, information that is lacking for most species of small cats (< 15 kg). Because of advances in methods and programs pertaining to camera trapping (e.g., Sollman et al., 2011; Tobler and Powell, 2013), this scenario is beginning to change for the smaller and lesser-known species of Felidae (Caruso et al., 2012; Mohamed et al., 2013; Naing et al., 2017). The northern tiger cat (*Leopardus tigrinus*) is a small-sized felid (ca. 2.4 kg; Figure 1) whose currently recognized range from Costa Rica to central Brazil is still being defined (Payan and de Oliveira, 2016; de Oliveira et al. unp. data). There is a very poor understanding of the demography, ecology and natural history of *L. tigrinus*, with very few available estimates of abundance and occupancy (Oliveira, 2011; Marinho et al., 2017; Oliveira, 2018; Dias et al., 2019). Furthermore, most ecological studies conducted before the species split investigated what is now considered *Leopardus guttulus* (e.g., Tortato and Oliveira, 2005; Oliveira-Santos et al., 2012). Only recently has *L. tigrinus* become the subject of long-term studies (Oliveira et al., 2008, 2018; Oliveira, 2011; Marinho et al., 2017; Oliveira, 2018; Dias et al., 2019). This species is the only carnivore listed as Endangered in Brazil and as Vulnerable worldwide (Oliveira et al., 2018a; Payan and de Oliveira, 2016).

Figure 1. Northern tiger cat (*Leopardus tigrinus*) in its key worldwide conservation area at Mirador State Park in the threatened northern/MATOPIBA savanna of Brazil.

It is increasingly known that the impacts of nonnative animals on native wildlife might be much greater than expected. Exotic carnivores can affect wild populations through direct predation, behavioral alteration, and disease transmission to other animals and humans (Weston et al., 2014; Doherty et al., 2017). The effects of predation and diseases of domestic dogs in natural areas are well documented (Young et al., 2011; Doherty et al., 2017). Transmitted diseases include canine distemper virus, parvovirus, and rabies, with cases of wildlife die-off due to these diseases documented within protected areas (Roelke-Parker et al., 1996; Woodroffe, 1999). Therefore, even in fully protected areas, wildlife may still be at risk if domestic dogs are present within them or in adjacent areas.

This raises the question as to whether certain key conservation units are indeed effectively protecting threatened wildlife.

The savannas of the Cerrado biome, a biodiversity hotspot, are currently facing the greatest threats related to habitat loss in Brazil; an annual loss rate of ca. 0.44% has been observed, with >51% of the biome having already been removed and only 8% off limits for development (IBAMA, 2015; NASA, 2018). Current removal is concentrated in the MATOPIBA region (an acronym for the states of Maranhão, Tocantins, Piauí and Bahia), Brazil's new agricultural frontier, where agricultural lands increased by 87% between 2000 and 2014 (IBAMA, 2015; NASA, 2018). This area comprises the northern savannas, which are the country's most extensive savannas, and areas of the highest conservation priority, including the entire remaining nonagricultural area surrounding Mirador State Park (MSP; MMA, 2017). This park hosts an impressive number of threatened species and faces several environmental problems (Oliveira, 2014). Among these is the very high presence of domestic animals, including domestic dogs. The tiger cat has long been found to live in the park (Oliveira, 1996), and given some abundance estimates, the park was noted as a possible key worldwide conservation area for the species in the IUCN Red List assessment (Payan and de Oliveira, 2016). Therefore, we asked two main questions: does MSP represent a key conservation area for the endangered northern tiger cat? Could the domestic dogs in the area pose a threat to this species? To answer these questions, the main goals of the current study were to provide estimates of the density and abundance of the population of northern tiger cats in MSP, and assess the role of the park in the long-term conservation and persistence of this species.

2. Study Area

MSP is a fully protected conservation area in the Brazilian mid-north (Figure 2). At 5,008 km^2 in size, MSP is the second largest protected area in the Brazilian Cerrado. The park encompasses a series of savanna formations, from open to forested, and includes gallery forests composed mostly of palms (see Rodrigues and Conceição, 2014 for a detailed description). The climate is subhumid, with an annual precipitation of 1,200 mm and mean maximum and minimum temperatures of 31.4-33.0°C and 19.5-21.0°C, respectively (Rodrigues and Conceição, 2014). Preliminary assessments indicated the presence of 28 species of mammals of conservation interest, making MSP a key biodiversity area (Oliveira, 2014). The study sites within MSP were established within three outposts: Mel, Cágados and Zé Miguel (Supplementary Material Fig. S1). Mel and Zé Miguel contain settlements, whereas Cágados does not. The vegetation structure is mostly dense woodland savannas at Mel, semiopen to dense woodland savannas at Cágados, and mostly open savannas at Zé Miguel. Wild and human-induced fires are the only impacts to the vegetation at the sites. Human slash-burn agriculture at the park is conducted mostly near the watersheds, away from the sampling sites. Thus, we considered all sampling sites to be representative of the area’s natural vegetative conditions, regardless of their proximity to human settlements.

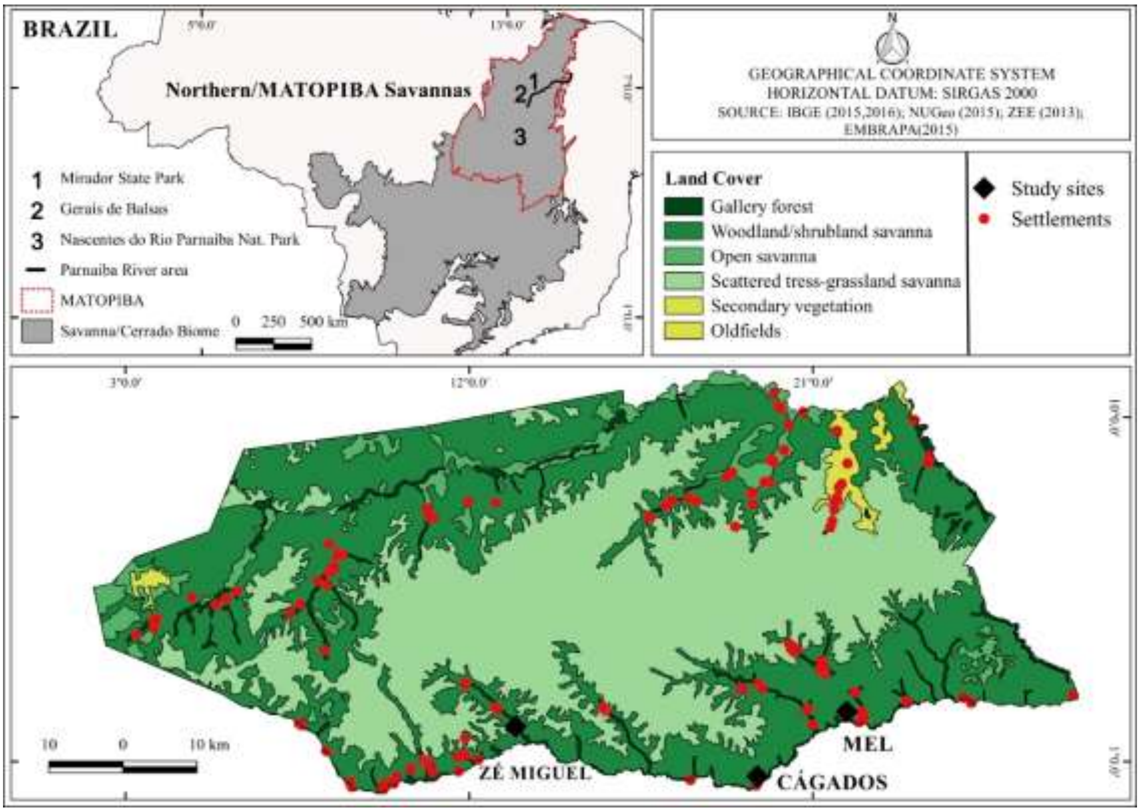


Figure 2. Locations of the study sites in the northern savannas of Brazil and the camera-trapping sites and human settlements in Mirador State Park.

3. Methods

3.1. Camera trapping protocol

We deployed passive detection camera traps, the infrared Bushnell Trophy Cam HD (Bushnell Outdoor Products, Overland Park/Kansas), and the white-flash ScoutGuard SG565 (Boly Inc., Santa Clara/California) and Reconyx PC850 (Reconyx Inc., Holmen/Wisconsin). Typically, >19 camera stations consisting of one unit each were used in each sampling area (Mel, Cágados). Camera placement followed the same protocol at all sites, always targeting small felids. All cameras were spaced from 0.5 km to 1 km apart to guarantee that no animals would have a zero detection probability based on the known minimum home range size of tiger cats and other Neotropical felids and the typical distance moved by these animals (e.g., Michalski et al., 2006; Oliveira et al., 2010; Kasper et al., 2016). The camera traps were typically placed 20-30 cm high along trails and at other sites with high potential for felid detection. This protocol has been very effective for the detection of felids (Oliveira et al., 2008). Overall, camera trapping was conducted from January 2014 to August 2018 (Table 1). For abundance comparisons, we also used data from four months of sampling in 2005 conducted with the same protocol and at the same sampling site in the Cágados area by the lead author. To assess the extent of dog use (ray of action), we determined the minimum and maximum distance moved from a camera location to the nearest and farthest households at the sites. A detailed study of the health of domestic carnivores is being conducted at the sites.

3.2. Population parameters

To determine relative abundance, consecutive photographic records of the same species were defined as independent occurrences when the individual(s) could be unambiguously distinguished or if the interval between records was >1 hour. Individual tiger cat identification was based on their characteristic spot patterns, body markings and other individual features (i.e., scars).

Population estimation was conducted using the traditional mark-recapture method with the *Rcapture* package (Baillargeon and Rivest, 2007) in R version 3.5.1 (R Development Core Team, 2016). Best-fit models were evaluated based on Akaike information criterion (AIC) values. We favored heterogeneity models (M_h), as they are widely considered to be more biologically appropriate for felids than other models because of the variation in capture probability among individuals (Chao et al., 2000). For capture probability (p^) and closure tests, we used the program Capture (White et al., 1978) because *Rcapture* does not provide these calculations. The camera polygon plus a buffer of the mean maximum distance moved by individuals (MMDM) (Dillon and Kelly, 2007; Maffei and Noss, 2008) were used to determine the effectively trapped area. We applied the same buffer for both trapping sites. We conducted density estimation at the Mel site for 11 months and six months, while density estimation was conducted for three months at the Cágados site. Trapping occasions (six for Mel and eight for Cágados) were implemented to minimize the number of sessions with zero captures and increase recaptures following the recommendations of Otis et al. (1978).

We also estimated tiger cat density through spatially explicit capture-recapture models (SECR) in a maximum likelihood framework (Borchers and Efford, 2008). SECR models assume that the population is closed during the survey period, that each individual has a fixed and circular home range and that the encounter rate of an individual decreases with distance from its home range center following a specific detection function. For this, we used a half-normal function with two parameters: the encounter rate at the home range center, g_0, and the scale parameter, sigma (σ), which describes the inverse relationship between the detection probability and distance from the home range center (Tobler et al., 2013; Jedrzejewski et al., 2017). For buffer width, we assumed that 95% of the activity in a circular bivariate normal home range is concentrated within a circle of radius 2.45σ (Petit et al., 2018). We divided the study period into 24-h capture occasions because short sampling intervals can improve the precision of SECR estimates for felids (Goldberg et al., 2015). All SECR analyses were performed using the *secr* package version 3.2 (Efford, 2019) in R.

To estimate the size of the adult tiger cat population at MSP and the population’s long-term viability, we used a digitized shapefile of vegetation formations and land use at the park determined on the basis of detailed satellite images (Landsat8-TM) that were georeferenced, field proofed, and analyzed in Q-GIS ver.3.4.7 LTR (Q-GIS Development Team, 2019). To define the available area, we excluded all unsuitable nonspecific vegetative formations, settlements and cultivated areas. Then, we applied density estimates (mean, minimum and maximum) to all areas deemed suitable. For areas close to households/settlements, we applied a buffer of 800 m in which we considered density to be 60% of the average values used elsewhere and 80% in areas of secondary/disturbed vegetation. We based this on the difference between the SECR density results between the two sites. This slight reduction was appropriate because preliminary occupancy estimates at MSP showed a probability of absence of 80% at that distance (Lima, 2019; Supplementary Material Fig. S2). Marinho et al. (2017) also showed that proximity to settlements affected the occupancy of northern tiger cats.

For the other protected areas of the MATOPIBA savannas, we used shapefiles of suitable and unsuitable habitats to estimate the tiger cat population size (Project MapBiomas, 2019). We applied the minimum and maximum known density estimates for small Neotropical cats (0.01-0.25 ind./km^2; Oliveira 2011; Oliveira et al., 2018a, b). For their expected population size, we made an assumption based on their abundance proportions in comparison to those of MSP estimates of approximately 60%. Thus, for sites other than MSP, expected population sizes were calculated using a density of 0.06 indiv./km^2. Lastly, we also estimated the population for the MATOPIBA portion of the buffer zone of the Cerrado Biosphere Reserve, which serves as a potential corridor for the protected areas in the region. We assessed habitat suitability within the reserve by excluding agricultural areas and vegetation types not used by the species. We performed the analysis using land use and vegetation maps from the Brazilian Institute of Geography and Statistics – IBGE (2018). Then we applied the minimum density values of Neotropical cats (0.01 – 0.02 indiv./km^2; Oliveira, 2011; Oliveira et al., 2018b) to all areas of suitable habitat within the biosphere reserve. We chose to be conservative because buffer zones are not strictly protected and there have been no camera trapping surveys done in this part of the region.

In this analysis, we calculated both the total (N) and effective population sizes (N_e), considered as 0.2N, following the genetically based recommendations for risk assessments and red list criteria adjustments (Frankham et al., 2014).

The potential impact of domestic dogs and human settlements on tiger cat density was estimated through the Heat Map plugin in QGIS. The estimate was made through a Kernel interpolation function, which expresses the density based on the number of points in a location and the overlap of the different layers (Bailey and Gatrell, 1995; Oliveira et al., 2015, 2016). The ray of potential dog impact was based on the mean maximum distance moved by dogs during the survey period (6 km; Supplementary Material Table S3), while the ray of human settlements influence was calculated based on tiger cat occupancy probabilities as a function of distance to human settlements (see “Population Viability Assessment”).

3.2.1. Population viability analysis

For the population viability analysis (PVA), we used the software VORTEX version 10.3.3 (Miller and Lacy, 2005), which has been widely used to model wildlife populations and, when tested against long-term field study datasets, was found to provide accurate predictions (Brook et al., 2000). For a detailed explanation of VORTEX and its use in PVA, see Miller and Lacy (2005). Literature on tiger cats and unpublished data on their natural history and ecology, complemented with data on other species of felids (notably jaguar and ocelot) as well as personal communications and best guesses offered by cat specialists, provided data on the life history parameters necessary for the population models (Supplementary Material Table S5). We used the baseline 100 iterations for a short-term scenario (100 years) and long-term scenario (1,000 years), which, with a 5-year generation length, represented 20 and 200 tiger cat generations, respectively. The initial population size was based on the average density of the more conservative estimates of the spatially explicit capture-recapture models for MSP, whereas, for carrying capacity (K), we added 20%. The main threat modeled was disease. Disease outbreak prevalence was established at 14% per generation, or 2.8% per year, based on felid data provided by Reed et al. (2003). We tested both a mild and strong outbreak scenario, in which survivorship percentages were 85% and 60% of the normal survival values, respectively. Given the predictions of habitat loss for the MSP area (Ferreira et al., 2013), we considered an annual loss of approximately 1.2% per year (for about 100 years). We also tested this threat separately and considering both scenarios of disease outbreaks for the short term only. We also tested the scenario of a 30% loss in K. This change in K is likely to occur if land use changes take place or if the populations of ocelots or other competitors increase, as seen in another tiger cat population in southern Brazil (Oliveira et al., 2010).

4. Results

4.1. Population parameters

We identified 21 individual northern tiger cats (98% of the species' photographs) over a trapping effort of 5,030 trap-days for MSP in 2014-15 and 2018 (Table 1), with an average relative abundance of 1.014 ind./100 trap-days. The different sites at the park showed different abundances, with higher abundances in the mostly dense formations and very low abundances in the predominantly open areas (0.124-2.168 ind./100 trap-days, Table

1). At Mel, the relative abundance was the same in 2014/15 and 2018, with ca. 1 tiger cat per 100 trap-days during both time periods. Interestingly, a 13-year comparison of the abundance at a single trapping site at Cágados showed a dramatic difference, from 0.00 to 2.168 ind./100 trap-days in 2005 and 2018, respectively. The abundance in the other study areas in the northern savannas also varied (mean: 0.368 ind./100 trap-days, range: 0.222-0.481 ind./100 trap-days) but was less than half of the MSP abundance on average.

Table 1. Relative abundances (number of individuals × 100 trap-days) of northern tiger cats in the northern savannas of Brazil.

Site	Sampling effort (trap-days)	Individuals/ 100 trap-days	Habitat type/integrity
MSP – Mel (01/2014-07/2015)[1]	2,729	0.953	Pristine/lightly disturbed dense savanna
– Mel (05-08/2018)[1]	711	0.985	
– Mel (01/2014-08/2018)[1]	3,440	0.959	
MSP – Zé Miguel (08/2014-07/2015)[1]	806	0.124	Pristine/lightly disturbed mostly open savanna
MSP – Cágados 2005[2]	450	0.000	Pristine/lightly disturbed moderately open to dense savanna
– Cágados (05-08/2018)[1]	784	2.168	
Mirador State Park (2014/2018)[1]	5,030	1.014	
Parnaíba River area[2]	1,580	0.400	Pristine to disturbed dense savanna
Gerais de Balsas[2]	450	0.222	Pristine/lightly disturbed dense savanna
Nascentes do Rio Parnaíba Nat. Park (MA/TO/PI)[3]	4,154	0.481	Pristine/lightly disturbed dense savanna

1. This study, 2. Oliveira et al. (2008), 3. Lima (2009)

At Mel, six different individuals (2 males, 2 females, 2 unidentified sex) were recorded 26 times in 2014. For a six-month period, this yielded a population estimate (M_h, M_0) of 5.3 ± 0.7 individuals (5.0-7.5) (Table 2). At Cágados, eight individuals were identified (3 males, 2 females, 3 unidentified sex) and recorded 16 times in a three-month period, which led to a population estimate (M_h, M_0) of 10.4 ± 2.4 individuals (8.0-17.9). The capture probability (p^) was estimated at 35.7% and 50.0% (M_h, M_0, respectively) at Mel and 21.9% and 18.7% (M_h, M_0) at Cágados. The MMDM for the park was 2.4 ± 1.05 km (range: 0.87-3.3 km). The effective trapped area was 45.1 km^2 for Mel and 41.9 for Cágados, which led to estimated densities of 12 ind./100 km^2 (13-19 ind./100 km^2) and 25 ind./100 km^2 (19-38 ind./100 km^2), respectively. Assessments for an 11-month period at Mel were similar (Supplementary Material Table S6). The densities estimated from the SECR models were smaller and were 8.68 ± 3.9 (3.75-20.1) ind./100 km^2 for the Mel site and 11.3 ± 5 ind./100 km^2 (5.0-25.5) for the Cágados site (Table 3).

Table 2. Abundance models for the northern tiger cat in Mirador State Park, Brazil, by means of traditional nonspatial methodology.

Site/Model	Abundance	SE ±	95% CI	Density (per km^2)	SE ±	95% CI	AIC
Mel							
M_0	5.3	0.7	5.0-7.0	0.12	0.016	0.11-0.16	39.137
M_t	5.0	0.0	5.0-5.7	0.11	0.00	0.11-0.13	34.486
M_h Chao	7.3	4.2	5.0-21.9	0.16	0.093	0.11-0.49	39.433
M_h Poisson	5.3	0.7	5.0-7.5	0.13	0.016	0.11-0.17	41.137
Cágados							
M_0	10.4	2.4	9.0-17.7	0.25	0.057	0.21-0.42	52.280
M_t	10.0	2.2	8.0-16.5	0.24	0.053	0.19-0.39	58.272
M_h Chao	10.4	2.4	8.0-17.9	0.25	0.057	0.19-0.43	52.280
M_h Poisson	8.5	1.2	8.0-12.1	0.20	0.024	0.19-0.29	52.918

Table 3. Density estimates of northern tiger cats in Mirador State Park, Brazil, by means of spatially explicit capture-recapture models.

Parameter	**Mel**	**Cágados**
Buffer (2.45*RPSV km)	3.37	3.56
D (+/- SE) per 1 km^2	0.087 ± (0.039)	0.11 ± (0.049)
95% CI	0.038-0.20	0.05-0.25
Sigma (km)	1.93	4.40
g_0	0.0061	0.0025

The total area of the park with habitat suitable for northern tiger cats is 2,629.12 km^2 (52.5% of the park – Figure 3,). This leads to an estimated population of 537 (464-827) or 287 (127-661) individuals according to nonspatial models or SECR models, respectively. Thus, the effective population size (N_e) would be 107 individuals (93-165) nonspatially or 57 individuals (25-132) spatially.

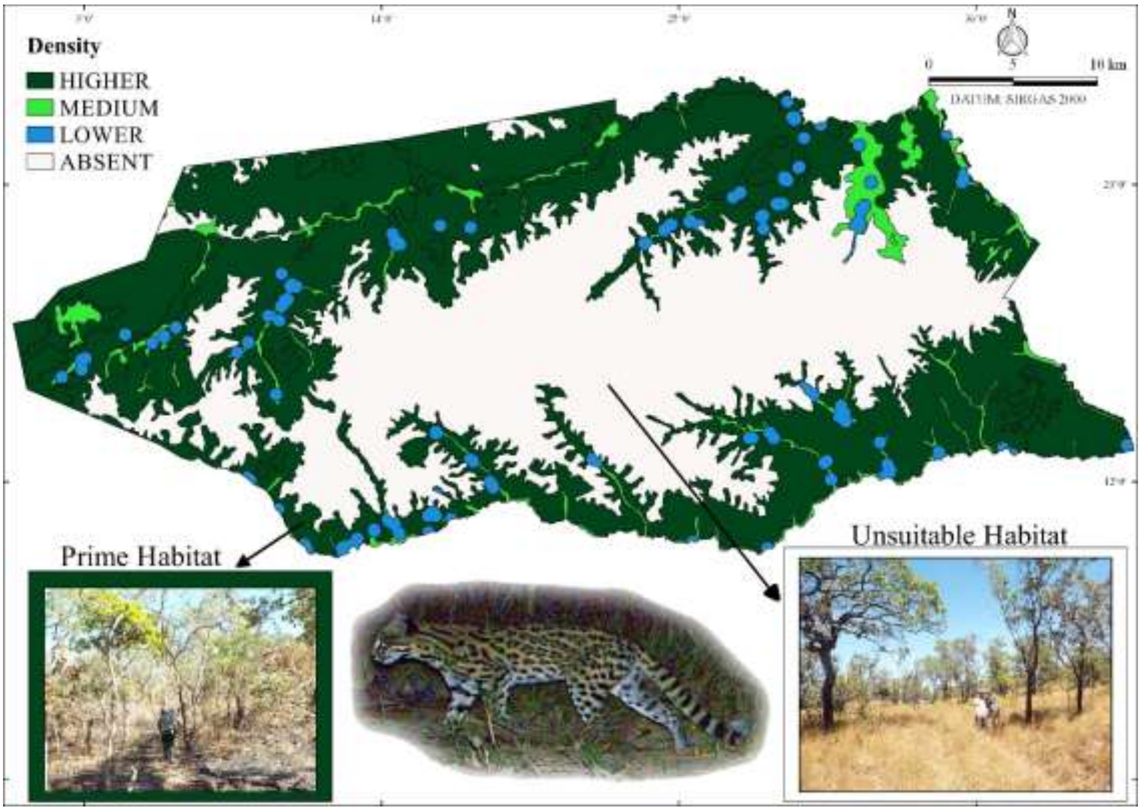
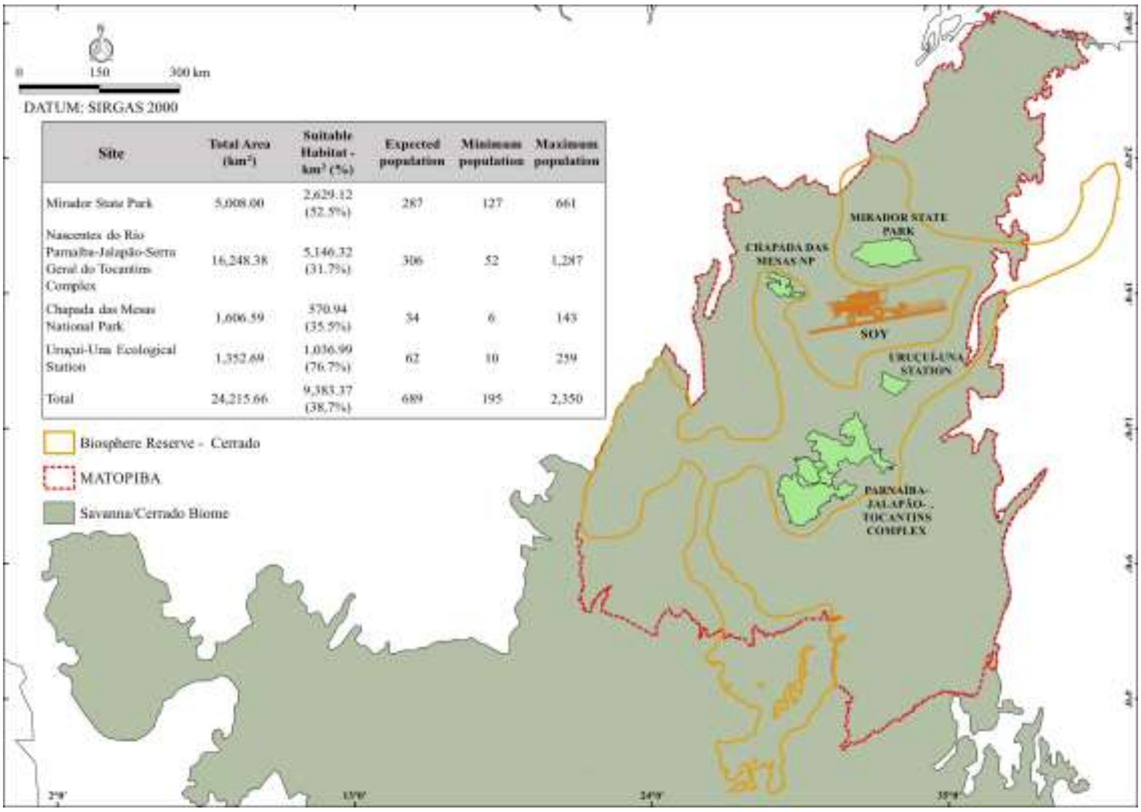


Figure 3. Expected density map of the northern tiger cat in its key worldwide conservation area in Mirador State Park in the northern savannas of the Cerrado biodiversity hotspot.

The expected population sizes in other protected areas within the MATOPIBA savannas varied (34-306 Figure 4) and were either equal or smaller than those of MSP. The total population for the protected area system was approximately 700 adult northern tiger cats (200-2,350). For the buffer zone of the Cerrado Biosphere Reserve in the MATOPIBA, the expected population size was 1,302-2,064 individuals (Supplementary Material Fig. S4). This means that the total expected tiger cat population for the whole MATOPIBA region could potentially reach 2,000 or 3,000 individuals.



Site	Total Area (km²)	Suitable Habitat - km² (%)	Expected population	Minimum population	Maximum population
Mirador State Park	5,008.00	2,629.12 (52.5%)	287	127	661
Nascentes do Rio Parnaíba-Jalapão-Serra Geral do Tocantins Complex	16,248.38	5,146.32 (31.7%)	306	52	1,287
Chapada das Mesas National Park	1,606.59	570.94 (35.5%)	34	6	143
Uruçui-Una Ecological Station	1,352.69	1,036.99 (76.7%)	62	10	259
Total	24,215.66	9,383.37 (38,7%)	689	195	2,350

Figure 4. Expected northern tiger cat population size based on habitat suitability for the protected areas of the MATOPIBA savannas and the corridor of the Cerrado Biosphere Reserve, whose shape is highly influenced by the soy belt.

4.2. Population viability assessment

With an estimated initial population of 287 animals and carrying capacity of 359 individuals, the tiger cat population would not go extinct in either a 100-year or 1,000-year period under catastrophe-free conditions, even if the carrying capacity decreased by 30% (Figure 5, Supplementary Material Table S7). The same would apply in a mild disease outbreak scenario or even with a stronger disease threat over the short term (100 years). However, over the long term (1,000 years), if the outbreaks resulted in survivorship of 60% of the regular values, the population would go extinct. The effect of habitat loss in the short-term scenario is also devastating in MSP. Considering the effective population size, the outcome is grim. In the short-term scenarios, the extinction probability ranges from 3% (no catastrophes) to 100% (e.g., moderate disease outbreaks, habitat loss). In the long-term scenario and in all simulations and with habitat loss, the average probability of extinction in all the scenarios is 88.6% (53-100% - Supplementary Material Table S7 and Fig. S8).

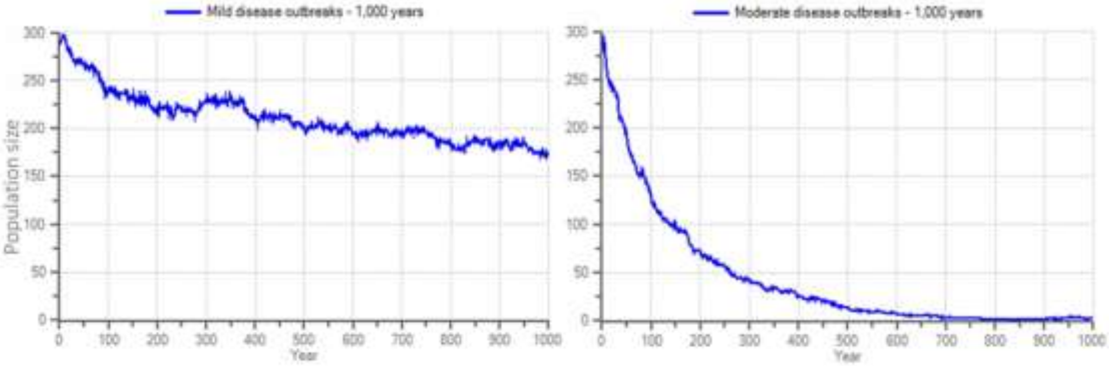


Figure 5. Long-term outcomes of northern tiger cat population viability analyses in Mirador State Park under scenarios of mild and moderate disease outbreaks.

4.3. Assessing domestic dog potential impact

Non-feral domestic dogs were identified in all studied areas in the park; there were 15 individuals at Mel and seven at Cágados (Supplementary Material Table S3). The distances moved by domestic dogs were 1.4-2.5 km for the Mel area and 8.0-11.2 km for the Cágados area. They appeared on 80% of all cameras that recorded tiger cats. Given the ray of action of dogs (6 km), the area of tiger cat suitable habitat potentially impacted by dogs is 1,815.24 km^2 (65.1%, Figure 6). Interviews and clinical evaluations conducted at the study sites on the health assessment of domestic carnivores showed dermatologic disorders (mange, dermatophytosis, mycosis), as well as unspecific clinical signs of anorexia, coughing, and apathy in all 50 dogs evaluated (Albuquerque et al., unp. data). Of very high concern were the neurologic signs indicating the presence of canine distemper virus in these free-ranging dogs in the park (Albuquerque et al., unp. data).

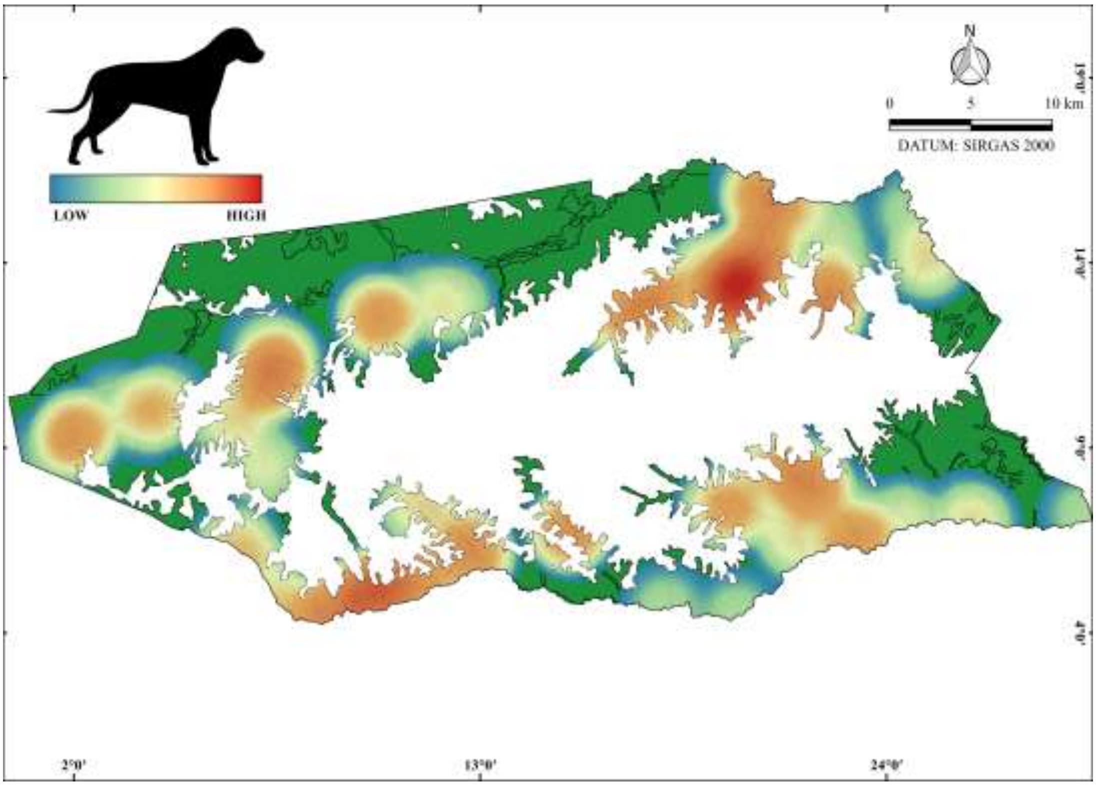


Figure 6. The area of suitable tiger cat habitats potentially impacted by domestic dogs in Mirador State Park is about 65%.

5. Discussion

5.1. Population assessment

The density estimates provided here represent the first estimates published for this species. The estimates are robust, with a higher-than-average likelihood of capture (p^) and a narrower 95% confidence interval than those provided by several density estimate studies of felids, where p^ is typically <15% and the CI is very broad (Karanth and Nichols, 1998; Silver et al., 2004; Kolowski and Alonso, 2010). Higher recapture rates are key for robust estimates (Sollmann et al., 2011). Nevertheless, spatial and nonspatial estimates differ, with spatially explicit estimates always being lower in studies that compared both methods (Sollmann et al., 2011; Tobler et al., 2013; Ávila-Nájera et al., 2015). Overall, our SECR estimates showed greater errors and wider confidence intervals than the traditional estimates. However, they were still in the same range or better than estimates from other felid studies conducted elsewhere (Sollman et al., 2011; Mohamed et al., 2013; Naing et al., 2017). The differences between the two sites could be related to slight differences in resource availability or to the fact that the Mel site is close to human settlements, whereas Cágados is not. Marinho et al. (2017) showed that proximity to settled areas decreased occupancy by northern tiger cats.

Unpublished estimates of northern tiger cat populations exist for two sites in the savannas of the Grande Sertão Veredas/Peruaçu National Parks conservation mosaic area. The reported densities, 9.1 ind./100 km^2 and 4.5 ind./100 km^2, were lower than those in MSP (Oliveira, 2018). The highest density reached by the smaller (< 6 kg) tropical species of Neotropical felids is 25 ind./100 km^2 and is only attained where ocelots are rare or absent, with an average high density of 10-15 ind./100 km^2; where such species are rare, the densities are typically < 1-5 ind./100 km^2 (Oliveira et al., 2010, 2018a, b; Oliveira, 2011). Other authors (Oliveira-Santos et al., 2012; Caso, 2013; Kasper et al., 2016; Oliveira, 2018) have corroborated these findings. Ocelots, the ecologically dominant mesopredators in the area, reach much higher densities, with an average density of 30 ind./100 km^2, but are able to reach densities of up to 80-100 ind./100 km^2 under favorable conditions (Kolowski and Alonso, 2010; Oliveira et al., 2010). All reported estimates for northern tiger cats are similar to the values of the other relatively small species of tropical America (1-25 ind./100 km^2 – Supplementary Material Fig S9; Oliveira, 2011, unp. data; Oliveira-Santos et al., 2012; Caso, 2013; Kasper et al., 2016; Oliveira, 2018; Oliveira et al., 2018b). This indicates that tiger cat densities at MSP are high for Neotropical felid standards, signifying the importance of the park.

Our data show that the northern tiger cat population at MSP is robust and more than twice abundant than that in other Brazilian mid-north savanna areas (Oliveira et al., 2008; Lima, 2009) and considerably higher than that in other savannas throughout Brazil. In the predominantly open savanna at Emas National Park, assessments conducted from 2001-2011 over 30,798 trap-days did not record the species (Giozza et al., 2017), even though one individual was trapped and radio-collared outside the park (Oliveira et al., 2010). The abundance at semiarid Caatinga scrub sites in NE Brazil was similar (0.036-0.493 ind./100 trap-days; Oliveira, 2011). Only at some sites in the semiarid Caatinga in Rio Grande do Norte were abundance estimates higher or equivalent to those at MSP (0.6-4.1 ind./100 trap-days; Marinho, 2015).

A rather startling finding was the difference in the abundance in the Cágados area between 2005 and 2018, where records went from 0.0 to 2.2 ind./100 trap-days, or from momentarily absent to 25 tiger cats per 100 km^2. Considerable population fluctuations have been noted to occur for Pampas cats (*Leopardus colocola*) and other carnivores in Emas National Park (Giozza et al., 2017). Changes in the abundance of northern tiger cats have also been reported in a Caatinga scrub/savanna mosaic in the Caetité area of Bahia state, where the population dropped by 25.9% between 2012 and 2015 (Meira et al. unp. data) and for several populations of the southern tiger cat and other felids in SE Asia (de Oliveira et al., 2016; Naing et al., 2017). Three nonexclusive hypotheses could be invoked to explain the findings: 1) conditions changed between the two survey periods, 2) differences in habitat or prey availability occurred, or 3) other factors, such as the occurrence of disease transmitted from dogs, caused the differences. The area sampled and camera protocol remained the same, as did the vegetation structure and integrity. This means that whatever caused the disappearance of tiger cats from the area in the 2005 catchment was not related to habitat integrity or methodology. The temporal change hypothesis associated with changes in prey availability seems to be an unlikely explanation, as Pampas cats and other mesocarnivores were relatively common at that time at the same site (Oliveira et al., 2008). The most plausible and compelling hypothesis is that a disease outbreak affected the species at the time, which has serious inherent implications for conservation. In the late 1980s and early 1990s, there was a crash in the fox population at the park, which was likely due to diseases transmitted by domestic dogs (Oliveira, 1996). We speculate that the same might have happened with tiger cats. In 2005, while tiger cats were absent, dogs were recorded on cameras. Unquestionable signs of the current and former occurrence of canine distemper were found in the domestic dogs observed in this study, and this disease is well known to cause serious impacts to carnivores worldwide (Woodroffe, 1999; Jorge et al., 2010).

What would make the tiger cat abundance twice as high in MSP than in other savannas? Small-mammal trapping showed a healthy prey base but nothing exceptional that could explain such differences (Oliveira, 2014, unp. data). MSP experiences multiple anthropogenic impacts, which should actually have a negative impact on this species. A possible explanation associated with prey availability could be the near absence of ocelots at this location. It has been documented that ocelots negatively affect the abundance of smaller competitors through interspecific killing, also known as the “ocelot effect” (Oliveira et al., 2010; Oliveira, 2011). Ocelots are present in MSP, but their abundance in the monitored areas is extremely low (0.020 ind./100 trap-days; Supplementary Material Table S10). With the camera-trapping rarity defined at 0.300 ind./100 trap-days (see de Oliveira et al., 2018), ocelots are exceedingly rare at the park, which could allow higher numbers of tiger cats to occur (Fig.7). This is in line with the intraguild hostility hypothesis (Maran et al., 1998). Oliveira et al. (2010) showed that where ocelot densities are higher than 15 ind./100 km^2, smaller felids are very low in abundance or absent. Other felids present in MSP (Supplementary Material Table S10) would also be considered rare according to camera-trapping efforts in Neotropical America (de Oliveira et al., 2018), which would suggest low competition and predation pressure for tiger cats at MSP, as has been observed to explain the leopard cat (*Prionailurus bengalensis*) abundance in Borneo (Mohamed et al., 2013). Notwithstanding, small Neotropical cats (< 6 kg) do not seem to negatively affect each other's numbers (Oliveira, 2011).

Figure 7. A healthy prey base with the near absence of the ocelot, the dominant mesopredator of tropical America and the tiger cat's interspecific killer, allows for the relatively high densities of *Leopardus tigrinus* found in Mirador State Park.

5.2. Northern tiger cat long-term conservation at the park and the northern savannas

Tiger cat populations in the MATOPIBA protected area system are much smaller than expected given their total area size due low levels of habitat suitability, which when combined represented only 39%. This is especially true for the largest area of them all, the Nascentes do Parnaíba-Jalapão-Serra Geral de Tocantins complex, which, at 16,248 km^2, has only 31.7% suitable habitat and, being three times larger than MSP, has the same expected population size.

The total number of northern tiger cats expected in the MATOPIBA protected area (approximately 700) is still below that proposed by Frankham et al. (2014) for the maintenance of evolutionary potential, even though its upper limits could fulfill the criterion. However, despite the rampant rates of habitat loss (IBAMA, 2015) in every direction due to the agricultural frontier, there are still extensive amounts of savannas that, if properly managed within the concept of biosphere reserves, could host approximately 1,300-2,000 individuals for total population size of 2,000-3,000 mature individuals and also maintain gene flow.

The results of the PVA suggest that short-term viability would be guaranteed for the tiger cat populations above 200 individuals at MSP. However, over the long term (1,000 years), stronger disease outbreaks would cause extinction if the population became isolated. In this scenario, over the long term, the probability of extinction increases sharply to 96%. Given the geography of MSP, local outbreaks are more likely than one simultaneously affecting the entire 5,008 km^2 area. Although mild-outbreak scenarios could predominate, severe disease outbreaks remain a clear and present danger at MSP.

In the N_e scenario PVA showed an unviable result. This striking difference in the PVA outcome of N and N_e raises serious concern. Frankham et al. (2014) stressed that, for the retention of evolutionary potential, the population would need to be > 1,000 individuals and to avoid inbreeding depression, >100 individuals. In a scenario of isolation, only short-term inbreeding depression could be avoidable at MSP. Thus, for the effective population to remain viable, maintenance of connectivity is vital. If properly managed, the established Cerrado Biosphere Reserve (MMA, 2016) could fulfill this need.

In most PVAs of other Neotropical hypercarnivores (jaguar, ocelot, bush-dog), survivorships were found to be considerably lower than those for the tiger cats in Mirador (Haines et al., 2006; Desbiez et al., 2013; Godoy et al., 2015). In fact, the PVAs using spatially explicit estimates for population size reflected the biological potential of the tiger cat population in the park. Thus, considering the total population size, MSP should indeed be considered a key conservation area for northern tiger cats.

In the other areas of the northern savannas, the data suggests smaller population sizes than those found in MSP. However, given the size and theoretical protection of the Nascentes do Rio Parnaíba National Park-Jalapão-Serra Geral de Tocantins protected area complex, even only half the abundance of individuals in MSP should be very important for the long-term species conservation. This is especially true considering the integration of the Cerrado Biosphere Reserve (MMA, 2016), which might prove needed for maintaining connectivity, gene flow and viability under the severe pressure of the agricultural frontier. In the scenario of connectivity, the PVA for the MATOPIBA Biosphere Reserve (N = 3,000; Ne = 750) suggests that the population would be self-sustaining over 1,000 years, with zero probability of extinction, even with moderate disease outbreaks.

5.3. Potential impact of dogs and park conservation issues

MSP hosts an estimated population of approximately 1,000 people in 61 small settlements, with 201 households and 201 families (1-18 families per settlement; Oliveira, 2014). Although poaching is a problem at MSP, we could not find evidence that it affects tiger cats. Habitat loss and conversion within the park boundaries do not pose a threat yet, although there are predictions that this might become a threat in the future (Ferreira et al., 2013). Dogs, on the other hand, could be a potential threat to tiger cats. At Mel, where settlements occur, dogs travelled 2.5 km away from their households, similar to the 3 km reported in the literature (Lessa et al., 2016), as opposed to 11 km at Cágados, where there are no settlements. Dogs roaming longer distances into the natural areas of MSP than regularly indicated by the literature increase the threat of disease transmission. Furthermore, domestic dogs were detected at 80% of the trapping stations at which tiger cats were also observed. Thus, these species overlap spatially in the study areas, which leads to the potential for disease transmission or even predation. The extensiveness of settlements throughout the park suggests that the area potentially impacted by dogs is widespread in MSP, especially in suitable tiger cat habitats.

Although laboratorial confirmation of the diseases affecting domestic carnivores in MSP has not yet been conducted, the neurologic signs of canine distemper virus found in the free-ranging dogs along with their high area of overlap with tiger cats makes us consider that dogs may pose a serious threat to the population of this felid at MSP. The overlap of the home ranges of dogs and wild carnivores provides an easy pathway for disease transmission and is a great zoonotic threat (Curi et al., 2010; Lessa et al., 2016).

Given the high potential threat of disease to tiger cats, actions should be taken to reduce the presence of domestic dogs in the park. Unfortunately, the literature offers few solutions for conservation issues involving dogs and wildlife interactions (Hughes and Macdonald, 2013). Domestic dog management in protected areas is socially complex and often opposed by people, making eradication attempts unsuccessful (WHO, 2005; Dorresteijn et al., 2015; Doherty et al., 2017). It requires management actions of control, restraint and eradication to reduce contact and the subsequent risk of disease transmission (Lessa et al., 2016).

5.4. Concluding Remarks

MSP harbors an important population of the endangered northern tiger cat in the threatened MATOPIBA savannas of northern Brazil. This species reaches high densities in the park that allow for a viable population to be maintained over the long term. This confirms that the park is a key conservation area for this felid. However, the high incidence of dogs, as well as signs of the highly dangerous canine distemper virus, and the association of dogs with extensive human settlements suggests that dogs pose a conservation threat to the local population of *L. tigrinus*, which will require serious conservation actions.

The data shows that without a refined analysis of habitat suitability, population estimates would be much higher than they actually are. Thus, integrating a refined population assessment proved to be very helpful and important for accurate and proper assessments of population size and viability; this information is of great importance for conservation planning and decision-making for managing threatened species.

Author contributions:

Study design and fieldwork: TGO, BL, LFR, RP; data analysis: TGO, BL, LFR, RP, EPA; article writing: all authors.

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Conflicts of interest: None.

Ethical standards: This research complies with GECCO's Code of Conduct.

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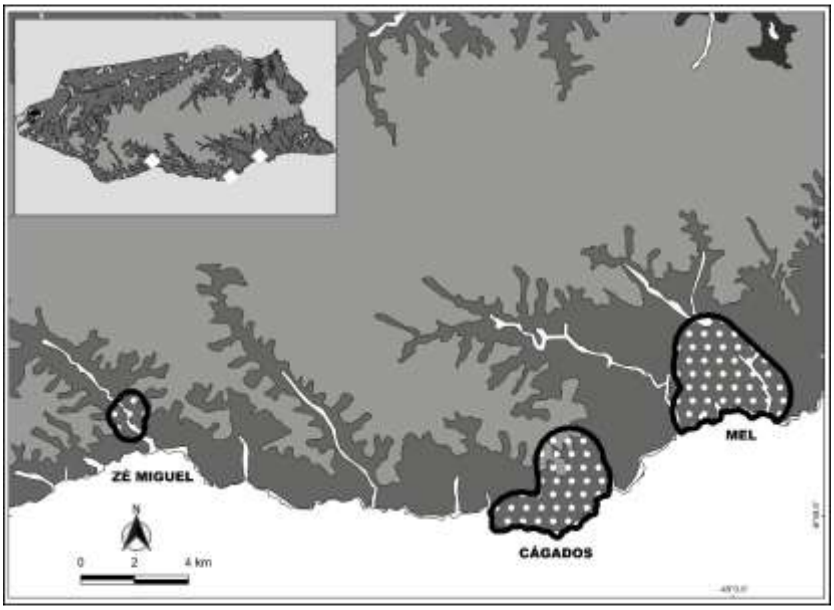


Figure S1. Camera trap sampling areas at the three sites, Mel, Cágados and Zé Miguel, in Mirador State Park in the northern/MATOPIBA savannas of Brazil. The first two sites provided density estimates, and the latter provided only relative abundance.

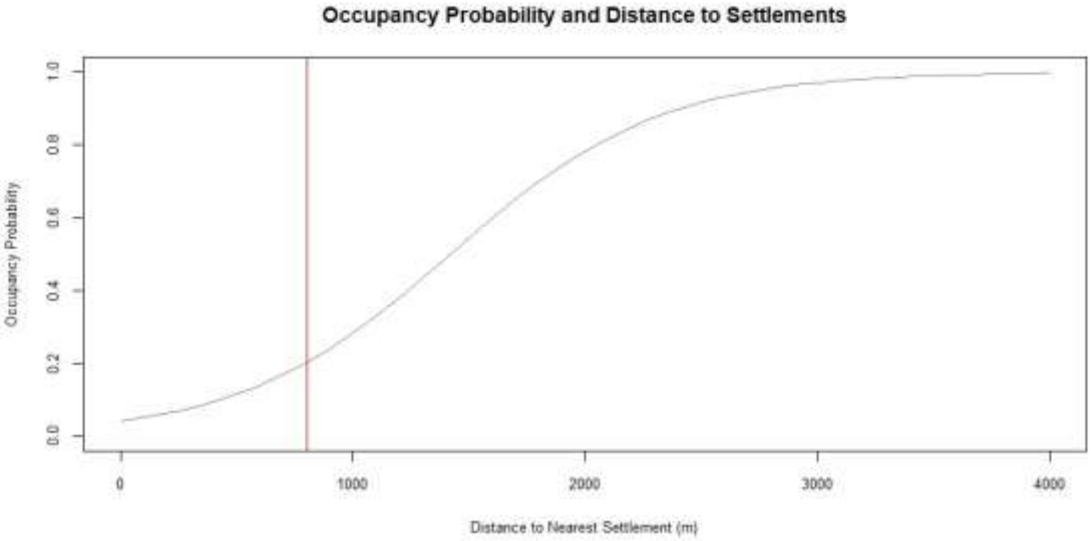
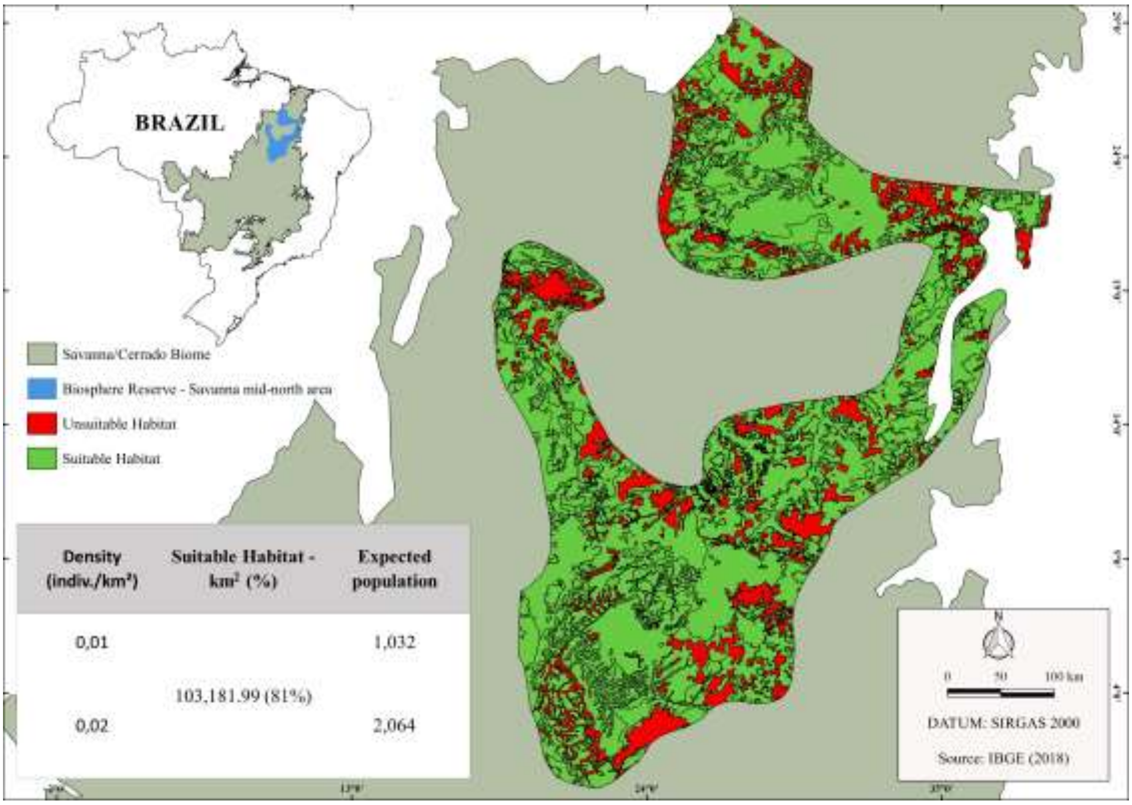


Figure S2. The occupancy probability and distance to households/settlements of northern tiger cats in Mirador State Park shows that at distances less than 800 m, tiger cat absence is 80%.

Table S3. Records of domestic dogs and distances travelled from the nearest households to the camera stations located in Mirador State Park, Brazil, the northern tiger cat's key worldwide conservation area.

Site	Relative abundance (photos/100 trap-days)	# individuals	Distance travelled by dogs	
			Mean maximum (km)	Mean minimum (km)
Mel	0.99	15	2.62 ± 1.07	1.9 ±0.87
Cágados	3.44	7	10.93 ± 1.36	9.04 ± 0.30
MSP Mean			6.02 ± 4.01	4.87 ± 3.41



Density (indiv./km²)	Suitable Habitat - km² (%)	Expected population
0,01	103,181.99 (81%)	1,032
0,02		2,064

Figure S4. Expected population size of the northern tiger cat in suitable areas within the MATOPIBA portion of the Cerrado Biosphere Reserve.

Table S5. Summary of parameter input values used in the baseline model for the *Leopardus tigrinus* population viability analysis.

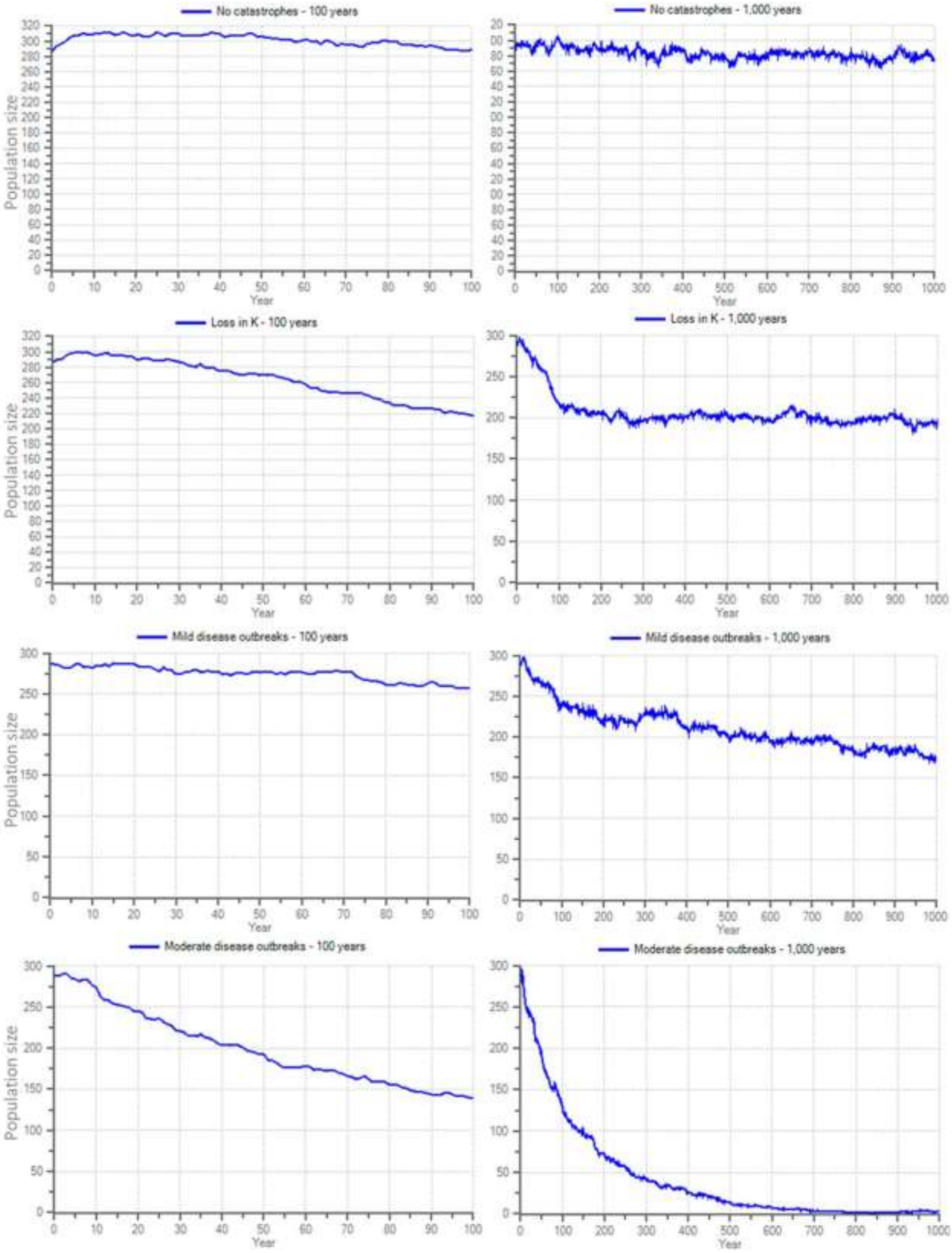
Parameter	**Baseline value**
Number of populations	1
Initial population size (N / $N_{e,}$ / MATOPIBA-N_e)	287 / 57 / 600
Carrying capacity (N / N_e/ MATOPIBA-N_e)	359 / 71 / 750
Inbreeding depression	6 LE
% of the effect of inbreeding due to recessive lethal alleles	50
Breeding System	Polygyny
Age of first reproduction (♀ / ♂)	2 / 2
Maximum age of reproduction	10
Annual % adult females reproducing (SD)	75% (10)
Number of litters per year	1
Average litter size	1.12
Density dependent reproduction?	No
Maximum litter size	2
Overall offspring sex ratio	50:50
% adult males in breeding pool	90
% mortality from age 0-1 (EV) (♀ / ♂)	42(7) / 42(7)
% mortality from age 1-2 (EV) (♀ / ♂)	22(5) / 37(5)
% annual mortality after age 2 (EV) (♀ / ♂)	13(2) / 13(2)
Catastrophe?	Disease outbreak
Annual frequency of occurrence	2.8%
Severity: reproduction (% of normal value)	0.95 / 0.80
Severity: survival (% of normal value)	0.85 / 0.60
Catastrophe	Habitat loss / fire
Annual frequency of occurrence	1.2%
Severity: reproduction (% of normal value)	0.95
Severity: survival (% of normal value)	0.50

Table S6. Abundance models for northern tiger cats at the Mel site in Mirador State Park, Brazil, for six and 11 sampling occasions.

Models	Abundance	± SE	95% CI	Density (#/per km^2)	± SE	95% CI	AIC
11 occasions							
M_0	6.5	0.8	6.0-8.5	0.14	0.018	0.13-0.19	65.815
M_t	6.2	0.5	6.0-7.4	0.14	0.01	0.13-0.16	59.853
M_h Chao	6.9	1.2	6.0-14.7	0.15	0.027	0.13-0.33	65.060
M_h Poisson	6.5	0.9	6.0-8.7	0.14	0.02	0.13-0.19	66.883
6 occasions							
M_0	5.3	0.7	5.0-7.0	0.12	0.016	0.11-0.16	39.137
M_t	5.0	0.0	5.0-5.7	0.11	0.00	0.11-0.13	34.486
M_h Chao	7.3	4.2	5.0-21.9	0.16	0.093	0.11-0.49	39.433
M_h Poisson	5.3	0.7	5.0-5.7	0.13	0.016	0.11-0.17	41.137

Table S7. Expected population parameters and probability of extinction of the northern tiger cat in Mirador State Park in the case of isolation after 100 and 1,000 years, with 287 individuals and a carrying capacity (K) of 359.

	Scenarios						
Parameters	No catastrophes	Mild disease outbreak	Moderate disease outbreak	Mild disease + habitat loss	Moderate disease + habitat loss	Habitat loss	Loss in K (no catastrophes)
	100 years (Mirador State Park)						
Initial population (K $_{SECR}$)	287 (359) individuals						
Probability of extinction - %	0.0	0.0	0.0	0.95	0.97	0.94	0.0
Time to extinction* (years)	-	-	-	56	47	53	-
Stochastic population growth – r (standard deviation)	0.008 (0.076)	0.003 (0.081)	-0.008 (0.120)	-0.073 (0.253)	-0.089 (0.276)	-0.077 (0.261)	0.008 (0.076)
Number left in population (std. Dev.)	289 (60)	256 (76)	139 (104)	14 (11)	10 (2)	26 (27)	217 (37)
	1000 years (Mirador State Park)						
Initial population (K $_{SECR}$)	287 (359) individuals						
Probability of extinction - %	0.0	0.17	0.99	-	-	-	0.01
Time to extinction* (years)	-	627	342	-	-	-	359
Stochastic population growth – r (standard deviation)	0.007(0.076)	0.002 (0.084)	-0.011 (0.139)	-	-	-	0.007 (0.077)
Number left in population (std. Dev.)	273 (84)	208 (99)	193	-	-	-	192 (52)
	1000 years (MATOPIBA)						
Initial population (K)	-	-	3000 (750)	-	-	-	-
Effective population - Ne	-	-	600	-	-	-	-
Probability of extinction - %	-	-	0.0	-	-	-	-
Time to extinction* (years)	-	-	-	-	-	-	-
Stochastic population growth – r (standard deviation)	-	-	0.013 (0.083)	-	-	-	-
Number left in population (std. Dev.)	-	-	655 (94)			-	-


No catastrophes - 100 years
No catastrophes - 1,000 years
Loss in K - 100 years
Loss in K - 1,000 years
Mild disease outbreaks - 100 years
Mild disease outbreaks - 1,000 years
Moderate disease outbreaks - 100 years
Moderate disease outbreaks - 1,000 years
Population size
Year
0
10
20
30
40
50
60
70
80
90
100
0
100
200
300
400
500
600
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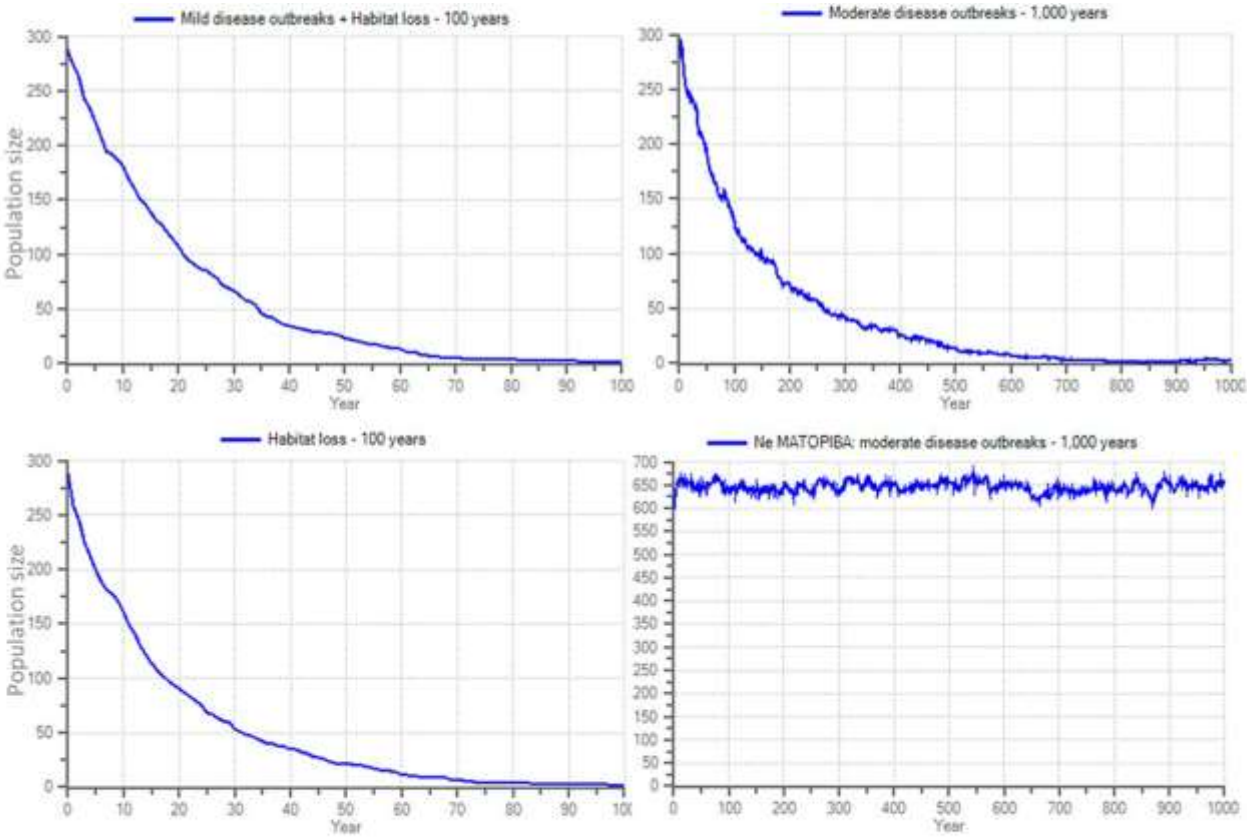

Figure S8. Population Viability Analysis estimates for Northern Tiger Cat in Mirador State park and the MATOPIBA savannas.

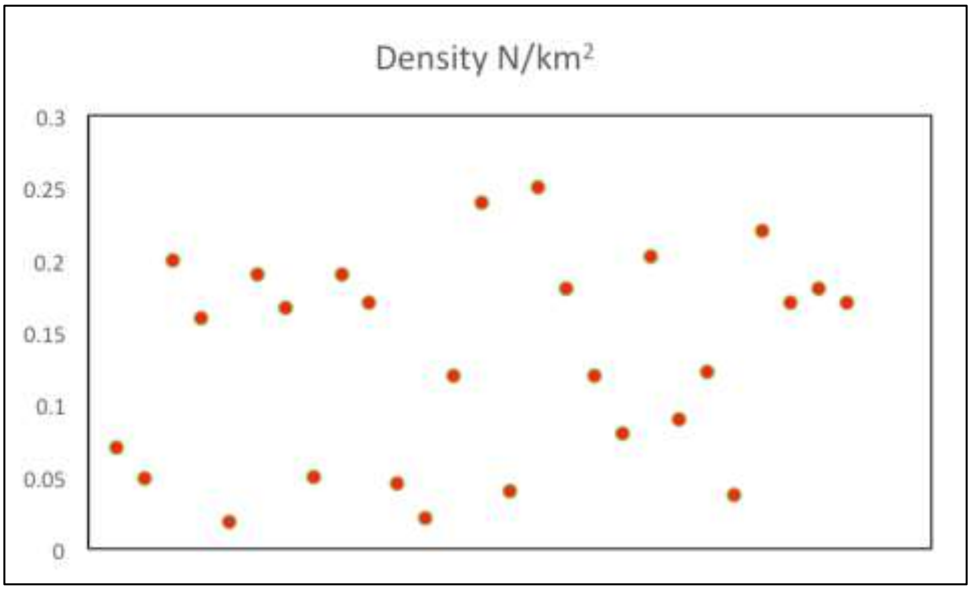

Figure S9. Densities of small cats in tropical America: jaguarundis (*Herpailurus yagouaroundi*), margays (*Leopardus wiedii*), and northern (*Leopardus tigrinus*) and southern (*Leopardus guttulus*) tiger cats. These are all densities where ocelots are absent or rare. In most areas where ocelots are abundant, small cats' densities are smaller than the lower values presented here (Oliveira et al., 2018b).

Table S10. Carnivore abundances in Mirador State Park in the threatened northern/MATOPIBA savannas of Brazil, as determined after 5,030 camera-trapping days.

Species		Individuals/100 trap-days
Northern tiger cat	*Leopardus tigrinus*	1.014
Pampas cat	*Leopardus colocola*	0.119
Ocelot	*Leopardus pardalis*	0.020
Jaguarundi	*Herpailurus yagouaroundi*	0.020
Puma	*Puma concolor*	0.239
Crab-eating fox	*Cerdocyon thous*	5.527
Hoary fox	*Lycalopex vetulus*	0.636
Domestic dog	*Canis lupus familiaris*	1.213
Coati	*Nasua nasua*	0.357
Hog-nosed skunk	*Conepatus semistriatus*	0.755

CAPITULO II

Artigo estruturado de acordo com as normas da Revista de interesse para publicação – Perspectives in Ecology and Conservation.

Of small cats and dogs: Interspecific relationships of wild and domestic carnivores in the northern savannas of Brazil

Abstract

Among the several ecological forces that dictate the structure of carnivore communities, interspecific relations could be considered relevant for the coexistence of several species within an area. At Mirador State Park, a key conservation area in the Brazilian Cerrado, the northern tiger cat (*Leopardus tigrinus*) and Pampas cat (*Leopardus colocola*) share space with domestic dogs and humans. We therefore addressed their influence as well as that of environmental variables on the spatio-temporal exploitation mechanisms of both felid species, using Generalized Linear (GLM) and Occupancy (OM) Models, as well as extrapolating their effects to our sampled sites. We also analyzed activity patterns of both felids and of other carnivores. Records were obtained between May 2018 and March 2019 with 30 camera traps installed on two areas within the park, totaling 4,312 trap-nights. We obtained a probability of habitat use of 0.012 and 0.99 for pampas cat and tiger cat, respectively. Detectability of both species was directly affected by vegetation structure, while habitat selection analyses showed that tiger cats avoided areas near human settlements and with high intensity of use by domestic dogs. Conversely, pampas cat habitat selection was mostly influenced by vegetation structure. Both felids and domestic dogs showed a moderate degree of temporal overlap, while there was a significant temporal segregation between both felids. The highest level of activity overlap was observed between tiger cat and crab-eating fox (*Cerdocyon thous*). Crab-eating foxes were not found to influence small felids' numbers or spatio-temporal ecologies. Domestic dogs did potentially influenced tiger cats' numbers and spatial ecology. However, the greatest menace of both canids on small cats is the potential of disease transmission. Our results suggest anthropic threats could act with more intensity than environmental factors in determining these species use of space, representing a risk for wildlife conservation in the park.

Keywords: *Leopardus tigrinus*; *Leopardus colocola*; northern savanna; domestic dogs; Occupancy models; temporal overlap

Highlights:

- We assess the first interspecific relations among tiger cat, pampas cat and dogs.
- We provide a refined habitat use analysis for both felid species.
- Domestic dogs and human presence greatly influence habitat use of small felids.
- High degree of temporal overlap between both felids and domestic dogs.
- Anthropogenic variables represent a conservation issue for both felids.

1. Introduction.

Understanding interspecific relations in their most varied context is a central part of the fields of modern ecology and conservation biology. In the carnivore guild of a given community, interspecific interactions are a key process modulating species co-occurrence. Species interactions may provide much needed resilience for ecosystems to resist negative impacts both of anthropogenic and natural origin (Polis et al. 1989; Ritchie e Johnson, 2009; Di Bitetti et al. 2010; Ripple et al. 2014; Heim et al. 2019). In this context, intraguild predation and interspecific killing may be considered the most active ecological forces in the structuring of carnivoran communities in South America. Generally, larger carnivores influence behavioral and demographic aspects of smaller species in the same guild (de Oliveira and Pereira, 2014; Ripple et al. 2014). Expansion of human activities across the globe has altered these interactions in some carnivoran communities, particularly in areas where exotic carnivores have been introduced (Ferreira et al. 2018). Kays et al. (2015) have shown that domestic cats are rare where coyotes run free in North America. This brings interesting ecological perspectives in canids and felids interspecific relationships, also bridging out on wild-domestic carnivorans interactions.

Negative effects from exotic carnivore introductions are well documented, and 58% of all recent vertebrate extinctions were caused by exotic predators (Weston et al. 2014, Doherty et al. 2016, 2017). Within this group, domestic dogs (*Canis familiaris*) have lived near humans since they were domesticated ca. 15,000 years ago (Driscoll and Macdonald, 2010), reaching high densities and occupying several areas of different ecosystems (Ordeñana et al. 2010; Paschoal et al. 2018). Domestic dogs affect wildlife populations through direct predation, behavioral change, prey predation, and disease transmission (Doherty et al. 2016, 2017; Ellwanger and Chies, 2019). Cases of predation by domestic dogs range from an increase in predation pressure on small mammals and ungulates (Young et al. 2011) to the extreme case of a single dog causing a 55% decline in a kiwi (*Apteryx australis*) population (Taborsky, 1988). In the savannas of the Brazilian Cerrado, prior research suggest that domestic dogs are the main suspect of pathogen transmission and behavioral alterations in wild carnivores, even within protected areas (Curi et al. 2006; Lacerda et al. 2009, Lessa et al. 2016). Therefore, quantifying interactions between domestic dogs and wild carnivores in protected areas is key in order to guarantee long-term survival of several species.

In the Cerrado Biodiversity Hotspot, several protected areas are recognized not only by their intrinsic value, but also by allowing important ecological processes to occur. Among these areas, Mirador State Park (MSP) is home to several threatened species both globally and nationally (Oliveira et al. 2014). The park has been recognized as a key area for the conservation of small felids (< 15 kg), particularly the globally Vulnerable northern tiger cat – *Leopardus tigrinus* (Schreber, 1775) and the Near Threatened pampas cat – *Leopardus colocola* (Molina, 1782) (Payan and de Oliveira, 2016; Lucherini et al. 2016; de Oliveira et al. 2020) (Fig.1). At MSP, these two species are sympatric with other wild carnivores (e.g. puma – *Puma concolor,* ocelot – *Leopardus pardalis,* jaguarundi – *Herpailurus yagouaroundi,* crab-eating fox – *Cerdocyon thous* and hoary fox – *Lycalopex vetulus*) (Oliveira et al. 2014, 2020). Both tiger cat (2.4 kg) and pampas cat (3.5 kg) have several natural history traits in common and also have overlapping distribution in the Cerrado biome in Brazil, which make them potential interspecific competitors (Oliveira et al. 2018, Queirolo et al. 2013, de Oliveira and Pereira 2014). Meanwhile, their spatial and temporal relations remain unknown. In order to address this issue and canid-felid interspecific relationships, we combined occupancy and activity analyses with the goal of answering the following questions: 1) How environmental and anthropogenic factors influence space use of small felids in savannas? 2) Are there any interspecific relationships modulating activity patterns for these species? 3) Do domestic dogs influence the ecological niche of both felids? Do the larger domestic and wild canids exert a demographic pressure on small cats? In order to answer these questions, we set up a camera trapping study aiming on understanding the interspecific relationship of tiger cat and pampas cat and to assess the potential role played by domestic dogs on their habitat usage and conservation needs. Our results will also help us evaluate the role that MSP plays in the conservation of small felids on the northern Cerrado savannas.

Fig. 1. Small threatened felids at Mirador State Park, northern tiger cat *Leopardus tigrinus* and pampas cat *Leopardus colocola.*

2. Methods.

2.1 Study site.

Mirador State Park is a fully protected area located in the northern savannas of the Cerrado biome, and with its 5,008 km^2 it is the second largest protected area in the entire biome (Fig. 2). MSP vegetation includes several savanna formations varying from open savannas to woodland savannas, tree cover ranges from 0 – 50% in most of the park. Tree cover is higher in gallery forests, which occurs along the park's rivers (Rodrigues and Conceição, 2014). Two sites within MSP were sampled: Mel and Cágados. Concerning vegetation structure, Mel has slightly denser vegetation than Cágados. The amount of human settlements and the degree of human activities is also higher at Mel. Brazilian environmental legislation prohibits extractive activities, poaching and livestock raising in protected areas such as MSP. Nevertheless, there are signs of these activities at our sampled sites as well as outside park limits (Oliveira et al. 2014).

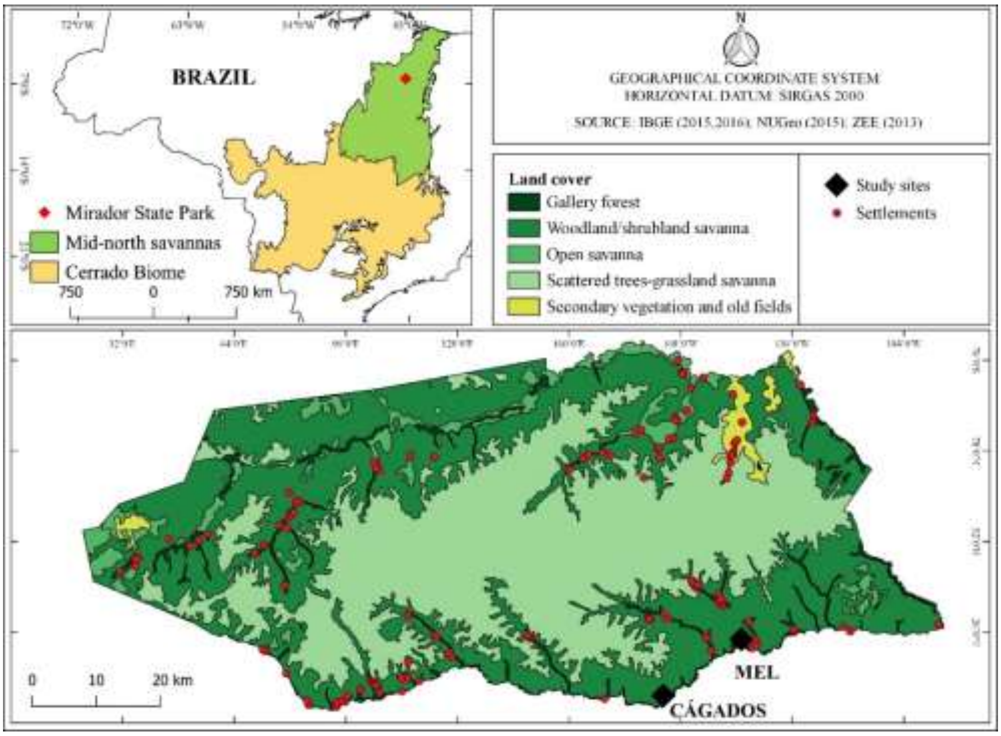

Fig. 2. Location of Mirador State Park with the sampled sites, human settlements, and land cover.

2.2 Camera trapping

The study was conducted between May, 2018 and March, 2019 with the use of camera traps, the infrared Bushnell Trophy Cam HD (Bushnell Outdoor Products, Overland Park/Kansas) and the white-flash ScoutGuard SG565 (Boly Inc., Santa Clara/California) and Reconyx PC850 (Reconyx Inc. Holmen/Wisconsin). We established 30 sampling points, 12 at Mel and 18 at Cágados, each of which consisted of a single camera trap. Camera trapping followed a well-established and effective protocol for small neotropical felids (Oliveira et al. 2008, 2020). Camera spacing considered the radius of the smallest home ranges known for small neotropical felids and varied from 0.5-1.0 km (Michalski et al. 2006; Oliveira et al. 2010; Kasper et al. 2016). With this arrangement, all individuals within the sampling landscape had a nonzero detection probability.

2.3 Habitat use covariates

We used the following six covariates associated with habitat quality and structure: 1) tree cover (%), 2) elevation (m), 3) conditional habitat use by domestic dogs (conditional ψ), 4) distance to nearest human settlement (m), 5) distance to nearest water source (m), and 6) distance to nearest non-paved road (m) (Table S1).

A 90,000 m^2 buffer was established around each sampling point. For each buffer, we estimated mean tree cover using data from the Global Forest Change Tree Cover Dataset (Hansen et al. 2013). On this dataset, trees are defined as vegetation taller than 5 m in height and are expressed as a percentage per 30x30 m pixel. We also estimated mean elevation above sea level for each buffer, using data from the United States Geological Survey (2019). All “distance to” covariates were measured from each camera trap: distance to non-paved roads and water sources were calculated using nearest neighbor analysis, while for human settlements, we averaged the distance to the three nearest settlements. All covariate values were extracted using QGIS ver. 3.4 (QGIS Development Team).

Conditional habitat use by domestic dogs represents the probability of domestic dogs using each sampling unit independently. We obtained these values using single-season occupancy models in the software PRESENCE 10.7 (Hines, 2006; Mackenzie et al. 2006), with the same number of sampling occasions as the main analysis (23 occasions). Model selection was carried out using Akaike information criterion, with the best models being those with ΔAIC ≤ 2 (Burnham and Anderson, 2002). All covariate values were z-scored and tested for collinearity using Pearson correlation tests, we excluded highly correlated covariates ($|r| \geq 0.8$) (Long et al. 2011).

2.4 Data Analysis

Possible influences of anthropogenic and environmental variables on the spatial ecology of the two felid species were assessed using two types of hierarchical models: Generalized Linear Models (GLMs) and Occupancy Models (OMs). Combining these two techniques is highly recommended in order to reduce the probability of excluding covariates that could be important from an ecological point of view (Gorosito, 2018), especially in cases with low species detections (Michalski et al. 2015). The two methods use different data matrixes (OM – presence/absence matrix; GLM – number of independent records). Both of them were treated as proxies for habitat use. In order to evaluate activity patterns of both species, as well as possible influences of interspecific relations on such patterns, we analyzed temporal overlap between them (Ridout and Linkie, 2008; Meredith and Ridout, 2018). All analyses were performed in R ver. 3.6.0 (R Development Core Team 2019) using specific packages.

2.4.1 Occupancy models (OMs)

We acknowledge that the field sampling protocol violated the closure assumption, that is, we cannot guarantee that there were no changes in occupancy of the sampled sites. We therefore interpret occupancy probability as probability of habitat use (Mackenzie et al. 2006; Guillera-Arroita et al. 2010).

Probability of use (ψ) and detection (p) were calculated using single season occupancy models (Mackenzie et al. 2002, 2006), with a binary detection history of 23 occasions, each composed of 13 days. We used a two-step approach for modeling purposes (Mackenzie et al. 2006). On the first step, we estimated the influence of each covariate on the detection probability of each species (p), leaving ψ constant. On the second step, we fixed the covariates of the best ranked model from the first step and tested the influence of all covariates on ψ. This approach allows for higher precision in testing covariates individually or in groups (Marinho et al. 2017). We selected the best models based on AIC, with the best models being those with $\Delta AIC \leq 2$ (Burnham and Anderson, 2002). All models were constructed using the *unmarked* package (Fiske and Chandler, 2019).

2.4.2 Generalized linear models (GLMs)

GLMs were done separately for each species using a negative binomial distribution, which is the recommended distribution for over dispersed and/or zero inflated data (Sileshi, 2008; Warton et al. 2016). We modeled the number of independent records at each sampling site as a function of the covariates, using the same model selection criterion as in the occupancy models ($\Delta AIC \leq 2$). GLM analyses were done using the *MASS* package (Ripley et al. 2019).

2.4.3 Temporal overlap of carnivores at MSP and canid-felid ratios

Besides exploring possible effects by domestic dogs on the activity patterns of tiger cat and pampas cat at MSP, we also assessed the potential effects of the crab-eating fox (*Cerdocyon thous*), the most abundant carnivore in the park and a potential competitor of the smaller felids. We built a matrix with independent records (those at least 1 hour apart, or less in the case of different individuals) for each species. We examined activity patterns and calculated overlap coefficients (Δ; 0 – no overlap; 1 – complete overlap), for each species pair. We chose the Δ_1 estimator as the species with the smallest sample had fewer than 75 records (Meredith and Ridout, 2018). In order to interpret Δ we followed the values proposed by Massara et al. (2018), $\Delta < 0.50$ as a low overlap value, $0.50 \geq \Delta \leq 0.60$ as moderate overlap, and $\Delta > 0.60$ indicating a strong degree of overlap. We estimated 95% confidence intervals as percentage intervals from 10,000 bootstrap samples (Meredith and Ridout, 2018). We assessed significance using a Mardia-Watson-Wheeler test with a significance level of 0.05. We used the packages *Activity* (Rowcliffe, 2019), *Overlap* (Meredith and Ridout, 2018), and *Circular* (Lund et al, 2017) for the analyses.

To shed light on the possible demographic influence of canids and felids, we identified individual tiger cat, fox and dog based on their characteristic spot patterns or color, body marks and features. Then, we compared their ratios. Pampas cat individuals could not be reliably identified because almost all were melanistic and lacked special features and marks to do so.

2.5 Predicting felid occurrence at MSP

In order to predict species occurrence at the sample sites, we used the β coefficients of the best occupancy models for each species. We divided the sampled areas with a 50x50 m grid, at each of which we extracted covariate values. For each area, we added a buffer equivalent to the mean maximum distance moved by northern tiger cat at MSP (2.4 ± 1.05 km). We used these buffers as base-maps for the predictors, which allowed us to avoid the disappearance of possible effects (Morris et al. 1987; Gorosito et al. 2018) and conditioned our predictions to effectively surveyed areas (Brozovic et al. 2018). Predictions maps were done using the packages *Lattice* (Sarkar, 2018) and *Raster* (Hijmans et al. 2019).

3. Results

3.1 Occupancy Models (OMs):

After a survey effort of 4,312 trap-nights, we obtained 21 independent records of pampas cat and 41 of northern tiger cat, with a naïve occupancy of 23% and 50% respectively, and a spatial overlap of 16% (corresponding to five sampling points). Detection probabilities for both species were influenced by the same three covariates on the best ranking models (Table 1). Among these covariates, tree cover had the greatest Akaike weight, resulting in detection probabilities of 0.16 (CI: 0.11-0.22) for northern tiger cat and 0.015 (CI: 0.002-0.094) for pampas cat. As expected, pampas cat was negatively affected by this covariate, suggesting they are more detectable on open areas. On the other hand, tiger cat was positively affected by tree cover, with higher predilection for areas with denser vegetation.

Table 1. Detectability and probability of habitat use models for Northern tiger cat and Pampas cat in Mirador State Park. Only models with ΔAIC < 2 are shown.

Best Models	nPar	AIC	ΔAIC	AICwt
Northern tiger detection models (step one)				
Ψ(constant) p(FC)	3	246.49	0.00	0.127
Ψ(constant) p(DOG)	3	247.05	0.56	0.096
Ψ(constant) p(null)	2	247.26	0.77	0.086
Ψ(constant) p(FC+DOG)	4	247.71	1.23	0.069
Ψ(constant) p(ELEV)	3	247.89	1.40	0.063
Ψ(constant) p(FC+ELEV)	4	247.97	1.48	0.060
Ψ(constant) p(DOG+ELEV)	4	247.98	1.50	0.060
Ψ(constant) p(SET)	3	248.22	1.73	0.053
Ψ(constant) p(FC+SET)	4	248.25	1.76	0.052
Pampas cat detection models				
Ψ(constant) p(FC)	3	119.30	0.00	0.399
Ψ(constant) p(FC+SET)	4	119.81	0.51	0.310
Ψ(constant) p(FC+DOG)	4	120.67	1.37	0.201
Northern tiger occupancy models (step two)				
Ψ(DOG+SET+WATER) p(FC)	6	242.04	0.00	0.368
Ψ(UROAD+SET) p(FC)	5	243.09	1.05	0.218
Pampas cat occupancy models				
Ψ(FC) p(FC)	4	115.04	0.00	0.406

FC: Tree cover; **DOG**: Conditional habitat use by domestic dogs; **ELEV**: Elevation; **SET**: Distance to nearest settlement; **UROAD**: Distance to nearest paved road; **WATER**: Distance to nearest water source.

The best model for domestic dogs had constant detection probability and habitat use influenced by forest cover ($\beta = 0.91$ SE ± 0.65, naïve occupancy = 0.50). The best models for habitat use (ψ) were markedly different between both species. The best model for pampas cat suggested low probability of habitat use ($\psi = 0.012$; 95% CI: 0.001-0.563) and a negative effect by tree cover, suggesting this species likely exploits open areas at MSP with higher frequency (Fig. 3a). For northern tiger cat there were two models with ΔAIC < 2 (Table 1). The positive influence of increasing distances to settlements, suggests this species avoids areas with human presence (Fig. 3b). This felid also avoided areas near non-paved roads and areas with high intensity of use by domestic dogs (Fig. 3c-d). The best models estimated a very high probability of habitat use and a wide confidence interval ($\psi = 0.99$-1.00; 95% CI: 0.10-1.0). Unexpectedly, distance to water sources had a positive effect on habitat use by northern tiger cat, suggesting that the species does not exclusively use the water sources identified during the study (Fig. 3e).

No other covariates were in the best models for detection or habitat use, and either had low explanatory power or did not converge (Table S2).

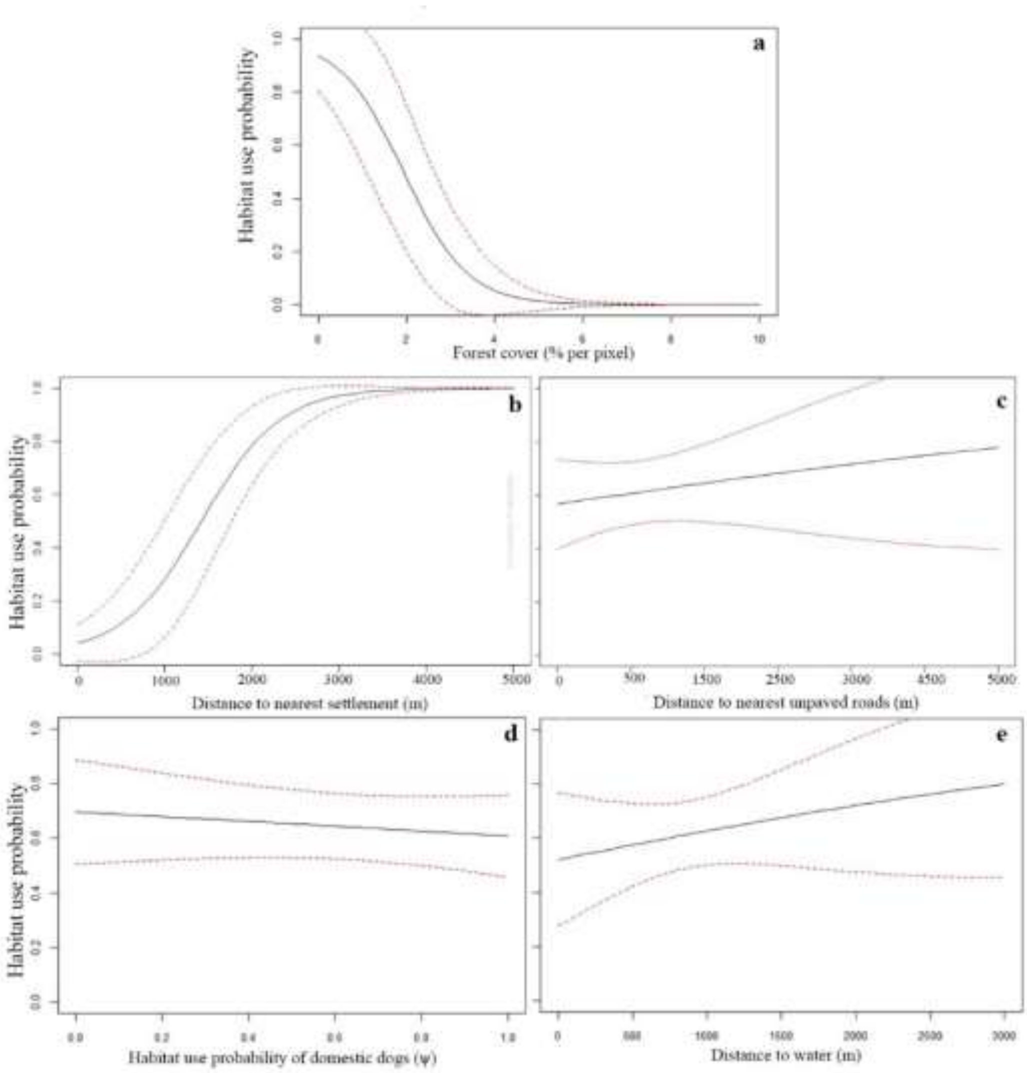

Fig. 3. Habitat use probabilities for small felids at MSP in relation to different covariates. Dotted red lines represent standard errors.

3.2 Generalized Linear Models (GLMs)

Following the same pattern observed on the OMs, the GLMs also showed differences between both felid species. Tree cover was statistically significant for explaining pampas cat abundance, with a negative influence, which further suggests the species preference for open areas at MSP. For tiger cat all models had a similar ΔAIC with no significantly important covariates in explaining its abundance at our sampled sites (Table 2).

Table 2. GLM model results for both felids at MSP.

Model	Npar	AIC	ΔAIC	Dispersion
Northern tiger cat				
Null model (Intercept)	2	110.10	0.00	1.060
Forest cover	3	110.90	0.80	1.123
Distance to nearest settlement	3	111.62	1.52	1.112
Habitat use probability of dogs	3	111.73	1.63	1.110
Elevation	3	111.78	1.68	0.903
Distance to water	3	111.96	1.86	0.903
Distance to nearest unpaved roads	3	111.96	1.86	0.903
Pampas cat				
Forest cover[a]	2	64.012	0.00	1.391
Null model (Intercept)	3	70.365	6.35	1.351
Habitat use probability of dogs	3	70.549	6.53	1.260
Elevation	3	71.812	7.80	1.300
Distance to water	3	72.001	7.99	1.300
Distance to nearest unpaved roads	3	72.001	7.99	1.300
Distance to nearest settlement	3	72.309	8.30	1.300

a: Statistically significant (*P* = 0.028)

3.3 Predicting felid occurrence at MSP

Due to the different values and signs of the coefficients, predictive maps showed interesting differences between both species. As expected, habitat use by pampas cat is smaller as tree cover increases, with the gallery forests showing very low probability of use ($\psi < 0.10$) (Fig. 4). Estimated predictions for tiger cat exhibited unusual patterns at the Cágados site, which could be due to hyper extrapolation of covariate coefficients or spatial autocorrelation between sampling points (Penjor et al. 2018). In general, anthropogenic covariates were extremely important for habitat use preferences of this species. Areas with high probability of use by domestic dogs were generally avoided by tiger cats. This pattern suggest that domestic dogs and human activities are directly limiting this species' capacity of exploiting different ecosystems at MSP (Fig. 4).

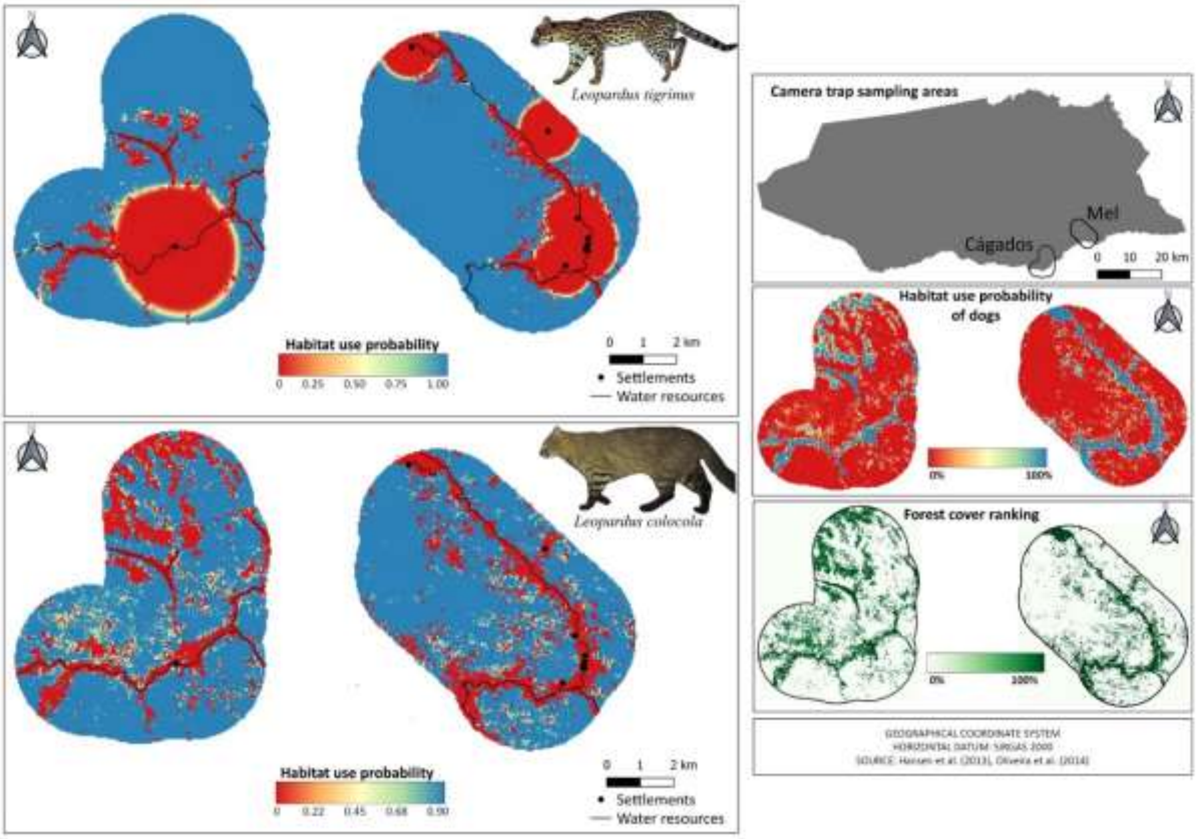

Fig. 4. Predictive occupancy maps for *L. tigrinus* and *L. colocola* on the effectively surveyed areas of MSP and maps for the main covariates.

3.4 Temporal overlap between carnivores at MSP and canid : felid ratios

Activity overlap between domestic dogs and wild carnivores differ for all species pairs. There was a moderate degree of overlap between domestic dog and tiger cat ($\Delta_1 = 0.59$; 95% CI: 0.44–0.75) (Fig. 5a); for pampas cat there was low overlap with domestic dogs ($\Delta_1 = 0.47$; 95% CI: 0.29 – 0.65); lastly, overlap between dog and crab-eating fox was high ($\Delta_1 = 0.61$ 95% CI: 0.48 – 0.74). Temporal overlap between crab-eating fox and the two felids had inverse results for both species: with tiger cat there was a high degree of overlap ($\Delta_1 = 0.82$; 95% CI: 0.72 – 0.92), while overlap with pampas cat was lower ($\Delta_1 = 0.47$; 95% CI: 0.30 – 0.64) (Fig. 5c-d). Temporal overlap between both felids was moderate ($\Delta_1 = 0.51$; 95% CI: 0.32 – 0.69) and significantly different ($w = 14.271$; $df = 2$; $p < 0.001$). Among all other species pairs, only pampas cat and crab-eating fox had significant differences ($w = 21.448$; $df = 2$; $p < 0.001$).

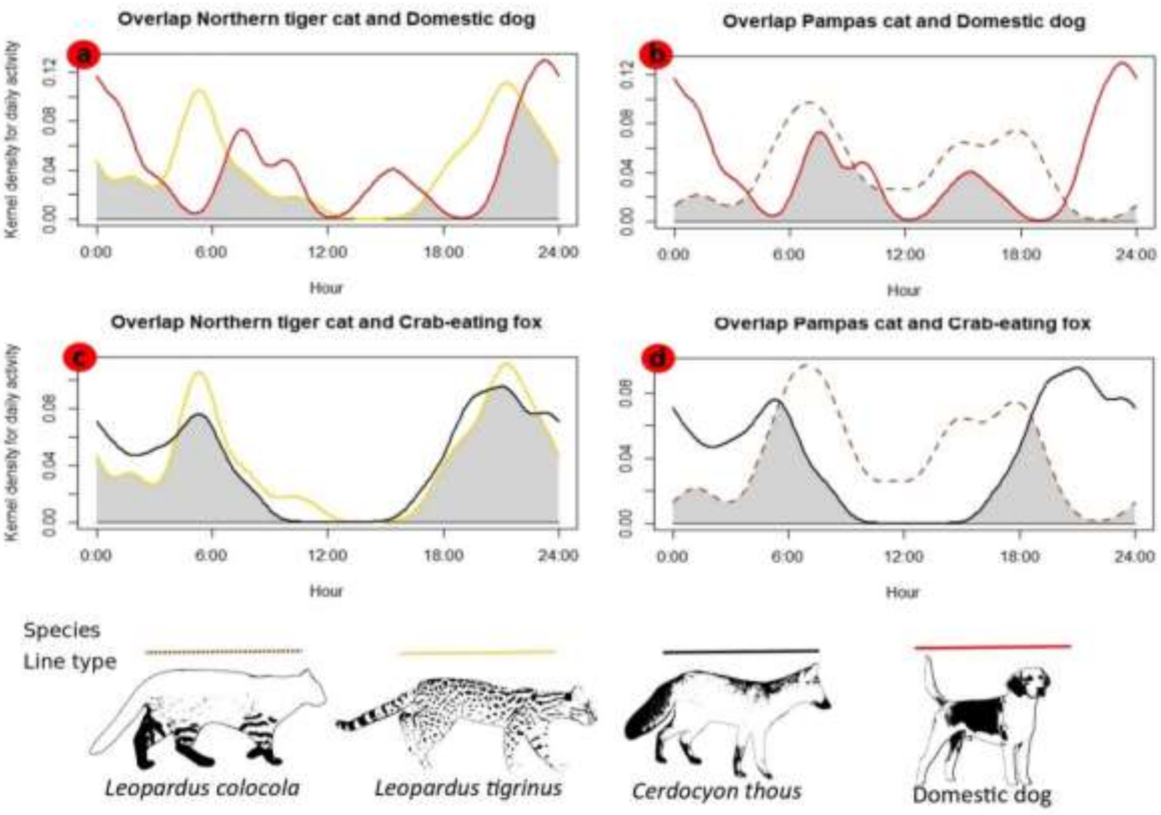

Fig. 5. Activity overlap plots of four carnivoran species (wild and domestic) from MSP. Shaded areas correspond to temporal overlap between species pairs.

At Mel, there were at least 12 individual foxes, 15 dogs and six tiger cats present, whereas at Cágados there were 21 foxes, seven dogs and eight cats This gives a ratio of 2 foxes: 1 cat and 2.7 foxes: 1 cat, respectively. For domestic dogs: tiger cats at Mel, ratio would be 2.5:1, whereas at Cágados it would be 0.9:1.

4. Discussion

4.1 *Small felid habitat use at MSP*

The combination of methodologies for identifying habitat use patterns allowed us to assess for the first time ever habitat preferences of threatened felids in the northern Cerrado. Thoroughness is extremely important when addressing ecological processes through correlations (Mackenzie et al. 2004). This is especially true for rare species, such as pampas, where lack of detection may result in biased estimates of habitat use (Mackenzie and Royle, 2005; Linkie et al. 2007). In our case, accounting for imperfect detection through occupancy models, and complementing this with the GLM, allowed us to avoid excluding ecologically important variables (Gorosito et al. 2018). At MSP, the sole application of a GLM would arbitrarily exclude anthropic covariates that act directly on the behavior and survival of tiger cats as reported in other studies (Oliveira et al. 1996, 2014, 2020). On the other hand, the exclusive use of OMs for pampas cat would not provide robust inferences, as OMs require a high number of detections in order to effectively identify habitat use patterns (Gorosito et al. 2018). Despite its importance, the lack of spatial independence between sampling points did not cause hamper to the analysis. This premise is often violated in studies with highly mobile species (Gould et al. 2019). Both felids have higher area requirements than what would be expected based on their body size (Oliveira et al, 2010; Payan and de Oliveira, 2016; Lucherini et al. 2016).

Detection probability estimates for *L. tigrinus* were in line with what has been found previously in the semi-arid Caatinga biome and in the Sertão Veredas/Peruaçú National Parks conservation area mosaic (MSVP). Our detection probability estimates were equal to those of MSVP and slightly higher of those in the Caatinga (Marinho et al. 2017; Oliveira et al. 2018). The lowest detection probabilities are reported for the Boqueirão da Onça region, with a value of 0.08 (0.04-0.11) (Dias et al. 2019). We had the highest values ever reported for the species for the probability of habitat use. Both occupancy and detection tend to be positively correlated with abundance (Lopez and Pfister, 2001; Royle and Nichols. 2003). This seems to be the case at MSP, which has a population of tiger cats twice as high as that in other Brazilian northern savanna areas (Oliveira et al. 2020).

In a similar fashion as Marinho et al. (2017) and Dias et al. (2019), probability of habitat use of tiger cats (interpreted as occupancy probability by both authors) was mainly influenced by anthropic covariates. In the Caatinga, tiger cats also avoided areas near human settlements, likely due to conflicts with domestic carnivores (Marinho et al. 2017). At MSP, predictive maps illustrated this as well, with areas within 800 m of human settlements having an 80% decline in probability of use by tiger cats. Although anthropic covariates were not present in the best models of pampas cats, the β coefficients showed that these covariates are of conservation interest at MSP. Direct predation by domestic dogs on pampas cat has been reported in the Brazilian Pampa (Lucherini et al. 2016) and just outside MSP there was a melanistic tiger cat killed by dogs (Oliveira 1996). Similarly in the Atlantic Forest, occupancy of southern tiger cat (*Leopardus guttulus*) and margay (*Leopardus wiedii*) declined as the number of domestic dog records increased (Cassano et al. 2014). It is known that domestic dogs can form packs and even attack larger carnivores (Lacerda et al. 2009; Oliveira 2011). At MSP, a significant portion of domestic dog records involved two or more individuals roaming together, thus representing a potential threat for the threatened felids.

Domestic dogs generally avoid areas in which apex predators are present (Foster et al. 2010). In the savannas of MSP, medium and large carnivores (i.e. jaguar (*Panthera onca*), puma and ocelot) are either absent or extremely rare (Oliveira, 1996, 2014, 2020). The lack of top down competitive pressure reflects on the high degree of spatial mobility of domestic dogs in MSP. During our study, 22 domestic dogs were identified, and they had a mean movement parameter of 6 km away from human settlements. These estimates suggest a spatial overlap of 65% with the suitable habitat available for *L. tigrinus* in the park (de Oliveira et al. 2020). This inference is caused mainly by human activities, and it could result in increased competition and predation pressure in natural environments (Heim et al. 2019), which on the long term could result in the local extinction of both felids at MSP.

From an ecological perspective, both pampas cat and tiger cat share similar environmental requirements in the savannas of the Brazilian Cerrado (Oliveira, 1994; Lucherini et al. 2016; Payan and de Oliveira, 2016). Resource exploitation strategies in relation to landscape characteristics and interspecific relations affect the spatial patterns of wild carnivores (Lyra-Jorge et al. 2009; de Oliveira and Pereira, 2014). Tree cover in particular, directly influenced pampas cat. This species is known to be associated with open habitats (Bagno et al. 2004; Lucherini et al. 2016), even being regularly detected in open savannas and agrarian landscapes of Emas National Park (Bagno et al. 2004; Godoi et al. 2010; Giozza et al. 2017). We expected the opposite result for tiger cats at MSP, as this species tens to present high densities in closed or moderately open savannas within the park (Oliveira et al. 2020). Therefore, besides prioritizing areas with good vegetation conditions in the Cerrado, it is also important to understand the influence of the horizontal stratification typical of savanna habitats on both felids.

Areas away from water sources showed high probability of habitat use by tiger cats. This, however, must be interpreted with caution since in arid and semi-arid environments water dictates abundance and survival of species (Wolff, 2001; de Oliveira and Diniz-Filho, 2010). Our result could be indicative of preference for smaller water sources that are not identifiable via satellite imagery (Marinho et al. 2018). Thus, we recommend future research prioritizing *in situ* search of water sources and analyzing the possible effects of seasonality.

4.2 Temporal overlap between carnivores at MSP, canid : felid ratios, and possible conservation effects

Interspecific relations between carnivores at temporal scales can create dynamics in carnivoran communities, directly influencing ecosystem functioning through changes in prey abundance and behavior (Roemer et al. 2009; Oliveira et al. 2011; Ripple et al. 2014; García-R et al. 2019). Small felid populations at MSP theoretically face little pressure from dominant wild carnivores (Maran et al. 1998; Oliveira et al. 2010).

In the absence of top-down competitive pressure from larger predators, small felid activity patterns tend to be modulated by prey availability (Palomares and Caro, 1999; Pereira, 2010; Gorini et al. 2011; Oliveira, 2011). Unsurprisingly tiger cats and pampas cats showed opposite patterns of diel activity, with the former being predominantly nocturnal and the latter mostly diurnal. In the Caatinga, activity patterns of northern tiger cats had a moderate overlap with small nocturnal mammals (Marinho et al. 2018), while its ecological equivalent from the Atlantic forest, the southern tiger cat (*L. guttulus*), was more diurnal in an area with larger felids (Oliveira et al. 2010, Massara et al. 2016). Prey base for pampas cat and tiger cat is similar, involving small mammals (< 100 g), birds, and squamates (Bagno et al. 2004; Oliveira, 2011). This high degree of dietary overlap along with similar body sizes increases the potential of competition, which results in segregation mechanisms. Besides temporal segregation between both species at MSP, there was a low degree of spatial overlap between them (ca. 16% of sampled points). Though these inferences are insightful, they are not enough to fully state that segregation between both species is exclusively to avoid competition. In order to disentangle this issue with greater precision, we would need to know the dietary composition of both cats, as well as their movement patterns related to habitat usage.

Domestic dogs' activity patters overlapped by more than 50% with those of tiger cat and their activity peaks did not differ significantly, which suggests dogs do not directly affect the diel activity of this felid. The same trend was observed for pampas cat. Nevertheless, this issue deserves attention, as domestic dogs are hosts of a variety of pathogens (Ellwanger and Chies, 2019). The degree of overlap between crab-eating fox and tiger cat (82%) and with pampas cat (47%) was even higher than the overlap with dogs.

In North America, coyote numbers affected those of domestic cats (Kays et al. 2015). However, this premise does not seem to apply at all for the felid–canid groups, e.g. tiger cat X crab-eating foxes/dogs at MSP. Body size alone puts this 6 kg fox as a potential predator of tiger cat, as it falls in the range of carnivores that could potentially benefit from interspecific killing smaller competitors, like the 2.4 kg tiger cat. Considering the typically high densities reached by the tiger cats in MSP, especially at Cágados (de Oliveira et al. 2020), where fox abundance was higher, fox numbers seems, in fact, to be ecologically irrelevant for the threatened felid. This should relate to the highly adaptable and abundant crab-eating fox being a generalist omnivore, not a hypercarnivore as tiger cats are (Donadio and Buskirk 2006, de Oliveira and Pereira 2014). Although domestic dogs can kill smaller carnivores, and the fact that there was an isolated historic predation of dogs on a black tiger cat outside park limits (Oliveira 1996), dogs also do not seem to affect wild felid ecology. However, it could be argued that the higher densities of tiger cats found at Cágados than at Mel (de Oliveira et al. 2020), could be related to the fact that in the former area ratios are about 1:1, whereas at the latter there are 2.5 X more dogs than tiger cats.

The scenario of high temporal overlap of dogs and foxes with both felids together with the high percentage of dogs and foxes with disease signs is favorable for disease transmission. Thus, it is more likely that crab-eating foxes and dogs represent a threat through potential disease transmission. At MSP, there are signs of dermatohological pathologies on different individuals (Albuquerque et al. unpublished data). Furthermore, dogs can potentially act as spillover bridges, facilitating pathogen transfer between wildlife and humans and vice versa (Ellwanger and Chies, 2019), turning a conservation issue into a public health problem. A population viability analysis for tiger cats at MSP showed that a scenario with moderate disease outbreaks and habitat loss could cause the local extinction of the species within 100 years (Oliveira et al. 2020). This is suggestive that disease outbreaks could have major consequences for the two small felids. Therefore, conservation actions are urgently needed before reaching an inflexion point (Doherty et al. 2017).

Concluding remarks

Our results suggest that anthropogenic covariates could act with higher intensity than environmental factors on the spatio-temporal distribution of threatened felids. Results are also suggestive that in areas that domestic dogs are prevalent, they are an important variable to be considered in occupancy and conservation assessments. Therefore, in protected areas it is of paramount importance to reduce the movement of domestic dogs and to have domestic dogs of the surrounding areas vaccinated to avoid possible disease outbreaks into wild carnivorans populations.

Different vegetation covers strongly influence habitat use, detectability, and segregation of tiger cats and pampas cats. A high-quality environment is also important for establishing conservation measures for these carnivores. In this sense, our results show that MSP fulfills the environmental needs of small felids, as long as anthropogenic threats are mitigated. Furthermore, quantifying interspecific interactions is crucial in order to fully understand the impacts of anthropogenic threats coming from free-roaming domestic animals. Thus, these factors should be integrated in future conservation assessments.

Our results illustrate the need for conservation actions in the park, and for them to be efficient, we recommend cooperation between researches and park managers. This should ensure the long-term survival of pampas and tiger cats at one of their most important conservation areas in the Brazilian Cerrado.

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Supplementary material

Table S1. Covariates employed in the analysis with their respective description, range, and mean

Covariates	Description	Range	Mean (SE)
Tree Cover (%)	Percent of trees > 5 m per pixel (30 x 30 m) in a 90,000 m² buffer	0 - 32	4.64 (6.32)
Elevation (m)	Elevation above sea level obtained through Shuttle Radar Topography Mission (SRTM) - USGS (30 x 30 m) data) in a 90,000 m² buffer	268 - 357	316 (20)
Habitat use probability of dogs (Ψ)	Habitat use probability for domestic dogs per camera trap obtained through the model (ψ[forest cover] p[constant])	0 - 1	0.58 (0.44)
Distance to settlements (m)	Euclidian distance to nearest 3 settlements from each camera trap	414 - 11,169	3,129 (2,410)
Distance to water sources (m)	Euclidian distance to nearest water source from each camera trap	21 - 2,603	1,186 (630)
Distance to unpaved roads (m)	Euclidian distance to nearest nonpaved road from each camera trap	0 - 2,461	765 (691)

Table S2. β coefficients for each covariate from the single season occupancy models.

	Northen tiger-cat				**Pampas cat**			
Covariates	β	SE	P	z	β	SE	P	z
Occupancy modeling								
FC	0.301	0.529	0.570	0.568	-0.927	5.040	0.065	-1.840
ELEV	0.151	0.701	0.829	0.216	did not converge	did not converge	did not converge	did not converge
OCCDOG	-0.468	1.210	0.699	-0.387	-2.630	2.540	0.300	-1.037
SET	4.030	2.850	0.158	1.410	-0.504	1.520	0.740	-0.332
WATER	0.104	0.395	0.792	0.264	-20.750	49.800	0.677	-0.416
UROAD	0.166	0.627	0.792	0.264	did not converge	did not converge	did not converge	did not converge
Detection modeling								
FC	0.227	0.131	0.008[a]	1.777	-2.970	1.358	0.002[a]	-2.190
ELEV	-0.279	0.244	0.025[a]	-1.140	0.325	0,586	0.058	0.554
OCCDOG	0.584	0.396	0.014[a]	1.480	-0.425	0.859	0.062	-0.495
SET	0.183	0.175	0.029a	1.050	0.674	0.395	0.008[a]	1.710
WATER	-0.060	0.116	0.060	-0.523	0.220	0.283	0.438	0.775
UROAD	-0.096	0.183	0.060	-0.530	0.348	0.450	0.043a	0.774
GLM								
FC	0.261	0.235	0.266	1.110	-2.743	1.249	0.028[a]	-2.197
ELEV	-0.183	0.282	0.516	-0.649	-0.381	0.413	0.356	-0.923
OCCDOG	0.356	0.585	0.545	0.605	-1.068	0.814	0.190	-1.312
SET	0.184	0.271	0.496	0.680	-0.107	0.425	0.801	-0.252
WATER	-0.061	0.168	0.714	-0.366	-0.183	0.252	0.469	-0.725
UROAD	-0.098	0.267	0.714	-0.366	-0.290	0.401	0.469	-0.725

* Statistically significant coefficient