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DOUGLAS DE MATOS DIAS

Influência antrópica sobre a probabilidade de ocupação de mamíferos carnívoros e as relações interespecíficas entre predadores e suas presas na Caatinga brasileira

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Tese apresentada ao programa de Pós-Graduação em Ecologia, Conservação e Manejo de Vida Silvestre (PPG-ECMVS) da Universidade Federal de Minas Gerais, como requisito parcial para obtenção do título de Doutor em Ecologia.

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“Quando uma árvore é cortada ela renasce em outro lugar. Quando eu morrer quero ir para esse lugar, onde as árvores vivem em paz”

(Tom Jobim)

Resumo

A perda e modificação de habitats, relacionadas direta ou indiretamente às atividades humanas, representam uma grave ameaça às populações de mamíferos em todo o mundo. Na Caatinga a situação não é diferente. Este bioma semiárido, caracterizado pela baixa umidade durante a maior parte do ano, está submetido a altas taxas de impacto antropogênico, como a pecuária extensiva, caça, introdução de espécies exóticas e a contínua expansão de parques eólicos em áreas bem conservadas. Nesse contexto, os mamíferos carnívoros, que estão entre os animais mais vulneráveis a essas modificações da paisagem, estão consideravelmente ameaçados. O uso da terra também pode induzir adaptações comportamentais nas espécies silvestres e isso pode ter implicações nas relações interespecíficas. Os predadores usam o espaço de uma maneira que maximize seu sucesso de forrageio, ocupando locais onde as presas são mais frequentes ou vulneráveis. Entretanto, pequenos carnívoros têm que lidar com demandas conflitantes entre ajustar suas atividades de acordo com a ocorrência de presas e evitar encontros agonísticos com predadores maiores. Neste estudo nós utilizamos armadilhas fotográficas para avaliar probabilidade de ocupação de carnívoros em relação às distâncias para povoados, parques eólicos e cursos de água em uma área prioritária para a conservação da biodiversidade na Caatinga. Do mesmo modo, exploramos como a ocorrência de cachorros domésticos, caçadores e o gado afetam a probabilidade de ocupação dos carnívoros silvestres. Investigamos também se a ocorrência de presas e de competidores dominantes como a jaguatirica *Leopardus pardalis* e predadores de topo (onça-parda *Puma concolor* e onça-pintada *Panthera onca*), influenciam a distribuição, detecção e os padrões de atividade diária de dois pequenos felinos neotropicais, o gato-pintado *Leopardus tigrinus* e o jaguarundi *Puma yagouaroundi*. A frequência de uso da jaguatirica foi menor nos sítios próximos aos povoados. A probabilidade de uso da onça-pintada correlacionou-se negativamente com a distância do parque eólico, enquanto que a detecção correlacionou-se positivamente com esta covariável. Encontramos uma correlação positiva entre a ocupação do jaguarundi e a distância para os parques eólicos. Nós encontramos maiores probabilidades de ocupação da onça-parda e do jaguarundi e de detecção da jaguatirica em locais próximos à água. A ocupação do cachorro-do-mato correlacionou-se positivamente com a presença de caçadores. Nós também encontramos maiores probabilidades de detecção do cachorro-do-mato nos sítios mais frequentados pelo gado. A probabilidade de ocupação do gato-pintado correlacionou-se positivamente com a presença do preá ($w_+ = 0.91$) e negativamente com a presença da jaguatirica ($w_+ = 0.75$). A ocorrência do mocó foi um importante preditor da detecção do gato-pintado ($w_+ = 0.50$). A ocorrência do preá foi a única covariável que influenciou a ocupação do jaguarundi ($w_+ = 1.00$). A probabilidade de detecção desse felino também foi correlacionada positivamente com a ocorrência dos principais predadores ($w_+ = 0.50$). O coeficiente de sobreposição temporal entre o gato-pintado e as duas espécies de presas menores foi alto ($\Delta_1 > 0.75$). O gato-pintado também apresentou um alto grau de sobreposição temporal com a jaguatirica ($\Delta_1 = 0.74$) e predadores de topo ($\Delta_1 = 0{,}76$). No caso do jaguarundi, houve considerável sobreposição com a cutia ($\Delta_1 = 0.76$). No entanto, o padrão de atividade predominantemente diurna desse felino refletiu-se na baixa sobreposição temporal com as outras espécies, tanto de presas quanto de predadores. De modo geral, e como esperado, as diferentes espécies apresentaram padrões distintos de respostas às influências antropogênicas na área de estudo. Nossos dados sugerem que as presas exercem mais influência do que os predadores de topo sobre o uso do habitat e o padrão de atividade dos pequenos felinos. No entanto, a jaguatirica parece ter uma forte influência sobre os pequenos felinos, principalmente sobre o gato-pintado, que tende a se segregar espacialmente. De modo geral, nosso estudo indica que os carnívoros estão expostos a uma série de perturbações de origem antropogênica e que medidas conservacionistas devem ser tomadas a fim de garantir a persistência das espécies, particularmente aquelas mais sensíveis e ameaçadas.

Abstract

The habitat loss and modification, directly or indirectly related to human activities, represent a serious threat to mammal populations around the world. The situation in Caatinga is no different. Characterized by low humidity rates for most of the year, this semi-arid biome is exposed to high anthropogenic impact rates, such as extensive livestock farming, hunting, introduction of exotic species and the continuous expansion of wind farms in preserved areas. In this regard, carnivorous mammals, one of the most vulnerable animals to landscape modifications, are widely threatened. Land use can also induce behavioral adaptations in wild species and this might have implications for interspecific relationships. Predators use space in a way that maximizes their foraging success. They occupy locations where the prey is most prevalent or vulnerable. However, small carnivores also have to deal with conflicting demands between adjusting their activities according to the occurrence of prey and avoiding agonistic encounters with larger predators. In this study we use camera traps to evaluate the occupancy probability of carnivores in relation to distances to settlements, wind farms and watercourses in a priority area for the conservation of biodiversity in the Caatinga. Similarly, we explore how the occurrence of domestic dogs, hunters and cattle affect the occupancy probability of wild carnivores. We also investigate whether the occurrence of prey and dominant competitors, such as the ocelot *Leopardus pardalis*, and top predators (puma *Puma concolor* and jaguar *Panthera onca*) influence the distribution, detection and daily activity patterns of two small neotropical felids, the northern tiger cat (*Leopardus tigrinus*) and the jaguarundi (*Puma yagouaroundi*). The frequency of use of the ocelot was lower in the ranches near the settlements. The probability of use of the jaguar was negatively correlated with the distance from the wind farm, while the detection was positively correlated with this covariate. We found a positive correlation between the jaguarundi occupancy and the distance to wind farms. We found higher probabilities of puma and jaguarundi occupancy and ocelot detection in sites near water. The wild dog occupancy positively correlated with the presence of poachers. We also identified greater odds of crab-eating fox detection in the sites mostly frequented by cattle. In general, and as expected, different species exhibited distinct response patterns to human influences in the study area. The occupancy probability of the northern tiger cat correlated positively with the presence of Spix’s cavy ($w_+ = 0.91$) and negatively with the presence of the ocelot ($w_+ = 0.75$). The occurrence of the rock cavy was an important predictor of the detection of the northern tiger cat ($w_+ = 0.50$). The occurrence of Spix's cavy was the only covariate that influenced the occupancy of the jaguarundi ($w_+ = 1.00$). The probability of detection of this feline was also correlated positively with the occurrence of the top predators ($w_+ = 0.50$). The coefficient of temporal overlap between the northern tiger cat and the two smaller prey species (the cavies) was high ($\Delta_1 > 0.75$). The northern tiger cat also presented a high degree of temporal overlap with the ocelot ($\Delta_1 = 0.74$) and top predators (Δ_1

= 0.76). In the case of the jaguarundi, there was considerable overlap with the agouti (Δ_1 = 0.76). However, the predominantly diurnal activity pattern of this feline was reflected in low temporal overlap with the other species, of both prey and predator. Our data suggest that prey wields more influence than top predators on habitat use and activity pattern of the small felids. However, the ocelot seems to have strong influence on small felines, especially on the northern tiger cat, which tends to spatially segregate itself. Overall, our study indicates that the carnivores are exposed to a number of human origin disturbances and that conservation measures should be taken to ensure the continuation of these species, specially those that are more sensitive and threatened.

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Introdução geral

A influência antrópica sobre o meio ambiente tem sido cada vez mais intensa, resultando no que alguns pesquisadores chamam de "crise" da biodiversidade, uma referência às extinções impulsionadas por diversos fatores relacionados às atividades humanas (Di Minin et al. 2016). As taxas atuais de extinções resultantes das atividades antropogênicas são sem precedentes e altamente incomuns na história da Terra (Ceballos et al. 2015). Estudos enfatizam a perda e a fragmentação do habitat como as principais ameaças à biodiversidade tropical e aos serviços ecossistêmicos, uma vez que as mudanças no uso da terra diminuíram drasticamente a cobertura florestal em todo o mundo (Laurance et al. 2014). Atividades como a caça ilegal, extração de produtos florestais madeireiros e não-madeireiros, bem como a pecuária extensiva, são exemplos de distúrbios antrópicos e importantes impulsionadores da perda de biodiversidade (Rito et al. 2016). Este cenário é particularmente preocupante nas florestas sazonalmente secas, que estão entre os ecossistemas mais ameaçados, devido aos impactos antrópicos e à vulnerabilidade frente às mudanças climáticas (Miles et al. 2006).

A Caatinga está entre as maiores florestas tropicais sazonalmente secas do mundo (Miles et al. 2006) e é também uma das regiões semiáridas mais populosas (Ribeiro et al. 2015). Esta região de floresta seca e vegetação xerófila se estende por mais de 800.000 km² no nordeste do Brasil e tem sofrido sucessivos impactos desde a colonização do país no século XVI (Silva & Barbosa 2017). Mas foi a partir do séc. XVII que os ocupantes desta região desenvolveram o hábito de desmatar e queimar a vegetação da Caatinga para abrir extensas pastagens, o que possibilitou o estabelecimento de povoados e cidades (Hemming 1978). Coletivamente, a agricultura de corte e queima, o pastoreio excessivo pela pecuária extensiva e a coleta de lenha impõem um contínuo de degradação que varia desde a redução da cobertura vegetal à completa desertificação (Leal et al. 2005). Estudos indicam que a pressão humana sobre a vegetação natural da Caatinga tem aumentado gradativamente ao longo os anos, resultando numa conversão de 63,3% dos ecossistemas naturais em paisagens antropogênicas (Silva & Barbosa 2017). O problema é ainda maior se levar em conta que um terço do bioma tem um alto potencial de desertificação (Sá & Angelotti 2009; Vieira et al. 2015).

Apesar de ser endêmica do Brasil e possuir uma rica biodiversidade, a Caatinga é um dos biomas brasileiros mais negligenciados do ponto de vista científico e governamental (Santos et al. 2011; Silva et al. 2018). Com isso, as perspectivas para sua conservação são pessimistas, uma vez que a apenas 1,5% da área do bioma está sob proteção integral e as Áreas de Proteção Ambiental (APA), compõem 80,8% de todas as áreas protegidas da Caatinga (Pacheco et al. 2018). A baixa representatividade de áreas de proteção integral e o predomínio de APAs, representam um desafio para a preservação dos remanescentes de Caatinga, pois categorias de áreas protegidas como as APAs, são permissivas em muitas atividades econômicas, admitindo o estabelecimento de infraestruturas de grande porte e de potencial impacto ambiental (Pacheco et al. 2018). Neste sentido, o desenvolvimento recente de infraestruturas como a expansão da matriz de energia eólica, tem exposto várias áreas de Caatinga a uma nova realidade (Pacheco & Santos 2012). No Brasil, a geração de energia a partir dos ventos bate recordes a cada ano e atualmente o país ocupa o oitavo lugar entre os maiores produtores mundiais neste setor (ABEEólica 2017). O estado da Bahia, por exemplo, está entre os maiores produtores do país, sendo o Boqueirão da Onça uma das regiões com o maior potencial eólico do estado (Atlas Eólico da Bahia 2013). Isto é particularmente preocupante, tendo em vista que os parques eólicos são construídos geralmente em locais remotos e sobrepostos às áreas de refúgios de muitas espécies de mamíferos, especialmente carnívoros (Eggermann et al. 2011, Costa et al. 2017).

A energia eólica é de fato uma alternativa importante para a produção de energia limpa e representa uma oportunidade valiosa para mitigar os efeitos das mudanças climáticas (Sims et al. 2003). No entanto, ela também gera impactos ambientais que devem ser considerados durante as fases de planejamento e implementação dos parques eólicos (Passoni et al. 2017). Modificações do habitat, abertura de estradas, aumento da presença humana em áreas anteriormente não perturbadas, mortes de animais por colisões com veículos, efeitos de ruídos e vibrações são alguns exemplos de impactos inerentes à construção e operação de parques eólicos (Costa et al. 2017). Embora o dano mais comum seja causado pela colisão direta de pássaros e morcegos com turbinas (Drewitt & Langston 2006, Kunz et al. 2007), os parques eólicos também exercem influência negativa sobre a fauna não-voadora (Lovich & Ennen 2013).

Alguns estudos de longa duração, por exemplo, mostram que a construção de parques eólicos pode afetar a ecologia e comportamento de lobos *Canis lupus* (Álvares et al. 2011, Helldin et al. 2012). Particularmente, durante as fases de construção e operação dessas infraestruturas, os lobos tendem a abandonar locais de reprodução e reduzirem suas taxas reprodutivas em áreas próximas aos aerogeradores, além de deslocarem suas áreas de vida para locais mais afastados desses empreendimentos (Álvares et al. 2011, Costa et al. 2017, Passoni et al. 2017). Tais respostas levantam preocupações quanto a conservação das espécies, particularmente quando a disponibilidade de habitats adequados é um fator limitante e os efeitos cumulativos de outras ameaças (por exemplo, perda de habitat, aumento da pressão de caça, maior frequência de animais domésticos, etc.) podem afetar as populações locais (Passoni et al. 2017). Contudo, alguns mamíferos de maior porte não respondem negativamente ao desenvolvimento da energia eólica. Um estudo realizado na América do Norte indicou que as variáveis climáticas e seus efeitos sobre a disponibilidade de forragem provavelmente influenciaram os movimentos de cervos (*Cervus elaphus*) em maior medida do que a construção de parques eólicos (Walter et al. 2006). Esses autores sugerem que, embora tenha havido um aumento no uso de áreas alternativas pelos cervos, em resposta à perda de habitat devido a instalação dos empreendimentos eólicos, os ungulados desenvolveram uma espécie de aclimatação comportamental para distúrbios humanos. Desta forma, a adaptação às alterações do habitat e ao distúrbio antrópico é possível quando há acesso a habitats capazes de cumprir os requisitos de sobrevivência e reprodução das espécies (Walter et al. 2006).

Este cenário de crescente degradação ambiental, depleção de presas e perseguição por humanos, tem sido comum em várias partes do mundo e tornou muitos carnívoros ameaçados de extinção (Karanth & Chellam 2009, Di Minin et al. 2016). Além disso, paisagens antropizadas também podem induzir alterações comportamentais em carnívoros (Schuette et al. 2013). Espécies envolvidas em conflitos com criadores, como a hiena manchada *Crocuta crocuta*, podem tornar-se mais reservadas ou noturnas em paisagens sob influência antrópica (Boydston et al. 2003). Tais mudanças comportamentais em predadores de topo podem dar início a uma "liberação comportamental" em competidores subordinados, através da ampliação de nichos temporais e espaciais (Di Bitetti et al. 2010, Schuette et al. 2013). Em geral, o padrão de atividade e o uso do habitat por um predador é influenciado pela disponibilidade de presas (Gorini et al. 2012). No entanto, a distribuição espacial de pequenos carnívoros é em grande parte o resultado de trade-off entre a ingestão de energia, risco de predação e competição intraguilda com predadores competitivamente dominantes (Palomares & Caro 1999). Desta forma, dado o efeito top down de grandes predadores, como as onças, espera-se maior segregação (espacial ou temporal) por parte dos carnívoros menores (Di Bitetti et al. 2010).

Embora a compreensão dos efeitos das ameaças humanas sobre a distribuição de carnívoros esteja entre as principais prioridades de conservação (Di Minin et al. 2016), as respostas das espécies às influências antrópicas na Caatinga permanecem desconhecidas. A escassez de informação é particularmente evidente em áreas prioritárias para a conservação, o que é crítico, considerando os requisitos espaciais dos carnívoros, principalmente aqueles que se encontram regionalmente ameaçados, como os felinos.

O objetivo geral deste estudo foi investigar os efeitos das atividades humanas sobre a ocupação de mamíferos carnívoros e avaliar as interações interespecíficas entre pequenos felinos e suas presas potenciais e com predadores de topo em uma área prioritária para a conservação na Caatinga. A tese está dividida em dois capítulos. No primeiro capítulo investigamos como as características do habitat relacionadas às atividades antrópicas (ex. assentamentos, parques eólicos, ocorrência de cachorros domésticos, gado e caçadores) e disponibilidade de água afetaram a distribuição de sete espécies de carnívoros (*Cerdocyon thous*, *Leopardus pardalis*, *Leopardus tigrinus*, *Panthera onca*, *Puma concolor*, *Puma yagouaroundi* e *Conepatus semistriatus*) nesta paisagem. No segundo capítulo, exploramos a partição espaço-temporal de dois pequenos felinos (*L. tigrinus* e *P. yagouaroundi*) com suas presas potenciais (*Galea spixii*, *Kerodon rupestris* e *Dasyprocta nigriclunis*) e com predadores competitivamente dominantes (*L. pardalis, P. concolor* e *P. onca*).

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Chapter 1 - Anthropic influence on the probability of occupancy of mammalian carnivores in the Brazilian Caatinga[1]

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Anthropic influence on the probability of occupancy of mammalian carnivores in the Brazilian Caatinga

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Abstract

Human activities result in modifications of the landscape, which cause impacts on a region's biodiversity. The Caatinga is a semi-arid biome, characterized not only by its greatly reduced humidity during most of the year, but also high rates of anthropogenic impact, such as the ongoing expansion of wind farms into well-conserved areas. In this context, the mammalian carnivores, which are among the animals most vulnerable to modifications of the landscape, are considerably threatened. We used data from camera traps and occupancy models to investigate the habitat use by carnivores in an area of Caatinga in northeastern Brazil. We found a negative correlation between the presence of wind farms and the probability of occupancy of the jaguar, and a positive relationship with the presence of the jaguarundi. Puma and jaguarundi occupied primarily sites in the vicinity of watercourses, whereas the occupancy of the crab-eating fox was correlated positively with the presence of poachers. The ocelot was detected more frequently at sites distant from settlements, whereas the jaguar was detected more often in areas far from wind farms. We found a negative correlation between the distance of water and the detection of the ocelot. The detection of the crab-eating fox was influenced positively by the detection of cattle. In general, and as expected, the different species presented distinct patterns of correlation with the variables analyzed, and we discuss the relevance and the implications of these findings for the conservation of the species that inhabit these landscapes and other similar environments.

Resumo

As atividades humanas resultam em modificações da paisagem, que causam impactos na biodiversidade de uma região. A Caatinga é um bioma semiárido, caracterizado não apenas pela umidade muito reduzida durante a maior parte do ano, mas também por altas taxas de impacto antropogênico, como a contínua expansão de parques eólicos em áreas bem conservadas. Nesse contexto, os mamíferos carnívoros, que estão entre os animais mais vulneráveis às modificações da paisagem, estão consideravelmente ameaçados. Utilizamos dados de armadilhas fotográficas e modelos de ocupação para investigar o uso de habitat por carnívoros em uma área da Caatinga no nordeste do Brasil. Encontramos uma correlação negativa entre a presença de parques eólicos e a probabilidade de ocupação da onça-pintada, e uma relação positiva com a presença do jaguarundi. O puma e o jaguarundi ocuparam primariamente sítios próximos dos cursos de água, enquanto a ocupação do cachorro-do-mato esteve correlacionada positivamente com a presença de caçadores. A jaguatirica foi detectada com maior frequência em locais distantes de assentamentos, enquanto o jaguar foi detectado com maior frequência em áreas distantes dos parques eólicos. Encontramos uma correlação negativa entre a distância da água e a detecção da jaguatirica. A detecção do cachorro-do-mato foi influenciada positivamente pela detecção de bovinos. Em geral, e como esperado, as diferentes espécies apresentaram padrões distintos de correlação com as variáveis analisadas, e discutimos a relevância e as implicações desses achados para a conservação das espécies que habitam essas paisagens e outros ambientes similares.

Key words: Biodiversity; Habitat use; Human activities; Semi-arid environment; Wind farm.

INTRODUCTION

HABITAT FRAGMENTATION, THE OVEREXPLOITATION OF NATURAL RESOURCES, AND THE INTRODUCTION OF INVASIVE SPECIES ARE INTER-RELATED IMPACTS ASSOCIATED WITH THE HUMAN OCCUPATION OF NATURAL LANDSCAPES, AND COMPRISE THE MAIN THREATS TO THE PLANET'S BIODIVERSITY (HOFFMANN *ET AL*. 2011). In this context, mammals of the order Carnivora are considered to be of the highest priority for conservation actions, due to their position at the top of trophic webs (Estes et al. 2011) and their vulnerability to the conversion of natural habitats into more inhospitable environments (Purvis et al. 2000). Global evaluations of the conservation status of carnivores have revealed a preoccupying scenario, and the urgent need for effective conservation measures (Ripple et al. 2014, Di Minin et al. 2016). Almost half of the carnivores found in Brazilian biomes are threatened as a result of the synergic impacts of habitat degradation, the depletion of prey populations, and illegal hunting (Beisiegel 2017). In the Caatinga biome, for example, five of the six wild felids are classified in some threat category (MMA 2014). The Caatinga is the largest seasonal dry forest in South America (Beuchle et al. 2015), and is one of the world's most densely-populated semi-arid ecosystems, with a total population of approximately 27 million inhabitants. The Caatinga is also the most ruralized region in Brazil, accounting for 32% of the country's ranches (Brasil 2017).

The Caatinga has already lost 63.3% of its original vegetation cover, due primarily to cattle ranching, deforestation and the harvesting of firewood, and the establishment of settlements, roads, and other infrastructure, such as wind farms (Silva & Barbosa 2017). Hunting has also had a long history in the Brazilian Caatinga, and hunting pressure is still intense, threatening the persistence of many native species, which have become locally extinct in many parts of the biome (Alves et al. 2016). Hunting with dogs is extremely popular in the region, and the dogs are typically under little control (Neto et al. 2012, Paschoal et al. 2016). This is worrying, since these canids can become very abundant in natural environments (Paschoal et al., 2016) and compromise the distribution of some wild carnivores (Massara et al., 2018). The ongoing expansion of human activities throughout the Caatinga has seen the progressive replacement of natural ecosystems by anthropogenic environments (Silva & Barbosa 2017).

Changes in the landscape caused by human activities may alter the distribution of animal species and provoke shifts in their behavior, given that the most sensitive animals will tend to avoid areas modified by human activities (Schuette et al. 2013). The establishment of wind farms in the Caatinga has raised profound concerns in the region's scientists. While wind power is an important alternative to fossil fuels, it does have impacts on the environment (Costa et al. 2017). Given the structure of the turbines, that is, high towers with moving blades, most research into the impacts of these structures on wildlife have focused on birds (Drewitt & Langston 2006) and bats (Arnett 2005), although they are known to affect other species (Helldin et al. 2012). The expansion of wind power operations has been identified as one of the principal threats to the existence of the largest American felids, the puma (*Puma concolor*) and the jaguar (*Panthera onca*) (Beisiegel 2017) in the Caatinga.

In addition to all these impacts, the carnivores of the Caatinga have to adapt to the region's intense scarcity of water. The biome becomes increasingly more arid towards its central portion, where long periods of intense drought often occur (Prado 2003). Given the loss of its natural vegetation cover and ongoing climate change (Schulz et al. 2017), permanent sources of water are becoming increasingly scarce in the Caatinga. This is likely to have profound impacts on its fauna, given that the availability of water is a primary factor determining the distribution of species in hot and arid environments, on a number of different scales (Thrash et al. 1995, Hawkins et al. 2003).

Given all these considerations, understanding how anthropogenic impacts and the availability of water influence the use of habitat by carnivores will be fundamental to the planning of land use and the development of effective conservation strategies. In the present study, we investigated the probability of occupancy of carnivores in relation to the distance from human settlements, wind farms, and watercourses within a priority area for the conservation of the biodiversity of the Caatinga, the Boqueirão da Onça (MMA 2016). While the carnivores of the study community face adverse conditions, some mid-sized species, such as the crab-eating fox (*Cerdocyon thous*) and the hog-nosed skunk (*Conepatus semistriatus*), present ecological attributes, such as plasticity in habitat use and generalist diets, that confer them with a relative tolerance of human activities (Dias & Bocchiglieri 2016, Dias 2017). Based on previous studies, we expected that these generalist mesocarnivores would prefer areas of greater anthropogenic impact due to the availability of feeding resources and refuge from their predators and main competitors (Schuette et al. 2013). On the other hand, we expected a positive correlation between the distance from settlements and wind farms and the probability of occupancy of the felines, which are more sensitive to anthropogenic impacts (De Angelo et al. 2011). In addition to the infrastructure itself, we expected the occupancy of all carnivores to be influenced negatively by the presence of poachers and dogs, given the potential risk they represent. However, we did expect the probability of occupancy of the jaguar and puma to be related positively with the occurrence of cattle, given that these animals are potential prey for the felines. As there are no known ecological interactions between cattle and the other native carnivores, we did not expect the occurrence of these domestic animals to influence the occupancy of the other species monitored in the present study. As water is a scarce and limiting resource in the Caatinga, we also expected a negative correlation between the probability of occupancy of the carnivore species and the distance to permanent watercourses.

We also expected the probability of carnivore detection to be influenced by infrastructure and the availability of water in a similar manner to the probability of occupancy. Furthermore, we expected that the detection of domestic dogs and poachers would have a negative influence on the detection probability of the native carnivores, given that these species would avoid areas in which dogs and poachers are detected, at least temporarily. Given the increasing number of reports of the predation of cattle within the study area, we expected jaguar and puma (but not other carnivores) to be detected at higher rates in areas in which cattle is more abundant. Finally, we predicted a positive relationship between the number of days of sampling and the detection probability of the species.

METHODS

STUDY AREA

The present study was conducted in a region known as Boqueirão da Onça, located in the north of the state of Bahia (Fig. 1). This region covers a total area of approximately 9,000 km², and is considered to be of "extremely high" importance for the conservation of biodiversity by the Brazilian Environment Ministry, due to the diversity of threatened and rare species, speleological patrimony, representativeness of ecosystems and vegetation cover (MMA 2016).

At Boqueirão da Onça, as in other parts of the Caatinga, the rains tend to be brief and unpredictable, with the short rainy season generally lasting from October to December. Over the past 10 years, mean annual precipitation was 563.6 mm, and the temperature was 27ºC, according to data from the Brazilian National Institute of Meteorology (INMET 2018). The arboreal-shrubby caatinga and the arboreal caatinga are the predominant vegetation types in this ecoregion (Velloso et al. 2002), although a mosaic of phytophysiognomies can be found within the area, including rock fields, plateau forests, and stands of palms, known as veredas

(Roos et al. 2012). Tracts of denser vegetation, with some emergent trees, can be found on escarpments and in deep valleys. As in most of this semi-arid region, there are few permanent streams, and the rare sources of water are derived from springs that flow throughout the year. Within the Boqueirão da Onça, we defined the study area as the zone influenced by the Sete Gameleiras and Delfina wind farms, located in the municipalities of Sento Sé and Campo Formoso, respectively.

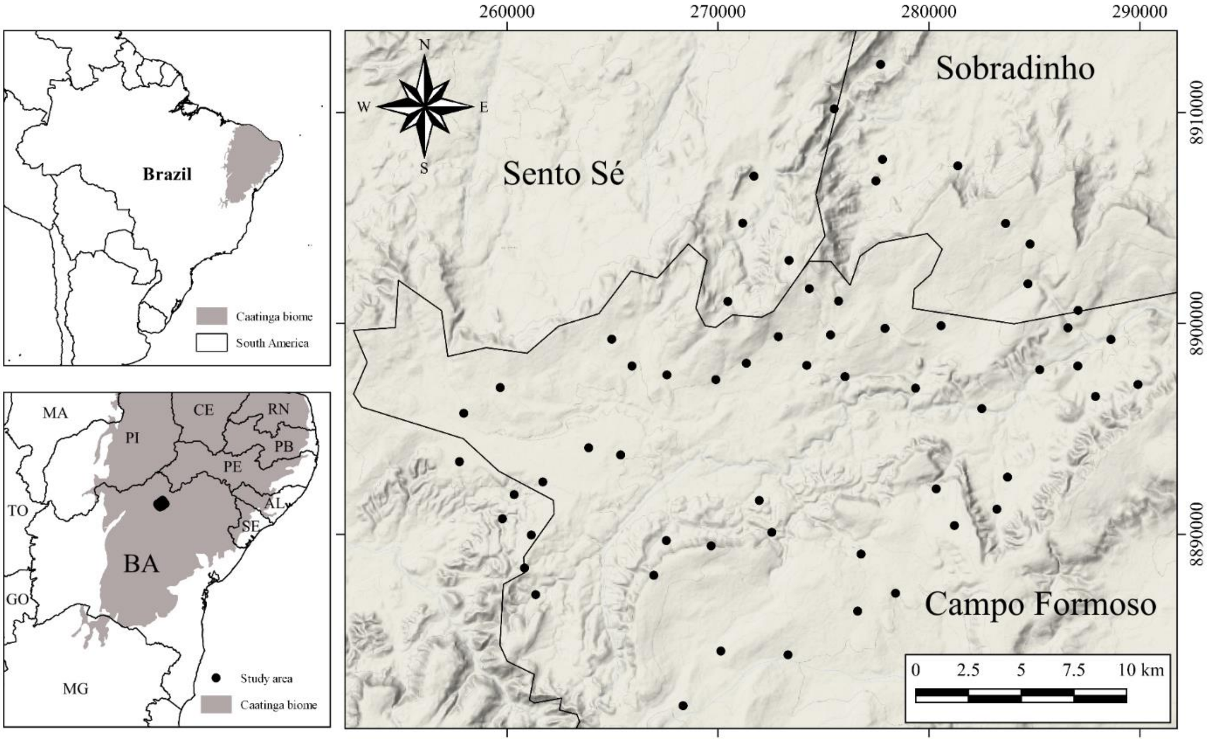

FIGURE 1. Distribution of the sampling sites (black dots) at Boqueirão da Onça, Bahia, Brazil. The insert in the upper left corner shows the Caatinga biome (gray) within Brazil, and the insert in the lower left corner indicates the study area (black dot) in northern Bahia state, northeastern Brazil

DATA COLLECTION

We established a 20-km x 30-km (600-km²) grid based on a satellite image, which was subdivided into 150 plots of 4-km². We selected 60 plots randomly to establish the sampling sites, and installed a camera trap in each plot to record carnivores, with a mean distance of 2.00-km (range: 1.5–3.28-km) between adjacent traps. We used Acorn LTL-5210 (n = 4) and Bushnell (n = 56) cameras traps. The traps were set to operate for 24 hours, and installed primarily on trails and unpaved roads, which are known to be access routes used by carnivores (Karanth 1995). We did not use baits to attract animals.

The study period encompassed the seven months of the dry season, from January to July 2017, and resulted in a total sampling effort of 8.678 trap-days. To calculate sampling effort, we excluded the traps that were stolen (n = 2) and the days on which the cameras were nonoperational. In the latter case, the day on which the last record was obtained was considered to be the last day on which the camera was operational for the calculation of sampling effort. We analyzed the records of seven carnivore species: crab-eating fox - *Cerdocyon thous*; ocelot - *Leopardus pardalis*; northern tiger cat - *Leopardus tigrinus*; jaguar - *Panthera onca*; puma - *Puma concolor*; jaguarundi - *Puma yagouaroundi*, and hog-nosed skunk - *Conepatus semistriatus*.

MODELING OCCUPANCY AND DETECTION PROBABILITIES

The probability of occupancy (Ψ) of a species is defined as the probability that site *i* is occupied by the species, while the probability of detection (*p*) is defined as the probability of detecting the species at site *i* and during time *t*, conditioning that the species occurs in the area. These parameters can be modeled as a function of the covariates (MacKenzie *et al*. 2002). In the present study, we interpreted the detection probability as a frequency (or intensity) of use (e.g., Cassano *et al*. 2014; Massara *et al*. 2018).

To investigate the influence of human activity on the probability of occupancy of the carnivores, we measured three covariates at each sampling site, that is, the distance from each site to the nearest (i) cattle ranch, (ii) settlement, and (iii) wind farm. As water is a limiting resource in the Caatinga, we also measured the distance from each site to the nearest permanent source of water (e.g., spring). We also investigated the direct influence of domestic dogs, cattle, and poachers on the probability of occupancy of the carnivores, estimating separately the conditional probability of occupancy ($\Psi_{\text{conditional}}$; MacKenzie *et al.* 2006) of dogs, cattle, and poachers at each site using the 'single-season' occupancy model in the PRESENCE program (Hines 2006). The conditional probability of occupancy is defined as the probability that the species is present at a site, since it was not detected. When a specie is detected at the site, its $\Psi_{\text{conditional}} = 1$ (MacKenzie *et al.* 2006). These conditional probabilities of occupancy were used as a site covariate in our analysis. We measured the distance covariates in QGis. 2.14 (http://www.qgis.org/en/site/) and used them as the site covariates in our analyses (Table 1).

TABLE 1. Covariates used to model the probabilities of occupancy (Ψ) and detection (p) of carnivores at Boqueirão da Onça, Bahia, northeastern Brazil. The mean (amplitude) of values are given for each covariate. The values for the detection of dogs, cattle, and poachers are the mean proportion of periods (20 in total) of the detection of these species among the different sites.

Covariates	Mean and range (minimum-maximum)
Distance from Settlements (m)	9656.7 (700-16300)
Distance from Wind farms (m)	8729.9 (950-19739)
Distance from watercourses (m)	5074.4 (220-15590)
$\Psi_{\text{conditional}}$ of Dog[a]	0.38 (0.00-1.00)
$\Psi_{\text{conditional}}$ of Cattle[a]	0.25 (0.00-1.00)
$\Psi_{\text{conditional}}$ of Poacher[a]	0.22 (0.00-1.00)
Dog detection	0.04 (0.00-0.08)
Cattle detection	0.09 (0.02-0.17)
Poacher detection	0.03 (0.00-0.07)
Days of camera operation	144.6 (30-200)

We also used covariates related to the distance of each site from the nearest cattle ranch, human settlement, wind farm, and watercourse to model the probability of detection (p) of the carnivores. To investigate the influence of the presence of domestic dogs, cattle, and poachers on the detection probability of the wild carnivores, we constructed three 'sampling covariates'. Each of these covariates is related to the detection (1) or not (0) of dogs, cattle, and poachers at each site during each sampling period. Finally, we considered the number of days on which each camera was operational at each site during each sampling period to evaluate for the influence of this covariate on the detection of the carnivores.

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[a] $\Psi_{\text{conditional}}$ is the probability that a site is occupied by the target species, given its specific detection history

We prepared a correlation matrix prior to running the analyses to determine whether pairs of predictor covariates were highly correlated, i.e., $r \geq 0.7$ (Goad *et al*. 2014). As the distance from cattle ranches was highly correlated with that from both settlements and wind farms (0.72 and 0.73, respectively), we excluded ranches from the subsequent analyses.

DATA ANALYSIS

We used a 'single-season' occupancy model (MacKenzie *et al*. 2002), run in the Mark program (White & Burnham 1999), to determine the influence of the covariates on the probabilities of occupancy and detection of the carnivores. The 200 days of sampling were grouped in 20 periods (occasions) of 10 days to characterize the history of detection of each species at each sampling site. Given the small number of detections of the jaguar, the data on this species were organized in 10 periods (occasions) of 20 days. As our primary objective was the identification of the predictor covariates that have the greatest effect or influence on the probabilities of occupancy and detection of the carnivores, we adopted a selection strategy model based on all the possible combinations contemplated by our *a priori* hypotheses. Specifically, we constructed 1094 models (see Table S1) based on all the possible additive combinations of the covariates that may have influenced the probabilities of occupancy (Ψ) and detection (p) of each carnivore. This approach resulted in a set of balanced models (Doherty *et al*. 2012), which allowed us to calculate the accumulative AICc (w_+) weights of each covariate (Burnham & Anderson, 2002) and evaluate which were the most likely ($w_+ \geq 0.50$) to have influenced the occupancy and detection probabilities of the carnivores.

We evaluated for a possible lack of independence (overdispersion) among sites using the goodness-of-fit test developed specifically for the analysis of 'single-season' occupancy (MacKenzie & Bailey 2004), analyzed in the PRESENCE program (Hines 2006). When overdispersion was found, the models were adjusted by the Quasi AICc (QAICc).

RESULTS

The goodness-of-fit test indicated significant overdispersion only for the northern tiger cat ($\hat{c}$ = 2.00; p = 0.01). The distance from wind farms was correlated negatively with the probability of occupancy of the jaguar (w_+ = 0.68; Table 2), and positively with that of the jaguarundi (w_+ = 0.84; Table 2). The distance from permanent watercourses was correlated negatively with the probability of occupancy of two species, the puma (w_+ = 0.60; Table 2) and the jaguarundi (w_+ = 0.53; Table 2). By contrast, the probability of occupancy of the crab-eating fox was correlated positively with the presence of poachers (w_+ = 0.94; Table 3). Neither the distance from settlements nor the presence of dogs or cattle had any influence on the probability of occupancy of any of the native carnivores (w_+ < 0.50; Table 2).

The number of days on which the cameras were operational had a positive influence on the probability of detection of all the species (w_+ > 0.50; Table 2), except for the jaguar (w_+ = 0.13; Table 2). The distance from settlements correlated positively with the probability of detection of the ocelot (w_+ = 0.99; Table 2). The distance from wind farms correlated negatively with the detection of the jaguar (w_+ = 0.71; Table 2). The distance from permanent sources of water correlated negatively with the detection probability of the ocelot (w_+ = 0.99; Table 2). The probability of detection of the crab-eating fox was correlated positively with the presence of cattle (w_+ = 0.58; Table 2). However, the detection of dogs and poachers not influenced the probability of detection of the wild carnivores (w_+ < 0.50; Table 2).

TABLE 2. Cumulative AICc weights for the covariates used to model the probabilities of occupancy (Ψ) and detection (p) of mammalian carnivores at Boqueirão da Onça, Bahia, northeastern Brazil. The estimates of the effects of the covariates (β parameters) are given for the most parsimonious model that included each covariate. The Ψ values were modeled as a function of the distance from water, settlements, and wind farms, with the $\Psi_{\text{conditional}}$ for domestic dogs (Dog$_{\text{cond}}$), cattle (Cattle$_{\text{cond}}$), and poacher (Poacher$_{\text{cond}}$). The p values were modeled as a function of the distance from water, settlements, and wind farms, and the detection of dogs, cattle, and hunters, and the number of days on which the cameras were operational. The mean values of occupancy ($\hat{\Psi}$ and detection ($\hat{p}$) of the species were obtained from the most parsimonious models, which included the covariates with the highest cumulative weight ($w_+ \geq 0.50$).

Covariates	Cumulative AICc Weights	β parameters			Real parameters		
		Estimate	Lower 95% IC	Upper 95% IC	Estimate	Lower 95% IC	Upper 95% IC
Crab-eating fox occupancy (Ψ)							
Poacher$_{\text{cond}}$	0.94	9.11	-2.99	21.22	-	-	-
Distance from Settlements	0.36	-4.8x10^{-4}	-8.2 x10^{-4}	-1.4 x10^{-4}	-	-	-
Dog$_{\text{cond}}$	0.33	2.10	0.15	4.04	-	-	-
Distance from watercourses	0.18	3.4 x10^{-4}	7.0 x10^{-5}	6.2 x10^{-4}	-	-	-
Cattle$_{\text{cond}}$	0.04	0.72	-0.86	2.31	-	-	-
Distance from Wind farms	0.03	-3.4x10^{-5}	-1.8x10^{-4}	1.2x10^{-4}	-	-	-
$\hat{\Psi}$	-	-	-	-	0.65	0.49	0.80
Crab-eating fox detection (p)					-	-	-
Camera operation	1.00	0.32	0.20	0.44	-	-	-
Cattle detection	0.58	0.80	0.29	1.31	-	-	-
Distance from watercourses	0.29	7.0x10^{-5}	1.5x10^{-5}	1.3x10^{-4}	-	-	-
Distance from Settlements	0.05	3.6x10^{-5}	-1.8 x10^{-5}	9.0 x10^{-5}	-	-	-
Distance from Wind farms	0.05	-6.5 x10^{-5}	-1.2 x10^{-4}	-4.7 x10^{-6}	-	-	-
Poacher detection	0.03	0.22	-0.55	0.99	-	-	-
Dog detection	0.02	-0.01	-0.78	0.77	-	-	-
$\hat{p}$	-	-	-	-	0.18	0.14	0.23
Ocelot occupancy (Ψ)							
Distance from Wind farms	0.12	-1.58x10^{-4}	-3.83x10^{-4}	6.8x10^{-5}	-	-	-
Distance from watercourses	0.10	-1.5x10^{-4}	-3.5 x10^{-4}	4.8 x10^{-5}	-	-	-
Cattle$_{\text{cond}}$	0.08	1.17	-1.16	3.50	-	-	-
Poacher$_{\text{cond}}$	0.07	1.17	-1.18	3.52	-	-	-
Dog$_{\text{cond}}$	0.06	-0.81	-2.41	0.79	-	-	-
Distance from Settlements	0.05	7.6x10^{-5}	-1.8x10^{-4}	3.3x10^{-4}	-	-	-
$\hat{\Psi}$	-	-	-	-	0.68	0.50	0.82
Ocelot detection (p)					-	-	-
Camera operation	1.00	0.31	0.16	0.45	-	-	-
Distance from watercourses	0.99	-2.33x10^{-4}	-3.26x10^{-4}	-1.40x10^{-4}	-	-	-
Distance from Settlements	0.99	2.35x10^{-4}	1.44x10^{-4}	3.26x10^{-4}	-	-	-
Poacher detection	0.22	1.6	-0.03	2.35	-	-	-
Distance from Wind farms	0.08	-6.3x10^{-5}	-1.7x10^{-4}	4.2x10^{-5}	-	-	-
Cattle detection	0.05	0.24	-0.39	0.87	-	-	-
Dog detection	0.04	0.22	-0.96	1.41	-	-	-
$\hat{p}$	-	-	-	-	0.13	0.08	0.17

TABLE 2. Cont.

Covariates	Cumulative AICc Weights	β parameters			Real parameters		
		Estimate	Lower 95% IC	Upper 95% IC	Estimate	Lower 95% IC	Upper 95% IC
Northern tiger cat occupancy (Ψ)[a]							
Dog$_{cond}$	0.21	1.11	-1.88	4.10	-	-	-
Cattle$_{cond}$	0.21	-0.89	-3.01	1.22	-	-	-
Distance from watercourses	0.16	4.8x10^{-6}	-2.8x10^{-4}	2.9x10^{-4}	-	-	-
Distance from Wind farm	0.16	2.8x10^{-5}	-2.1x10^{-4}	2.6x10^{-4}	-	-	-
Distance from Settlements	0.16	3.1x10^{-5}	-2.7x10^{-4}	3.3x10^{-4}	-	-	-
Poacher$_{cond}$	0.15	0.66	-2.16	3.48	-	-	-
$\hat{\Psi}$	-	-	-	-	0.64	0.38	0.84
Northern tiger cat detection (p)[a]					-	-	-
Camera operation	0.99	0.42	0.01	0.83	-	-	-
Distance from Settlements	0.29	-8.6x10^{-5}	-2.2 x10^{-4}	4.4 x10^{-5}	-	-	-
Poacher detection	0.22	0.77	-0.69	2.24	-	-	-
Cattle detection	0.22	0.60	-0.55	1.75	-	-	-
Distance from Wind farms	0.20	-4.4 x10^{-5}	-1.4 x10^{-4}	5.3 x10^{-5}	-	-	-
Distance from watercourses	0.16	-4.3 x10^{-5}	-1.9 x10^{-4}	1.1 x10^{-4}	-	-	-
Dog detection	0.14	0.31	-1.26	1.87	-	-	-
$\hat{p}$	-	-	-	-	0.08	0.04	0.11
Jaguar occupancy (Ψ)							
Distance from Wind farms	0.68	-1.01x10^{-3}	-2.6x10^{-3}	5.7x10^{-4}	-	-	-
Distance from watercourses	0.18	1.3x10^{-4}	7.4x10^{-4}	4.8x10^{-4}	-	-	-
Dog$_{cond}$	0.17	1.18	-2.80	5.16	-	-	-
Cattle$_{cond}$	0.16	1.45	-2.61	5.52	-	-	-
Poacher$_{cond}$	0.15	0.57	-3.13	4.27	-	-	-
Distance from Settlements	0.14	2.4x10^{-4}	-5.3x10^{-4}	0.001	-	-	-
$\hat{\Psi}$	-	-	-	-	0.56	0.30	0.83
Jaguar detection (p)					-	-	-
Distance from Wind farm	0.71	7.8x10^{-4}	2.4x10^{-4}	1.3 x10^{-3}	-	-	-
Cattle detection	0.47	-18.40	-15053.1	15016.3	-	-	-
Dog detection	0.30	-19.65	6.2x10^{-7}	-19.65	-	-	-
Distance from Settlements	0.16	-1.5x10^{-4}	-5.7x10^{-4}	2.7x10^{-4}	-	-	-
Poacher detection	0.16	0.96	-1.48	3.40	-	-	-
Camera operation	0.13	0.04	-0.11	0.20	-	-	-
Distance from watercourses	0.13	6.1x10^{-5}	-2.5x10^{-4}	3.8x10^{-4}	-	-	-
$\hat{p}$	-	-	-	-	0.10	-0.01	0.22
Puma occupancy (Ψ)							
Distance from watercourses	0.60	-7.4x10^{-4}	-1.7x10^{-3}	2.5x10^{-4}	-	-	-
Cattle$_{cond}$	0.36	2.08	-0.14	4.29	-	-	-
Distance from Wind farms	0.23	-4.4x10^{-4}	-1.1 x10^{-3}	2.7 x10^{-4}	-	-	-
Distance from Settlements	0.09	4.4x10^{-5}	-2.8 x10^{-4}	.7 x10^{-4}	-	-	-

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[a] Result of the adjusted model for QAICc.

TABLE 2. Cont.

Covariates	Cumulative AICc Weights	β parameters			Real parameters		
		Estimate	Lower 95% IC	Upper 95% IC	Estimate	Lower 95% IC	Upper 95% IC
Poacher$_{cond}$	0.07	-0.76	-4.50	2.97	-	-	-
Dog$_{cond}$	0.07	-0.43	-3.16	2.29	-	-	-
$\hat{\psi}$	-	-	-	-	0.23	0.05	0.42
Puma detection (p)					-	-	-
Camera operation	0.88	0.89	-1.74	3.53	-	-	-
Cattle detection	0.43	1.10	-0.05	2.26	-	-	-
Distance from Wind farms	0.37	-5.7 x10^{-4}	-9.5 x10^{-4}	-2.0 x10^{-4}	-	-	-
Distance from Settlements	0.34	5.4 x10^{-4}	1.6 x10^{-4}	9.2 x10^{-4}	-	-	-
Distance from watercourses	0.11	1.9x10^{-4}	-2.2 x10^{-4}	6.1 x10^{-4}	-	-	-
Poacher detection	0.10	1.42	-0.94	3.78	-	-	-
Dog detection	0.08	0.91	-1.38	3.19	-	-	-
$\hat{p}$	-	-	-	-	0.06	0.02	0.10
Jaguarundi occupancy (Ψ)							
Distance from Wind farms	0.84	4.3x10^{-4}	-3.3x10^{-5}	8.9x10^{-4}	-	-	-
Distance from watercourses	0.53	-1.3x10^{-3}	-2.4x10^{-3}	-1.8x10^{-4}	-	-	-
Distance from Settlements	0.35	8.2x10^{-4}	4.3x10^{-5}	1.6x10^{-3}	-	-	-
Cattle$_{cond}$	0.11	1.82	-1.86	5.51	-	-	-
Poacher$_{cond}$	0.07	-1.08	-5.06	2.90	-	-	-
Dog$_{cond}$	0.05	-0.01	-3.33	3.31	-	-	-
$\hat{\psi}$	-	-	-	-	0.54	0.29	0.79
Jaguarundi detection (p)					-	-	-
Camera operation	0.86	0.23	0.01	0.44	-	-	-
Distance from Wind farms	0.29	-1.5x10^{-4}	-2.9x10^{-4}	-4.8x10^{-6}	-	-	-
Distance from watercourses	0.29	-1.6x10^{-4}	-3.0x10^{-4}	-2.6x10^{-5}	-	-	-
Poacher detection	0.20	-19.94	-1.6x10^{4}	1.5x10^{4}	-	-	-
Distance from Settlements	0.08	-7.5x10^{-5}	-2.3x10^{-4}	8.4x10^{-5}	-	-	-
Cattle detection	0.06	-0.56	-2.01	0.88	-	-	-
Dog detection	0.05	-0.08	-2.13	1.97	-	-	-
$\hat{p}$	-	-	-	-	0.04	0.03	0.06
Striped hog-nosed skunk occupancy (Ψ)							
Dog$_{cond}$	0.41	-15.18	-36.4	6.04	-	-	-
Distance from Settlements	0.31	-1.0x10^{-3}	-2.5x10^{-3}	5.5x10^{-4}	-	-	-
Cattle$_{cond}$	0.22	-3.99	-21.43	13.43	-	-	-
Poacher$_{cond}$	0.16	-9.31	-23.43	4.81	-	-	-
Distance from watercourses	0.15	4.6x10^{-4}	-5.6x10^{-4}	1.5x10^{-3}	-	-	-
Distance from Wind farms	0.14	1.6x10^{-4}	-5.5x10^{-4}	8.7x10^{-4}	-	-	-
$\hat{\psi}$	-	-	-	-	0.47	0.19	0.76
Striped hog-nosed skunk detection (p)					-	-	-
Camera operation	0.96	0.50	-0.27	1.28	-	-	-
Poacher detection	0.33	-19.99	-20.00	-19.99	-	-	-

TABLE 2. Cont.

Covariates	Cumulative AICc Weights	β parameters			Real parameters		
		Estimate	Lower 95% IC	Upper 95% IC	Estimate	Lower 95% IC	Upper 95% IC
Distance from Settlements	0.32	$-9.8x10^{-4}$	$-2.5x10^{-3}$	$5.5x10^{-4}$	-	-	-
Distance from watercourses	0.14	$-5.9x10^{-5}$	$-2.2x10^{-4}$	$1.1x10^{-4}$	-	-	-
Dog detection	0.13	1.49	-0.75	3.73	-	-	-
Cattle detection	0.13	-0.19	-1.68	1.29	-	-	-
Distance from Wind farms	0.12	$-1.1x10^{-5}$	$-1.2x10^{-4}$	$9.9x10^{-5}$	-	-	-
$\hat{p}$	-	-	-	-	0.04	0.01	0.06

DISCUSSION

As expected, the different carnivore species responded in distinct ways to the anthropogenic impacts evaluated in the present study. The distance from wind farms was the human variable that most influenced the probability of occupancy of two felines, the jaguar and the jaguarundi. In contrast with our expectations, however, the jaguar presented a higher probability of occupancy at sites closer to wind farms. Previous research in the Caatinga has indicated a positive relationship between the probability of occurrence of the jaguar and highland areas (Morato *et al*. 2014, Astete *et al*. 2016), which correspond with the location of wind farms. As they are more remote, these areas tend to be less affected by habitat loss, which would favor the occurrence of the jaguar, which is highly dependent on areas of natural vegetation (De Angelo *et al*. 2011). These areas of better preserved habitat may also harbor populations of the prey species most frequently targeted by the jaguar in the study area, and this demands further investigation, given that the presence of top predators tends to be correlated positively with the presence of their prey (Karanth *et al*. 2004). Alternatively, the higher probability of occupancy of the jaguar in these areas may be associated with thermoregulation. The presence of deep valleys and ravines on the slopes of the upland areas offer a refuge from the extreme temperatures of the Caatinga (Astete *et al*. 2016). Given this, we believe that the synergic effects of these two factors (availability of prey and thermoregulation) may account for the pattern of occupancy of the jaguar observed within the study area.

By contrast, the jaguarundi presented a positive relationship with the distance from the wind farms, which may be related to the use of less dense habitats, given that this feline is an adaptable generalist able to occupy more open areas, and even habitats that have suffered anthropogenic impacts (Oliveira *et al*. 2010). One potential alternative, however, is that this pattern of occupancy in the jaguarundi represents a behavioral response to the presence of the jaguar. As jaguars may prey on the jaguarundi, the larger carnivores of this trophic guild may influence the behavior and distribution of the smaller species (Oliveira & Pereira 2014). In particular, smaller felines may avoid larger ones by occupying habitats of lower quality (Di Bitetti *et al*. 2010), although their contrasting patterns of activity – while jaguarundi are typically diurnal, the jaguar is primarily nocturnal – may minimize the possibility of direct contact. The exact nature of the interaction between these two species will only be elucidated with more detailed data on their patterns of spatial and temporal niche partitioning.

The probabilities of occupancy of the jaguarundi and the puma also increased with the proximity of watercourses. This association with sources of water has been noted in previous studies of both jaguarundi (Giordano 2016) and puma (Astete *et al*. 2016). In semi-arid environments like the Caatinga, the availability of water is without doubt one of the primary factors limiting biological diversity (Oliveira & Diniz-Filho 2010). Given this, one important management strategy practised in some of the biome’s protected areas is the installation of artificial watering troughs in an attempt to guarantee the survival of the resident species, especially during prolonged droughts (Astete *et al*. 2016, Dias *et al*. 2017). The findings of some studies indicate that the preference of carnivores for sites in the vicinity of water sources is related to the presence of denser vegetation in these areas, which provides shelter and the opportunity to encounter prey species dependent on water (Schuette *et al*. 2013). The correlation between the the occupancy of jaguarundis and pumas, and water sources in Boqueirão da Onça may also be related to the fact that the present study was conducted during the dry season. In this case, we expected to find differences in the occupancy of these species during the rainy season, when water accumulates in intermittent streams and the temporary pools (lajedos) that form within rock formations.

Contrary to our predictions, the presence of poachers only had a marked effect on the occupancy of the crab-eating fox, and in this case, with a positive association. This indicates that this fox is relatively tolerant of the presence of humans, which is consistent with its adaptability to a wide range of environmental conditions (Dias & Bocchiglieri 2016). The crab-eating fox is a generalist carnivore in many aspects of its ecology, including its activity patterns, habitat use, and diet, which suggests that its association with sites occupied by poachers may be related to the availability of resources such as animal carcasses and discarded food leftovers.

Both biological and technical factors determine the probability of some species will be detected at a given study site. Our study has shown that the proximity of human settlements affected the intensity (or frequency) of habitat use by the ocelot, with its detection probability being influenced negatively by this covariate. Despite being relatively well adapted to different types of habitat, including farmland (Oliveira *et al*. 2010), the sum of the evidence indicates that the ocelot is associated strongly with native habitats (Massara *et al*. 2015, 2018). This pattern of habitat use is thought to be related to the cryptic behavior of this feline and its preference for forest-dwelling prey (Lyra-Jorge *et al*. 2010). In addition to these factors, we believe that its reduced frequency in the areas adjacent to human settlements is related to conflicts with shepherds and goat-herders. Local residents in the study area, including poachers, reported that this feline is persecuted as a retaliation for the predation of lambs and goat, which are one of the principal sources of income in the local settlements. This would account for the evasive behavior of the ocelot, which tended to avoid areas occupied by humans.

The distance from wind farms also had a strong influence on the detection of the jaguar. While the majority of the sites occupied by this species were in the vicinity of these installations, they were visited only very infrequently during the study period. In other words, while these areas encompass better-preserved native vegetation with potential jaguar prey, the areas directly adjacent to the wind farms are exposed to noise from the turbines, intense traffic of heavy vehicles and humans, and an excess of artificial light (Costa *et al*. 2017). These areas are also affected by an increase in hunting pressure due to the availability of access roads (Helldin *et al*. 2012), and the occurrence of microtremors and noise caused by the use of explosives for the preparation of the foundations of the turbines. The synergic effects of these impacts may contribute to the avoidance of these areas by the jaguar. Similar patterns of habitat use have been reported in other big cat species, indicating that a fear of humans is widespread in this group, and induces shifts in behavior patterns and habitat use (Smith *et al*. 2015). In Africa, for example, lions (*Panthera leo*) adopt alternative behavioral strategies in areas with a high risk of human contact, such as more rapid movements (Oriol-Cotterill *et al*. 2015). In North America, pumas will spend less time feeding on their prey in areas occupied by humans, resulting in an increase in predation rates to compensate for the loss of energy intake (Smith *et al*. 2015). In this context, while areas in the vicinity of wind farms may represent important source of resources for the jaguar, it may use these sites relatively infrequently to avoid contact with humans.

Our observations indicate a strong influence of the presence of water on the probability of detection of the ocelot. A similar pattern has been observed in other regions, where the association with riparian habitats may be related to the greater availability of prey in these environments (Goulart *et al*. 2009). In the case of our study area, we believe that the higher rates of use of sites near sources of water by the ocelot were associated with the availability of the water itself, given that this resource is available at a small number of sites during the dry season. There is no evidence of physiological adaptations in small-bodied mammals in the Caatinga, related to the scarcity of water, although many species may adapt to this condition behaviorally (Carmingnotto & Astúa 2017). As there are no data on larger-bodied mammals, we believe that carnivores, such as the ocelot, may visit water sources more frequently during the dry season, shifting their behavior during the rainy season, when water becomes more abundant. Further research will be necessary to better understand potential seasonal fluctuations in habitat occupancy and detection by carnivores, and their physiological adaptations.

The crab-eating fox was the only carnivore whose detection was influenced by the occurrence of cattle. Previous studies have shown that this canid is a generalist and is tolerant of anthropogenic impacts (Dias & Bocchiglieri 2016). The compaction of the soil and the elimination of undergrowth by grazing cattle reduce the availability of refuges for many organisms, which may favor some opportunistic predators by increasing the detectability of their prey, and as a consequence, their capture rates (Preston 1990). Research in semi-arid environments in Australia indicates an association between lizards and area grazed by cattle (Read & Cunningham 2010). In addition to the effects of grazing, areas occupied by cattle are characterized by widespread deposits of fecal matter, which attract a diversity of coprophagous organisms, including coleopterans (Aidar *et al*. 2000). The crab-eating fox is known to be a generalist predator, and in the Caatinga, lizards and beetles may represent an important component of its diet (Olmos 1993, Dias & Bocchiglieri 2016). In this case, the foxes may visit areas occupied by cattle relatively frequently due to the abundance of easily-captured prey items.

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

In a region exposed to a wide range of anthropogenic impacts, such as Boqueirão da Onça, the availability of water may also have a profound influence on the occurrence of many other species. However, the inconclusive findings on the northern tiger cat (*L. tigrinus*) reinforce the need for further ecological research and the investigation of the factors that may threaten the persistence of this endangered species. To our knowledge, this is the first study in the Neotropical region to evaluate the influence of wind farms on habitat use by medium- and large-bodied mammals, and we hope that our findings will provide an incentive for further research in other regions of the world, where these facilities have been installed or are under construction. Understanding the impacts of wind farms on larger mammals will provide important insights for wildlife managers and the companies operating in this sector, and contribute to the development of strategies for the effective mitigation of the negative impacts of these installations. The negative response of endangered species, such as the jaguarundi and the jaguar, raises concerns for the conservation of the species over the short to medium term. Despite this, areas affected by wind farms also appear to be important to the jaguar, which emphasizes the need for the implementation of conservation measures directed at this species. The collection of data using telemetry may provide more systematic insights into the intensity of use of these areas by this carnivore. This may have important implications for the conservation of the jaguar in Boqueirão da Onça, given that a number of new wind farms are planned for the region.

Landscapes occupied by human populations are expanding continually, with a concomitant reduction in the availability of areas capable of supporting a diverse predator community (Wang *et al*. 2015). Recent estimates indicate that the natural vegetation of the Caatinga decreases year on year, and currently, 63.3% of its total area has been modified by anthropogenic impacts (Silva & Barbosa 2017). Boqueirão da Onça is one of only a few regions with extensive areas of continuous caatinga vegetation, which harbor one of the biome's last surviving jaguar populations, and further reinforces its classification as a priority area for the conservation of biodiversity (MMA 2016). The potential for the protection of areas such as Boqueirão da Onça is becoming increasingly difficult in the Caatinga, given the advanced stage of degradation of its natural habitats (Silva & Barbosa 2017). Given this, we emphasize the urgent need for intervention by government agencies in our study area, to protect its extremely diverse biota. Our findings also indicate that anthropogenic impacts on the carnivore community should not be overlooked, and that their potential effects must be evaluated separately for each species. Given the rapid modification of the landscape in which Boqueirão da Onça is inserted, effective measures are required from environmental agencies in order to guarantee that the development of the region is not prioritized to the detriment of the conservation of its biodiversity.

Our findings indicate that both human activities and the availability of water have some influence on the use of habitats by carnivores in semi-arid environments. The replication of our research in other systems vulnerable to similar pressures will permit the systematic evaluation of the compatibility of the conservation of local biodiversity with the expansion of human development and infrastructure. As different carnivore species have distinct ecological roles, they may also be more or less sensitive to anthropogenic disturbances (Lyra-Jorge *et al*. 2010). In this context, we have shown that some carnivores do not respond as intensively as others to the availability of water or anthropogenic impacts, and this emphasizes the importance of community-level research, to identify the most sensitive species and determine appropriate measures for the conservation and management of landscapes and their wildlife. While some landscapes impacted by human activities may be able to support carnivore communities (Lyra-Jorge *et al*. 2010), increasing development may threaten many species (Wang *et al*. 2015). This highlights the need for the creation of protected areas, which can mitigate anthropogenic pressures (Andam *et al*. 2008), contribute to the conservation of key groups, such as carnivores (Nagy-Reis *et al*. 2017), and protect springs and other important resources for the local wildlife.

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SUPPORTING INFORMATION

TABLE S1. —Results of the selection of the top 10 models used to model the probabilities of occupancy (Ψ) and detection (*p*) of the carnivores of Boqueirão da Onça, Bahia, in northeastern Brazil. The Ψ values are modeled based on the distance from water, settlements (Sett), and wind farms (Wind), while the $\Psi_{conditional}$ values are based on domestic dogs (Dog$_{cond}$), cattle (Catt$_{cond}$), and poachers (Poach$_{cond}$). The *p* values are modeled as a function of the distance from of watercourses, settlements, and wind farms, and the detection of dogs, cattle (Catt), and Poachers (Poach), and the number of days on which the cameras were operational (Cam).

Model^{a}	AICc	ΔAICc	AICc Weights	Number of parameters	Deviance
Crab-eating fox					
Ψ (Poach$_{cond}$) p (Water + Catt + Cam)	729.39	0.00	0.17	6	715.81
Ψ (Dog$_{cond}$ + Poach$_{cond}$) p (Catt + Cam)	729.52	0.13	0.16	6	715.93
Ψ (Water + Sett + Poach$_{cond}$) p (Cam)	729.69	0.30	0.15	6	716.11
Ψ (Sett + Poach$_{cond}$) p (Catt + Cam)	730.49	1.09	0.10	6	716.90
Ψ (Sett + Dog$_{cond}$ + Poach$_{cond}$) p (Cam)	732.55	3.16	0.03	6	718.97
Ψ (Dog$_{cond}$ + Poach$_{cond}$) p (water + Cam)	732.58	3.19	0.03	6	719.00
Ψ (Poach$_{cond}$) p (Catt + Cam)	732.82	3.43	0.03	5	721.71
Ψ (Sett + Poach$_{cond}$) p (Water + Cam)	733.43	4.04	0.02	6	719.84
Ψ (Poach$_{cond}$) p (Sett+ Catt + Cam)	733.62	4.23	0.02	6	720.03
Ψ (Poach$_{cond}$) p (Water + Wind + Cam)	733.63	4.24	0.02	6	720.05
Ocelot					
Ψ (.) p (Water + Sett + Poach + Cam)	610.74	0.00	0.22	6	597.15
Ψ (.) p (Water + Sett + Cam)	611.72	0.98	0.13	5	600.60
Ψ (Wind) p (Water + Sett + Cam)	611.92	1.18	0.12	6	598.34
Ψ (Water) p (Water + Sett + Cam)	612.24	1.51	0.10	6	598.66
Ψ (Catt$_{cond}$) p (Water + Sett + Cam)	612.75	2.02	0.08	6	599.17
Ψ (.) p (Water + Sett + Wind + Cam)	612.84	2.11	0.08	6	599.26
Ψ (Poach$_{cond}$) p (Water + Sett + Cam)	612.91	2.17	0.07	6	599.32
Ψ (Dog$_{cond}$) p (Water + Sett + Cam)	613.25	2.52	0.06	6	599.67
Ψ (.) p (Water + Sett + Catt + Cam)	613.64	2.90	0.05	6	600.05
Ψ (Sett) p (Water + Sett + Cam)	613.85	3.12	0.05	6	600.27
Northern tiger cat*					
Ψ (.) p (Cam)	220.57	0.00	0.03	3	214.14
Ψ (.) p (Sett + Cam)	221.24	0.67	0.02	4	212.51
Ψ (.) p (Catt + Cam)	221.89	1.32	0.01	4	213.17
Ψ (.) p (Poach + Cam)	221.93	1.36	0.01	4	213.21
Ψ (.) p (Wind + Cam)	222.10	1.52	0.01	4	213.37
Ψ (Dog$_{cond}$) p (Cam)	222.16	1.59	0.01	4	213.44
Ψ (Catt$_{cond}$) p (Cam)	222.20	1.62	0.01	4	213.47
Ψ (.) p (Sett + Poach + Cam)	222.46	1.89	0.01	5	211.35
Ψ (.) p (Water + Cam)	222.54	1.97	0.01	4	213.81
Ψ (Poach$_{cond}$) p (Cam)	222.63	2.06	0.01	4	213.90
Jaguar					
Ψ (Wind) p (Wind + Catt)	87.27	0.00	0.05	5	76.16
Ψ (Wind) p (Wind + Dog + Catt)	88.70	1.43	0.02	6	75.11
Ψ (Wind) p (Wind + Dog)	88.78	1.51	0.02	5	77.67
Ψ (Sett + Wind) p (Wind + Catt)	89.16	1.89	0.02	6	75.57
Ψ (Wind + Catt$_{cond}$) p (Wind + Catt)	89.21	1.94	0.02	6	75.63
Ψ (Wind) p (Wind + Poach)	89.26	1.99	0.02	5	78.15
Ψ (Wind) p (Sett + Wind)	89.26	1.99	0.02	5	78.15
Ψ (Wind) p (Wind + Catt + Poach)	89.34	2.07	0.02	6	75.76
Ψ (Wind + Dog$_{cond}$) p (Wind + Catt)	89.35	2.08	0.02	6	75.76
Ψ (Wind) p (Wind + Catt + Cam)	89.37	2.10	0.02	6	75.79
Puma					
Ψ (Water) p (Sett + Wind + Cam)	156.97	0.00	0.11	6	143.38
Ψ (Water + Catt$_{cond}$) p (Catt + Cam)	158.56	1.59	0.05	6	144.97
Ψ (Water + Wind) p (Catt + Cam)	159.19	2.23	0.04	6	145.61
Ψ (Catt$_{cond}$) p (Sett + Wind + Cam)	159.28	2.31	0.03	6	145.69
Ψ (Water + Catt$_{cond}$) p (Cam)	159.61	2.64	0.03	5	148.50
Ψ (Water) p (Catt + Cam)	159.65	2.68	0.03	5	148.54
Ψ (.) p (Sett + Wind + Cam)	160.00	3.03	0.02	5	148.89
Ψ (Water + Catt$_{cond}$) p (Wind + Cam)	160.74	3.77	0.02	6	147.15
Ψ (Water) p (Sett + Catt + Cam)	161.01	4.04	0.01	6	147.42
Ψ (Water) p (Catt + Poach + Cam)	161.01	4.05	0.01	6	147.43

TABLE S1. Cont.

Model[a]	AICc	ΔAICc	AICc Weights	Number of parameters	Deviance
Jaguarundi					
Ψ (Water + Sett + Wind) p (Cam)	243.17	0.00	0.15	6	229.59
Ψ (Water + Wind) p (Wind + Cam)	245.22	2.05	0.05	6	231.63
Ψ (Wind) p (Water + Cam)	245.63	2.46	0.04	5	234.52
Ψ (Wind) p (Wind + Cam)	246.04	2.87	0.04	5	234.93
Ψ (Wind) p (Water + Poach + Cam)	246.10	2.93	0.03	6	232.51
Ψ (Water + Wind) p (Poach + Cam)	246.22	3.05	0.03	6	232.64
Ψ (Wind) p (Wind + Poach + Cam)	246.50	3.32	0.03	6	232.01
Ψ (Wind + $\text{Cattle}_{\text{cond}}$) p (Water + Cam)	246.50	3.33	0.03	6	232.92
Ψ (Wind) p (Water + Wind + Cam)	246.56	3.39	0.03	6	232.98
Ψ (Water + Wind) p (Cam)	246.72	3.55	0.02	5	235.61
Striped hog-nosed skunk					
Ψ (Sett + Dog_{cond}) p (Sett + Cam)	192.41	0.00	0.04	6	178.83
Ψ (Sett + Dog_{cond}) p (Cam)	192.57	0.16	0.03	5	181.46
Ψ (Sett + Dog_{cond}) p (Dog + Cam)	193.77	1.36	0.02	6	180.18
Ψ (Sett + Dog_{cond}) p (Poacher + Cam)	194.02	1.61	0.02	6	180.44
Ψ (Water + Sett + Dog_{cond}) p (Cam)	194.03	1.62	0.02	6	180.44
Ψ (Dog_{cond}) p (Sett + Cam)	194.36	1.95	0.01	5	183.25
Ψ (.) p (Sett + Cam)	194.39	1.98	0.01	4	185.66
Ψ (Dog_{cond}) p (Cam)	194.39	1.98	0.01	4	185.66
Ψ (Sett + Dog_{cond}) p (Water + Cam)	194.52	2.11	0.01	6	180.93
Ψ (.) p (Cam)	194.55	2.14	0.01	3	188.12

[a] The plus (+) signal means an additive effect between two or more covariates and the dot (.) means no covariate effect on both parameters. * Result of the adjusted model for QAICc.

Chapter 2 - Feline predator-prey relationships in a semi-arid biome in Brazil[2]

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[2] Paper under review at Journal of Zoology.

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

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Abstract

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

Key words: Neotropics; mesocarnivores; species interactions; spatial segregation; temporal segregation.

Introduction

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

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

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

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

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

Material and Methods

Study area

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

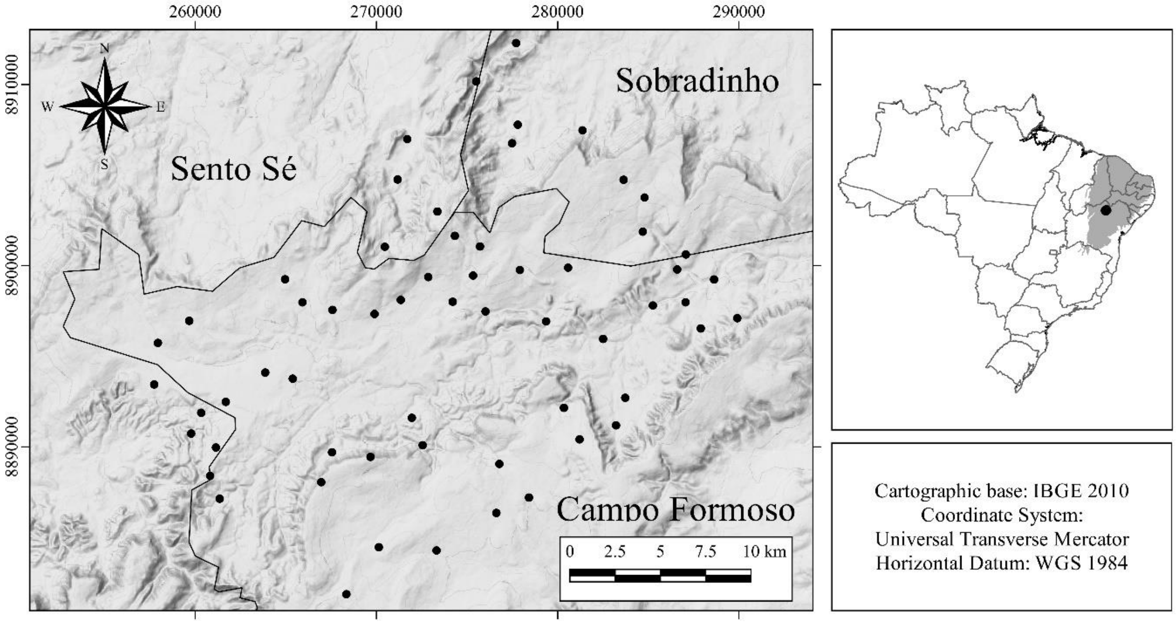

Figure 1. Distribution of the camera traps (black dots) in the Boqueirão da Onça, Bahia, Brazil. The gray lines represent the limits of the three municipalities Sento Sé, Sobradinho, and Campo Formoso. The insert (top right) shows the study site (black dot) within the Caatinga biome (gray shading) in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

Data collection

We established a 20 km x 30 km grid (600 km²) on the study area, which we subdivided into 150 plots of 4 km². As 60 camera traps were available, we randomized 60 sampling points. We installed a camera trap at each point to record mammals, with a mean distance of 2 km (range: 1.50 km–3.30 km) between traps. The traps were regulated to operate during 24 hours, and were installed primarily on tracks and unpaved roads, which are the typical travel routes of the local carnivorous mammals. We did not use bait to avoid biasing the frequency of records of the focal species. The study covered 200 days of the dry season period, between January and July, 2017, with a total sampling effort of 8678 trap-days (not including two stolen traps and the days on which the traps had malfunctioned). In the case of malfunction, the trap was assumed to have been working up until the date of the last record for the calculation of sampling effort.

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

Modeling the occupancy and detection probabilities of the study species

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

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

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

We used the 'single-season' occupancy model (MacKenzie *et al*., 2002) in the Mark program (White & Burnham, 1999) to analyze the influence of these covariates on the probability of occupancy and detection of the northern tiger cat and jaguarundi. The 200 sampling days were divided into 20 sampling periods of 10 days, to compile the detection history of each species at each sampling point. As the objective of the present study was to identify the predictor covariates that had the greatest influence on the probability of occupancy and detection of the northern tiger cat and jaguarundi, we selected the model based on all the possible combinations that would satisfy our a priori hypothesis. Specifically, we constructed 563 models (Supplementary Data) based on all the possible combinations of covariates that may influence the probability of occupancy (Ψ) and detection (p) of the northern tiger cat and jaguarundi. This approach resulted in a set of balanced models (Doherty, White & Burnham, 2012) that permitted the calculation of the cumulative AICc (w_+) weight of each covariate (Burnham & Anderson, 2002) and identify which were most likely ($w_+ \geq 0.50$) to influence the probability of occupancy and detection of the northern tiger cat and jaguarundi. We also tested the data for a possible lack of independence (overdispersion) among the sites using the goodness-of-fit test developed specifically for the analysis of ‘single-season’ occupancy (MacKenzie & Bailey, 2004), in the PRESENCE program (Hines, 2006).

Activity patterns and temporal overlap

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

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

Using the Overlap package (Meredith & Ridout, 2018), we estimated the density of the activity of each species using the kernel density, a nonparametric approach that evaluates the probability function of the density of a random variable (Worton, 1989). We then calculated the most adequate overlap coefficient (Δ), which varies from 0 (no overlap) to 1 (complete overlap) of each pair of species (Meredith & Ridout, 2018). We used the Δ_1 estimator, which is recommended when the smaller sample has less than 75 observations (see Meredith & Ridout, 2018) and calculated 95% confidence intervals of Δ_1, based on 10,000 bootstrap replicates. We considered Δ_1 values of less than 0.50 to represent a low level of overlap, values of between 0.50 and 0.60 to reflect moderate overlap, and values of over 0.60 to represent a high level of overlap (Massara *et al*., 2018). We ran these analyses in the R software (R Development Core Team, 2012). To complement this analysis, we compared the

24-hour cycles between species using the Mardia-Watson-Wheeler test (W), run in Oriana 4.01 (Kovach Computing Services, Anglesey, UK).

Results

We obtained a total of 1,764 independent records of the focal species, including 161 of ocelot, 63 of northern tiger cat, 35 of the top predators, and 33 of the jaguarundi. The most common prey species was Spix's cavy (n = 828 records), followed by the rock cavy (n = 347), and the agouti (n = 297). The occupancy probability of the northern tiger cat correlated positively with the presence of Spix's cavy ($w_+ = 0.91$) and negatively with the presence of the ocelot ($w_+= 0.75$; Table 2). The occurrence of the rock cavy was an important predictor of the detection of the northern tiger cat ($w_+ = 0.50$; Table 2). The occurrence of Spix's cavy was the only covariate that influenced the occupancy of the jaguarundi, with a very strong, positive relationship ($w_+ = 1.00$; Table 2). The probability of detection of this feline was also correlated positively with the occurrence of the top predators ($w_+ = 0.50$). The number of days on which the camera traps were operational also had a positive influence on the probability of detection of both small felids ($w_+ > 0.50$; Table 2).

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

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

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

Table 3. Rayleigh's uniformity test (Z) for temporal activity patterns, with the critical Z value being defined for a significance level of p = 0.05, based on the number of independent records (N) collected for each species. The classification of the activity pattern was based on the proportion of observations recorded during each period of the circadian cycle.

	Z	*p*	$Z_{critical}$	N	Distribution	Activity
Oncilla	4.83	0.008	2.98	63	Non-uniform	Predominantly nocturnal
Jaguarundi	6.05	0.002	2.97	33	Non-uniform	Predominantly diurnal
Spix's cavy	200.46	$1x10^{-12}$	2.99	828	Non-uniform	Predominantly nocturnal
Rock cavy	60.78	$1x10^{-12}$	2.99	347	Non-uniform	Predominantly nocturnal
Agouti	63.29	$1x10^{-12}$	2.99	297	Non-uniform	Predominantly diurnal
Ocelot	46.16	$1x10^{-12}$	2.99	161	Non-uniform	Predominantly nocturnal
Top predators	8.60	$1x10^{-4}$	2.97	35	Non-uniform	Predominantly nocturnal

The coefficient of temporal overlap between the northern tiger cat and the two smaller prey species (the cavies) was high ($\Delta_1 > 0.75$; Figure 2), declining to moderate ($\Delta_1 = 0.54$) for the agouti. Even so, the W test indicated significant differences between the circadian distribution of the northern tiger cat and those of Spix's cavy (W = 15.1; d.f = 2; P < 0.001), the rock cavy (W = 13.5; d.f = 2; P = 0.001) and the agouti (W = 48.3; d.f = 2; P < 0.001). The northern tiger cat also presented a high degree of temporal overlap with the ocelot (Δ_1 = 0.74), although the distribution of the daily records of these two species were dissimilar (W = 19.9; d.f = 2; P = 0.001). However, while the northern tiger cat also overlapped highly with the top predators ($\Delta_1 = 0.76$; Figure 2), there was no difference in the distribution of their daily records (W = 5.1; d.f = 2; P = 0.07).

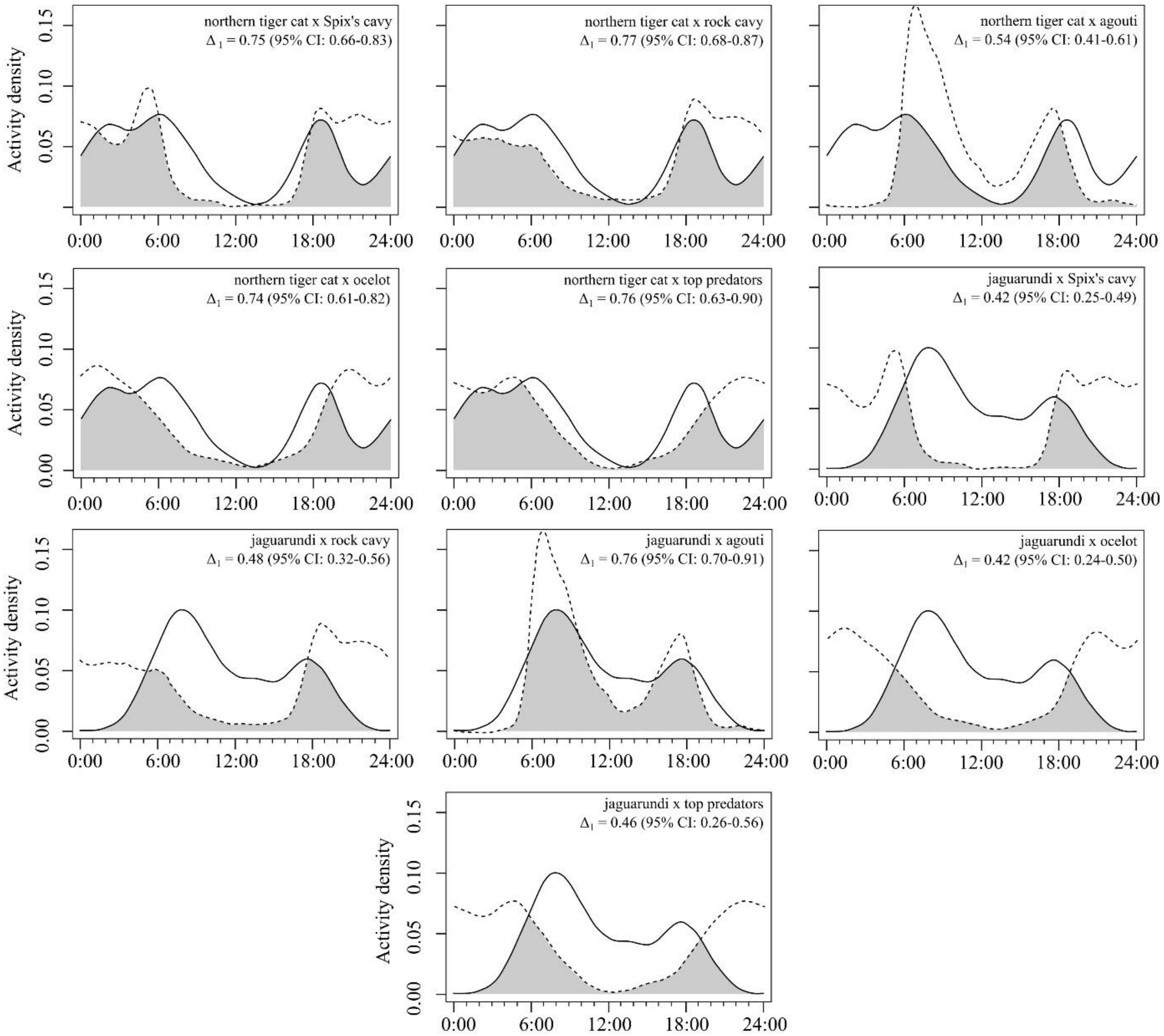

Figure 2. Temporal activity of the small felids (northern tiger cat and jaguarundi), represented by the solid lines, and the degree of overlap (95% CI's) with the three prey species, the ocelot and the top predators, represented by the dotted lines, in the Boqueirão da Onça, Bahia, Brazil. The overlap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

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

Discussion

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

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

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

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

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

The activity patterns recorded in the present study were consistent with those described in Oliveira *et al*. (2013), which have shown the northern tiger cat to be nocturnal and crepuscular, and the jaguarundi to be diurnal (Oliveira, 1998). In extreme environments, such as semi-arid ecosystems, carnivores are believed to adopt more nocturnal habits, as a way of avoiding the intense heat of the daytime period (Penido *et al*., 2017), as in the specific case of the northern tiger cat in the Caatinga, despite the fact that more nocturnal habits increase its temporal overlap with larger felids. In the Atlantic Forest, where temperatures are generally less intense, Massara *et al*. (2016) observed more diurnal behavior in the northern tiger cat, possibly in response to the presence of the larger felids.

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

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

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

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

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

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Supplementary data

Results of the selection of the top 10 models used to model the probabilities of occupancy (Ψ) and detection (*p*) of the small felids of Boqueirão da Onça, Bahia, in northeastern Brazil. The $\Psi_{\text{conditional}}$ values are based on Spix's cavy (Cavy$_{\text{cond}}$), rock cavy (Rock$_{\text{cond}}$), agouti (Agouti$_{\text{cond}}$), ocelot (Ocelot$_{\text{cond}}$) and top predators (Pred$_{\text{cond}}$). The *p* values are modeled as a function of the detection of Spix's cavy, rock cavy, agouti, ocelot, and top predators (Pred), and the number of days on which the cameras operated (Cam).

Model[a]	AICc	ΔAICc	AICc Weights	Number of parameters	Deviance
Northern tiger cat					
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Rock + Cam)	415.84	0.00	0.32	6	402.25
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Cavy + Cam)	416.42	0.59	0.24	6	402.84
Ψ (Cavy$_{\text{cond}}$) p (Cavy + Rock + Cam)	419.16	3.32	0.06	6	405.57
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Pred + Cam)	419.56	3.72	0.05	6	405.98
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Ocelot + Cam)	420.39	4.56	0.03	6	406.81
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Cam)	420.44	4.61	0.03	5	409.33
Ψ (Cavy$_{\text{cond}}$ + Rock$_{\text{cond}}$ + Agouti$_{\text{cond}}$ + Ocelot$_{\text{cond}}$ + Pred$_{\text{cond}}$) p (Cavy + Rock + Agouti + Ocelot + Pred + Cam)	421.18	5.34	0.02	13	387.26
Ψ (Ocelot$_{\text{cond}}$) p (Cavy + Rock + Cam)	421.26	5.42	0.02	6	407.68
Ψ (Cavy$_{\text{cond}}$) p (Rock + Pred + Cam)	421.31	5.48	0.02	6	407.73
Ψ (Cavy$_{\text{cond}}$) p (Cavy + Pred + Cam)	421.93	6.09	0.02	6	408.35
Jaguarundi					
Ψ (Cavy$_{\text{cond}}$) p (Pred + Cam)	243.13	0.00	0.10	5	232.02
Ψ (Cavy$_{\text{cond}}$) p (Cam)	244.25	1.11	0.06	4	235.52
Ψ (Cavy$_{\text{cond}}$) p (Agouti + Pred + Cam)	244.76	1.62	0.05	6	231.17
Ψ (Cavy$_{\text{cond}}$) p (Ocelot + Pred + Cam)	245.21	2.08	0.04	6	231.63
Ψ (Cavy$_{\text{cond}}$) p (Rock + Pred + Cam)	245.24	2.11	0.04	6	231.66
Ψ (Cavy$_{\text{cond}}$ + Agouti$_{\text{cond}}$) p (Pred + Cam)	245.34	2.21	0.03	6	231.76
Ψ (Cavy$_{\text{cond}}$) p (Cavy + Pred + Cam)	245.50	2.36	0.03	6	231.91
Ψ (Cavy$_{\text{cond}}$ + Rock$_{\text{cond}}$) p (Pred + Cam)	245.56	2.42	0.03	6	231.97
Ψ (Cavy$_{\text{cond}}$ + Pred$_{\text{cond}}$) p (Pred + Cam)	245.57	2.43	0.03	6	231.98
Ψ (Cavy$_{\text{cond}}$ + Ocelot$_{\text{cond}}$) p (Pred + Cam)	245.61	2.48	0.03	6	232.02

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[a] The plus (+) signal means an additive effect between two or more covariates and the dot (.) means no covariate effect on both parameters

Considerações finais

Neste estudo demonstramos que as espécies de carnívoros respondem de maneira distinta aos diferentes fatores de origem antrópica no Boqueirão da Onça. Essas respostas refletem o comportamento de cada espécie. Por exemplo, a onça-pintada, o jaguarundi e a jaguatirica evitaram locais próximos aos parques eólicos e aos povoados, corroborando a natureza elusiva deste grupo de carnívoros (Nowell & Jackson 1996). Por outro lado, espécies mais generalistas como o cachorro-do-mato e o cangambá (Dias & Bocchiglieri 2016, Dias 2017) exibiram baixa sensibilidade às influências antropogênicas. Nossos resultados sugerem que a disponibilidade de presas tem uma importância maior sobre o uso do habitat e o padrão de atividade dos pequenos felinos do que a ocorrência de predadores de topo. No entanto, os pequenos felinos tendem a evitar encontros com a jaguatirica segregando no espaço ou no tempo. Portanto, nossos achados suportam a hipótese do "*efeito pardalis*" (Oliveira et al. 2010). Além disso, considerando os estudos prévios e os nossos resultados, sugerimos que a extensão da área pode ter um efeito significativo sobre a resposta comportamental do gato-pintado, quando em simpatria com a jaguatirica.

Além das interações interespecíficas, a água também exerceu uma influência importante sobre a distribuição dos carnívoros. O padrão único de precipitação da Caatinga e as altas temperaturas, tornam a água o recurso limitante mais importante para o bioma, dada sua baixa disponibilidade ao longo de vários meses do ano (Fonseca et al. 2017). Nossos resultados corroboram isso, considerando que a maioria dos felinos ocuparam ou foram mais frequentes em habitats próximos aos cursos d'água. Em ambientes áridos, fonte de água permanente é um recurso raro e atrai muitas espécies de carnívoros, o que potencializa a competição (Edwards et al. 2015). No Boqueirão da Onça isso não é diferente, pois o número de fontes perenes de água está cada vez menor. Segundo moradores locais, muitas fontes que antigamente eram permanentes, têm secado nos últimos anos, devido aos longos períodos de estiagem, desmatamentos e queimadas provocadas pela ação do homem. No entanto, um resultado intrigante é a falta de relação de algumas espécies com este recurso vital, particularmente a onça-pintada. De fato, espera-se que as espécies de carnívoros difiram em sua dependência da água, o que pode, por sua vez, afetar a detectabilidade em locais próximos a este recurso (Edwards et al. 2016). Entretanto, as informações sobre as necessidades de água ou o quanto os mamíferos da Caatinga estão fisiologicamente adaptados ou não à escassez de água, não é conhecido (Carmignotto & Astúa 2017).

Na região do árido Kalahari, o consumo de água por leopardos *Panthera pardus* ocorre em fontes superficiais quando disponíveis e pela ingestão de fluídos corporais das presas (Bothma 2005). Assim, o uso oportunista de água superficial e o abate regular de presas, podem suprir principalmente as necessidades de água de um grande felino em ambientes sem fontes de água permanentes (Nowell & Jackson 1996, Bothma 2005). De qualquer forma, o balanço hídrico de grandes felinos em ecossistemas secos, pode ocorrer também através de uma função comportamental que limita a perda de água. Neste sentido, esses animais podem restringir sua atividade aos horários de temperaturas mais amenas e se abrigar em refúgios sombreados durante os momentos mais quentes do dia (Bothma 2005). Isto foi sugerido para onças-pintadas em estudos realizados em áreas de Caatinga (Astete et al. 2016, e neste estudo).

Estas questões levantam preocupações quanto a expansão de infraestruturas de energia eólica sobre áreas importantes para os carnívoros no Boqueirão da Onça. Somente na nossa área de estudo existem dois grandes complexos de parques em operação e mais três estão previstos para serem construídos em curto prazo, isso sem levar em conta as dezenas de Torres Anemométricas espalhadas por todo o Boqueirão da Onça. Estudos indicam que o estabelecimento dessas infraestruturas na área de ocorrência de uma das poucas populações remanescentes de onça-pintada na Caatinga, põe em risco a persistência do felino, bem como de outras espécies (Paula et al. 2012, Morato et al. 2014, Beisiegel 2017). Destacamos aqui, que essas preocupações não se restringem apenas aos parques eólicos em si, mas aos impactos cumulativos associados a esses empreendimentos. A crescente especulação de novas áreas para construção de parques eólicos, resultou num surto de demarcação de terras por proprietários ou não. Essas demarcações incluem incontáveis variantes (trilhas que representam linhas de fronteira entre propriedades), que foram abertos em áreas onde poucas pessoas haviam se aventurado visitar. Esses novos acessos têm facilitado os deslocamentos dos caçadores e consequentemente aumentado a pressão de caça e as incursões de animais domésticos, especialmente de cães na vegetação nativa (DM Dias, obs. pess.). Prevê-se que a distância de movimento dos animais aumente proporcionalmente com a perturbação da paisagem (Fahrig 2007). Dito isso, a crescente modificação do habitat pode causar o aumento da área de vida de onças-pintadas, acrescendo a exposição desses animais ao risco, incluindo caça (Morato et al. 2016) e conflitos com criadores de gado. Tais mudanças comportamentais em uma espécie dominante podem ter implicações sobre a estrutura da comunidade (Schuette et al. 2013).

Em ambientes extremos como o Boqueirão da Onça, onde a disponibilidade de fontes de água permanentes está cada vez menor, a caça intensa e predatória sobre a base de presas impõe uma pressão ainda maior sobre os carnívoros. Assim, quando há perda de habitat, depleção de presas e abate excessivo, grandes áreas protegidas tornam-se estritamente importantes para a conservação dos carnívoros. Felizmente, em abril de 2018 foi criado o mosaico de áreas protegidas, formado pela Área de Proteção Ambiental Boqueirão da Onça (505.692 hectares) e o Parque Nacional Boqueirão da Onça (346.908,10 hectares), Decreto nº 9.336, de 5 de abril de 2018 (ICMBio 2018). Com o estabelecimento dessas áreas protegidas, esperamos que todos esses problemas sejam atenuados. No geral, para minimizar o cenário atual de pressão antrópica sobre o Boqueirão da Onça, sugerimos medidas efetivas de repressão à caça e ao desmatamento. Mitigação de conflitos entre predadores e criadores de gado, ovino e caprinos através de suporte técnico para melhoria do manejo dos rebanhos. Além disso, o potencial de invasão de cachorros domésticos deve ser considerado. Apesar de não encontrarmos evidências de uma influência direta sobre a ocorrência dos carnívoros silvestres, a alta frequência de cães pode ter implicações negativas sobre os outros representantes da fauna nativa. Em algumas regiões do Brasil, os cães tornaram-se mais abundantes que os carnívoros nativos, mesmo em áreas protegidas (Paschoal et al. 2016). A ocorrência de cães em habitats naturais pode provocar sérios danos sobre os mamíferos, através do assédio e predação (Galetti & Sazima 2006, Campos et al. 2007). Ações de conscientização dos donos de cães nos povoados do entorno do Boqueirão da Onça são extremamente necessárias. Sugerimos também controle sanitário e campanhas de vacinação desses animais nas comunidades, dado seu potencial de transmissão de doenças para a fauna silvestre (Curi et al. 2016).

Como considerações gerais, um aspecto importante relacionado ao principal objetivo de avaliar a influência humana sobre os carnívoros é que a área que nós amostramos é uma matriz complexa de fontes de perturbação misturadas no espaço (assentamentos, parques eólicos, caça, abundância de animais domésticos, conflito homem x predador, desmatamentos, queimadas, etc.). Nossos resultados são relevantes e ajudarão os futuros gerentes das áreas protegidas a avaliar o grau em que a conservação da biodiversidade é compatível com desenvolvimento de infraestrutura e presença humana no Boqueirão da Onça. Finalmente, sob a nova legislação de proteção, amparada pelo Sistema Nacional de Unidades de Conservação (Lei Federal nº 9985, de 18 de julho de 2000), o Boqueirão da Onça agora está sob normas e restrições para o uso da terra. Assim, espera-se que os novos empreendimentos planejados para a região, atendam as condicionantes e realizem os devidos estudos de impactos ambientais exigidos pelos órgãos de controle.

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