UNIVERSIDADE FEDERAL DE MINAS GERAIS (UFMG)
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Abundância, uso do habitat e interações ecológicas da jaguatirica em áreas protegidas da Mata Atlântica

(Abundance, habitat use and ecological interactions of the ocelot in Atlantic forest protected areas)

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Belo Horizonte, 2016

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“The problem with the world is that the intelligent people are full of doubts, while the stupid ones are full of confidence” (Charles Bukowski)

Resumo

A fragmentação e a perda de habitat são as maiores ameaças para a biodiversidade. Para prevenir um aumento na atual taxa de perda da biodivesidade, a maioria dos países têm implementado áreas protegidas. Entretanto, é incerto se as áreas protegidas são adequadas para uma conservação a longo prazo das espécies em todo o mundo, especialmente nos trópicos. Na Mata Atlântica, mais de 80% dos remanescentes florestais são pequenos (50 ha) e 61% destes estão isolados das áreas protegidas, as quais protegem apenas 9% da floresta remanescente e estão imersas em uma matriz manejada pelo homem. Este atual cenário é ineficaz para a persistência de grandes espécies de mamíferos, como a onça-pintada e a onça-parda, o que pode resultar em uma cascata trófica. Apesar da jaguatirica ser uma espécie oportunista, com características de história de vida que poderia permitir com que a mesma substituísse os predadores de topo (onça-pintada e onça-parda) em áreas de Mata Atlântica, ela possui uma alta afinidade por áreas de floresta densa. Portanto, não se sabe se esta espécie está substituindo os predadores de topo e se beneficiando nestes remanescentes florestais, possivelmente causando efeitos deletérios em outros mesocarnívoros (isto é, liberação do mesopredador), ou se a abundância e a distribuição da jaguatirica é similarmente influenciada pela perda de grandes áreas de floresta. Neste estudo nós utilizamos um protocolo padronizado de armadilhas fotográficas para investigar o status populacional da jaguatirica em seis áreas protegidas da Mata Atlântica, quantificando sua abundância, densidade e distribuição (probabilidade de uso). Do mesmo modo, exploramos como feições da paisagem (por exemplo: áreas de matriz e tamanho da reserva) e covariáveis individuais afetam a espécie neste atual cenário. Nós também investigamos se a jaguatirica representa uma potencial ameaça para outros mesocarnívoros ou se potenciais competidores (isto é, predadores de topo e cães domésticos) influenciam a abudância, a distribuição ou a detecção da jaguatirica. Nós exploramos fatores adicionais que poderiam causar diferenças na probabilidade de detecção entre nossas localizações de amostragem e ajustamos essas diferenças para obter estimativas não enviesadas dos parâmetros de interesse. A abundância da jaguatirica e a probabilidade de uso correlacionaram-se positivamente com a presença dos predadores de topo e negativamente com o número de cães. A abundância da jaguatirica também correlacionou-se positivamente com o tamanho da reserva. Nós encontramos maiores probabilidades de detecção em áreas menos florestadas e em áreas com maior quantidade de eucalipto. Nós suspeitamos que menores áreas de vida e maiores taxas de movimentação em áreas menores e mais degradadas aumentam a detecção. Adicionalmente, o eucalipto parece servir como uma importante e mais protegida rota de deslocamento para conectar habitats naturais da Mata Atlântica. Nossos dados sugerem que a ocorrência da jaguatirica não influencia o uso do habitat por outros mesocarnívoros e que a habilidade de algumas espécies (jaguarundi, gato do mato pequeno, quati e irara) ajustarem seus padrões de atividade para evitar um contato direto com jaguatiricas, possa facilitar suas coexistências nestes remanescentes de Mata Atlântica. De modo geral, nossos achados indicam que áreas protegidas com ambos os predadores de topo e circundadas por matrizes permeáveis, como o eucalipto, podem ser fundamentais para a persistência de jaguatiricas no atual cenário da Mata Atlântica. Adicionalmente, nossos dados não corroboram a hipótese da liberação do mesopredador. Contrariamente, nossos dados indicam que as jaguatiricas respondem negativamente à perda do habitat e que sobrepõem temporalmente e espacialmente com os predadores de topo em grandes áreas protegidas.

Abstract

Fragmentation and habitat loss are the main threats to biodiversity. To prevent an increase in the current rate of biodiversity loss, most countries have implemented protected areas. However, it is uncertain whether protected areas are adequate for the long-term conservation of species worldwide especially in the tropics. In the Atlantic Forest, > 80% of forest remnants are small (≤50 ha) and 61% of these are isolated from protected areas, which protect only 9% of the remaining forest and are embedded in a human-managed matrix. This current scenario is ineffective for the persistence of large mammal species, such as jaguars and pumas, which may result in trophic cascades. Although the ocelot is an opportunistic species with life-history characteristics that may allow it to replace top predators (jaguar and puma) in Atlantic forests remnants, it has a high affinity for closed canopy forested areas. Therefore, it is unknown whether the species is replacing top predators and flourishing in these forest remnants, possibly causing deleterious effects on other mesocarnivores (i.e., mesopredator release), or if ocelot abundance and distribution is similarly influenced by the loss of large forested areas. In this study we used a standardize camera trap protocol to investigated ocelot status in six Atlantic Forest protected areas, quantifying its abundance, density and distribution (probability of use). Likewise, we explored how landscape features (e.g., matrix areas and reserve size) and individual covariates affect the species in this current scenario. We also investigated whether ocelots represent a potential threat to other mesocarnivores or if potential competitors (i.e., top predators and domestic dogs) influence ocelot abundance, distribution or detection. We explored additional factors that may cause differences in detection probabilities among our sampling locations and adjusted for these differences to obtain unbiased estimates of the parameters of interest. Ocelot abundance and use were positively correlated with the presence of top predators and negatively correlated with the number of dogs. Ocelot abundance was also positively correlated with reserve size. We found higher detection probabilities in less forested areas and in areas with more eucalyptus. We suspect that smaller home ranges and higher movement rates in smaller, more degraded areas increased detection probabilities. Additionally, eucalyptus appear to serve as an important and more protected travel route for connecting natural habitats of Atlantic Forest. Our findings suggest that ocelot occurrence did not influence the habitat use of other mesocarnivores and the ability of some species (jaguarundi, little spotted cat, coati and tayra) to adjust their activity patterns to avoid a direct contact with ocelots may facilitate their coexistence in these Atlantic Forest remnants. Overall, our findings indicate that protected areas with both top predators and surrounded by permeable matrices, such as eucalyptus, may be critical to the persistence of ocelots in the current scenario of the Atlantic Forest. Additionally, our data do not corroborate the hypothesis of mesopredator release. Rather, our data indicates that ocelots respond negatively to habitat loss and overlap temporally and spatially with top predators in large protected areas.

Contents

General Introduction

Currently, fragmentation and habitat loss are some of the greatest threats to biodiversity (Fahrig, 2003). Large expanses of forest are becoming fragments of different sizes that are isolated from each other (Gascon, Williamson & Fonseca, 2000). Often/generally a population's persistence is directly related to fragment size, thus mammal species have higher population viability in large fragments (> than 20,000 ha; Chiarello, 1999). In the Atlantic Forest, deforestation is extremely serious, requiring emergency action plans. The vast majority of remnants (over 80%) are smaller than 50 ha and 61% of these are more than 25 km from protected areas, which protect only 9% of the remaining forest and 1% of the original biome (Ribeiro *et al.*, 2009). To prevent a steadily increase in the current rate of biodiversity loss, most countries have implemented protected areas (Chape *et al.*, 2005; Butchart *et al.*, 2010). However, many aspects of protected areas, such as whether or not they are suitable for the long-term conservation of species, have not been fully examined (Ceballos, 2007). Human activities, especially in the tropics, are common inside protected areas and in their immediate surroundings, resulting in widespread deforestation pressure in some areas (Spracklen *et al.*, 2015). In the Atlantic Forest protected areas are embedded in a human-managed matrix, which are ineffective for the long-term conservation of large carnivores (Tabarelli *et al.*, 2010).

The large terrestrial species in the order Carnivora (i.e., top predators) are some of the world's most charismatic mammals but, ironically, are also some of the most threatened species (Ripple *et al.*, 2014). Because they have large home ranges and thus, require large areas to thrive, they are unlikely to persist in this current scenario (Crooks, 2002; Sunquist & Sunquist, 2002). As a consequence of the loss of these top predators, a top-down cascading effect has occurred in different systems worldwide (Estes *et al.*, 2011). Large carnivores often exert a strong system-level influence by limiting medium to large herbivores through predation (Ripple *et al.*, 2014). As a result, the loss of top predators may increase the intensity of herbivory and decrease the abundance and composition of plants (Silliman & Angelini, 2012). In some forested patches in Venezuela, for example, the absence of jaguars (*Panthera onca*) and pumas (*Puma concolor*) resulted in an explosion of herbivores and in an extremely low densities of seedlings and canopy trees (Terborgh *et al.*, 2001). Top predators also control mesocarnivore populations through intraguild competition (Crooks & Soulé, 1999; Prugh *et al.*, 2009), thus structuring different systems worldwide (Estes *et al.*, 2011; Ripple *et al.*, 2014).

Mesocarnivores are classified as species belonging to the order Carnivora that are neither large nor considered as top predators (Roemer, Gompper & Valkenburgh, 2009). Instead, they are small or medium-sized species (< than 20 kg), which may be solitary to highly social, frugivorous to strictly carnivorous and have a high ecological plasticity (Roemer *et al.*, 2009). Due to their smaller size, smaller home ranges and ability to adapt to various environments, some mesocarnivores may be the most abundant carnivores in many fragments (Roemer *et al.*, 2009). The absence or reduced density or distribution of a top predator may result in an increase in the abundance, density or habitat use of a medium predator, a phenomenon termed as mesopredator release, which may result in deleterious effect in different ecosystems (Brashares *et al.*, 2010). For example, the decline and disappearance of the coyote (*Canis latrans*; top predator) in some areas in California increased the domestic cat (*Felis catus*; mesopredator) population, which negatively affected the distribution and abundance of the avian community (Crooks & Soulé, 1999).

Given their important ecological role, numerous studies have focused on habitat preferences of top predators to protect their habitats as well as those of species in lower trophic levels. From tigers (*Panthera tigris*) in Asia (Khan & Chivers, 2007; Singh *et al.*, 2009), lions (*Panthera leo*) and leopards (*Panthera pardus*) in Africa (Visser *et al.*, 2009; Toni & Lodé, 2013) to gray wolves (*Canis lupus*) in North America (Mladenoff, Sickley & Wydeven, 1999; Milakovic *et al.*, 2011) and jaguars (*P. onca*) and pumas (*P. concolor*) in South America (De Angelo, Paviolo & Di Bitetti, 2011; De Angelo *et al.*, 2013), these efforts have resulted in useful information to protect top predators and their habitat. In many Atlantic Forest fragments, the mammal community have been modified in response to the absence or rarity of jaguars and pumas (Canale *et al.*, 2012).

The ocelot (*Leopardus pardalis*) may capitalize on small forest patches where top predators are absent or rare, enlarging its trophic niche (Moreno, Kays & Samudio, 2006) and expanding the diversity of items in its diet (Bianchi, Mendes & Júnior, 2010). Although rare, the ocelot can also prey on other mesocarnivores (Emmons, 1987; Chinchilla, 1997), and can potentially hunt or harass other smaller felines, such as jaguarundi, *Puma yagouaroundi*, margay, *Leopardus wiedii* and oncilla, *Leopardus tigrinus*, which is referred to as "effect pardalis" hypothesis (Oliveira *et al.*, 2010). This hypothesis predicts that in fragments where ocelot density is low, the density of other felines is high due to the reduction of intraguild predation by ocelot (Oliveira *et al.*, 2010). The ocelot has characteristics of interspecific competition that may favour its prevalence in

Atlantic Forest fragments, but it has a high affinity for closed canopy forested areas (Haines *et al.*, 2006; Horne *et al.*, 2009). The species can be negatively influenced by factors within and in the immediate surroundings of the forest reserve, especially in areas with a high incidence of agriculture (e.g., pasture), or where domestic dogs (*Canis familiaris*) are frequent due to the greater proximity to the forest edge. If it is the case, the scenario may be even worse for the overall system because jaguars and pumas are already difficult to conserve in this biome and ocelots could fill their role, helping to lessen the cascading effect in Atlantic Forest remnants (Prugh *et al.*, 2009). For example, in the absence of top predators, such as wolves (*Canis lupus*), coyotes can form larger packs and hunt or harass larger herbivores in Yellowstone National Park (Gese & Grothe, 1995).

Ocelot studies in the Atlantic Forest have focused on abundance and density (Di Bitetti *et al.*, 2008; Goulart *et al.*, 2009a; Paschoal *et al.*, 2012), activity patterns (Di Bitetti, Paviolo & Angelo, 2006), diet (Bianchi *et al.*, 2010; Bianchi *et al.*, 2014; Santos *et al.*, 2014), home range size (Di Bitetti *et al.*, 2006) and habitat preferences (Di Bitetti *et al.*, 2006; Goulart *et al.*, 2009b; Di Bitetti *et al.*, 2010). However, these studies had limited detection modeling and use of appropriate covariates to estimate habitat use by ocelots or to assess its interaction with other mesocarnivores and potential competitors (i.e., top predators and domestic dogs). Importantly, these studies did not explore the influence of inhospitable habitats or human-related habitat features (e.g., agricultures) on ocelots' occurrence within protected areas of Atlantic Forest.

Therefore, the choice of appropriate methods, such as capture-recapture (Otis *et al.*, 1978) and occupancy models (MacKenzie *et al.*, 2006), which can estimate ocelot abundance and use as a function of specific covariates, respectively, are important to assess whether the species is thriving or not in this biome. At the same time, methods that can directly measure the influence of top predators on ocelot occurrence as well as the influence of this latter on other mesocarnivores are important to better clarify the ecological interactions between these species (MacKenzie *et al.*, 2006; Ridout & Linkie, 2009). These methods can be combined with data from camera traps, which are cost-effective, flexible and useful to estimate species use, population abundance and density (McCallum, 2013). Additionally, time stamp data from camera traps can be used to determine activity pattern of the species and also measure the overlap of activity patterns between species of interest (Linkie & Ridout, 2011).

Here we investigated the ocelot population status in Atlantic Forest, quantifying its abundance, density, use, activity pattern and ecological interactions with sympatric carnivores in six protected areas of this biome. We explored how human-related habitat features (e.g., pasture, cropland, and eucalyptus) affected the species in this landscape. We investigated whether ocelot presented a potential threat to other mesocarnivores or if potential competitors (i.e., top predators and domestic dogs) presented a potential threat to ocelot. We also explored factors that may cause differences in detection probabilities among our locations and adjusted for these differences to obtain unbiased estimates of the parameters of interest. This thesis is presented in four chapters as follow: (1) Ocelot population status in protected Brazilian Atlantic forest; (2) Factors influencing the probability of use of Atlantic Forest protected areas by ocelots; (3) Activity patterns and temporal overlap between ocelot and top predators in protected areas of Atlantic Forest; and (4) Ecological interactions between ocelot and other sympatric mesocarnivores in protected areas of Atlantic Forest. Finally, this thesis ends with a general conclusion, where we use our main findings to provide recommendations to protect ocelots as well as other mammal carnivores in the current context of the Brazilian protected areas.

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Chapter 1 - Ocelot Population Status in Protected Brazilian Atlantic Forest

Ocelot Population Status in Protected Brazilian Atlantic Forest

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Abstract

Forest fragmentation and habitat loss are detrimental to top carnivores, such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), but effects on mesocarnivores, such as ocelots (*Leopardus pardalis*), are less clear. Ocelots need native forests, but also might benefit from the local extirpation of larger cats such as pumas and jaguars through mesopredator release. We used a standardized camera trap protocol to assess ocelot populations in six protected areas of the Atlantic forest in southeastern Brazil where over 80% of forest remnants are < 50 ha. We tested whether variation in ocelot abundance could be explained by reserve size, forest cover, number of free-ranging domestic dogs and presence of top predators. Ocelot abundance was positively correlated with reserve size and the presence of top predators (jaguar and pumas) and negatively correlated with the number of dogs. We also found higher detection probabilities in less forested areas as compared to larger, intact forests. We suspect that smaller home ranges and higher movement rates in smaller, more degraded areas increased detection. Our data do not support the hypothesis of mesopredator release. Rather, our findings indicate that ocelots respond negatively to habitat loss, and thrive in large protected areas inhabited by top predators.

Introduction

Fragmentation and habitat loss are serious threats to tropical forest biodiversity [1, 2] and the Atlantic Forest is no exception [3–5]. The vast majority of remnants (> 80%) in this biome are smaller than 50 ha and 61% of these are more than 25 km from protected areas (PAs), which protect only 9% of the remaining forest and 1% of the biomes' original area [4]. This biome scenario is inadequate for the long-term conservation of top predators such as jaguars (*Panthera onca*) and mountain lions

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(*Puma concolor*) [6, 7].

While impacts of forest loss and fragmentation are well documented for large predators [8,9], the effects on mesocarnivores are less clear. Mesocarnivores are species belonging to the order Carnivora that are neither large nor top predators [10]. They are small or medium-sized species (less than 15 kg); may be solitary to highly social, frugivorous to strictly carnivorous, and have high phenotypic plasticity [10]. These life-history characteristics might allow some species of mesocarnivores to "replace" top predators when such species are absent or declining, altering the food chain (mesopredator release theory; [11]).

The ocelot (*Leopardus pardalis*) is a mesocarnivore in neotropical forests that may thrive in forest patches where top predators are absent or rare [12]. In these circumstances, ocelot might expand its trophic niche in response to a competitive release [12]. Normally, ocelot diets are composed of small mammals (<2.0 kg; [13]), but recent studies suggest that in the absence of top predators, especially jaguars, ocelots take larger prey [14–16]. Ocelots can also prey on other mesocarnivores [17–19] and hunt or harass smaller felines, such as jaguarondi (*Puma yagouaroundi*), margay (*Leopardus wiedii*) and oncilla (*Leopardus tigrinus*) [20, 21]. Together, these findings suggest that ocelots are opportunistic, ecologically plastic and may thrive in fragmented landscapes [22, 23].

However, ocelots may be more sensitive to fragmentation than other mesocarnivores because the species may have high affinity for closed canopy forests [24, 25]. The species is considered vulnerable in fragmented areas outside the Brazilian Amazon, such as the Atlantic Forest [26]. Thus, two opposing forces may be affecting ocelot populations in fragmented landscapes. The abundance of ocelots may be increasing due to mesopredator release or, abundance may be decreasing due to fragmentation and habitat loss. To test these two main hypotheses, and to understand the ecological process driving ocelot population dynamics and conservation status, we estimated ocelot abundance in a range of Atlantic Forest PAs. Specifically we assessed the effects of the amount of habitat (percent of forest cover and reserve size), impact of an invasive domestic species (relative abundance of free-ranging domestic dogs) and presence of top predators (mountain lions and jaguars) on ocelot abundance. We hypothesize a positive relationship between ocelot abundance and reserve size because larger forested areas could support more ocelots [6, 7, 27]. We expect a negative relationship between ocelot abundance and domestic dogs and top predators, because these species are considered potential competitors to ocelots [28, 29].

Camera traps are a common tool used to assess ocelot density [29–33], but few studies have accounted for potential variation in detection probability (p). To prevent potential biases caused by such variation, we tested several hypotheses involving factors that may influence detection. We expected that detection probability may vary among the sexes: females may have a higher detection probability than males because they have smaller home ranges that they use more intensively [13]. Alternatively, males travel larger distances [34], and they may be exposed to more cameras than females and thus have a higher detection probability. We expected a trap shy behavioral response in which recapture probability (c) of ocelots would be lower than the initial detection probability (p) because of the camera flash [35, 36]. We also expected ocelots to be more elusive and restrict their movements in areas with a higher abundance of top-predators or dogs [28, 29]. The number of unpaved roads within a reserve could also influence detection because ocelots often use trails or unpaved roads to move around the landscape [37–39]. We hypothesized that detection probability would be negatively correlated with density of travel routes because we could not survey many routes with our few cameras. Further, detection may be influenced by the location of cameras. Given the known affinity of ocelots for unpaved roads, we expected a positive relationship between detection and proportion of cameras installed on unpaved roads. We also expected a low detection probability in large densely, forested areas (the preferential habitat of the species; [24, 40]), because individuals have more area to explore and may have larger home ranges. Finally, we expected a higher detection probability in dry seasons because ocelots may be more active in the dry season due to resource scarcity [41].

In summary, our main objective is to estimate ocelot abundance and density in six Atlantic Forest reserves in southeastern Brazil, while correcting for factors that may influence detection. We also assess the ability of reserve and individual ocelot variables to explain variation in ocelot abundance and detection. Finally, we compare our estimates with other estimates to assess the current ocelot population status in Atlantic Forest remnants.

Materials and Methods

Ethics statement

Sampling was performed under licenses obtained from the State Forest Institute (Instituto Estadual de Florestas—IEF) of the State Parks (UC: 080/10, 081/ 10 and 082/10) and under permission from the responsible (the owner of the land) of the private reserves. Data collection used non-invasive, remotely activated camera traps and did not involve direct contact or interaction with animals.

Study areas

We sampled six protected areas in the Atlantic Forest located in the State of Minas Gerais, southeastern Brazil (Fig 1). These include one large (> 20,000 ha) and two medium-sized (10,000–20,000 ha) state parks, respectively: Rio Doce (RD), Serra do Brigadeiro (SB) and Sete Salões (SS), and three small (< 10,000 ha) private reserves: Feliciano Miguel Abdala (FMA), Mata do Sossego (MS), and Fazenda Macedônia (FM). Vegetation in all areas is classified as semi-deciduous seasonal forest [42]. Elevation in these areas ranges from 150 m (RD) to 2,075 m (SB) [43] and the climate is classified as humid tropical in SB and semi-humid in the other PAs [44]. We considered RD as a reference area since it is one of the largest PAs remaining in the Atlantic Forest of southeastern Brazil, with a diverse mammal community, including jaguars, mountain lions, tapirs (*Tapirus terrestris*) and giant armadillos (*Priodontes maximus*) [45, 46]. Although jaguars, tapirs and giant armadillos are absent in the other PAs, mountain lions can be detected in SB, SS, FMA and FM (Paschoal et al., in prep.).

Sampling design

We used a standardized camera trap protocol to detect ocelots in the six reserves. Cameras were set to operate for 24 hours with an interval of five minutes between photos. Reserves were sampled for 80 consecutive days in each season (dry: April-September; wet: October-March).

In each study area, we selected 20 random sampling points (camera locations) from satellite images using ArcGIS 9.2 [49]. We distributed camera locations to ensure that at least one trapping station was located in a circular area equivalent to the smallest known home range of ocelots (76 ha; [50]). Any two adjacent trapping stations were up to 1 km apart, thus maximizing the probability of recording every individual present in the area. In the field, camera locations were placed as close as possible to the predetermined coordinates, usually within 50 m or 100 m, but preferentially placed along game trails, human paths, or unpaved roads because ocelots use these as travel routes [37–39]. We recorded the actual camera location using a GPS unit.

We installed camera traps in pairs to obtain simultaneous recording of the right and left sides of ocelots, allowing for individual identification. Because we only had ten cameras, we randomly moved pairs of cameras among sampling locations. We left cameras in place for 20 consecutive days before moving them to another five random points in the reserve, until all 20 points were sampled (total of 80 days). When we moved cameras, we also changed film and

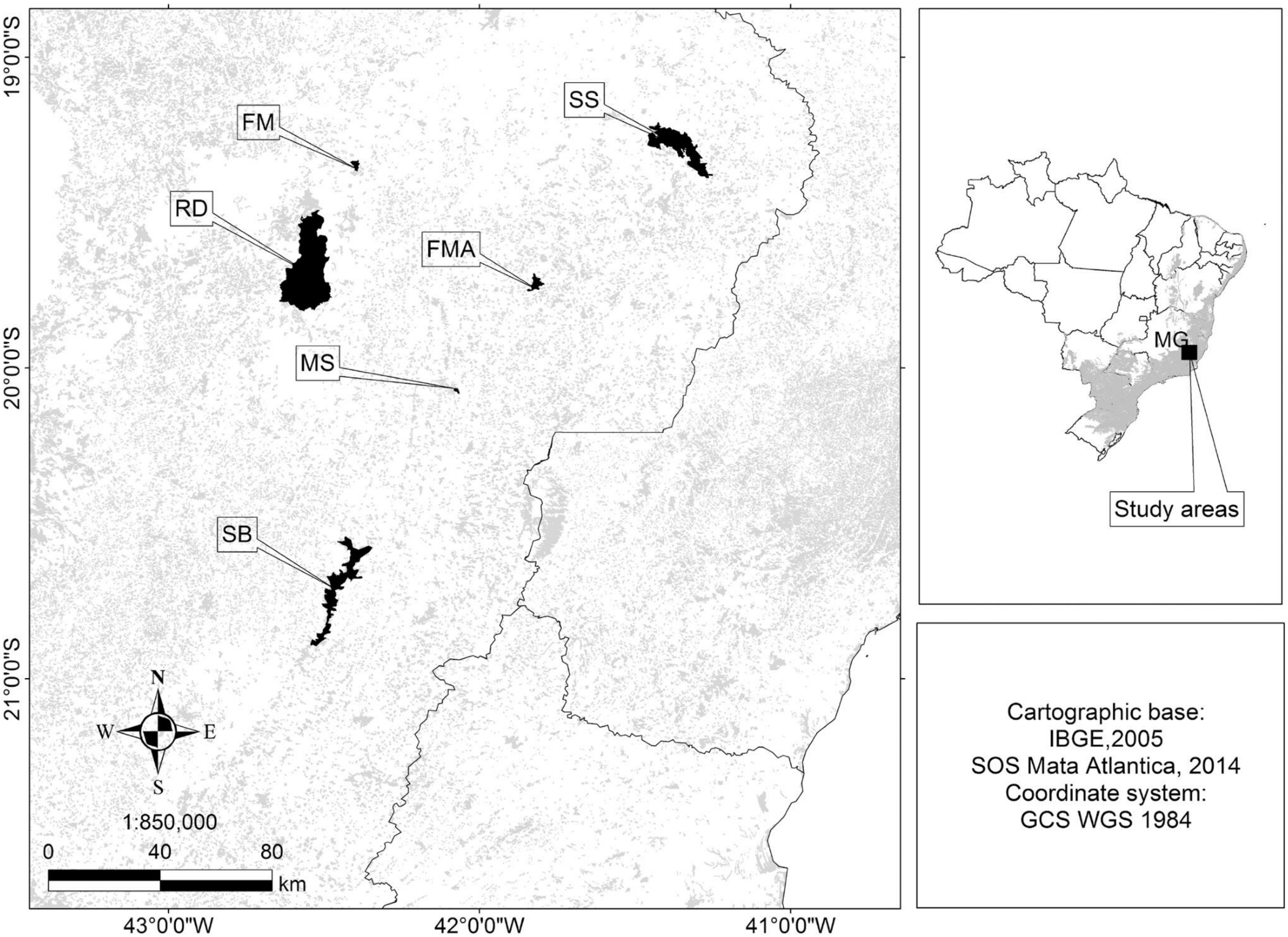

Fig 1. Atlantic Forest reserves sampled for ocelot populations in State of Minas Gerais (MG), southeastern Brazil. FM = Fazenda Macedônia Reserve; FMA = Feliciano Miguel Abdala Reserve; MS = Mata do Sossego Reserve; SB = Serra do Brigadeiro State Park; SS = Sete Salões State Park; RD = Rio Doce State Park. The current distribution of Atlantic Forest remnants are shown in the insert (grey area) as defined by the SOS Mata Atlântica Foundation [47]. The state divisions are from the Brazilian Institute of Geography and Statistics [48].

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batteries. The total sampling effort, considering the pair of cameras at each location as a single sampling unit, was 800 camera trap-days in each reserve (400 camera trap-days /season).

Estimating abundance, density and detection probability

We individually identified ocelots by stripe patterns on flanks, which are unique among individuals. Sex was determined by observation of genitals and the presence or absence of testes were used to distinguish between males and females. From these observations, we developed encounter histories for the 80 days of sampling in each season in each reserve depending on whether each individual was detected (1) or not (0). We collapsed our 80 days into groups of ten days (i.e., each individual encounter history contained eight occasions) in order to increase detection probabilities and improve estimates, as suggested by previous studies with elusive carnivores [51, 52]. We included sex as an individual covariate and used the Huggins closed capture model [53, 54] in Program MARK [55] to estimate abundance.

Table 1. Area covered by camera traps (minimum convex polygon—MCP—area), buffer area and effective trapping areas (ETA) based on two distances (MMDM = 2,718.61 m and ½ MMDM = 1,359.31 m) derived from camera traps in six Atlantic Forest reserves in southeastern Brazil.

Reserve	MCP (ha)	Buffer Area (ha)		ETA (ha)			
		MMDM	½MMDM	Total Area (MMDM)	Total Area (½MMDM)	Forest Area (MMDM)	Forest Area (½MMDM)
Fazenda Macedônia Reserve	1,073.32	5,910.70	2,374.68	6,984.02	3,448.00	429.48	429.48
Feliciano Miguel Abdala Reserve	754.05	5,545.87	2,192.08	6,299.92	2,946.13	2,237.29	1,450.65
Mata do Sossego Reserve	433.83	4,785.97	1,812.05	5,219.80	2,245.88	2,461.71	1,454.59
Serra do Brigadeiro State Park	1,334.51	6,309.67	2,574.25	7,644.18	3,908.76	3,974.50	2,343.11
Sete Salões State Park	980.41	6,119.87	2,479.44	7,100.28	3,459.85	3,781.25	2,193.14
Rio Doce State Park	830.97	5,481.00	2,159.95	6,311.97	2,990.92	3,544.83	2,074.27

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We mapped the land cover types by interpreting and classifying Landsat 5 images of each sampled area, using the technique of supervised classification and a maximum similarity algorithm in program ERDAS Image 8.4 [56]. We calculated the minimum convex polygon (MCP) formed by the outer sampling points in each reserve, which covered on average 910.6 ha (range 433.8 to 1,334.5 ha; Table 1). We added an additional buffer of about 3 km based on the mean maximum distance movement (MMDM; [57]) by ocelots detected in all reserves (Table 1). Inside this area (MCP + MMDM buffer) we calculated the proportion of forest and road network coverage (composed mainly by unpaved roads) in each reserve. To check if the proportion of forest inside the MPC + MMDM buffer accurately represented the amount of forest available in the larger landscape around the sampled areas, we mapped the proportion of forest inside an area of 10,000 ha centered around the MPC centroid of each reserve. This fixed area was large enough to accommodate the MPC + MMDM buffer. After that we performed a Pearson Correlation test between the proportion of forest mapped inside the MPC + MMDM buffer and inside the 10,000 ha area and found that both were highly correlated (r = 0.99). From this, we assumed that the proportion of forest inside the MPC + MMDM buffer accurately represented the amount of forest in the surrounding landscape. We used these predictor variables (i.e., covariates) for the analyses.

We also considered the size of each reserve for the analyses as well as the number of free-ranging domestic dogs photographed in each reserve (i.e., the number of individuals that could be uniquely identified). We identified dogs based on their specific phenotypic differences and pelage coloration [29]. Finally, we considered the presence of both top predators (jaguar and mountain lion), which were detected only in the largest reserve (RD). Before using these covariates in our analysis, we tested for correlation among them using a Pearson Correlation Matrix, which indicated that none of the variables were highly correlated ($|r| \leq 0.50$ in all cases).

We used four variables (percent of forest area, reserve size, number of free-ranging domestic dogs, and presence of both top predators; Table 2) in a variance components analyses in Program MARK [55]. We used a variance components analyses to focus on explaining the biological process variance (δ^2), which should not be confused with the sampling variance of ocelot abundance estimates [58, 59]. We estimated the percent of ocelot abundance variation explained by each variable. However, models from this analysis could not be compared using a model selection approach (e.g., AIC) because abundance ($\widehat{N}$) is not in the likelihood in Huggins models. Therefore, we ran a mean model (intercept only) to obtain an overall estimate of process variance for each season. We then constructed additional models including each of these four variables alone for each season. We interpreted the resulting difference between the overall process variance (intercept only) and the process variance of a particular variable model as the amount of process variance explained by the variable. We also calculated the proportion of the biological variation explained as the difference divided by the overall process variance for each variable in each season.

We calculated ocelot density by dividing $\widehat{N}$ by the effective trapping area (ETA) in each reserve (Table 1). However, the estimated abundance of ocelots ($\widehat{N}$) in one small reserve (FMA) was not reliable because we only recorded a single ocelot in each season and detection probabilities were very low (see Results). When the detection probability for rare and elusive carnivores is low (≤ 0.10) and each individual in the population is detected less than 2.5 times, the Huggins model has difficulty estimating abundance accurately [60]. Therefore, we used the observed abundance of ocelot to estimate density in FMA. We considered four different levels of ETA to estimate ocelot density (Table 1): MMDM buffer + MCP; ½ MMDM + MCP, and actual forest area within each of these previous levels of ETA. We considered forest area in calculating ocelot density because ocelots are considered a forest dependent species [24,40, 61]. Although MMDM has been considered a more accurate approach than ½ MMDM for estimating the area effectively sampled by cameras [34,62, 63], we also used the latter for two reasons. First, to make comparisons with other studies. Second, given the size of our MCPs, we judge the ½ MMDM may portray more faithfully the area of influence around the camera traps [62]. In one small reserve (MS), for example, the MMDM was almost ten times larger than the area sampled by cameras (MPC; Table 1) and, therefore, the MMDM may underestimate the ocelot density for this reserve. We calculate the polygons, buffers, and ETA using ArcGIS 9.2 [49].

Additionally, we modelled detection (p) and recapture (c) probabilities to estimate abundance ($\widehat{N}$) for each season in each reserve. We considered detection structures with the effects of behavior (trap shy), sex (male vs female), season (dry vs wet), presence of both top predators (reserve with both predators -largest reserve; RD- vs other reserves; Table 2), landscape features (percent of forest area, percent of road network coverage and reserve size), PAs (or reserves), number of free-ranging domestic dogs and percent of cameras installed on unpaved roads (Table 2).

Model selection and assumptions

We considered detection probabilities structures with all possible additive combinations of reserve (or covariates associated with each reserve), trap effect, season, and sex. We used

Table 2. List of covariates used to model the variation in detection probability of ocelots among reserves, specifically the percentage of land covered by road networks and Forest Area, percentage of cameras installed on unpaved roads, the number of dogs detected in the reserve, reserve size and the presence of both Top Predators. Forest Area, Number of Dogs, Reserve size and Presence of both Top Predators were also used to model the process variance in abundance estimates of ocelot populations in six Atlantic Forest reserves in southeastern Brazil.

Reserve	Road Network Coverage (%)	Cameras Installed on Unpaved Roads (%)	Forested Area (%)	Number of Free-Ranging Domestic Dogs	Reserve Size (ha)	Presence of both Top Predators
Fazenda Macedônia Reserve	2.64	55.00	6.15	18	560	No
Feliciano Miguel Abdala Reserve	1.27	59.09	35.5	47	958	No
Mata do Sossego Reserve	0.14	0.00	47.14	9	134	No
Serra do Brigadeiro State Park	0.62	0.00	51.98	6	14,985	No
Sete Salões State Park	0.00	3.85	53.21	16	12,520	No
Rio Doce State Park	0.65	35.00	56.12	0	35,970	Yes

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Akaike's Information Criterion adjusted for small sample size (AICc), the relative AICc difference among models (ΔAICc), and associated model weights (AICc weights) to assess strength of candidate models [64]. This strategy resulted in a balanced model set and allowed us to calculate the cumulative AICc weights for each predictor variable [65]. Because of model selection uncertainty, we calculated model-averaged estimates of detection probability and abundance [64].

We examined violations of assumptions for closed population capture-recapture models [66]. We used the median $\hat{c}$ goodness-of-fit approach in Program MARK [67], which indicates no overdispersion (or independence among the sampled ocelots) when the $\hat{c}$ value is close to "1". Our models assume that the population is closed geographically – no movement on or off the study area – and demographically – no births or deaths [66]. We tested for closure using the POPAN model in Program MARK, which allowed us to analyze the survival (phi) or egress (1 -phi) and ingress rates (pent) among capture occasions [68]. Using ΔAICc we compared models in which phi and pent parameters were fixed as "1" and "0" respectively (i.e., no egress or ingress) to models that allowed egress and ingress to vary to assess whether closure was achieved.

Results

We did not detect overdispersion ($\hat{c}$ = 1.06 with 95% CI = 0.90–1.23) and our closure test revealed no violation (ΔAICc of the model without closure = 3.00).

The largest State Park (RD) and one small private reserve (FM) had the highest abundance and density estimates of ocelots (Table 3). Another small private reserve (FMA) had the lowest abundance and density estimates of ocelots among all reserves (Table 3) and one medium-sized reserve (SS) had the lowest abundance and density estimates of ocelots among the State Parks; no ocelots were detected there during the wet season (Table 3). When we look at the confidence intervals, however, we noticed that abundances and densities were similar among all areas, except for RD (Table 3).

Reserve size, presence of both top predators and number of free-ranging domestic dogs all contributed to explaining variance of ocelot abundance (Table 4); ocelot abundance responded positively to reserve size and to presence of both top predators and negatively to abundance of

Table 3. Abundance and density estimates for ocelots derived from camera-trap studies conducted in six Atlantic forest reserves, southeastern Brazil.

Reserve	Season	Abundance (±95% CI)	Density (ocelots/km^2± 95% CI)			
			MMDM	½ MMDM	Forest MMDM	½ Forest MMDM
Fazenda Macedônia Reserve	Dry	5.04 (4.65–5.42)	0.07 (0.07–0.08)	0.15 (0.14–0.16)	1.17 (1.08–1.26)	1.17 (1.08–1.26)
	Wet	4.04 (3.62–4.46)	0.06 (0.05–0.06)	0.12 (0.11–0.13)	0.94 (0.84–1.04)	0.94 (0.84–1.04)
Feliciano Miguel Abdala Reserve	Dry	1	0.02	0.03	0.05	0.07
	Wet	1	0.02	0.03	0.05	0.07
Mata do Sossego Reserve	Dry	3.20 (2.18–4.22)	0.06 (0.04–0.08)	0.14 (0.10–0.19)	0.13 (0.09–0.17)	0.22 (0.15–0.29)
	Wet	1.07 (0.48–1.67)	0.02 (0.01–0.03)	0.05 (0.02–0.07)	0.04 (0.02–0.07)	0.07 (0.03–0.12)
Serra do Brigadeiro State Park	Dry	3.49 (1.79–5.19)	0.05 (0.02–0.07)	0.09 (0.05–0.13)	0.09 (0.05–0.13)	0.15 (0.08–0.22)
	Wet	4.70 (2.59–6.82)	0.06 (0.03–0.09)	0.12 (0.07–0.17)	0.12 (0.07–0.17)	0.20 (0.11–0.29)
Sete Salões State Park	Dry	2.21 (1.16–3.26)	0.03 (0.02–0.05)	0.06 (0.03–0.09)	0.06 (0.03–0.09)	0.10 (0.05–0.15)

	Wet	0	0	0	0	0
Rio Doce State Park	Dry	8.39 (5.28–11.51)	0.13 (0.08–0.18)	0.28 (0.18–0.39)	0.24 (0.15–0.33)	0.41 (0.26–0.56)
	Wet	8.51(5.26–11.76)	0.14 (0.08–0.19)	0.29 (0.18–0.39)	0.24 (0.15–0.33)	0.41 (0.25–0.57)

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free-ranging domestic dogs (Table 4). Further, the amount of variance explained by each of these variables varied seasonally (Table 4). The precision of these variance estimates were low (e.g., overlapping confidence intervals), suggesting that the differences in variance explained, both among variables and between seasons, should be considered with care.

Overall, the most parsimonious model in our candidate set indicated that the detection probability of ocelots varied among reserves (Table 5). Based on this model, detection probability of ocelots was higher in two small reserves (FM and MS), and lower in one small reserve (FMA) and in the largest reserve (RD; Fig 2). Of the reserve covariates used to model detection, the percent of forest was the only covariate that had more influence (cumulative AICc weights = 39.37%) on ocelot detection; the percent of forest had a negative relationship (β = -0.02 ± SE 0.01) with ocelot detection (Table 6). As expected, detection probability of ocelots was lower in more forested reserves, such as RD (Table 2; Fig 2), and higher in reserves with a lower proportion of forest cover, such as FM and MS (Table 2; Fig 2). The detection probability of ocelots in FM, for example, was more than two times higher than in RD (Fig 2), which has the highest forested area among all reserves (Table 2), but precision was low (large confidence intervals) due to small sample sizes (Fig 2). Although behavior, seasonality and sex had some influence on ocelot detection, they had low cumulative AICc weights (< 35%; Table 6). Road network coverage, reserve size, presence of both top predators, percent of cameras installed on unpaved roads and number of free-ranging domestic dogs had, respectively, the lowest cumulative AICc weights (< 6%) among the variables tested (Table 6).

Discussion

Contrary to our expectations, we did not find higher abundance and density in fragments where the top predators were absent or rare. Rather, the presence of both top predators (jaguar and mountain lion) in the largest reserve (RD) correlated positively with an increased abundance of ocelots, especially during the dry season. Top predators may increase the area of forest by controlling the herbivory rates [69, 70], which might increase ocelot abundance because this species is dependent to canopy cover [24, 25]. In addition, high abundance and densities of territorial carnivores may positively correlate to prey density [71]. Jaguars, for example, were found only in RD and their presence may be related to a higher diversity of prey for this species, especially those of large body size, such as deer (*Mazama americana*) and collared peccary

Table 4. The percent of biological process variation in ocelot abundance explained by four reserve variables among six Atlantic Forest reserves in southeastern Brazil. Negative process variances were considered zero. See Methods for details.

Variables	Dry Season			Wet Season		
	δ^2 Variance (±95% CI)	Beta Values (±95% CI)	% of Variation Explained	δ^2 Variance (±95% CI)	Beta Values (±95% CI)	% of Variation Explained
Intercept only model	4.96 (1.62–32.87)	3.61 (1.75–5.47)	-	7.33 (2.03–68.25)	3.53 (1.04–6.01)	-
Reserve Size	3.05 (1.02–26.19)	0.1×10^{-3} (-0.3×10^{-5}–0.3×10^{-3})	38.59	1.34 (0.39–19.46)	0.2×10^{-3} (0.8×10^{-4}–0.3×10^{-3})	81.73
Presence of both Top Predators	2.11 (0.73–17.76)	4.81 (1.08–8.53)	57.47	3.19 (0.87–47.81)	5.34 (0.65–10.04)	56.50
Number of Domestic Dogs	3.33 (0.95–30.86)	-0.09 (-0.19–0.01)	32.90	5.74 (1.46–88.41)	-0.09 (-0.23–0.04)	21.63
Percent of Forest	5.57 (1.91–56.89)	-0.4×10^{-2} (-0.12–0.11)	0	8.38 (2.53–143.52)	0.03 (-0.11–0.18)	0

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Table 5. Model selection results for variables expected to influence ocelot detection probability in six Atlantic Forest reserves in southeastern Brazil. Only models with an AICc weights ≥ 0.01 are presented here.

Model*	AICc	ΔAICc	AICc Weights	Parameters	Deviance
p(Reserve) = c(Reserve)	353.86	0.00	0.17	6	341.58
p(Reserve) c(Reserve)	354.63	0.77	0.11	7	340.25
p(Forest) = c(Forest)	354.77	0.91	0.11	2	350.73
p(Forest+Sex) = c(Forest+Sex)	355.66	1.80	0.07	3	349.58
p(Forest+Season) = c(Forest+Season)	355.92	2.06	0.06	3	349.84
p(Reserve+Season) = c(Reserve+Season)	355.97	2.11	0.06	7	341.59
p(Forest) c(Forest)	356.16	2.30	0.05	3	350.08
p(Reserve+Sex) = c(Reserve+Sex)	356.25	2.39	0.05	7	341.87
p(Reserve+Season) c(Reserve+Season)	356.51	2.65	0.04	8	340.03
p(Forest+Sex) c(Forest+Sex)	356.78	2.92	0.04	4	348.64
p(Forest+Season+Sex) = c(Forest+Season+Sex)	356.78	2.92	0.04	4	348.65
p(Reserve+Sex) c(Reserve+Sex)	357.23	3.37	0.03	8	340.75
p(Forest+Season) c(Forest+Season)	357.33	3.47	0.03	4	349.20
p(Reserve+Season+Sex) = c(Reserve+Season+Sex)	357.55	3.69	0.03	8	341.06

p(Reserve size) = c(Reserve size)	358.72	4.86	0.01	2	354.68

*The detection (p) and recapture (c) probability of ocelots modeled as function of: each reserve (Reserve); proportion of forest in each reserve (Forest); reserve size in ha (Reserve size); males and females (Sex) and; Season (Dry vs Wet). The equal signal (=) indicates that p and c have the same values for detection probability. The plus signal (+) means an additive effect between two or more tested variables.

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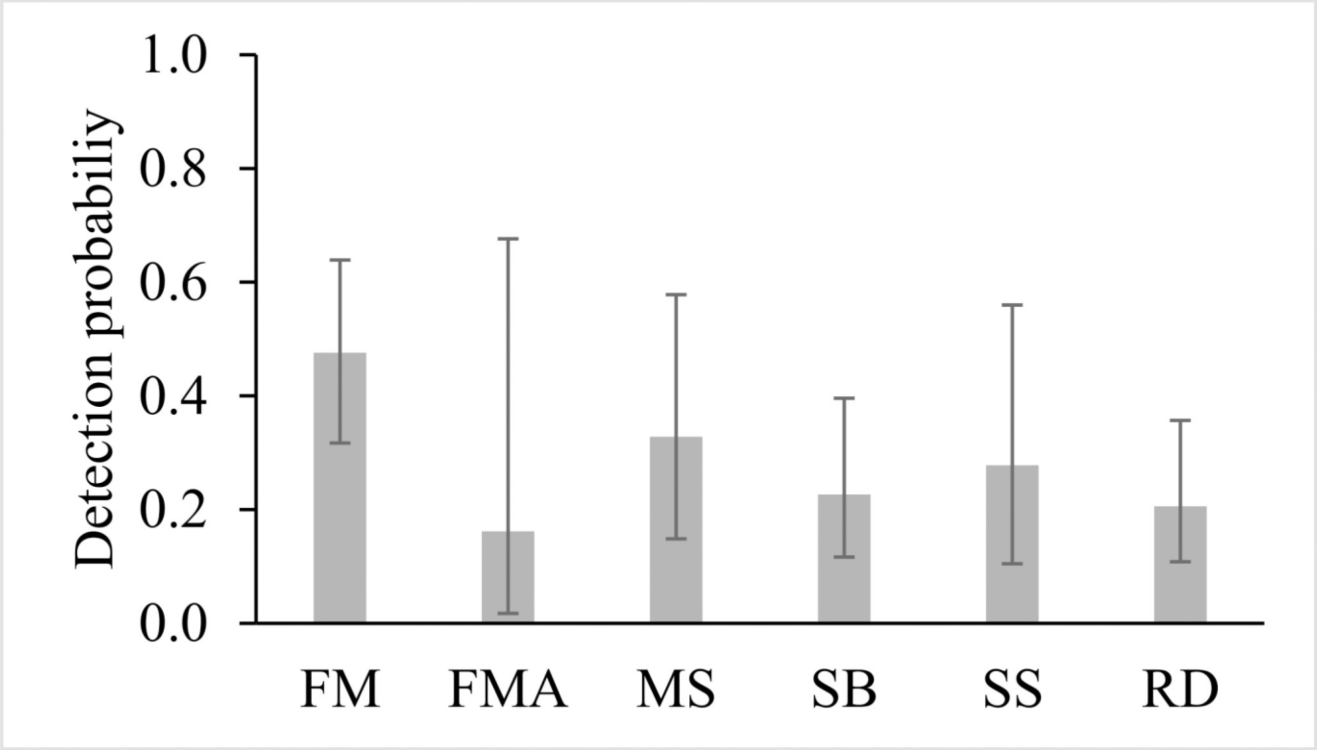

Fig 2. Model-averaged estimates of ocelot detection probabilities (p; ± 95% CI) in six Atlantic Forest reserves, southeastern Brazil. FM = Fazenda Macedônia Reserve; FMA = Feliciano Miguel Abdala Reserve; MS = Mata do Sossego Reserve; SB = Serra do Brigadeiro State Park; SS = Sete Salões State Park; RD = Rio Doce State Park.

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Table 6. Cumulative AICc weights for variables used to model ocelot detection probabilities in six Atlantic Forest reserves in southeastern Brazil.

Variables	Cumulative AICc Weights (%)
Reserve	49.10
Forested Area (%)	39.37
Behavior Effect (trap shy)	34.62
Seasonality Effect (Dry vs Wet)	29.39
Sex Effect	29.17
Road Network Coverage (%)	5.20
Reserve Size (ha)	5.02

Presence of both Top Predators	1.11
% of Cameras Installed on Unpaved Roads	0.10
Number of Free-Ranging Domestic Dogs	0.08

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(*Pecari tajacu*) [72]. Our other study areas have less forest area and prey densities may not allow for ocelot, jaguar and mountain lion coexistence. In other words, the positive relationship between jaguars and ocelots might result from the fact that jaguar presence means better habitat for ocelots [28, 73] and for other carnivores. Jaguar abundance was positively related with mountain lion occupancy in the Cerrado of Central Brazil [74], and another study indicated that coexistence of both top predators are mediated mainly by food resources [75]. The presence of top predators, especially the jaguar in the Atlantic Forest, may be key in controlling the food chain and maintain prey availability in an ecosystem [9, 76].

Alternatively, jaguar occurrence may be positively correlated with ocelot abundance or density through the predation and/or harassment of potential ocelot competitors. We found a negative influence of dogs on ocelot abundance; the highest ocelot abundance was found in the largest reserve (RD) where we did not detect dogs. Therefore, the presence of jaguars may reduce the abundance of domestic dogs in a reserve via predation or interference competition [77]. Although domestic dogs did not exhibit a direct influence on the detection probability of ocelots, this exotic species may decrease prey availability [78] especially in small reserves, such as in FMA.

In a recent study, Paschoal et al. [29] found approximately 40 domestic dogs in FMA at a density about six times higher than that of ocelots, suggesting potential deleterious effects on ocelots. The current estimate of dog abundance in FMA seems to be almost two times higher (Paschoal et al., in prep.) than the abundances considered here (Table 2), which suggest that the influence of domestic dogs on the ocelot ecology could be stronger. For example, domestic dogs were also responsible for negatively affecting ocelot use (or distribution) in the same reserves of Atlantic Forest (Massara et al., in prep.) as well as the distribution of other felids in this biome, such as the margay (*Leopardus wiedii*) and the oncilla (*Leopardus tigrinus*) [79]. However, we do not know exactly the ecological mechanisms behind domestic dog occurrence that resulted in a decreasing on ocelot abundance in the studied reserves. These dogs are classified as rural free-ranging domestic dogs, which are owned or peripherally associated with human settlements but are not confined in a restrict area [80]. Although considered weak competitors, they may become important competitors and predators of wildlife because high densities of these dogs are subsidized by humans that live near natural habitats [78, 80]. Additionally, these dogs cause a variety of impacts apart from direct predation on wildlife, including the spread of disease [81]. At the same time, domestic dogs can exert more intrusive edge effects in more fragmented and smaller reserves, which are surrounded by a high density of human settlements and human-modified habitats, such as agricultural lands [80, 82]. In these reserves, these dogs can even form packs and explore natural areas, which make their impacts even higher upon medium- to large- sized mammals [29]. It may explain, for example, the high dog abundance and low ocelot abundance in smaller reserves, such as in FMA, which is dominated and surrounded by agriculture and human habitations. However, little is known about the variables that may indeed facilitate dog entrance in Brazilian natural areas or their direct effects on different species [29, 79, 83]. As domestic dogs are one of the most commonly recorded mammal species in the Atlantic Forest [29, 79, 84], managers of protected areas should start acting to mitigate or eliminate this hazard.

Reserve size also correlated positively with abundance of ocelots. Though it is difficult to compare densities among studies due to the lack of a standard sampling protocols and the inconsistency in quantifying the effective trapping area [62, 85], we found that larger areas usually have higher ocelot abundances and densities in the Atlantic Forest remnants (Table 7). Further, reserve size was negatively correlated (r = -0.92) with the edge ratio of each reserve, which suggests that our largest reserve (RD) may provide better quality of habitat for wildlife and suffer less edge effects, such as those exerted by the exotic species (e.g., domestic dogs).The proportion of forested area, however, did not positively correlate with ocelot abundance in the reserves. We suspect that it might be a reflection of one sampled reserve (i.e., Fazenda Macedônia; FM).

Fazenda Macedônia had a relatively small size (560 ha), a high abundance and density of ocelots, and no jaguars (Tables 2 and 3). We believed that due to the proximity (15 km) of this reserve to the largest reserve (RD) and the existence of several smaller fragments connecting these two areas, the flow of ocelots among these fragments may be facilitated, making RD act as possible source of ocelots to FM. Young male ocelots (two or three years old), can disperse more than 10 km [13]. Further, FM has had potential prey species reintroduced, especially Galliformes and Tinamiformes birds [86], which may also attract predators, such as ocelots, to the area. However, longer-term studies and radio-tracking approaches are needed to test this hypothesis. At the same time, the high estimates of ocelot density in FM obtained using some buffers (i.e., Forest MMDM and ½ Forest MMDM; Table 3) relies on the fact that this area has

Table 7. Abundance and density estimates for ocelots derived from camera-trap studies conducted in Atlantic forest sites. Estimates are provided for two levels of buffers (MMDM, ½MMDM) according to their availability in each study. Ninety-five percent confidence intervals (95% CI) are presented, unless not included in a study.

Reserve	Country	Season	Sampling Effort (Trap—days)	Area (ha)	Abundance (± 95% CI)	Density (ocelots/km^2)	
						MMDM	½MMDM
Yabotí Biosphere Reserve[1]	Argentina	Wet	1,871	274,200	39 (35–54)	0.05	0.09
Iguazú National Park[1] / San Jorge Forest Reserve[1]	Argentina/ Brazil	Wet	2,059	259,400	86 (75–111)	0.10	0.17
Iguazú National Park[2]	Argentina	Both	1,631	170,000	55 (42–87)	0.13	0.20
Uruguaí Private Reserve[2]	Argentina	Both	1,409	113,243	20 (18–35)	0.08	0.13
Ilha do Cardoso State Park[3]	Brazil	Dry	585	15,100	6	0.21	-
Caraguatá Ecological Reserve[4]	Brazil	Both	4,250	4,300	3.07	-	0.04
Feliciano Miguel Abdala Reserve[5]	Brazil	Dry	450	957	2	0.16	0.35

[1] [30]

[2] [31]

[3] [32]

[4] [33]

[5] [29]

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the smallest proportion of forest among all reserves (Table 2), which may inflate the ocelot density through a mathematical artifact.

Although we did not detect closure violations, detecting such violations is difficult with small data sets. If the ocelot population is open then we are technically estimating a super-population (i.e., all individuals that use the sampled area during sampling; [68]). A super-population definition also aligns with potentially high turnover of ocelots among occasions and seasons, especially inside small or medium-sized fragments. In one small reserve (FMA) for example, we detect just one different individual in each season and no ocelots were recorded in one medium-sized reserve (SS) during the wet season. Further, in FMA the ocelots were only detected in a single occasion. The super-population concept may imply the existence of a metapopulation dynamic among fragments [87], reinforcing our suggestion of a flow of ocelot individuals between the largest reserve (RD) and one small reserve (FM).

Ocelots of different sex may have different home ranges [22,31, 34], and ranges may vary by season [34, 88]. Ocelots may use large trails or unpaved roads to move around the landscape [37–39]. However, we did not find strong support for these variables affecting detection probability of ocelots. Although the proportion of forest had just some influence (AICc weights = 39.37%) on ocelot detection, it was the reserve variable that best explained the variation in ocelot detection. Low detectability in more forested areas may relate to large ocelot home ranges in these areas, where individuals have a larger amount of forested area to use. Conversely, in areas poorly covered by forests, ocelots may have smaller home ranges (i.e. Bolivia; [62]) and concentrate travel (about 3 to 7 km per night) in a smaller area to attain their daily energy requirements [22, 24, 89], which can increase their detection probabilities. This reasoning however does not explain our results in one small reserve (FMA), which has the second lowest proportion of forest among all sampled areas (Table 2) but the lowest detection probability (Fig 2). We believe that some other variables that we did not measure in this present study may better explain the variation in ocelot detection probability among reserves and should be investigated in future studies. Some obvious possibilities that are known to affect mammal populations includes degree of surveillance or poaching pressure [3, 90]. We refrain to speculate about these, given that an accurate assessment of such effects are lacking for our six reserves.

We do have data on the immediate surrounding landscapes of our reserves. One of our small and least forested reserve (i.e., FM) for example, is surrounded by eucalyptus, which may be used constantly by ocelots as travel routes to move between native habitats within or outside the reserve [91]. Because ocelot is a forest dependent species [25,61, 92], it may uses eucalyptus more often than open habitats (e.g., pasture or croplands) to find native habitats (e.g., native forest). Therefore, reserves surrounded by more permeable matrices may have higher ocelot detection than areas surrounded by more inhospitable habitats (e.g., pasture around FMA).

Overall, our findings suggest that top predators, especially the jaguar, seem to act as an umbrella species for ocelots and other sympatric mesocarnivores [73] and that ecological processes that are detrimental to top predators may also be detrimental to ocelots. By protecting top predators we may also protect other species, such as ocelots. Indeed, top predators have been target by conservation initiatives to protect entire communities in different ecosystems [76]. Although our data show that the ocelot is able to inhabit smaller reserves, the lower densities (except for FM) indicate that these reserves might represent poor habitats. These results corroborates other authors working on the effects of forest fragmentation in the Atlantic forest, which show that only large fragments in the range of 20,000 ha or more can sustain viable populations of medium to large sized mammal species [6, 7, 27].

Low densities in small fragments translates to small populations with low viability. In the USA, for example, only two known isolated ocelot populations occur in southern Texas. For these isolated populations, conservation concerns include loss of dense forest habitat, mortality from vehicle-collisions, and genetic drift [93]. A habitat-based population strategy was adopted for the recovery efforts of these populations [92, 93]. The long-term recovery strategy included the restoration of ocelot habitat and the establishment of a dispersal corridor between ocelot breeding populations [92]. Whether increased connectivity will be able to overcome genetic drift or the reduction in the genetic diversity is unknown [94–96]. Unfortunately, a similar situation may be occurring among the remnant ocelot populations in the Atlantic Forest. A recent study found the first report of a unilateral cryptorchidism (i.e., the absence of one testis from the scrotum) in an wild adult ocelot, an inherited condition linked to low genetic variability in inbred wild cats [97]. This finding is especially concerning because it comes from the largest of our study areas (RD, with 36,000 ha). Therefore, without increased connectivity, the outlook for ocelots in the Atlantic Forest may be pessimistic, a view also backed by others [30, 31].

Conclusion and Recommendations

Our findings do not support the hypothesis of mesopredator release. Rather, our analyses indicate that presence of top predators and reserve size correlated positively with an increased abundance of ocelots in the Atlantic Forest reserves. The implementation of biodiversity corridors could protect and increase the current ocelot population in small Atlantic Forest fragments, reducing the isolation of small populations and augmenting structural and functional connectivity among forest patches. However, a better alternative might be based on improving connections via native vegetation and protection through the Brazilian Forest code (Federal Law number 12,651 from May 25, 2,012). Preliminary data of an ongoing project carried out in São Paulo state show, for example, that ocelots do inhabit areas of permanent protection (Áreas de Proteção Permanente—APPs), even when these are immersed in sugar cane or eucalyptus matrices [98]. According to the Brazilian forest code, these APPs protect mainly watercourses. Therefore, the possibility that these areas act like true corridors might indeed be real. We note that one small reserve (FM) and the largest reserve (RD) are linked by the Rio Doce River. Implementing the Forest Code law would therefore translate to increasing structural connectivity between these two protected areas via restoration of riparian forests along the Rio Doce River. Future studies should, investigate more closely these areas and their surrounding matrices in order to assess their use by ocelots.

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Author Contributions

Conceived and designed the experiments: RLM AMOP AGC. Performed the experiments: RLM AMOP. Analyzed the data: RLM PFDJ. Contributed reagents/materials/analysis tools: PFDJ AH. Wrote the paper: RLM AMOP PFDJ AGC.

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Chapter 2 – Factors influencing the probability of use of Atlantic Forest protected areas by ocelots

Factors influencing the probability of use of Atlantic Forest protected areas by ocelots

Use probability of ocelots in Atlantic Forest reserves

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Abstract

Over 80% of the remnant Atlantic Forest patches are small (<50 ha) and protected areas are embedded in a matrix dominated by human activities, which undermines the long-term persistence of carnivores. The ocelot is an opportunistic species, but little is known about its preferences and the influence of other species on ocelot use in these areas. We used camera traps to assess ocelot use and detection in protected areas of Atlantic Forest in southeastern Brazil. We found a strong, positive relationship between ocelot use and presence of top predators (jaguars and pumas), and a weaker negative effect between ocelot use and abundance of domestic dogs. Ocelot detection was higher at sites with more eucalyptus, suggesting that ocelots may use these areas as corridors. Protected areas with top predators, surrounded by permeable matrices, such as those associated with silviculture, may be critical to the persistence of ocelots in the current degraded scenario of the Atlantic Forest.

Keywords: *Leopardus pardalis,* habitat loss, mesocarnivores, occupancy, protected areas

Introduction

The uncontrolled growth of human populations is causing a severe reduction and loss (i.e., extinction) of species worldwide (Gascon, Williamson & Fonseca, 2000; Fahrig, 2003). Recent studies have suggested that drivers linked to human activities, mainly related to agriculture, account for 70% of the projected loss of terrestrial biodiversity (SCBD, 2014). To prevent a steadily increase in the current rate of biodiversity loss, most countries have implemented protected areas, such as national parks, biosphere reserves, and wildlife sanctuaries (Chape *et al.*, 2005; Butchart *et al.*, 2010). Currently, protected areas cover ~ 13% of earth's land area (Jenkins & Joppa, 2009); however, many aspects of protected areas, such as whether or not they are suitable for the long-term conservation of species, have not been fully examined (Ceballos, 2007). It is unlikely that all native species can be protected within these protected areas, especially those that lack proper administration, management or funding (SCBD, 2014). For example, in the tropics, human activities are common inside protected areas and in the surrounding areas, resulting in widespread deforestation pressure in some areas (Spracklen *et al.*, 2015).

In Brazil, protected areas can be divided in two groups: strictly protected and sustainable use (Federal Law # 9985; July 18, 2000), which were created according to the IUCN (The World Conservation Union) protected area management categories (IUCN, 1994). The main objective of the strictly protected category is nature conservation, but activities related to educational, scientific and recreational purposes are allowed. This category also includes Private Natural Heritage Reserves (acronym in Portuguese - RPPNs), which are usually small but not less important for nature conservation. Sustainable use areas combine nature conservation with sustainable use of natural resources. Unfortunately, most protected areas in Brazil are insufficiently managed, and human activities as well as the presence of exotic species (e.g., domestic dogs) are common within their boundaries (Paschoal *et al.*, 2012).

In Atlantic Forest protected areas, for example, native forest remnants are embedded in a matrix of human-managed habitats, dominated by pastures, croplands, and eucalyptus monocultures (Tabarelli *et al.*, 2010). Over 80% of the remnant Atlantic Forests patches are smaller than 50 ha and protected areas cover only 9% of the remaining biome, revealing a serious situation (Ribeiro *et al.*, 2009). The scenario is even worse for top predators, such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), that require large protected areas for the long-term conservation of their populations (De Angelo *et al.*, 2013; De Angelo, Paviolo & Di Bitetti, 2011). The loss of top predators may cause extensive and cascading effects worldwide (Estes *et al.*, 2011), especially in degraded Atlantic Forest biome (Jorge *et al.*, 2013). A recent study found that ocelot abundance was positively correlated with both reserve size and presence of top predators (jaguars and pumas) in the Atlantic Forest, which may indicates that top predators occurrence may act as indicator of better-protected areas for ocelots and other mammal species (Massara *et al.*, 2015).

Previous ocelot studies in South America have focused on the species' ecology, including studies on abundance and density (Di Bitetti *et al.*, 2008; Goulart *et al.*, 2009a; Massara *et al.*, 2015), activity patterns (Di Bitetti, Paviolo & De Angelo, 2006), diet (Bianchi *et al.*, 2014; Santos *et al.*, 2014) and home range size (Di Bitetti *et al.*, 2006). Few studies assessed habitat preference by ocelot (Di Bitetti *et al.*, 2010; Di Bitetti *et al.*, 2006; Goulart *et al.*, 2009b) and most did not account for variation in detection probability. Importantly, these studies did not explore the influence of inhospitable habitats (e.g., agriculture) or the presence of competitors on ocelots' occurrence within protected areas.

Here we employ occupancy models to investigate factors influencing ocelot occupancy (hereafter, ocelot use) within protected areas (or reserves) that contain Atlantic Forest. Specifically, we explored how human-related habitat features influenced ocelot use. While it is widely known that ocelot have a high affinity for closed canopy forested areas (Haines *et al.*, 2006; Horne *et al.*, 2009), less is known about the effect of other landscape features on ocelot use. Human-related habitat features, such as silviculture (Lyra-Jorge, Ciocheti & Pivello, 2008) and unpaved roads (Srbek-Araujo & Chiarello, 2013; Di Bitetti *et al.*, 2010) may be more permeable to ocelots and facilitate movement, while other features may be avoided, such as natural fields and pasture and croplands. Likewise, we explored whether the presence of native top predators or non-native species influenced local ocelot use. We also explored variables that may cause differences in ocelot detection probability among our locations (MacKenzie *et al.*, 2006). Finally, we use our results to provide recommendations to protect the current ocelot populations within protected areas containing Atlantic Forest fragments.

Materials and Methods

Study areas

We sampled within six protected areas of Atlantic Forest located in the State of Minas Gerais, southeastern Brazil, including three State Parks protected under the strictly protected category, and three smaller private areas protected under the sustainable use category (Fig. 1). Elevation within these protected areas ranges from 150 m (Rio Doce) to 2075 m (Serra do Brigadeiro; Miranda, 2005) and the climate is classified as humid tropical or semi-humid (IBGE, 2012).Vegetation in all areas is classified as semi-deciduous seasonal forest (SOS Mata Atlântica, 2015). Rio Doce is considered the most pristine reserve in our study, with a diverse mammal community, including resident populations of jaguars and pumas (Massara *et al.*, 2015).

Fig. 1 here

Sampling design and field methods

We sampled 120 camera trap sites (i.e., our sampling units), being 20 sites randomly selected within each of the six areas using ArcGIS 9.2 (ESRI, 2008). However, due to the small size of MS and FM, 11 and 10 sites respectively, were placed out of the legal boundaries of these two protected areas. Originally, our sampling design was set to estimate ocelot abundance and thus, two cameras were placed at each of 120 sites to identify individual ocelots and the maximum distance between camera sites was 1 km (see details in Massara *et al.*, 2015). Because the camera spacing was relatively small in relation to the ocelot home ranges (Sunquist & Sunquist, 2002), we interpreted occupancy estimates as the probability of use (MacKenzie *et al.*, 2006), and detection probability as a proxy for the intensity or frequency of use (Cassano, Barlow & Pardini, 2014).When cameras could not be installed in their original locations due to logistic constraints (e.g., no site access), we relocated the site within <100 m and recorded the new GPS location. When possible, we elected to place cameras along game trails, human paths, or unpaved roads to maximize the opportunity to detect carnivores in the area (Srbek-Araujo & Chiarello, 2013; Di Bitetti *et al.*, 2010).

Sampling occurred between 2008-2012; each area was sampled for 80 days in both the dry (April-September) and wet (October-March) seasons. We were limited to only ten cameras, so we rotated cameras among random sites within each area. We deployed cameras at five sites for 20 consecutive days, then we exchanged film and batteries and moved the cameras to five different sites within the area. We repeated this process until all 20 sites were sampled (total of 80 days/season). Cameras were set to operate for 24 hours with an interval of five minutes between pictures.

Modelling ocelot use and detection as a function of covariates

Ocelot use (Ψ)

To explore the influence of features around the camera site (termed site covariates) on ocelot use (Ψ), we classified land cover types by interpreting Landsat 5 images using program ERDAS Image 8.4 (Erdas, 1997). Using a 500 m radius buffer around each camera site, we quantified the area (ha) of eucalyptus, natural field and pasture, cropland and unpaved roads (Table 1). We chose a 500 m radius buffer because it is similar to the smallest recorded ocelot home range size (76 ha; Crawshaw & Quigley, 1989). We did not test for native forest because: (1) most of our sites were within protected areas where Atlantic Forest is the natural cover, and we were interested in the effects of non-native habitats (i.e., human-related habitat features) within these areas and (2) the area of native forest within the buffer was highly correlated with eucalyptus area (r = -0.78). We expected a negative relationship between ocelot use and eucalyptus area and open canopy areas, such as natural fields and pasture and croplands (Haines *et al.*, 2006).We also expected lower ocelot use in areas with more unpaved road because unpaved roads represent a threat to native cats, contributing to habitat loss and fragmentation (Silva *et al.*, 2014).

In addition to land covers, we expected ocelot use to be influenced by the occurrence or relative abundance of other predators or competitors (Table 1). We expected a positive relationship between the presence of top predators and ocelot use because their presence may indicate better habitat quality (e.g., more resource availability; Massara *et al.*, 2015). Conversely, we expected ocelots to avoid areas with high abundances of free-ranging domestic dogs as dogs can harass and/ or compete with ocelots (Paschoal *et al.*, 2012). We estimated the conditional occupancy probability ($\Psi_{\text{conditional}}$; MacKenzie *et al.*, 2006) of top predators (jaguar and puma combined) for each site using the single season occupancy model in Program PRESENCE (Hines, 2006). Due to limited detections of jaguars (detected only in RD), we could not estimate different occupancy probabilities for this species. However, estimates of $\Psi_{\text{conditional}}$ were similar when considering puma detections only, indicating that jaguars and pumas were detected at the same camera sites in RD. We also recorded the number of domestic dogs photographed at each site and used this as a site covariate in our analysis (Table 1). We identified individual dogs based on their specific phenotypic differences (Paschoal *et al.*, 2012).

Finally, we considered the reserve size as a covariate to model variation in ocelot use (Ψ) among areas (Table 1). Ocelot abundance is often positively correlated with reserve size in our biome (Massara *et al.*, 2015), and reserve size was negatively correlated with the edge ratio of each reserve ($r = -0.92$), suggesting that larger reserves may represent better habitat quality for native fauna (Gascon *et al.*, 2000). Therefore, we expected a positive relationship between ocelot use and reserve size because large areas may harbor more ocelots, likely increasing ocelot distribution (or use) within the reserve.

We tested for correlation among our selected covariates, but none were highly correlated ($|r| \leq 0.50$ in all cases).

Ocelot detection (p)

We used the same land cover covariates to model potential variation in ocelot detection (p) at used sites (Table 1). We expected detection probability would vary among sites due to eucalyptus area, but we were unsure of the direction of the relationship. Sites with more eucalyptus may have a higher detection probability because eucalyptus may be more permeable to native carnivores than any other anthropogenic land cover (Lyra-Jorge *et al.*, 2008). Therefore, in this scenario ocelots may use eucalyptus as travel routes to move between native forests, which may increase detection probability. Alternatively, eucalyptus may limit the detection radius/camera sensitivity thereby decreasing detection probability in these areas. We expected that sites within larger reserves, may have higher ocelot detection because larger reserves harbor more individuals compared to smaller areas (Massara *et al.*, 2015). Conversely, used sites with more area of natural field, pasture, or croplands may have lower ocelot detection probability because the species may restrict their movement in open canopy areas (Haines *et al.*, 2006).

We also considered four additional covariates that were used to model detection probability only. First, we recorded if the camera was located on (1) or off (0) an unpaved road, because previous studies have suggested that ocelot may use unpaved roads frequently as travel routes, which may increase detection probability (Srbek-Araujo & Chiarello, 2013; Di Bitetti *et al.*, 2010). Next, we constructed two 'survey' covariates that varied for each site and occasion: (1) whether or not domestic dogs were detected, and (2) whether or not top predators were detected. We expected a negative relationship between ocelot detection probability and both of these covariates, as ocelot may restrict their movements (or frequency of use) during occasions when dogs (Paschoal *et al.*, 2012) or larger predators (Di Bitetti *et al.*, 2010) were seen at a site. We also recorded the number of days that the cameras were operable in each site expecting a positive relationship between this covariate and ocelot detection.

Table 1 here

Data Analysis

For each camera site we recorded whether an ocelot was detected (1) or not (0) during each five-day period that cameras were deployed, so each site was sampled on four occasions in each season (each occasion represented a five-day period). Using these data, we first explored possible changes in occupancy state (i.e., occupancy dynamics) and detection probability between dry and wet seasons, using a dynamic occupancy model (MacKenzie *et al.*, 2003). We fit four models, where the dynamic parameters (colonization and extinction) were either estimated (non-zero) or fixed to 0 (i.e., occupancy state is static between seasons) and detection varied or not between seasons. Using Akaike's Information Criterion adjusted for small sample size (AICc) for model selection (Burnham & Anderson, 2002), a static model with constant detection probability among seasons was best supported (ΔAICc values for the best dynamic and variable detection models were 2.90 and 4.90, respectively). Therefore, we used a single season occupancy model with eight occasions (both seasons) and did not test for seasonality effect (Dry vs. Wet) in ocelot detection in our subsequent analysis (MacKenzie *et al.*, 2002).

We built 1942 models consisting of all possible additive covariate combinations (Doherty, White & Burnham, 2012) for occupancy (Ψ) and detection probability (p) and fit these in Program MARK (White & Burnham, 1999). This strategy resulted in a balanced model set necessary to interpret the cumulative AICc weights (w_+) for each covariate (Burnham & Anderson, 2002). We explored the potential for lack of independence among the camera locations, using the goodness-of-fit test incorporated in Program PRESENCE (MacKenzie & Bailey, 2004), using our global model structure (composed of all covariates for Ψ and p).

Results

Our goodness-of-fit test revealed no evidence of overdispersion ($\chi^2 = 283.31$; p-value = 0.18; $\hat{c} = 1.16$). Due to our large candidate model set, our most parsimonious model had weight of 0.15, but this model was ~ four times more likely than any other model in our candidate set (Table 2).

Table 2 here

Consistent with our a priori expectations, the probability of ocelot use showed a strong positive relationship with the occurrence of top predators ($w_+ = 0.94$) and a negative relationship with the relative abundance of free-ranging dogs ($w_+ = 0.50$; Table 3; Fig. 2). All other covariates had $w_+ < 0.30$ and did not influence the probability of ocelot use at sites in the sampled reserves (Table 3). Using the mean values of top predator occurrence and the number of free-ranging domestic dogs among sites for each reserve, we found a higher probability of ocelot use in two State Parks (RD and SB) and in one private reserve (FM; Fig. 3).

The amount of eucalyptus (ha) had a strong positive relationship on ocelot detection probability ($w_+ = 0.85$; Table 3; Fig. 2). All other variables had $w_+ < 0.30$ and did not influence the detection probability of ocelots at used sites (Table 3).

Table 3, Fig. 2 and Fig. 3 here

Discussion

The presence of top predators correlated positively with the probability that ocelots used a site in Atlantic Forest protected areas, which suggests that ocelots do not spatially partition habitat with these top predators, a finding supported by other studies (Di Bitetti *et al.*, 2010). A recent study in the same biome found higher ocelot abundances in protected areas with top predators (Massara *et al.*, 2015). The presence of a diversity of predators indicates adequate prey resources in the system (Ritchie & Johnson, 2009). Unfortunately, we could not directly test the effects of prey metrics on ocelot use because we did not sample their main prey (small mammals; Sunquist & Sunquist, 2002), instead our cameras were placed to maximize the opportunity to detect carnivores. Because the presence of carnivores may indeed correlate positively to prey density (Srivathsa *et al.*, 2014; Zanin *et al.*, 2015), future sampling designs should collect information on prey density and investigate its influence on ocelot use.

Our findings suggest that ecological processes that are detrimental to top predators, such as quality and quantity of Atlantic Forest habitat, may also be detrimental to ocelots. Presence of top predators may act as a biodiversity indicator, designating habitats capable of supporting both large and presumable smaller, prey species. Additionally, the presence of top predators designate areas with adequate protection and presumably with low poaching pressure on prey and predators. Serra do Brigaderio (SB) and Rio Doce (RD) are the most protected areas in our study, with more park rangers and higher levels of surveillance. We recorded large prey species in these State Parks, such as deer (*Mazama* spp.) and collared peccary (*Pecari tajacu*), the most preferred species by hunters in Atlantic forest remnants (Chiarello, 1999; Cullen, Bodmer & Valladares-

Padua, 2001). Finally, the presence of top predators may also increase local ocelot use through the predation and/or harassment of potential competitors, including domestic dogs.

We found a negative relationship between dog abundance and ocelot use. Ocelot use at sites with a high number of dogs, such as those sampled in Feliciano Miguel Abdala (FMA), is almost four times lower than at sites with no dogs, such as those sampled in RD (Table 1; Fig. 2; Fig. 3). Free-ranging domestic dogs cause a variety of impacts on wildlife, such as predation and spread of disease (Curi *et al.*, 2014; Young *et al.*, 2011), and their occurrence negatively affects the distribution of other mammal species, such as maned wolf (*Chrysocyon brachyurus*) and giant anteater (*Myrmecophaga tridactyla*) in the Brazilian Cerrado (Lacerda, Tomas & Marinho-Filho, 2009), and margay (*Leopardus wiedii*), oncilla (*Leopardus tigrinus*), golden-headed lion tamarin (*Leontophitecus chrysomelas*) and naked-tailed armadillo (*Cabassous* sp.) in the Brazilian Atlantic Forest (Cassano *et al*., 2014). Our results suggest that ocelot can be added to this list of species whose local distribution is influenced by domestic dogs. Management practices to control high densities of free-ranging domestic dogs should be developed to avoid a further deteriorating scenario in this and other biomes, as this exotic species is increasingly among the most common mammal species in Brazilian natural areas (Espartosa, Pinotti & Pardini, 2011; Paschoal *et al.*, 2012; Cassano *et al.*, 2014). Such plans could involve dog vaccination, sterilization campaigns and management practices to restrict their use of natural areas (Curi *et al.*, 2014; Curi *et al.*, 2016).

Contrary to our expectations, reserve size did not influence the use or detection of ocelots. This finding may be a reflection of one small private reserve (Fazenda Macedônia; FM) which supports pumas and high ocelot use. FM has large native prey (deer, *M. gouazoubira*) and reintroduced avian species, such as Galliformes and Tinamiformes birds (CENIBRA, 2014), which may help sustain predators. Additionally, FM occurs near (~ 15 km) RD and the matrix between these reserves is composed of supposedly permeable eucalyptus and other smaller native fragments which may facilitate movement of ocelots, top predators and other species among these fragments (Lyra-Jorge *et al.*, 2008).

We found that ocelot detection was higher at used sites with relative high amounts of eucalyptus, indicating that the species frequents these locations. However, this result should be interpreted cautiously because eucalyptus plantations appeared only in two protected areas (FM and RD). Nevertheless, eucalyptus plantations/forests are expanding within the biome, becoming more common in many Atlantic Forest remnants (Tabarelli *et al.*, 2010; Ribeiro *et al.*, 2009). For example, eucalyptus plantations occupied ~ 6 Mha of the area of planted trees in Brazil, representing ~ 72% of the total, and are located mainly (~ 43%) in southeastern Brazil (IBÁ, 2015). The influence of such expansion on native fauna should be better investigated. While recent studies have showed that eucalyptus plantations are frequented by native carnivores (Lyra-Jorge *et al.*, 2008) and birds (Millan, Develey & Verdade, 2015) as forest remnants, it is important to clarify that these finding may not necessarily apply to all eucalyptus plantations. In our scenario, reserves are primarily patches of natural/native forests, occasionally separated by eucalyptus, that may promote or facilitate ocelot movement between natural/native forest patches. Additionally, management practices in eucalyptus plantations might either attract or repel carnivores. For example, in FM the understory vegetation in eucalyptus plantations are maintained until the end of their commercial cycle (~ 7 years), except when plague control practices are needed (CENIBRA, 2016). The maintenance of the understory vegetation in eucalyptus plantations might be associated with an increase in the proportion of bird (Millan *et al.*, 2015) and small mammal (Umetsu & Pardini, 2006) species that are able to occupy this matrix, which may potentially attract ocelots. Conversely, ocelot records were five times less frequently in agricultural landscapes than in native forests in the State of São Paulo, where eucalyptus plantations covered a much higher proportion of the landscape (Dotta & Verdade, 2011). The same relationship was showed for a carnivore community in the Mediterranean basin, which is being threatened by afforestation, most notably with eucalyptus (Cruz, Sarmento & White, 2015).

The value of agricultural and silvicultural lands for native fauna and connectivity might depend on the permeability of the crop type, management practices and landscape context. Quantifying these differences and their effect on predator distributions may influence conservation decisions regarding which type of matrix is more suitable for connecting natural habitats in protected areas of Atlantic Forest. In our study, eucalyptus appears to serve as an important and more protected travel route than open areas, such as pasture. It may be even more important in small and less forested reserves, where ocelots may move constantly to meet their energetic requirements or find better habitats (e.g., with low dog densities). Species with medium or large home-ranges, such as ocelots, jaguars and pumas (Sunquist & Sunquist, 2002), are unlikely to thrive in this fragmented scenario and a permeable matrix may allow dispersal of young individuals and the persistence of a rich carnivore assemblage in a human-dominated landscape (Lyra-Jorge *et al.*, 2008). However, to achieve efficient connection among these forest patches to facilitate sustainable activity, we need to incorporate ecological knowledge of silvicultural practices.

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Figures

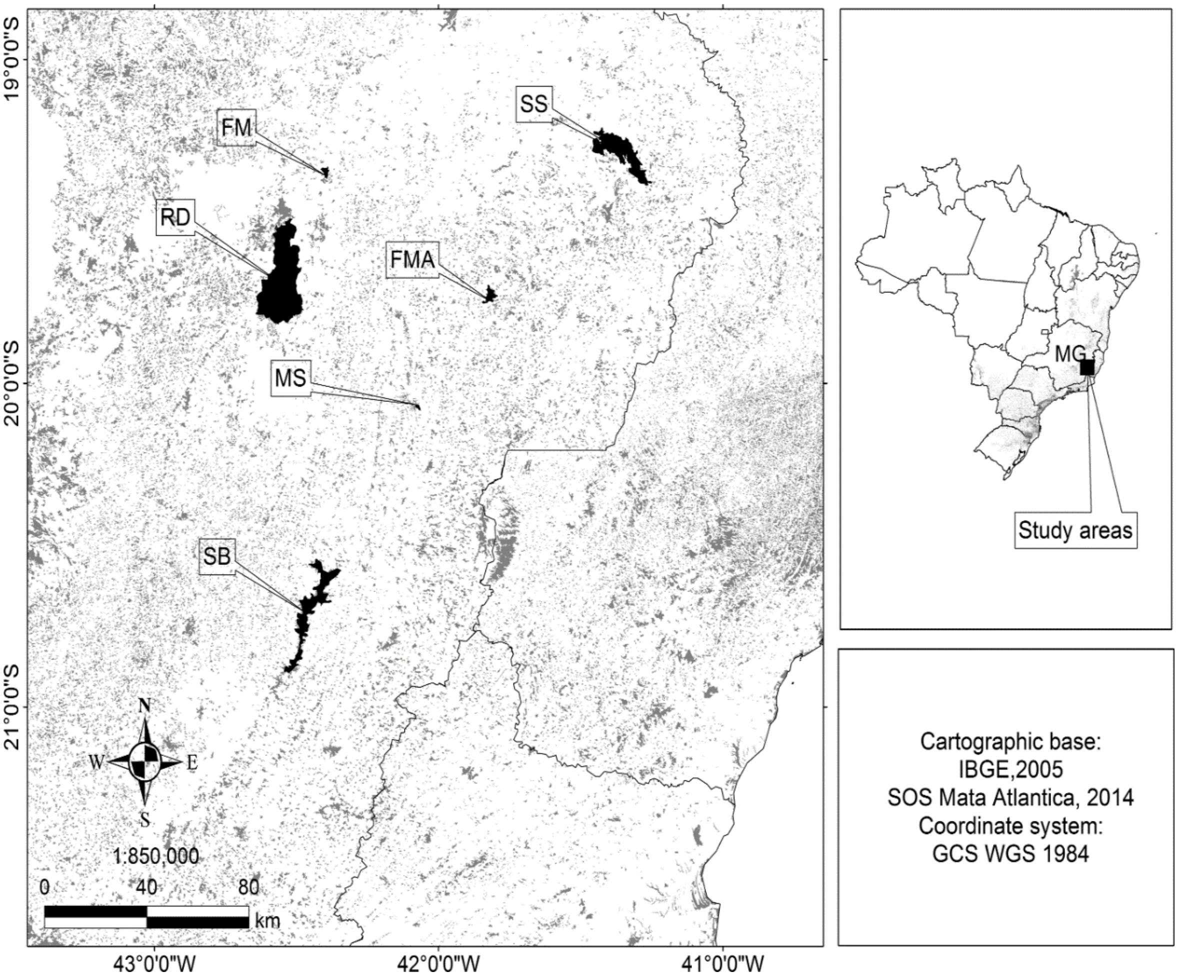

Figure 1 Locations of the six Atlantic Forest reserves, including three State Parks (SS= Sete Salões State Park; SB= Serra do Brigadeiro State Park; RD= Rio Doce State Park) and three private reserves (FMA= Feliciano Miguel Abdala Reserve; MS= Mata do Sossego Reserve; FM= Fazenda Macedônia Reserve) sampled for ocelot in the State of Minas Gerais (MG), southeastern Brazil. The current distribution of Atlantic Forest remnants are shown in the insert (gray area) and follow SOS Mata Atlântica (2014) . The state divisions are from the Brazilian Institute of Geography and Statistics (IBGE, 2005).

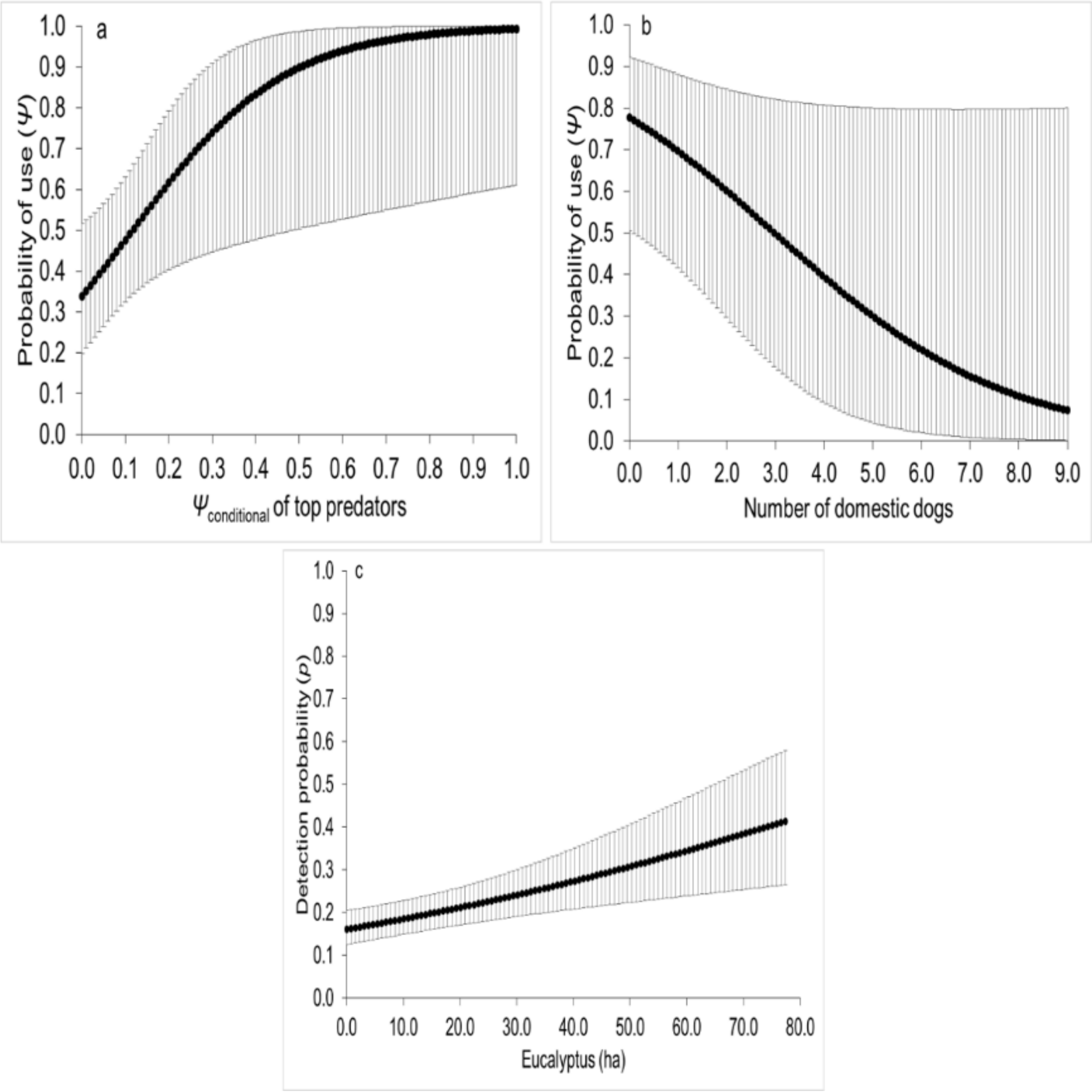

Figure 2 Probability of ocelot use (± 95% CI) as a function of site-specific conditional use ($\Psi_{\text{conditional}}$) of top predators (a) or number of domestic dogs (b). Ocelot detection probability (± 95% CI) as a function of area of eucalyptus (c) at used sites. Estimates are from the most parsimonious model that included those covariates, Ψ ($\Psi_{\text{conditional}}$ of top predators and number of domestic dogs), and p (Area of eucalyptus).

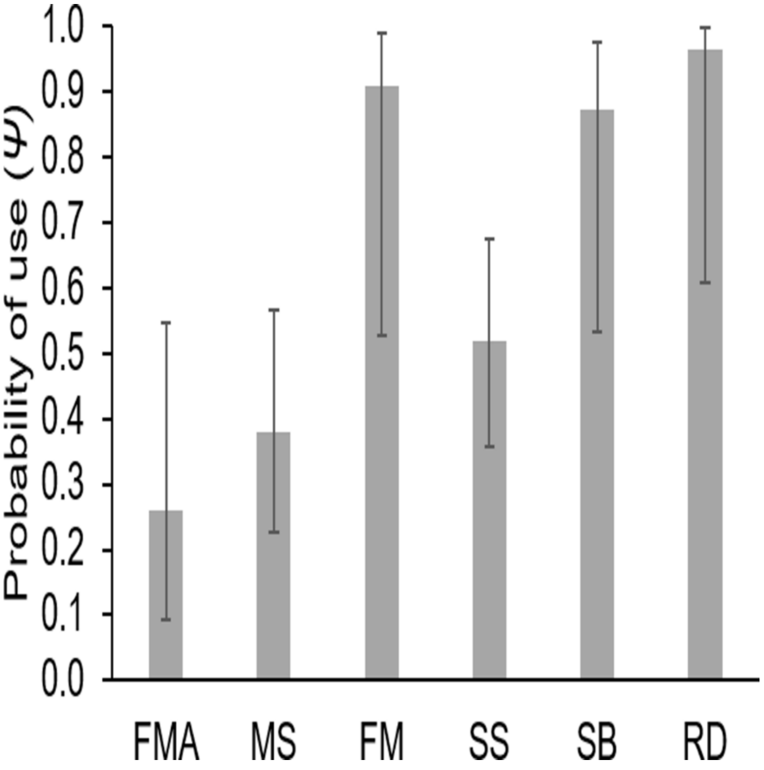

Figure 3 Probabilities of use (± 95% CI) by ocelots in six Atlantic Forest reserves (FMA= Feliciano Miguel Abdala Reserve; MS= Mata do Sossego Reserve; FM= Fazenda Macedônia Reserve; SS= Sete Salões State Park; SB= Serra do Brigadeiro State Park; RD= Rio Doce State Park) in southeastern Brazil. Estimates are based on the mean values of $\Psi_{\text{conditional}}$ of top predators and number of free-ranging domestic dogs for each reserve, using the most parsimonious model that included those covariates, Ψ ($\Psi_{\text{conditional}}$ of top predators and number of domestic dogs), and p (Area of eucalyptus).

Tables

Table 1 Covariates used to model the probabilities of use (Ψ) and detection probability (p) of ocelots in six Atlantic Forest reserves in southeastern Brazil. Mean and range (minimum - maximum) of each covariate are given for each reserve. Land cover covariates (*Area of eucalyptus*, *area of field and pasture*, *area of croplands* and *area of unpaved road*) are given within 500 m radius buffer around each camera site (out of 20 total sites / reserve). The values for *Detection of top predators* or *Detection of domestic dogs* are the proportion of occasions (out of 8 total) with top predators or domestic dog detections, respectively, averaged across sites. *Located on unpaved roads* indicates the number of camera sites that were installed on unpaved roads in each reserve. See methods for details

	Feliciano Miguel Abdala	**Mata do Sossego**	**Fazenda Macedônia**	**Sete Salões**	**Serra do Brigadeiro**	**Rio Doce**
Area of eucalyptus (ha)	0.00 (0.00-0.00)	0.00 (0.00-0.00)	21.66 (0.00-77.38)	0.00 (0.00-0.00)	0.00 (0.00-0.00)	4.56 (0.00-25.00)
Area of field and pasture (ha)	7.28 (0.00-31.89)	1.93 (0.00-12.08)	24.02 (0.00-59.53)	7.52 (0.00-30.88)	6.80 (0.00-34.48)	0.00 (0.00-0.00)
Area of croplands (ha)	2.96 (0.00-16.59)	0.00 (0.00-0.00)	3.31 (0.00-15.89)	3.84 (0.00-17.88)	0.00 (0.00-0.00)	0.07 (0.00-1.31)
Area of unpaved road (ha)	0.14 (0.00-3.02)	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.00 (0.00-0.00)	0.62 (0.00-4.19)	0.00 (0.00-0.00)

Number of domestic dogs	3.05 (0.00-9.00)	0.35(0.00-2.00)	0.55(0.00-3.00)	0.38 (0.00-3.00)	0.20 (0.00-2.00)	0.00 (0.00-0.00)
$\Psi_{\text{conditional}}$ of top predators [a]	0.10 (0.05-1.00)	0.00 (0.00-0.00)	0.50 (0.33-1.00)	0.10 (0.02-1.00)	0.41 (0.09-1.00)	0.64 (0.20-1.00)
Days of camera operation	32.14 (2.00-40.00)	40.00 (40.00-40.00)	40.00 (40.00-40.00)	30.04 (9.00-40.00)	39.00 (20.00-40.00)	40.00 (40.00-40.0)
Detection of top predators	0.01 (0.00-0.13)	0.00 (0.00-0.00)	0.04 (0.00-0.25)	0.01 (0.00-0.13)	0.05 (0.00-0.25)	0.19 (0.00-0.75)
Detection of domestic dogs	0.35 (0.00-1.00)	0.09 (0.00-0.38)	0.11 (0.00-0.63)	0.09 (0.00-0.50)	0.06 (0.00-0.38)	0.00 (0.00-0.00)
Located on unpaved road	13	0	11	1	0	7
Reserve size (ha)	958	134	560	12,520	14,985	35,970

[a] $\Psi_{\text{conditional}}$ is the probability that a site is used by top predators, given its particular detection history in each reserve.

Table 2 Model selection results for the top 10 models consisting of the probabilities of use (Ψ) and detection (*p*) of ocelots in six Atlantic Forest reserves in southeastern Brazil. Ψ modeled as function of: $\Psi_{\text{conditional}}$ of top predators (PRED), number of free-ranging domestic dogs (DOG), reserve size (RSZ), area of natural field and pasture (AFP) and area of unpaved road (AUR). *p* modeled as function of: area of eucalyptus (AEU), AFP, detection of top predators in each sampling occasion (PRED-t), camera location (On or off unpaved road; CL) and RSZ. The plus signal (+) means an additive effect between two or more tested covariates

Model	**AICc**	**Δ AICc**	**AICc Weights**	**Parameters**	**Deviance**
Ψ (PRED+DOG+RSZ), p (AEU)	595.81	0.00	0.15	6	583.11
Ψ (PRED), p (AEU+AFP+PRED-t)	598.30	2.49	0.04	6	585.60
Ψ (PRED+DOG), p (AEU+PRED-t)	598.32	2.51	0.04	6	585.62
Ψ (PRED+DOG+AFP), p (AEU)	598.39	2.58	0.04	6	585.69
Ψ (PRED+DOG), p (AEU+CL)	598.54	2.73	0.04	6	585.85
Ψ (PRED+DOG), p (AEU+AFP)	599.19	3.39	0.03	6	586.50
Ψ (PRED+RSZ), p (AEU+PRED-t)	599.92	4.12	0.02	6	587.23
Ψ (PRED), p (AEU+AFP+RSZ)	599.98	4.17	0.02	6	587.28
Ψ (PRED+DOG+AUR), p (AEU)	600.19	4.39	0.02	6	587.50
Ψ (PRED+DOG), p (AEU)	600.20	4.39	0.02	5	589.70

Table 3 Cumulative AICc weights for covariates used to model the probabilities of use (*Ψ*) and detection (*p*) of ocelots in six Atlantic Forest reserves in southeastern Brazil. Estimates of covariate effects (β parameters) are given for the most parsimonious model that included the covariate

Covariate	**Cumulative AICc Weights (%)**	**β parameters**		
		Estimate	**Lower 95%CL**	**Upper 95%CL**
Ocelot use (*Ψ*)				
$\Psi_{\text{conditional}}$ of top predators	93.81	8.04	0.47	15.61
Number of domestic dogs	50.02	-0.63	-1.21	-0.06
Reserve size	27.27	$-0.76\text{x}10^{-4}$	$-0.14\text{x}10^{-3}$	$-0.12\text{x}10^{-4}$
Area of field and pasture	16.67	0.06	-0.01	0.13
Area of eucalyptus	15.89	0.08	-0.10	0.25
Area of unpaved road	10.52	-1.21	-2.55	0.13
Area of croplands	4.47	0.08	-0.09	0.26
Ocelot detection (p)				
Area of eucalyptus	85.26	0.02	0.01	0.03
Detection of top predators	25.26	0.90	0.18	1.61
Area of field and pasture	18.08	0.02	$0.20\text{x}10^{-2}$	0.03
Camera location [a]	14.76	0.52	0.01	1.03
Days of camera operation	10.37	0.05	-0.02	0.11
Reserve size	6.65	$0.21\text{X}10^{-4}$	$0.34\text{x}10^{-6}$	$0.42\text{x}10^{-4}$
Area of cropland	5.46	-0.05	-0.13	0.02

Detection of domestic dogs	3.74	0.25	-0.55	1.05

[a] β parameter value based on camera sites that were installed on unpaved road.

Chapter 3 - Activity patterns and temporal overlap between ocelot and top predators in protected areas of Atlantic Forest

Activity patterns and temporal overlap between ocelot and top predators in protected areas of Atlantic Forest

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Abstract

Temporal segregation may be one of the most effective mechanism to reduce interspecific killing. Recent studies in the Atlantic Forest showed that ocelot occurrence is strongly and positively correlated with the presence of large carnivores (jaguars and mountain lions). We hypothesized temporal segregation by ocelots as the main strategy of reducing interference competition, allowing ocelots to coexist with large carnivores. We compared the activity patterns of jaguars, mountain lions and ocelots, using camera-traps and measured the degree of activity overlap ($\widehat{\Delta}_1$) between ocelots and the other species. Overall, all species showed an intensive nocturnal and crepuscular activity, which resulted in a high overlap of the daily activity pattern between large carnivores and ocelots ($\widehat{\Delta}_1 \geq \sim 0.70$ or 70%). Our finding suggest that other strategies, such as dietary segregation may allow for the coexistence of the species of focus in Atlantic Forest remnants. Our results enhance our understanding of the mechanisms through which closely related sympatric felids can coexist in the current scenario of the Atlantic Forest.

Key words: mesocarnivores, apex predators, tropical forest, interspecific competition

Resumo

A segregação temporal pode ser um dos mecanismos mais eficazes para reduzir a morte interespecífica. Estudos recentes na Mata Atlântica mostraram que a ocorrência da jaguatirica está fortemente e positivamente correlacionada com a presença de grandes carnívoros (onças-pintadas e onças-pardas). Trabalhamos com a hipótese de que a segregação temporal seria a principal estratégia adotada pelas jaguatiricas para reduzir a competição por interferência, permitindo com que as jaguatiricas coexistam com os grandes carnívoros. Foram comparados os padrões de atividade das onças-pintadas, onças-pardas e jaguatiricas usando armadilhas fotográficas e medido o grau de sobreposição de atividade (Δ_1) entre as jaguatiricas e as outras espécies. No geral, todas as espécies apresentaram uma intensa atividade noturna e crepuscular, o que resultou em uma alta sobreposição no padrão diário de atividade entre os grandes carnívoros e as jaguatiricas ($\Delta_1 \geq \sim 0.70$ ou 70%). Nossa descoberta sugere que outras estratégias, como a segregação da dieta, possam permitir a coexistência das espécies foco em remanescentes de Mata Atlântica. Nossos resultados melhoram a nossa compreensão sobre os mecanismos através dos quais os felinos simpátricos estreitamente relacionados podem coexistir no atual cenário da Mata Atlântica.

Palavras-chave: mesocarnívoros, predadores de topo, floresta tropical, competição interspecífica

Introduction

Animals may reduce interspecific competition and thus increase niche segregation, by minimizing temporal overlap with similar species [1]. Carnivores are no exception and temporal segregation by ecologically similar species is likely to occur in different systems [2-4]. The temporal segregation of the daily activity patterns may be one of the most effective mechanism to reduce competition, especially when interspecific competition can result in interspecific killing [1, 5, 6]. Interspecific killing is broadly defined as the killing of potentially competing species without any immediate energetic gain to the predator [6]. The intensity of interspecific killing may reach a maximum when the larger species is 2.0-5.4 times larger than the smaller species [7]. The consequences of interspecific competition may be even stronger when the amount of available habitat is limited due to forest fragmentation and habitat loss [8, 9].

Currently, forest fragmentation and habitat loss are the greatest threats to wildlife worldwide, but its consequences is even more dramatic in biodiverse tropical biomes, such as in the Atlantic Forest [10, 11]. In this biome, the high demand for large areas of arable lands and land-use intensification have reduced the original cover to less than 20% [10, 12, 13]. Additionally, over 80% of the Atlantic Forest remnants are smaller than 50 ha [10], which are ineffective for the persistence of large species, such as jaguar (*Panthera onca*) and mountain lion (*Puma concolor*) [14-16]. Additionally, recent studies show that the occurrence and abundance of ocelot (*Leopardus pardalis*) is positively correlated with the presence of these large carnivores, suggesting they may not spatially segregate [2, 17, 18]. Given that the amount of available habitat for the persistence of these three species is limited in this biome, ocelots may exhibit temporal segregation with dominant competitors, such as jaguars and mountain lions, to avoid interspecific killing [19]. This temporal segregation may prevent the local loss of the subordinate competitor (ocelot) in the system (competitive exclusion) [20] and allow the coexistence of ocelots and these large carnivores in this fragmented biome.

Recent statistical developments enables estimating overlap in daily activity between sympatric species using camera-trap data. It has been broadly used among different species and systems [4, 21, 22]. The advantage of this method is that the measures of overlap between circular random variables (i.e., time-of-day) are estimated nonparametrically using kernel density estimates, which include a measure of precision estimated by bootstrapping [23]. However, the only study to date that explored temporally segregation between ocelots and large carnivores in this Atlantic Forest did not use this approach [2].

Here we compared the activity patterns of jaguars, mountain lions and ocelots, using camera-traps to answer the following question: do ocelots show temporal activity avoidance with jaguars and mountain lions in Brazilian Atlantic Forest remnants, which would suggest a strategy of reducing interference competition and allowing for species coexistence?

Methods

Study areas

We worked in six Atlantic Forest reserves (or protected areas) located in the State of Minas Gerais, southeastern Brazil (Fig. 1). These areas consist of three smaller private reserves: Feliciano Miguel Abdala (FMA), Mata do Sossego (MS), and Fazenda Macedônia (FM), and three state parks: Serra do Brigadeiro (SB), Sete Salões (SS), and Rio Doce (RD). Rio Doce is the most pristine reserve among the sampled areas; it is one of the largest reserves remaining in the Atlantic Forest, with a diverse mammal community, including the presence of large and resident species such as tapirs (*Tapirus terrestris*), giant armadillos (*Priodontes maximus*), jaguars and mountain lions [18]. The vegetation is classified as semi-deciduous seasonal forest in all areas [24]. The topography varies among reserves, with the elevation ranging from 150 m (RD) to 2075 m (SB) [25]. The climate is classified as humid tropical in SB and semi-humid in other reserves [26].

Fig. 1 here

Sampling design and field methods

Twenty camera sites were randomly selected from satellite images of each reserve using ArcGIS 9.2 [27]. All camera sites were a maximum of 1km apart from each other and two cameras were placed at each of 20 camera sites. Cameras were set to operate for 24 hours with a minimum interval of five minutes between photos. When cameras could not be installed in their original locations due to constraints (e.g., no site access), we moved them to the nearest site (within <100 m) and recorded the locations again using a GPS unit. When possible, we elected to place cameras along game trails, human paths, or unpaved roads to maximize the opportunity to detect the focal species [2, 28, 29].

Sampling occurred from 2008 to 2012; each reserve was sampled for 80 days in both the dry (April-September) and wet (October-March) seasons. We were limited to only ten cameras, so we rotated cameras among sites within each reserve. We deployed cameras at five sites for 20 consecutive days. After that period, we exchanged film and batteries before moving cameras to another five sites within the reserve. We repeated this process until all 20 sites were sampled (total of 80 days/season).

Data analysis

We only used photographs of the same species from the same camera that had been taken more than one 1 h apart, thus minimizing the non-independence of consecutive photographs [22].

To assess whether large carnivores (jaguar or mountain lion) occurrence influenced the activity pattern of ocelots, the activity hours of each species were transformed into solar time to adjust the actual time to the dial cycle of each carnivore [22, 23]. The time adjustments and transformations were based on times of sunrise and sunset at each reserve, which was extracted using the software Tropsolar 5.0 [30]. The average time of sunrise and sunset in all reserves during our sampling was 6:14 and 18:09, respectively. We categorized the activity of the species into diurnal (activity predominantly between 1 h after the sunrise and 1 h before the sunset), nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise) and crepuscular (activity occurred 1 h before and after sunrise and sunset).

We estimated the activity pattern of each species using kernel density (i.e., density of activity), a nonparametric method for evaluating the probability density function (PDF) of a random variable [31]. We then calculated the most suitable coefficient of overlapping ($\widehat{\Delta}_1$), which varies from 0 (no overlap) to 1 (complete overlap), between each large carnivore and ocelot [23]. We used the $\widehat{\Delta}_1$ estimator because it is the preferable estimator for small sample size (i.e., number of registers < 75) [23]. We calculated the 95% confidence intervals for $\widehat{\Delta}_1$ from 10,000 bootstrap samples [23]. Statistical analyses were implemented in R Software [32].

Because each reserve was sampled in different periods (i.e., years and months) and are located in different regions in the Brazilian Atlantic Forest (Fig. 1), we first used a series of pairwise comparisons to test for differences in activity patterns of mountain lions and ocelots among reserves. This test revealed no strong differences in activity periods for these species among reserves (minimum value of $\widehat{\Delta}$ for mountain lion and ocelot was 0.53 with 95% CI = 0.34-0.88 and 0.56 with 95% CI = 0.32-0.75, respectively). Thereafter, we pooled the data from all reserves for both species in the subsequent analysis. Because jaguars were registered just in one reserve (RD), we use only the registers of the ocelot in this reserve to measure the most suitable coefficient of overlapping between it and jaguars for this area.

Results

We obtained a total of 185 independent registers of jaguars, mountain lions and ocelots. Ocelot was the most recorded species (n= 122), followed by mountain lion (n=55) and jaguar (n=8).

Overall, all species showed an intensive nocturnal and crepuscular activity but preferred the crepuscular and day hours slightly differently (Fig. 2). Jaguars and mountain lions showed some diurnal activity whereas diurnal activity by ocelots was almost inexistent (Fig. 2).The similarities among the activity patterns resulted in a high overlap of the daily activity pattern between the large carnivores and the ocelots ($\widehat{\Delta} \geq 0.68$ or 68 % ; Fig. 3). Although the estimates from the jaguar analyses had low precision, the lower bound of the 95 % confidence interval suggests that ocelot and jaguar activity patterns overlap by ~ 60 % (Fig. 3).

Fig. 2 and 3 here

Discussion

Our findings showed a similar activity pattern among species, which resulted in a high degree of temporal overlap between ocelots and the larger cats (jaguar and mountain lion). One possible explanation for the lack of temporal segregation between ocelots and these larger cats may relate to the low densities of these species in Atlantic Forest remnants, which may lead to fewer interactions [18, 33, 34]. In addition to temporal segregation [2-4], carnivores may reduce interspecific competition by minimizing spatial [2, 35, 36] and dietary overlap [37-39] with a dominant competitor. However, ocelots may not spatially segregate with these larger cats in these protected areas. Contrary, recent studies carried out by us in the same reserves showed that the use probability of ocelots in Atlantic Forest sites (Massara et al. in prep.) as well as ocelot abundance [18] strongly and positively correlated with the occurrence of these large predators, supporting the idea that occurrence of these species may positively correlates with better-protected areas [2, 33, 34].Therefore, the coexistence between ocelots and these larger species appear to be facilitated by diet segregation.

Competition for food and high diet overlap among mammalian carnivores has been suggested as a one of the key factors precipitating interspecific competition (i.e., interspecific killing) [6, 40]. Although ocelots occasionally prey on large mammals in these Atlantic Forest remnants, it may be a reflection of the opportunistic habit of the species [41-43]. Ocelots prey mainly on small to medium mammals, whereas jaguars and mountain lions prey mainly on large ungulates [44-46]. Therefore, temporal overlap between ocelots and these larger predators may be mediated mainly by the existence of prey of various sizes. For example, the only reserve where we detected the three cat species together was in Rio Doce State Park (RD) and their presence may be related to a higher diversity of prey for these species, especially those of large body size, such as deer (*Mazama americana*) and collared peccary (*Pecari tajacu*) [18]. However, illegal hunting on synergetic species may have negative consequences in the Atlantic Forest remnants and thus, on the coexistence of these species [11, 15, 47].

The effect of hunting pressure in the Atlantic Forest remnants is even more disastrous because the game hunters have greater access to forest remnants due to the current fragmented scenario of the biome [14]. Most forest patches are isolated, which may not allow for immigration or recolonization of the wildlife populations depleted by game hunters [14, 47]. Ungulates are one the most preferred group of game species targeted by hunters in Atlantic forest remnants [14, 47, 48]. Because the presence of carnivores, even in low densities, may correlates positively to their prey density, the persistence of jaguars and mountain lions is highly threatened in this biome [49-51]. Alternatively, these large and opportunistically species might begin to prey on smaller species, such as armadillos and medium to large caviomorph rodents [44, 52], and to adjust their activity patterns to reduce interactions with humans [53, 54]. For example, mountain lions might become more crepuscular and nocturnal in less protected Atlantic Forest areas [33]. This activity behavior change might further increase the overlap of the daily activity pattern between the large carnivores and the ocelots, a crepuscular and nocturnal species (Fig. 2). For example, animals being more active during restricted temporal periods can potentially increase interaction opportunities among them (i.e., greater temporal overlap) [9]. In other words, these dietary and activity behavior changes coupled with the alarming rates of habitat loss and fragmentation in this biome, may increase the encounter rates between these large felids and ocelots, which might result, for example, in interspecific killing of the latter species [8, 19, 55].

Implications for conservation

Overall, our finding suggest that temporal segregation is not a mechanism adopted by the studied species to avoid interspecific competition. Other mechanisms, such as dietary segregation, may allow for the coexistence of the focus species in the Atlantic Forest. However, some human anthropogenic disturbances may change when and what animals eat, and how they interact with each other in these forest patches [9, 56]. Although hunting in Brazil is illegal, we have noticed different types of hunting activities, which varies in its intensity among our study areas (Massara pers. comm.). Hunting, for example, was more intense in Sete Salões State Park (SS) than in Rio Doce State Park (RD). Conservationists need starting to consider how the hunting pressure and the presence of other human activities affect the behavior of some species, and how these changes in animals' behavior affects species interactions. Additionally, we need to improve connection among our forest remnants because the amount of available habitat for the persistence of these three species is scarce [16]. Unfortunately, the selection of Brazilian protected areas still fails to create connectivity among the legally protected forest remnants, which are essential for the long-term persistence of medium-large carnivores in the Atlantic Forest [57]. Some elements of human-modified landscapes, such as tree monocultures, may offer excellent initiatives for biodiversity corridors and might be more logistically feasible than the creation of new protected areas [11, 47]. Therefore, without landscape connectivity and the immediate enforcement of the Brazilian environmental laws the overlook for these feline populations is pessimistic.

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Figures:

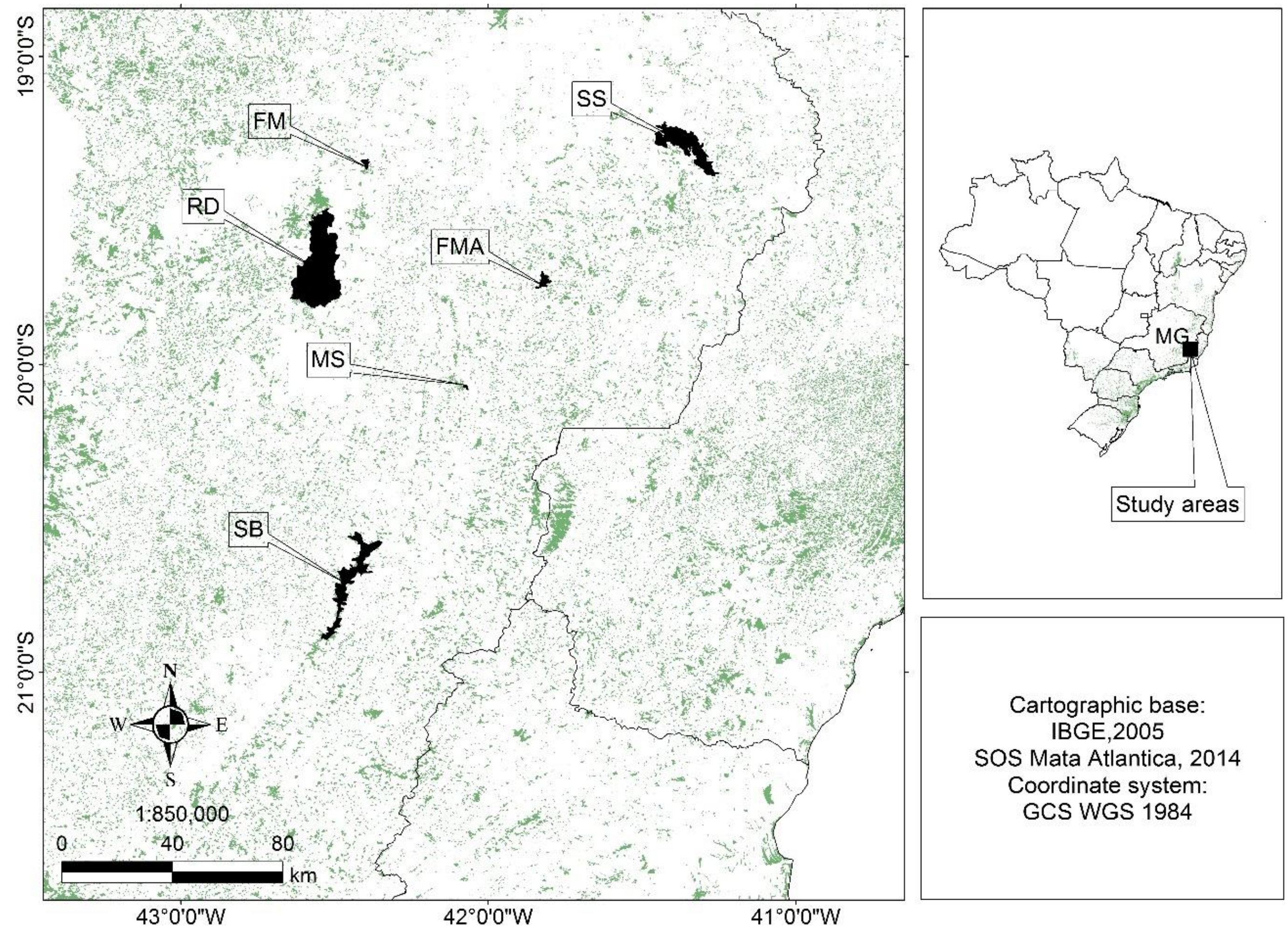

Fig. 1. Locations of the six Atlantic Forest reserves (MS= Mata do Sossego Reserve, 134 ha; FMA= Feliciano Miguel Abdala Reserve, 958 ha; FM= Fazenda Macedônia Reserve, 560 ha; SS= Sete Salões State Park, 12,520 ha; SB= Serra do Brigadeiro State Park, 14,985 ha; RD= Rio Doce State Park, 35,970 ha) sampled for carnivores in the Atlantic Forest, State of Minas Gerais (MG), southeastern Brazil. The current distribution of Atlantic Forest remnants are shown in the insert (gray area).

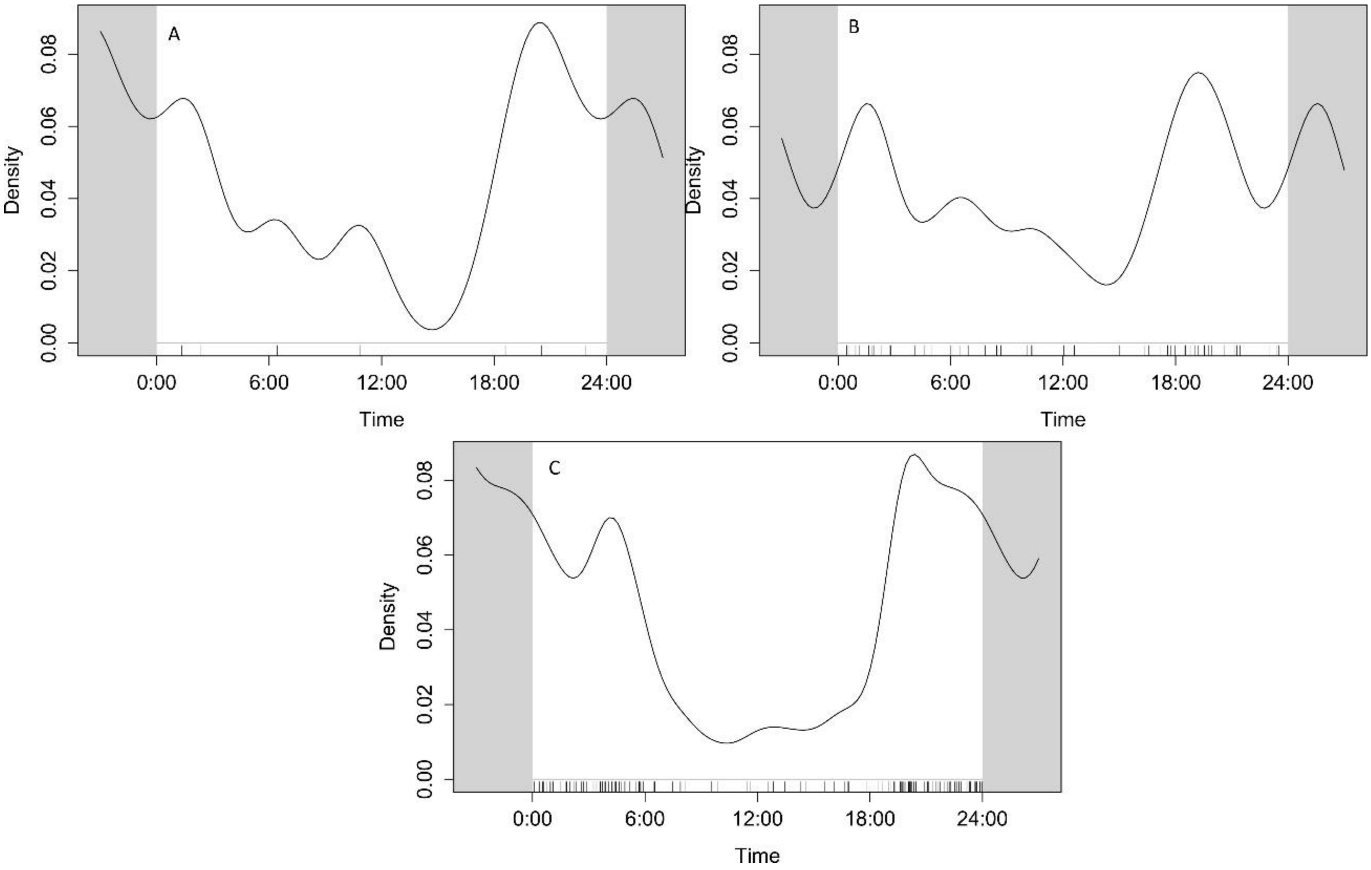

Fig. 2. Temporal activity patterns of three carnivores in six Atlantic Forest reserves, southeastern Brazil. A= jaguars in RD. B and C = mountain lions and ocelots, respectively, in all areas combined. Tick marks on the x-axis represent all activity samples (independent records) for each species. The y-axis range is the kernel density (density of temporal activity), where higher density represents increased activity. The activity periods were categorized into diurnal (activity predominantly between 1 h after the sunrise and 1 h before the sunset), nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise) and crepuscular (activity occurred 1 h before and after sunrise and sunset). The average time of sunrise and sunset in all reserves during our sampling was 6:14 and 18:09, respectively.

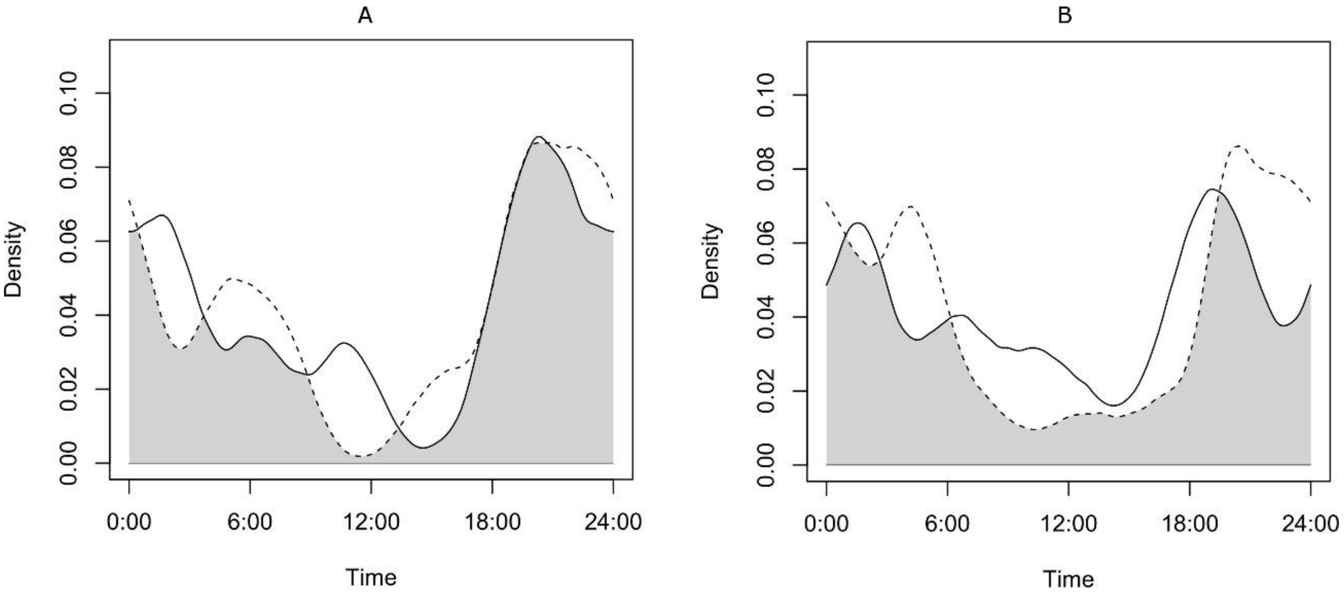

Fig. 3. Activity overlap between ocelot and large carnivores in six Atlantic Forest reserves in southeastern Brazil. A = ocelot vs. jaguar in RD; $\widehat{\Delta}_1$= 0.68 with 95% CI= 0.59-1.00. B = ocelot vs. mountain lion in all areas combined; $\widehat{\Delta}_1$= 0.78 with 95% CI= 0.66-0.87. Dotted (…) lines indicate registers from ocelot and solid (—) lines indicate registers from either jaguar (A) or mountain lions (B). Overlap between activity periods is represented by the shaded area. The x-axis represent the activity periods [diurnal (activity predominantly between 1 h after the sunrise and 1 h before the sunset); nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise) and crepuscular (activity occurred 1 h before and after sunrise and sunset)]. The y-axis range is the kernel density (density of temporal activity), where higher density represents increased activity. The average time of sunrise and sunset in all reserves during our sampling was 6:14 and 18:09, respectively.

Chapter 4 – Ecological interactions between ocelot and other sympatric mesocarnivores in protected areas of Atlantic Forest

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Ocelot interactions with mesocarnivores

Ecological interactions between ocelot and other sympatric mesocarnivores in protected areas of Atlantic Forest

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ABSTRACT

Over 80% of the Atlantic Forest remnants are smaller than 50 ha and now lack resident populations of large predators (jaguars, *Panthera onca*, and pumas, *Puma concolor*). Mesopredators with opportunistic life-history characteristics (e.g., ocelots, *Leopardus pardalis*), are now hypothesized to be the dominant competitor(s) in these systems and may negatively affect the spatial or temporal distribution of other sympatric and subordinate mesocarnivores. Here we used camera trap data and employed occupancy methods and temporal overlap indexes to explore whether ocelot occurrence influenced the habitat use or activity patterns of six mesocarnivores in reserves of the Brazilian Atlantic Forest. Our data suggests that ocelot occurrence did not influence the habitat use of these mesocarnivores. Moreover, the ability of some mesocarnivore species, especially the little spotted cat (*L. guttulus*), to adjust their activity patterns to avoid direct contact with ocelots may facilitate their coexistence in these Atlantic Forest remnants. Ocelot occurrence did not influence the activity pattern of two nocturnal species (the crab-eating fox, *Cerdocyon thous*, and the crab-eating raccoon, *Procyon cancrivorus*), suggesting that these species are more tolerant of ocelots than other mesocarnivores. Overall, our finding indicates that the mesocarnivores use correlated negatively with reserve size and that the probability of occupancy (use) was different among species, with tayra (*Eira barbara*) and South American coati (*Nasua nasua*) having the highest occupancy estimates. Because mesocarnivores are important drivers of ecosystem function, structure, and dynamics and they may occupy unique roles that cannot be filled by larger carnivores, future studies should assess other environmental factors that may influence the use of each mesocarnivore species in these small remnants of Atlantic Forest.

Key words: carnivores, competition, *L. pardalis*, tropical forest

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INTRODUCTION

Interspecific competition can be divided broadly into exploitative and interference competition. Exploitative competition is an indirect interaction among species for a common limiting resource, whereas interference competition occurs when one species is directly antagonistic towards another (Glen and Dickman 2005). The most extreme forms of interference competition are known as intraguild predation and interspecific killing. Intraguild predation can be defined as the killing and eating behavior among potential competitors (Arim and Marquet 2004), whereas interspecific killing is defined as the killing of potentially competing species without any immediate energetic gain to the predator (Polis et al. 1989). As a result, strong and dominant competitors may lead to the local extinction of weaker or subordinate competitors in the system (competitive exclusion; Gause 1932).

Interspecific competition may be exacerbated when the amount of available habitat is limited, which may increase contact rates among species and, consequently, a dominant competitor might affect the occurrence and activity patterns of a subordinate species (Gehrt et al. 2010; Buchmann et al. 2013; Lewis et al. 2015a). In the Brazilian Atlantic Forest, deforestation is mainly due to agricultural activities, which demand large areas of arable lands with land-use intensification (Lyra-Jorge et al. 2008; Ribeiro et al. 2009; Cassano et al. 2014). Today the existing Atlantic Forest covers less than 20% of the historic biome (Ribeiro et al. 2009) and over 80% of its remnant patches are smaller than 50 ha (Ribeiro et al. 2009).

The ocelot (*Leopardus pardalis*) has opportunistic life-history characteristics that define it as a dominant competitor that may negatively affect other sympatric and subordinate mesocarnivore species in remnants of Atlantic Forest, especially when the subordinate species is 2.0-5.4 times smaller than the dominant competitor (Donadio and Buskirk 2006). For example, a recent study identified *L. pardalis* as a potential killer of most mesocarnivores in South America (Oliveira and Pereira 2014). *L. pardalis* can prey on many mesocarnivores (Chinchilla 1997; Bianchi et al. 2014; Oliveira and Pereira 2014) and control the abundance and density of other wild cats, such as jaguarundi (*Puma yagouaroundi*), margay (*Leopardus wiedii*) and little spotted cat (*Leopardus guttulus*; Oliveira et al. 2010; Oliveira-Santos et al. 2012).

However, *L. pardalis* may only influence other mesocarnivores in reserves where the species is either abundant or in specific locations where it is likely to occur. Current knowledge suggest that *L. pardalis* is sensitive to deforestation (Di Bitetti et al. 2006; Di Bitetti et al. 2008) so, in theory, this cat might fare better in larger reserves and fragments than in smaller ones. However, larger and better protected reserves (> 10,000-20,000 ha) might also harbor larger cats, such as jaguars (*Panthera onca*) and pumas (*Puma concolor*; De Angelo et al. 2013; Castilho et al. 2015). The presence of these big cats in large reserves could limit *L. pardalis* abundance through either interference or exploitative competition. Rather surprisingly, however, recent studies in the Atlantic Forest have shown that *L. pardalis* is more abundant in larger, better protected areas inhabited by *P. onca* and *P. concolor* (Di Bitetti et al. 2010; Massara et al. 2015). Therefore, it is pertinent to investigate if ocelots are differently affecting other mesocarnivores in areas with and without big cats.

In these areas mesocarnivores may reduce interspecific competition by minimizing temporal (Di Bitetti et al. 2009; Di Bitetti et al. 2010; Gerber et al. 2012), spatial (Creel and Creel 1996; Gehrt and Prange 2006; Di Bitetti et al. 2010) and dietary overlap (Konecny 1989; Caro and Stoner 2003; Cupples et al. 2011) with a dominant competitor, such as *L. pardalis*. Carnivores might use scent marking (e.g., via scats urinations, and scent glands) as an important way of communication among species, where animals may use olfactory and visual signs to either avoid or challenge dominant competitors spatially and temporally (Caro and Stoner 2003; Lewis et al. 2015a). Unfortunately, few studies explore whether *L. pardalis* occurrence influences the spatial and temporal use or activity patterns of other mesocarnivores in the Atlantic Forest (Di Bitetti et al. 2010; Oliveira-Santos et al. 2012). Existing studies do not model occupancy and detection probability of mesocarnivores as a function of *L. pardalis* presence or measured the overlap of activity patterns between *L. pardalis* and other mesocarnivore species (MacKenzie et al. 2006; Ridout and Linkie 2009). However, studies in other systems have demonstrated the advantages of using camera-trap data to investigate potential spatial (Lewis et al. 2015a; Sunarto et al. 2015) and temporal (Linkie and Ridout 2011; Farris et al. 2015) segregation among sympatric carnivores.

Here we employed occupancy methods to explore if *L. pardalis* presence influences the occupancy probability of six mesocarnivore species (hereafter, mesocarnivores use), namely: South American coati (*Nasua nasua*), tayra (*Eira barbara*), crab-eating raccoon (*Procyon cancrivorus*), crab-eating fox (*Cerdocyon thous*), jaguarundi (*P. yagouaroundi*) and little spotted cat (*L. guttulus*) in protected areas (or reserves) of the Brazilian Atlantic Forest. Although *L. pardalis* is nocturnal, we expected the species to influence the spatial distribution of all mesocarnivore species including diurnal species, such as *N. nasua*, *E. barbara* and *P.*

yagouaroundi (Wilson and Mittermeier 2009). Despite clear differences in temporal activity patterns, these species are potentially under threat from intraguild predation and interspecific killing by *L. pardalis* (Oliveira and Pereira 2014) and thus, may spatially avoid *L. pardalis*. Alternatively, we expected the influence of *L. pardalis* on the probability of use may vary among mesocarnivores according to the natural history characteristics of each species. For example, we expected a negative influence of *L. pardalis* on the use probability of nocturnal species (*P. cancrivorus*, *C. thous* and *L. guttulus*) but a neutral influence of *L. pardalis* on the use probability of diurnal species (Wilson and Mittermeier 2009). Finally, temporal activity partitioning may be a possible mechanism behind the coexistence of *L. pardalis* and other mesocarnivores in this fragmented biome, thus we assessed if mesocarnivores, especially the nocturnal species, demonstrated temporal segregation with *L. pardalis*.

MATERIALS AND METHODS

Study Areas

We worked in six Atlantic Forest reserves located in the State of Minas Gerais, southeastern Brazil (**Fig. 1**). These comprised three state parks: Rio Doce (RD), Serra do Brigadeiro (SB), and Sete Salões (SS), and three smaller private reserves: Feliciano Miguel Abdala (FMA), Mata do Sossego (MS), and Fazenda Macedônia (FM). The topography varies among reserves, with the elevation ranging from 150 m (RD) to 2,075 m (SB; Miranda 2005). The climate is classified as humid tropical in SB and semi-humid in other reserves (IBGE 2012). The vegetation is classified as semi-deciduous seasonal forest in all areas (SOS Mata Atlântica 2015). Rio Doce is the most pristine reserve among the sampled areas and has a diverse mammal community, including the presence of large and resident species such as *P. onca*, *P. concolor*, tapirs (*Tapirus terrestris*) and giant armadillos (*Priodontes maximus*; Massara et al. 2015).

Fig. 1 here

Sampling Design and Field Methods

We sampled a total of 120 camera sites (i.e., our sampling units), consisting of 20 camera sites randomly selected within each of the six reserves using ArcGIS 9.2 (ESRI 2008). The minimum and mean distance between cameras was 200.55 m and 571.98 m, respectively. Two cameras were placed at each site for 20 consecutive days per season, and operated for 24 hours within a minimum interval of five minutes between photos. Due to limited number of cameras, we rotated cameras among sites within each reserve. Specifically, we deployed cameras at five sites for 20 consecutive days, then we exchanged film and batteries before moving cameras to another five sites within the same reserve. We repeated this process until all 20 sites were sampled (total sample duration for a reserve: 80 days / season). Each reserve was sampled for 80 days in one dry (April-September) and one wet (October-March) season during the period from 2008 to 2012.

We prioritize game trails, human paths, or unpaved roads to install the cameras to maximize the opportunity to detect carnivores (Goulart et al. 2009; Srbek-Araujo and Chiarello 2013). As our camera spacing was relatively small in relation to the mesocarnivore home ranges (Sunquist and Sunquist 2002; Reis et al. 2011), we interpreted occupancy estimates as the probability that a mesocarnivore used a site in each reserve (MacKenzie et al. 2006) and we account for possible lack of independence (overdispersion) using an estimated variance inflation factor (MacKenzie and Bailey 2004; see Data Analysis section below).

Data Analysis

Modelling mesocarnivores use and detection as a function of covariates.–To explore the influence of *L. pardalis* on mesocarnivore use (Ψ) we estimated the conditional occupancy probability ($\Psi_{conditional}$) of *L. pardalis* for each camera site in each reserve using the single season occupancy model (MacKenzie et al. 2002) in Program PRESENCE (Hines 2006; **Table 1**). The conditional occupancy probability is defined as the probability that *L. pardalis* was present at a site given it was sampled; if *L. pardalis* was detected at a site, $\Psi_{conditional} = 1$ (MacKenzie et al. 2006; p.97-98). In a previous study conducted in the same Atlantic Forest reserves, we found that *L. pardalis* use was positively related to top predator occurrence (*P. onca* and *P. concolor*) and negatively related to the abundance of domestic dogs (*Canis familiaris*). Additionally, *L. pardalis* detection probability was positively correlated with area of eucalyptus. We used these covariates to derive site-specific estimates of $\Psi_{conditional}$ of *L. pardalis*, and used $\Psi_{conditional}$ as a covariate for our mesocarnivore analysis. We also explored the influence of *L. pardalis* on mesocarnivores use at a reserve scale. A previous study conducted in the same reserves found that *L. pardalis* abundance was significantly higher in the larger, better protected reserve (Rio Doce State Park) , the only reserve where both top predators are present (Massara et al. 2015). Thus, we created a categorical covariate (termed RD) that distinguished Rio Doce (RD = 1) from other reserves (RD = 0).

Next, we explored spatial and temporal variation in detection probability for our mesocarnivore species using another *L. pardalis* covariate. To explore the influence of *L. pardalis* at a finer temporal scale, we modeled detection probability (*p*) of mesocarnivores as a function of whether or not *L. pardalis* was detected in a given occasion (five-day period; see below for further details; **Table 1**). We also considered the number of days that each camera site was operable (total = 40 days for both seasons combined) to model variation in detection probability (covariate termed camera operation; **Table 1**). We expected a positive relationship between this covariate and mesocarnivore detection (e.g., Lewis et al. 2015a; Lewis et al. 2015b).

We tested for species-specific differences in the probabilities of use and detection (covariate termed mesocarnivores), as is typically recommended for multispecies studies (MacKenzie et al. 2006; Shannon et al. 2014). We expected that detection and use of mesocarnivores would be negatively related to *L. pardalis* occurrence (i.e., additive relationships) because *L. pardalis* is a strong competitor and all mesocarnivores may spatial or temporally avoid this species (Oliveira et al. 2010; Oliveira-Santos et al. 2012; Oliveira and Pereira 2014). Alternatively, we tested species-specific differences in the influence of *L. pardalis* on probability of use using natural history characteristics of mesocarnivore species (i.e., interactive relationships). Specifically, we created two covariates that distinguished species that were diurnal (1) from nocturnal (0) species (covariate termed activity period; **Table 2**), and omnivorous (1) from carnivorous (0) species (covariate termed diet; **Table 2**). Additionally, we created one continuous covariate related to the average body weight of each mesocarnivore (**Table 2**). We expected a negative relationship between use of mesocarnivores and *L. pardalis* abundance (RD) or local occurrence ($\Psi_{conditional}$) but only for nocturnal or carnivorous species or those 2-5.4 times smaller than *L. pardalis*.

Finally, we considered another reserve scale covariate (reserve size) to model variation in mesocarnivores use and detection among reserves (**Table 1**). In our system, reserve size was highly correlated with patch size (r = 0.99). To calculate patch size, we used ArcGis 9.2 (ESRI 2008) to map forest patches inside and outside our reserves. We assumed that forest remnants ≤ 250 m from our sampled forests are functionally connected because this distance is transposable by most mammal species (Magioli et al. 2016). Because these two metrics were highly correlated, we chose to use reserve size in our analysis. We expected use and detection probability of mesocarnivores would vary according to reserve size, but we were unsure of the direction of the relationship. Generally, large reserves may represent better habitat quality for native fauna (Gascon et al. 2000), which may increase mesocarnivores distribution (use) within these reserves. However, our studied species may thrive quite well in small reserves. *Procyon cancrivorus, N. nasua* and *C.thous* are generalist and/or matrix - tolerant species (Lyra-Jorge et al. 2008; Ferraz et al. 2010; Cassano et al. 2012) and may benefit from agricultural activities close to small reserves. *Eira barbara* is also a habitat and diet generalist and, apparently, tolerant to forest fragmentation (Mendes Pontes et al. 2016; but see Canale et al. 2012). The more carnivorous species, such as *P. yagouaroundi* and *L. guttulus*, may benefit from an increased abundance of potential preys (i.e., small mammals) in pastures or open fields surrounding small reserves (Di Bitetti et al. 2010).

Table 1 and 2 here

For each camera site we considered whether each mesocarnivore was detected (1) or not (0) during each five-day period that cameras were deployed, yielding a detection matrix where each camera site was sampled on four occasions during each season (each occasion represented a five-day period when cameras were operating at the site). Using these data, we first explored possible changes in mesocarnivore occupancy state (i.e., occupancy dynamics) and detection probability between dry and wet seasons, using a dynamic occupancy model (MacKenzie et al. 2003). We fit four models, where the dynamic parameters (colonization and extinction) were either estimated (non-zero) or fixed to 0 (i.e., occupancy state is static between seasons) and detection varied or not between seasons. We used Akaike's Information Criterion adjusted for small sample size (AICc) and the relative AICc difference among models (ΔAICc) to evaluate which model was better supported by our data (Burnham and Anderson 2002). The dynamic occupancy model was better supported (ΔAICc for the static model = 3.48) but there was uncertainty about a constant detection probability between seasons (ΔAICc for detection varying between seasons = 1.25). However, we had trouble fitting dynamic occupancy models due to our small number of primary periods (one dry and one wet season), and the main focus of our study related to species use, not in factors that may influence changes in species use between seasons. Thus, we used the single season occupancy model (MacKenzie et al. 2002) and considered ‘season’ as another covariate (dry or wet) when modeling either use or detection of mesocarnivores in our subsequent analysis.

We first built 353 models consisting of all additive covariate combinations (Doherty et al. 2012) for use ($\Psi_{conditional}$ of *L. pardalis*, RD, mesocarnivores, reserve size and season) and detection probability (ocelot detection, mesocarnivores, camera operation, reserve size and season) and fit these in program MARK (White and Burnham 1999). This strategy resulted in a balanced model set that allowed us to calculate the cumulative AICc weights for each predictor variable (or covariate) to account for model selection uncertainty (Burnham and Anderson 2002). We explored the potential for lack of independence among the camera sites, using the goodness-of-fit (GOF) test incorporated in Program PRESENCE (MacKenzie and Bailey 2004), using our global model structure, Ψ ($\Psi_{conditional}$ of *L. pardalis* + reserve size + season + mesocarnivores), *p* (ocelot detection + camera operation + reserve size + season + mesocarnivores). As anticipated, the GOF test indicated a lack of independence among the camera sites ($\chi^2 = 42.06$; $P < 0.01$; $\hat{c} = 3.22$) and, therefore, we used the resulting $\hat{c}$ estimate to adjust model selection results and estimates of precision. In other words, we used the Akaike's Information Criterion adjusted for small sample bias and overdispersion (QAICc) in our subsequent analysis (Burnham and Anderson 2002).

We also tested 12 *a posteriori* interactive models to compare their performance (i.e., according to model selection approach) with our previous additive models. These interactive models represented those hypotheses where the response to *L. pardalis* abundance (RD) or local occurrence ($\Psi_{conditional}$ of *L. pardalis*) could differ among mesocarnivore species according to natural history characteristics (i.e., covariate termed Activity period and Diet) or their average body weight. Specifically, we paired six occupancy (Ψ) structures (Diet * RD, Diet * $\Psi_{conditional}$ of *L. pardalis,* Activity period * RD, Activity period * $\Psi_{conditional}$ of *L. pardalis,* Average body weight * RD, and Average body weight * $\Psi_{conditional}$ of *L. pardalis*) with the two detection (*p*) structures in our top additive models [*p* (.) or *p* (Reserve size); see Results section for details].

Activity pattern of mesocarnivores and temporal segregation with ocelots.–We defined an activity sample as all photographs of the same species detected at a camera location within a 1h period, thus minimizing the non-independence of consecutive photographs (Linkie and Ridout 2011).

In order to assess whether *L. pardalis* presence influenced the activity pattern of other mesocarnivores, especially the nocturnal species (**Table 2**), the hour of each activity sample (taken by the camera traps) was transformed into solar time (based on times of sunrise and sunset at each reserve) to adjust the actual time of day to the dial cycle of each mesocarnivore (Ridout and Linkie 2009; Linkie and Ridout 2011). We categorized the activity of the species into diurnal (activity predominantly between 1 h after the sunrise and 1 h before the sunset), nocturnal (activity predominantly between 1 h after the sunset and 1 h before the sunrise), cathemeral (peaks of activity through the diurnal and nocturnal period) and crepuscular (activity occurred 1 h before and after sunrise and sunset). We determined the exact time of sunset and sunrise using the freely-available software Tropsolar 5.0, which used the time of day, date and coordinates of each reserve (Cabús 2015). The approximate time of sunrise and sunset in all reserves during our sampling was 6:00 and 18:00, respectively.

We estimated the activity pattern of each species using kernel density (i.e., density of activity), a nonparametric method for evaluating the probability density function of a random variable (Worton 1989). We calculated the most suitable coefficient of overlap ($\widehat{\Delta}$), which varies from 0 (no overlap) to 1 (complete overlap), between each mesocarnivore and *L. pardalis* (Ridout and Linkie 2009). We used the $\widehat{\Delta}_4$ estimator when the number of independent registers of at least one species had more than 75 photographs. Otherwise (< 75 photographs), we used the $\widehat{\Delta}_1$ estimator (Ridout and Linkie 2009). We calculated the 95% confidence intervals for $\widehat{\Delta}$ from 10,000 bootstrap samples (Ridout and Linkie 2009). Statistical analyses were implemented in R Software (R Development Core Team 2012).

Because each reserve was sampled in different periods (i.e., years and months) and are located in different regions in the Atlantic Forest, we first investigated if there were differences in the activity period of our focal species among reserves using the method described above. This test revealed no differences in the activity period of the species among reserves (minimum value for $\widehat{\Delta}$ was 0.6). Thereafter, we pooled the data from all reserves for each species in the subsequent analysis.

RESULTS

Mesocarnivore registers

We obtained a total of 426 independent registers of all species. *L. pardalis* was the most recorded species (n = 122), followed by *N. nasua* (n = 87), *E. barbara* (n = 76), *P. cancrivorus* (n = 63), *C. thous* (n = 35), *P. yagouaroundi* (n = 30) and *L. guttulus* (n = 13).

Use and Detection Probabilities of Mesocarnivores

Due to our large candidate model set, our most parsimonious model had a low model weight (QAICc weight = 0.07; **Table 3**). The additive model structures were better supported by model selection approach than any interactive model structures; the most parsimonious interactive model structures had a ΔQAICc = 7.06. Therefore, our prediction that *L.pardalis* may influence the mesocarnivores similarly was better supported than our prediction that *L. pardalis* may differentially influence mesocarnivores according to the natural history characteristics or average body weight of the species. However, even those additive model structures that contained *L. pardalis* covariates (i.e., RD or $\Psi_{conditional}$ of *L. pardalis*) had low cumulative QAICc weights and, therefore, this species abundance or occurrence did not strongly influence the probability that a mesocarnivore used a site in the sampled reserves (**Table 4**).

The probability of use was different among mesocarnivore species and was highest for *E. barbara* and *N. nasua* (**Table 4**; **Fig. 2**). Reserve size had a negative relationship ($\hat{\beta}$ = -0.8 x 10^{-4}; *SE* = 0.3 x 10^{-4}) with the probability of mesocarnivores use; estimates of mesocarnivores use were over twice as high in MS (134 ha) compared to RD (35,970 ha, **Fig. 2**). All other covariates had low cumulative QAICc weights (< 0.30) and did not influence the probability that mesocarnivores used a site in the sampled reserves (**Table 4**).

Table 3, 4 and Fig. 2 here

Although previous analyses (i.e., dynamic model) suggested that mesocarnivores use was different between seasons, the subsequent analyses indicated that season had a weak effect on mesocarnivores use and detection when tested together with other more important variables (**Table 4**).

Reserve size was the only covariate that influenced mesocarnivore detection probabilities (**Table 4**). The effect of reserve size was negative, but detection probabilities were similar among areas (*p* for MS, FM and FMA = 0.15; *SE* = 0.04; *p* for SS and SB = 0.12; *SE* = 0.04; and *p* for RD = 0.08; *SE* = 0.07). All other variables had lower cumulative QAICc weights (< 0.35) and did not influence the detection probability of mesocarnivores at used sites (**Table 4**).

Overall, *L. pardalis* showed an intensive nocturnal and crepuscular activity, a similar pattern showed by *P. cancrivorus* and *C. thous* (**Fig. 3**). These two mesocarnivore species showed a high temporal overlap with *L. pardalis* ($\widehat{\Delta} > 0.70$; **Fig. 3**). Although presenting some preference for the first half of nighttime hours, *L. guttulus* was primarily diurnal as well as *E. barbara*, *P. yagouaroundi* and *N. nasua* (**Fig. 3**), which resulted in a low temporal overlap of these mesocarnivores with *L. pardalis* ($\widehat{\Delta} < 0.45$; **Fig. 3**).

Fig. 3 here

DISCUSSION

Contrary to our expectations, *L. pardalis* occurrence did not influence the spatial distribution of mesocarnivores in the Atlantic Forest reserves, which indicates that these mesocarnivores are likely to overlap spatially with *L. pardalis* in the sampled reserves. Our finding was surprising because the studied mesocarnivores share at least one characteristic of natural history with *L. pardalis* and most are 2.0-5.4 times smaller than this cat (**Table 2**). For example, even the smaller and strictly carnivorous cats (*P. yagouaroundi* and *L. guttulus*) did not avoid areas used by *L. pardalis*. Because *L. guttulus* and *P. yagouaroundi* share similar food resources (i.e., small mammals) with *L. pardalis* (Oliveira et al. 2010; Silva-Pereira et al. 2011), we thought these species might spatially segregate with *L. pardalis*. While recent studies showed that high densities of *L. pardalis* have a negative influence on the abundance and density of these smaller cats (Oliveira et al. 2010; Oliveira-Santos et al. 2012; Kasper et al. 2016), our findings suggest that *L. pardalis* fails to completely exclude smaller cats. Moreover, our findings suggest that some species may avoid interspecific competition through temporal segregation (Di Bitetti et al. 2010; Oliveira-Santos et al. 2012).

Dietary overlap may motivate interspecific killing and intraguild killing is one mechanism that may explain the observed temporal segregation between *L. pardalis* and both *P. yagouaroundi* and *L. guttulus* in our sampled reserves (Oliveira et al. 2010; Oliveira and Pereira 2014). It is widely known that *P. yagouaroundi* is diurnal and *L. guttulus* nocturnal (**Table 2**). However, *L. guttulus* exhibited primarily diurnal activity in our sampled reserves. A recent study showed that *L. guttulus* might become more diurnal or cathemeral when it occurs with larger cats, such as *L. pardalis* (Oliveira-Santos et al. 2012). This activity flexibility may decrease temporal overlap with *L. pardalis* and other larger felines and facilitate their coexistence, especially for smaller species, such as *L. guttulus* (**Table 2**). Even though *E. barbara* and *N. nasua* are omnivorous, they also temporally segregated with *L. pardalis*. However, these species are naturally diurnals (**Table 2**), possibly to avoid contact with stronger and dominant competitors. For example, both *E. barbara* and *N. nasua* have been reported in *L. pardalis* diets (Bianchi et al. 2010; Bianchi et al. 2014). We were surprised by the lack of influence of *L. pardalis* on two nocturnal species (*P. cancrivorus* and *C. thous*). Previous studies reported these species in *L. pardalis* diets (Crawshaw JR. 1995; Bianchi et al. 2010); however, *L. pardalis* may only occasionally predate on these species (Oliveira and Pereira 2014). Even though these species are omnivorous (**Table 2**), they may consume more plant material, fruits and invertebrates than small vertebrates (Gatti et al. 2006; Rocha-Mendes et al. 2010; Quintela et al. 2014), which may decrease their dietary overlap with *L. pardalis* and thus, minimize interspecific competition with the latter species. Additionally, these species, especially *P. cancrivorus*, might share similar body sizes with *L. pardalis*, also minimizing interspecific competition with the latter species (**Table 2**).

Mesocarnivores use was negatively influenced by reserve size (**Fig. 2**). This is not entirely surprising because most of or study species (*E.barbara*, *N. nasua*, *P. cancrivorus*, *C.thous*) are habitat and diet generalist and/or matrix-tolerant species and, therefore, may benefit from agriculture expansion and habitat fragmentation in the Atlantic Forest (Lyra-Jorge et al. 2008; Cassano et al. 2012; Mendes Pontes et al. 2016). It is relevant to mention that our system of forest remnants is entirely composed by protected areas and, further, that our smallest reserve (i.e., MS, 134 ha) is not small compared to the vast majority of Atlantic forest remnants (< 50 ha; Ribeiro et al. 2009). Species such as *P. yagouaroundi* and *L. guttulus* may benefit even further from smaller reserves due to the absence or low abundance of larger and stronger competitors (Oliveira et al. 2010). Recent studies suggested, for example, that *L. guttulus* are more abundant in smaller protected areas probably as a result of competitive release from *P. concolor* and *L. pardalis* (Di Bitetti et al. 2010; Oliveira-Santos et al. 2012). Our study showed that both *L. guttulus* and *P. yagouaroundi* occurrences were not influenced by *L. pardalis* presence, but the presence of other large carnivores, such as *P. concolor* and *P. onca* may indeed negatively correlate with the occurrence of these smaller cats and should be investigated in future studies.

We cannot exclude the possibility that prey abundance for these small cats is higher in smaller and more degraded Atlantic Forest reserves (Di Bitetti et al. 2010). In fact, these species may take advantage of the higher amount of open areas in smaller reserves of Atlantic Forest (Ribeiro et al. 2009; Tabarelli et al. 2010). Open areas, such as pasture and fields, may promote population explosions of some small granivorous/folivores mammals mainly because these species prefer areas with higher herbaceous cover and relatively low woody cover (Paglia et al. 1995; Vieira 2003; Henriques et al. 2006). Alternatively, closed canopy areas tend to have higher densities of semi-arboreal and arboreal frugivorous/insectivorous small mammals (Vieira 2003; Henriques et al. 2006), which are less likely to be predated by *P. yagouaroundi* and *L. guttulus* because these species do most of their hunting on the ground (Sunquist and Sunquist 2002; Tófoli et al. 2009).

Additionally, our results indicate that the probability of use was higher for *E. barbara* and *N. nasua* than any other mesocarnivore (**Fig. 2**). Both species are usually common in camera trap studies in fragmented areas of Atlantic Forest (Lyra-Jorge et al. 2008; Paschoal et al. 2012; Cassano et al. 2014); however, the relatively low probability of use by the other mesocarnivores is concerning.

In our study, we found low detection probabilities among mesocarnivore species, which resulted in a low precision of our use estimates (i.e., large confidence intervals). However, low detection probabilities are common among carnivore studies and our 'average' detection probability obtained from our most parsimonious model was $\hat{p} = 0.14$, which is comparable to estimates reported for other carnivore studies: $\overline{p} = 0.17$; range: 0.02 to 0.79 (Harmsen et al. 2011; Foster and Harmsen 2012).

Overall, we observed contrasting temporal patterns, indicating that some mesocarnivore species, notably *L. guttulus*, may adjust their activity patterns to avoid a direct contact with *L. pardalis*, thus facilitating their coexistence in Atlantic Forest remnants. For other species, *L. pardalis* occurrence did not influence their activity pattern, which may reflect their tolerance to *L. pardalis* or their lower degree of dietary overlap with this species. Other studies found similar results: a lack of spatial avoidance among sympatric carnivores in Central America (Davis et al.

2011) and in Asia (Sunarto et al. 2015), which suggests that temporal and diet avoidances seem stronger segregators than spatial avoidance among sympatric carnivores (Sunarto et al. 2015).

Finally, dietary investigations may clarify and add information about how these sympatric species share or segregate food resources in this potentially competitive scenario of the Atlantic Forest. Additionally, other variables should also be tested to better understand the relation between *L. pardalis* and other mesocarnivores and clarify why related species may have different use probabilities and tolerances in this human-managed biome. Species interactions may vary across a habitat or land-use gradients (Lewis et al. 2015a) and thus, land cover types might be responsible for a direct and different influence on mesocarnivores use in this biome. For example, two of our reserves (i.e., FM and RD) are surrounded by permeable eucalyptus, which *L. pardalis* may utilize as travel routes to move between native habitats within or outside reserves (Massara et al. 2015). *L. pardalis* is a forest dependent species (Sunquist and Sunquist 2002) and may avoid reserves surrounded by open areas (e.g., pasture), such as in FMA. Conversely, native habitats surrounded by pasture and croplands might be used frequently by matrix tolerant species, such as *N. nasua*, *E. barbara, P. cancrivorus* and *C. thous* (Lyra-Jorge et al. 2008; Ferraz et al. 2010; Mendes Pontes et al. 2016). Therefore, it is likely that the characteristic of the matrix may either increase or decrease the contact rates among sympatric carnivores, influencing the interspecific competition and the mesocarnivore use probabilities. Thus, future studies should investigate how these variables may affect mesocarnivore dynamics in these small remnants of Atlantic Forest to avoid future declines in this biome.

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List of tables

Table 1. Covariates used to model species-specific probabilities of use (*Ψ*) and detection (*p*) of mesocarnivores in six Atlantic Forest reserves in southeastern Brazil. Mean and range (minimum - maximum) of each covariate are given for each reserve combining dry and wet seasons. The Ocelot detection value reported here is the mean proportion of occasions (out of 8 total) with ocelot detections among sites.

Covariate	**Reserve**					
	Mata do Sossego	**Fazenda Macedônia**	**Feliciano Miguel Abdala**	**Sete Salões**	**Serra do Brigadeiro**	**Rio Doce**
$\Psi_{conditional}$ of *L. pardalis*	0.52 (0.10-1.00)	0.92 (0.24-1.00)	0.23 (0.01-1.00)	0.45 (0.11-1.00)	0.64 (0.11-1.00)	0.76 (0.22-1.00)
Ocelot detection	0.09 (0.00-0.63)	0.23 (0.00-0.50)	0.02 (0.00-0.13)	0.06 (0.00-0.50)	0.09 (0.00-0.25)	0.16 (0.00-0.50)
Camera operation	40.00 (40.00-40.00)	40.00 (40.00-40.00)	32.14 (2.00-40.00)	30.04 (9.00-40.00)	39.00 (20.00-40.00)	40.00 (40.00-40.00)
Reserve size (ha)	134	560	958	12,520	14,985	35,970

Table 2. Natural history characteristics used to model species-specific probabilities of use (Ψ) of mesocarnivores in six Atlantic Forest reserves in southeastern Brazil. Diet and activity period data are from Emmons and Feer (1999) and Wilson and Mittermeier (2009), and average body weight data are from Oliveira and Pereira (2014) and Wilson and Mittermeier (2009).

Species	**Average body weight (kg; minimum – maximum)**	**Diet**	**Activity period**
Leopardus pardalis	11.0 (6.60 - 15.50)	Carnivorous	Nocturnal
Procyon cancrivorus	8.80 (2.00 - 12.00)	Omnivorous	Nocturnal
Cerdocyon thous	5.70 (4.50 - 8.50)	Omnivorous	Nocturnal
Puma yagouaroundi	5.20 (3.00 - 7.60)	Carnivorous	Diurnal
Eira barbara	4.60 (2.70 - 7.00)	Omnivorous	Diurnal
Nasua nasua	3.90 (2.00 - 7.20)	Omnivorous	Diurnal
Leopardus guttulus	2.40 (1.50 - 3.50)	Carnivorous	Nocturnal

Table 3: Model selection results for the top 10 models of the probabilities of use (Ψ) and detection (p) of mesocarnivores in six Atlantic Forest reserves in southeastern Brazil.

Model[a]	**QAICc**	**Delta QAICc**	**QAICc Weights**	**Parameters**	**QDeviance**
Ψ (Mesocarnivores + Reserve size), p (.)	596.76	0.00	0.07	8	580.66
Ψ (Mesocarnivores), p (Reserve size)	598.07	1.31	0.04	8	581.97
Ψ (.), p (Mesocarnivores + Reserve size)	598.36	1.60	0.03	8	582.26
Ψ (Mesocarnivores + Reserve size), p (Ocelot detection)	598.37	1.61	0.03	9	580.25
Ψ (Mesocarnivores + Reserve size + $\Psi_{conditional}$ of *L. pardalis*), p (.)	598.41	1.68	0.03	9	580.32
Ψ (Mesocarnivores + Reserve size), p (Reserve size)	598.47	1.71	0.03	9	580.34
Ψ (Mesocarnivores + Reserve size), p (Camera operation)	598.59	1.83	0.03	9	580.46
Ψ (Mesocarnivores + Reserve size), p (Season)	598.67	1.91	0.03	9	580.54
Ψ (Mesocarnivores + Reserve size + Season), p (.)	598.78	2.03	0.03	9	580.66
Ψ (Mesocarnivores), p (Ocelot detection + Reserve size)	599.59	2.83	0.02	9	581.46

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

Table 4. Cumulative QAICc weights for covariates used to model the probabilities of use (Ψ) and detection (p) of mesocarnivores in six Atlantic Forest reserves in southeastern Brazil.

Covariate	**Cumulative QAICc Weights (%)**
Use (Ψ)	
Mesocarnivores	69.49
Reserve size	55.18
$\Psi_{conditional}$ of *L. pardalis*	28.35
Season	19.33
RD	09.15
Detection (p)	
Reserve size	54.77
Mesocarnivores	31.33
Ocelot detection	21.99
Season	19.79
Camera operation	19.74

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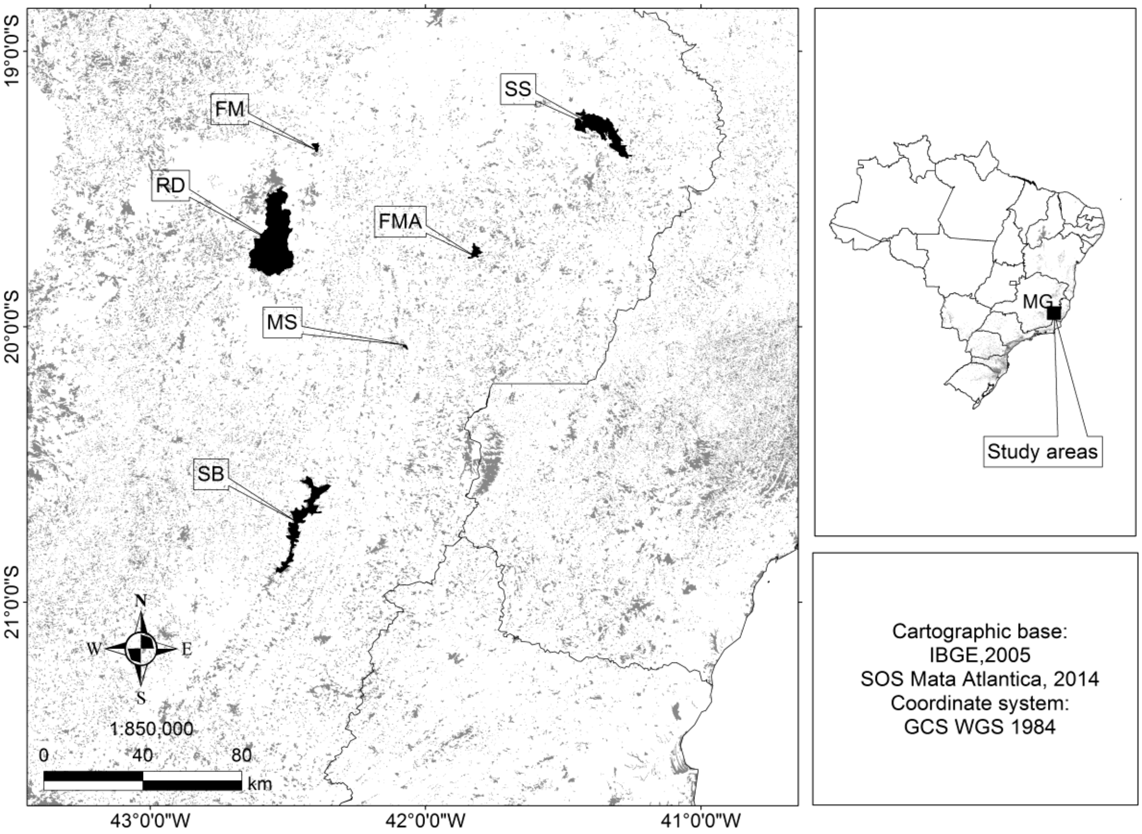

Fig. 1.–Locations of the six Atlantic Forest reserves (MS= Mata do Sossego Reserve; FMA= Feliciano Miguel Abdala Reserve; FM= Fazenda Macedônia Reserve; SS= Sete Salões State Park; SB= Serra do Brigadeiro State Park; RD= Rio Doce State Park) sampled for mesocarnivores in the Atlantic Forest, State of Minas Gerais (MG), southeastern Brazil. The current distribution of Atlantic Forest remnants are shown in the insert (gray area) and follow SOS Mata Atlântica (2014). The state divisions are from the Brazilian Institute of Geography and Statistics (IBGE 2005).

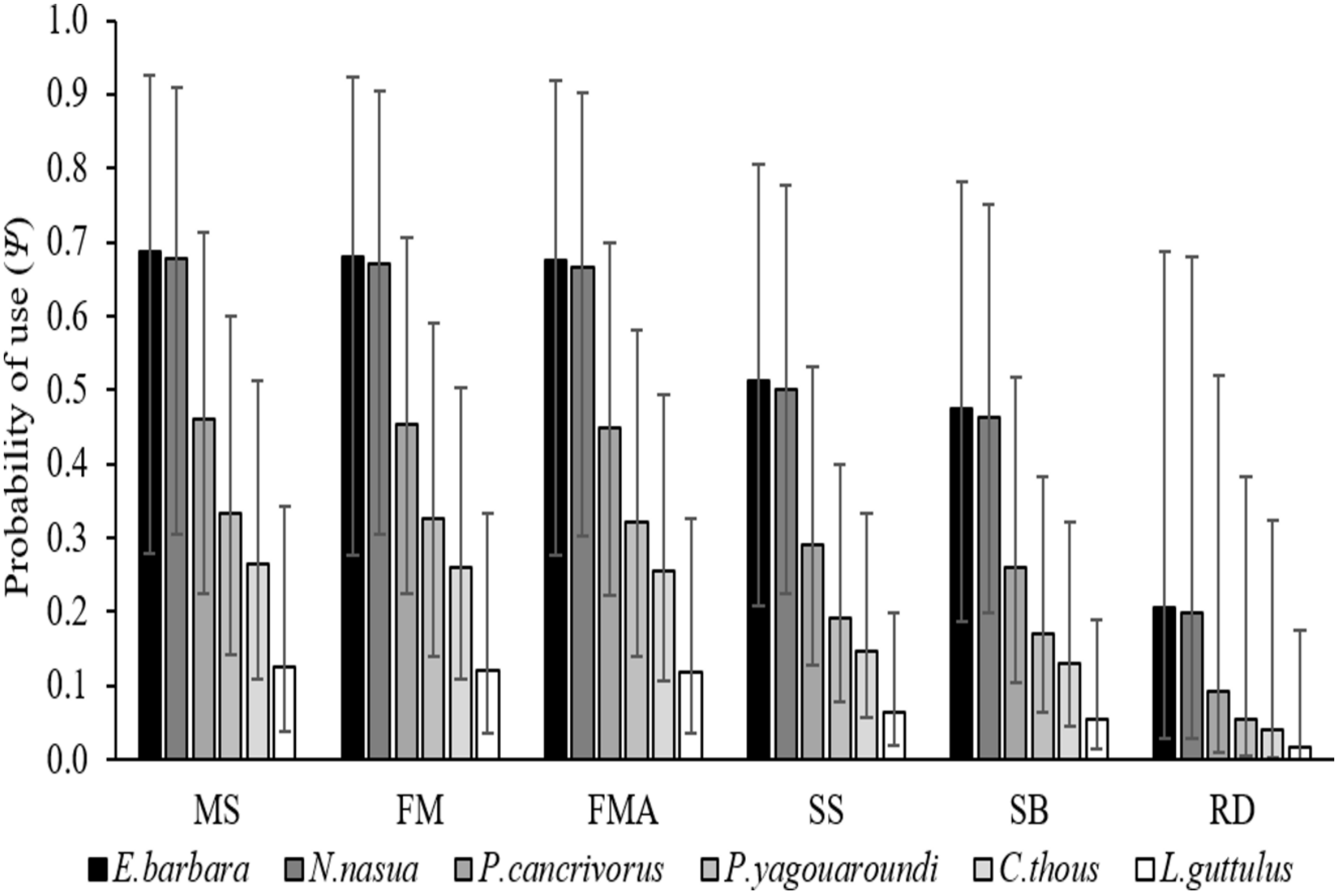

Fig. 2.–Estimated probabilities of use of mesocarnivores at sites in six Atlantic Forest reserves in southeastern Brazil (MS= Mata do Sossego Reserve, 134 ha; FM= Fazenda Macedônia Reserve, 560 ha; FMA= Feliciano Miguel Abdala Reserve, 958 ha; SS= Sete Salões State Park, 12,520 ha; SB= Serra do Brigadeiro State Park, 14,985 ha; RD= Rio Doce State Park, 35,970 ha). These estimates are from the most parsimonious model that included those covariates that had the highest cumulative QAICc weights for Ψ (Mesocarnivores + Reserve size) and p (Reserve size).

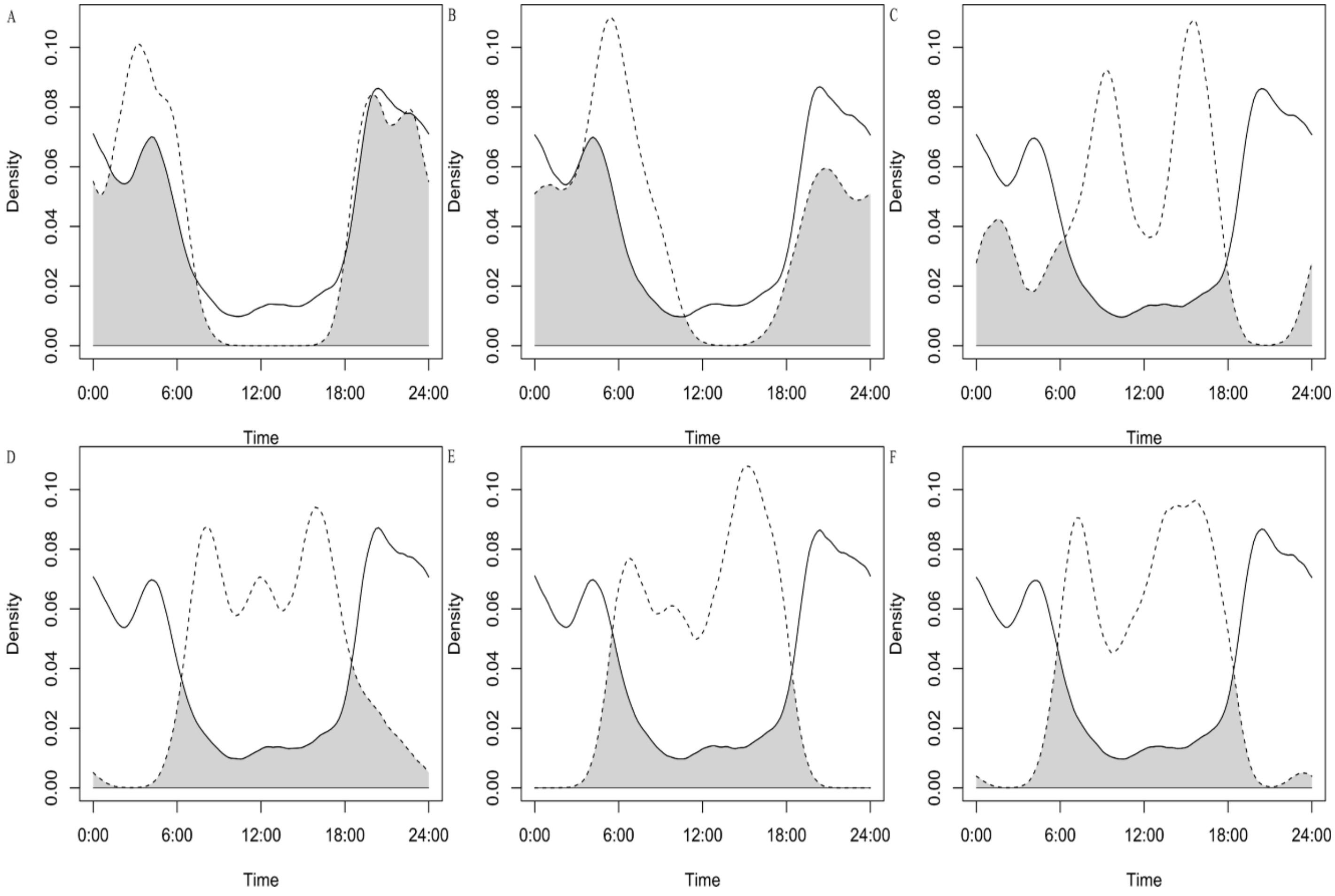

Fig. 3.–Temporal activity of mesocarnivores and degree of overlap between ocelot (*L. pardalis*, solid line) and mesocarnivores (dotted lines). Figures include: (A) *P. cancrivorus*; $\hat{\Delta}_1$ = 0.81 with 95% CI = 0.73-0.91, (B) *C. thous*; $\hat{\Delta}_1$ = 0.74 with 95% CI = 0.60-0.88, (C) *L. guttulus*; $\hat{\Delta}_1$ = 0.44 with 95 % CI = 0.22-0.60, (D) *E. barbara*; $\hat{\Delta}_4$ = 0.38 with 95% CI = 0.25-0.44, (E) *P. yagouaroundi*; $\hat{\Delta}_1$ = 0.36 with 95% CI = 0.19-0.40, and (F) *N. nasua*; $\hat{\Delta}_4$ = 0.33 with 95% CI = 0.21-0.38. Overlap between activity periods is represented by the shaded area. The x-axis represents time, where sunrise and sunset are approximately 6:00 and 18:00 respectively. The y-axis range is the kernel density.

Conclusion and recommendations

Our main findings indicate that ocelots respond negatively to habitat loss, and thrive in protected areas (or reserves) inhabited by top predators, where the presence of exotic species, such as domestic dogs, is less likely. Therefore, our results do not support the hypothesis of mesopredator release. Instead, other environmental factors influence ocelot abundance and its distribution (i.e., probability of use) in Atlantic Forest remnants, such as the level of protection and quantity and quality of forest remnants. Additionally, our findings suggest that ocelots can be an effective focal species to evaluate the degree of landscape-level connectivity (or fragmentation) in Atlantic Forest remnants. For example, ocelots may still persist (e.g., high abundance and probability of use) in small remnants but only those that have adequate connections to larger protected areas, such as Fazenda Macedônia reserve, which is connected with the largest protected area (Rio Doce State Park) by smaller native fragments and permeable areas of eucalyptus. Therefore, without increased connectivity and an appropriate protective legislation, the outlook for these carnivores in the Atlantic Forest is pessimistic.

A good conservation strategy might be to improve connections via native vegetation and protection through the Brazilian Forest Code (Federal Law number 12651 from May 25, 2012). However, the new Brazilian Forest Code reduced Brazil's environmental debt by ~ 60% (Soares-Filho *et al.*, 2014). The changes implemented in 2012 mean that Legal Reserves (LRs: native vegetation in rural properties) and Riparian Preservation Areas (RPAs: riverside forest buffers in rural properties) deforested illegally before 2008 that would have required restoration under the previous Brazilian Forest Code (Federal Law number 4771 from September 15, 1965), no longer need to be restored. These changes were accomplished by forgiving the Legal Reserve debt and relaxing Riparian Preservation Areas restoration requirements in "small" properties ranging in size from 20 ha in southern Brazil to 440 ha in the Amazon (Soares-Filho *et al.*, 2014). As a result, 90% of Brazilian rural properties qualify for amnesty (Soares-Filho *et al.*, 2014). Relative to the previous Forest Code, this current amnesty given for illegal deforestation decreased the total area to be restored by ~ 60% for LRs and by 70% for RPAs in the Atlantic Forest (Soares-Filho *et al.*, 2014). Additionally, this new Forest Code removed protections for other natural areas, allowing farmers and ranchers to deforest and convert some of these areas. These losses may have a negative effect on carnivore conservation, especially in the Atlantic Forest, where less than 20% of the original forest cover remains (Ribeiro *et al.*, 2009).

On the other hand, the new Brazilian Forest Code brought some potential advantages in preserving the remaining native habitats, which might be used for connecting protected areas in the Atlantic Forest. The new Brazilian Forest Code created the environmental rural registry (acronym in Portuguese, CAR), which establishes that the owners or occupiers of rural lands must enroll their properties in the CAR. The CAR is mandatory and provides a digital database for monitoring and combating illegal deforestation of protected native vegetation, such as RPAs and LRs, within rural properties. The deadline to register in the CAR is the end of May 2016 and if the rural land owner fails to comply with this environmental regulation, they will be subjected to criminal liabilities. According to information provided by the Brazilian Environmental Ministry, ~ 240 Mha (out of ~ 400 Mha total) has already been registered in the CAR (MMA, 2015). The CAR therefore will help the government agencies to find properties that are not compliant with the Forest Code, serving at least in theory, as a mechanism to promote restoration practices by owners of private lands, where most of remaining native vegetation in Brazil is located (Sparovek *et al.*, 2012).

Our findings suggest that eucalyptus intermingled with native areas may connect reserves, acting as a movement habitat for carnivores and may help to mitigate the problem of protected area isolation. We believe management solutions that combine conservation with production goals need to be considered, especially in a biome where most areas have already been converted into different production systems (Tabarelli *et al.*, 2010). For example, eucalyptus plantations occupied ~ 6 Mha of the area of planted trees in Brazil, representing ~ 72% of the total, and are located mainly (i.e., ~ 43 %) in southeastern Brazil (IBÁ, 2015). Eucalyptus is cultivated in different management systems and for different purposes, such as for pulp production and wood for furniture (IBÁ, 2015). Obviously, the different management systems do not have the same capabilities to promote connection among the remaining native vegetation. It is crucial, therefore, to investigate the characteristics of the matrix for maintaining the remaining fauna (Millan, Develey & Verdade, 2015). For example, future studies should compare different management practices of eucalyptus and highlight those that are potentially useful to improve the connectivity among nature habitats.

Our study also highlights the importance of buffer zones (i.e., areas external to natural reserves where human activities are subject to specific norms and restrictions) for improving the viability of carnivore populations in Atlantic Forest protected areas. Theoretically, buffer zones were created to minimize threats to the protected ecosystem but in practice, it is in the hands of the managers of the protected areas together with the licensing institution to indicate the most appropriate activity within buffer zones (Vitalli, Zakia & Durigan, 2009). For example, these areas could minimize threats related to edge effects, especially those related to the entrance of domestic dogs. According to the Brazilian system of protected areas (acronym in Portuguese, SNUC), the size of the buffer zone must be defined by the management plan of each reserve (Federal Law number 9985 from July 18, 2000). If the protected area was established without a clear definition of the buffer zone area, it must encompass a buffer of 3 km from the perimeter of the reserve (Federal Resolution number 428 from December 17, 2010). However, this size may not be adequate for protecting species from external threats. Domestic dogs, for example, are able to travel (linear) distances of up to 5.5 km between their residence and the nearest protected area (Paschoal *et al.*, 2012). Additionally, the potential invasion of dogs may be facilitated by the edge proximity of the Atlantic Forest remnants. Over 70% of the remaining Atlantic forest is <250 m from any non-forest area (Ribeiro *et al.*, 2009). Therefore, if management plans fail to include an effective buffer zone for each specific protected area, it is unlikely that native carnivores, such as ocelots, can be protected within these reserves. For example, our study indicates that planted forests in the buffer zone, especially eucalyptus, may be an interesting alternative to favor native carnivore movements between protected areas.

Overall, to minimize the current scenario of the Brazilian Atlantic Forest deforestation and thus conserve the medium and large size mammal carnivores, we suggest increasing connectivity among protected areas using the already available native habitats within private rural lands as well as those permeable habitats in the surrounding reserves (i.e., eucalyptus). Because buffer zones can be explored or modified either to protect or to impact native fauna inside protected areas, allowing for example, the dispersion of exotic species through the protected area, an adequate management of buffer zones are mandatory, especially because most Atlantic Forest protected areas are embedded in matrices greatly modified by human activities. Surprisingly, however, studies addressing the importance of buffer zone or assessments of its adequate dimension and / or restrictions are still very few in Brazil (Massara *et al.*, 2012).

Our suggestions might also be applied in a broader context because mammalian carnivores are facing serious threats and experiencing large population declines worldwide (Ripple *et al.*, 2014). These population declines are mainly related to anthropogenic impacts and our main challenge is finding smart solutions to maintain viable populations of these species in the actual scenario of alternative land uses (Ripple *et al.*, 2014). For example, the proportions of geographic ranges of medium to large carnivores that lie within large protected areas remain low in most cases (Cantú-Salazar & Gaston, 2010). Therefore, it is unlikely that we can find very large and adequate protected areas required to house viable populations of carnivores in a scenario with other societal demands. This means that the immediate surrounding matrix must also be managed for protecting carnivores. For example, large carnivore distributions in Europe are generally expanding, which is likely related to matrix suitability and protective legislation rather than to the contribution of the protected area system (Chapron *et al.*, 2014). Finally, we suggest that without protective legislation, supportive public opinion, and matrix alterations, the outlook for carnivores in the current scenario of human-managed habitats is pessimistic.

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