Programa de Pós-Graduação em Ecologia e Conservação
Centro de Ciências Biológicas e da Saúde
Universidade Federal de Mato Grosso Do Sul

Space and time partitioning among carnivore mammals in the Pantanal wetland

Vania Cristina Foster

Campo Grande
August 2017

Space and time partitioning among carnivore mammals in the Pantanal wetland

Vania Cristina Foster

Thesis presented as a requirement for obtaining the PhD degree in Ecology, by the Ecology and Conservation Graduate Program, Universidade Federal de Mato Grosso do Sul.

Advisor: Erich Fischer
Co-advisor: Pedro Bernardo Marques da Silva Rodrigues Sarmento and Carlos Manuel Martins Santos Fonseca.

Advisory Committee

Dra. Marina Zanin Gregorini
[Universidade Federal do Espírito Santo]

Dr. Guilherme de Miranda Mourão
[Universidade Federal de Mato Grosso do Sul]

Dr. Luiz Gustavo Rodrigues Oliveira Santos
[Universidade Federal de Mato Grosso do Sul]

I would like to dedicate this thesis to my parents for all love, dedication and comprehension;

Also, I would like to dedicate this dissertation to my friends and colleagues that help to build this history.

Acknowledgments

I thank Erich Fischer for his support and guidance during this project, for his friendship during these years and for his encouraging words to continue when things were not working out. I also tank Pedro Sarmento for patient help with statistical analysis and reviewing on early drafts with important comments and suggestions.

I also want to thank the Programa de Pós-Graduação em Ecologia e Conservação da Universidade Federal de Mato Grosso do Sul (UFMS) for all logistic support, with special thanks to Rosilene Bejarano who helped me whenever I needed, thank you so much!

I thank the Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul for a scholarship grant (23/200.652/2013), and the Conselho Nacional de Desenvolvimento Científico e Tecnológico for a sandwich scholarship (PDSE 6207/15-4) for a PhD stage in the Universidade de Aveiro, Portugal. I especially thank Carlos Fonseca for all support during my PhD stage in the Departamento de Vida Selvagem, Universidade de Aveiro.

I am grateful to Panthera for financial support for the conservation of *Puma yagouaroundi* under its Small Cat Action Fund (SCAF) grant scheme, and Idea Wild and Departamento de Vida Selvagem, Universidade de Aveiro for donation of the camera traps.

I also thank the partners of this project and farmers: Camilo Barros (Sagrado ranch), Vicente Gomes (Cáceres ranch), Mônica Fiore (Mata Grande ranch), Henrique Concone (San Francisco Hotel Ranch) and Instituto Homem Pantaneiro (IHP), for all support and for have believed in my work, and thank André Coelho for help with maps and to landscape analyses.

Special thanks to Grasiela Porfírio who gently offered her data from the natural reserve Eliezer Batista, reviewed and made important comments and suggestions on the manuscript, and encouraged the work. I also thank Wellington Fava (Weg) for all support in these years, to hear me and help during the most difficult times, and mainly to said me "it is the time to stop" at the right moment. Weg thank you so much my friend!

I also thank Marina Portugal, Ale Bertassoni, Rita Torres, Tania Caetano, Patricia Salvarani, Cristiane Fukaiama and Iana Ciarlini for their friendship, encouraging words and for being with me every time, in the good and bad times! You guys are very important in my life!

Thanks also to all the students and friends of the Laboratório de Ecologia do Instituto de Biologia (Inbio): Alêny Francisco, Alan Eriksson, Carol Santos, Nina Attias, Gabriel Ghizzi, Vanessa Nobrega, Ricardo Leroy and Walfrido Tomas. This project took some years to accomplish and during all this time I met and worked with many friends, colleagues and special peoples that will be impossible to mention, but I will always remember them and thank them for all their help and support.

Finally, special thanks to my parents, to understand my absence during my field work, for all love, and principally to understand all my stress during this final period. Thanks to Fred to stay by my side in this worst period, with love and comprehension!

To all of you many thanks! Without you, none of this would be possible!

Index

Abstract

Carnivores are considered a key component of animal communities, influencing the structures and dynamics of most communities around the world. However, carnivores represent some of the most threatened species as a result of the land-use changes, loss or degradation of habitat, persecution by humans, decline of their natural preys, and diseases. Once large carnivores control both herbivores populations, through predation, and mesopredator carnivore populations though intraguild competition, their decline result in cascading effects. Additionally it is known that species of carnivores can negatively interact through competition by interference or exploitation. Therefore, coexistence of potential competitors may depend upon temporal and/or spatial partitioning of resources.

In the present thesis, I address habitat selection, circadian rhythm and intraguild competition in the use of space by the Pantanal carnivore species. I access richness and distribution of carnivore species, estimate their occupancy rates and the factors affecting occupancy and detectability, and evaluate potential spatial and temporal partitioning between the predator and mesopredator species. Data was obtained using camera trapping and analyzed by single season species occupancy models, accounting for imperfect detection. I used kernel density to describe activity patterns, and pairwise co-occurrence approach to evaluate the co-occurrence among carnivore species in four regions of the Pantanal wetland.

Combining all study sites and camera trap stations, was recorded 11 carnivore species in 1109 independent records. Among the study sites Sagrado ranch was the richest (11 species detected) site. Regarding the probability of occupancy (ψ), the outcome varied among focal species with the highest probability of occupancy for the coati ($\psi = 0.79 \pm 0.10$) and the lowest for the tayra ($\psi = 0.35 \pm 0.11$). The species exhibited a notorious variability of detection probabilities (p), with the highest value for the crab-eating fox ($p = 0.50 \pm 0.06$), and the lowest one for the puma ($p = 0.18 \pm 0.04$). The inclusion of variables in the occupancy models showed that presence of top predators, such as puma, has the most consistent effect on the mesopredator community, with positive influence, followed by the habitat categories. Unlike expected, puma was present in the occupancy models of four species with a positive influence which can be an indicator of aggregation between them probably as a result of same habitat selection patterns. Prey availability had the most consistent effect on the predator community with positive influence in the occupancy estimative of jaguar and pumas. Regarding to detectability, the habitat categories was the most important predictor, influencing positively or negatively the detection probability of carnivore species. The general activity patterns found in the present study resemble those reported elsewhere for most carnivore species, with crepuscular or nocturnal activity, except that tayra, coati and jaguarundi are mostly diurnal in the Pantanal. According to the pairwise co-occurrence approach, most pairs of species co-occurred more than expected by chance, an evidence of low spatial avoidance among the Pantanal carnivores.

Finally, the major findings of this study were that carnivores largely use similar resources, with the share of space and/or time between few species, thus showing a low general level of niche partitioning in the Pantanal. In addition, different circadian rhythms contributed more than spatial partitioning for niche segregation among carnivores. In conclusion, the ability of carnivore species in modifying their activity patterns to avoid predators or competitors, or to adjust to the availability of their main preys, is a likely main character that facilitates their coexistences in the Pantanal.

Keywords: Carnivores, Coexistence, Activity Patterns, Occupancy, Detectability, Pantanal

Resumo

Carnívoros são considerados componentes chave na comunidade animal, influenciando a estrutura e a dinâmica da maioria das comunidades ao redor do mundo. No entanto, os carnívoros representam algumas das espécies mais ameaçadas, resultado das mudanças no uso do solo, perda e degradação de habitat, perseguição por humanos, declínio de suas presas principais e doenças. O declínio de grandes carnívoros resulta em um efeito cascata, uma vez que eles controlam as populações de herbívoros por meio da predação e as populações de mesopredadores por meio de competição intraguilda. Adicionalmente, espécies de carnívoros podem interagir negativamente por meio de competição por interferência ou exploração. Assim, a coexistência entre potenciais competidores pode depende da partilha temporal e/ou espacial de recursos.

Na presente tese estudei a seleção de habitat, os ritmos circadianos e a competição intraguilda quanto ao uso do espaço pelas espécies de carnívoros do Pantanal. Analisei a riqueza e distribuição de espécies de carnívoros, estimei suas taxas de ocupação e os fatores que afetam a ocupação e a detectabilidade, e avaliei a partilha espacial e temporal

entre grandes predadores e mesopredadores. Os dados foram obtidos com auxílio de armadilhas fotográficas e analisados meio de modelos de ocupação, considerando a detecção imperfeita. Utilizei densidade de kernel para descrever o padrão de atividades, e uma abordagem de co-ocorrência par-a-par para avaliar a co-ocorrência entre as espécies de carnívoros em quatro regiões do Pantanal.

Combinando todas as áreas de estudo e estações de armadilhas fotográficas, 11 espécies foram registradas em 1109 registros independentes. Dentre as áreas de estudo a Fazenda Sagrado foi a que apresentou maior riqueza de espécie (11 espécies detectadas). Relativamente à probabilidade de ocupação (ψ), os resultados variaram entre as espécies focais, com a maior probabilidade de ocupação registrada para o coati ($\psi = 0.79 \pm 0.10$) e a menor para a irara ($\psi = 0.35 \pm 0.11$). As espécies exibiram uma notória variabilidade na probabilidade de detecção (p), com o maior valor verificado para o cachorro-do-mato ($p = 0.50 \pm 0.06$), e o menor para a onça-parda ($p = 0.18 \pm 0.04$). A inclusão de variáveis nos modelos de ocupação demostrou que a presença de predadores de topo, como por exemplo a onça-parda, possuem o efeito mais consistente na comunidade de mesopredadores, com influência positiva, seguida pelas categorias de habitat. Ao contrário do esperado a onça-parda esteve presente nos modelos de ocupação de quatro espécies de mesopredadores com influência positiva o que pode ser considerado um indicador de agregação entre eles, provavelmente como um resultado de um padrão de seleção dos mesmos habitats. A disponibilidade de presas, teve o efeito mais consistente na comunidade de predadores com influência positiva na estimativa de ocupação de onça-pintadas e onça-pardas. Em relação à detectabilidade, categorias de habitats foi o preditor mais importante, influenciando positiva e negativamente a probabilidade de detecção das espécies de carnívoros. Os padrões gerais de atividade encontrados no presente estudo se assemelham com os já relatados em outros lugares para a maioria das espécies de carnívoros, com atividade crepuscular ou noturna, com excessão da irara, coati e jaguarundi, os quais são majoritariamente diurnos no Pantanal. De acordo com a abordagem de co-ocorrência par-a-par, a maioria dos pares de espécies estudadas ocorreram mais vezes do que o esperado por chance (aleatoriamente), uma evidência de baixa evasão espacial.

Por fim, os resultados deste estudo permitem concluir que os carnívoros utilizam amplamente recursos similares, com compartilhamento do espaço e/ou do tempo entre poucas espécies, demonstrando assim, em geral, baixa segregação de nicho no Pantanal. Adicionalmente, diferentes ritmos circadianos contribuíram mais que a partilha espacial

para a segregação de nicho dentre os carnívoros. Concluindo, a habilidade das espécies de carnívoros em modificar seus padrões de atividade para evitar predadores ou competidores, ou para ajustarem-se à disponibilidade de suas presas principais, é provavelmente a principal característica que facilita a coexistência delas no Pantanal.

Palavras - chaves: Carnívoros, Coexistência, Padrão de Atividade, Ocupação, Detectabilidade, Pantanal

Introduction

Carnivores (Mammalia: Carnivora) are a group of ecological importance in several ecosystems (Gese 2001, Gittleman et al. 2001, Barea-Azcon et al. 2006). They comprise species of different sizes that play a significant role in maintaining the structures and dynamics of most communities around the world (Prugh et al. 2009, Prevosti & Pereira 2014, Ripple et al. 2014). Carnivores includes large-sized specialized top predators, which occupy the higher position in food webs, and mesopredators, that comprise medium-sized species situated in trophic levels below top predators (Ritchie & Johnson 2009, Roemer et al. 2009). These predators contribute in a variety of ways as indicators of ecosystem health (Noss et al. 1996), regulation and evolution of prey populations (Terborgh et al. 2001), seed dispersal (López-Bao & González-Varo), control of disease transmissions (Pongsiri et al. 2009), carbon storage to buffer climate change (though the herbivores control) and biodiversity enhancement (Terborgh et al. 2010). Nonetheless, carnivores have suffered a global decline as a result of the land-use changes, loss or degradation of habitat, persecution by humans, decline of their natural preys, and diseases (Gese 2001, Di Minin et al. 2016). Since they often require large areas and occur in low population densities, these environmental alterations have caused substantial reduction of their populations (Gese 2001). For this reason, the carnivore guild globally shows a significant number of species threatened to extinction, especially the largest ones (Ripple et al. 2014).

Large carnivores can control both herbivores populations through predation, thereby limiting the pressure in the plant communities, and mesopredator carnivore populations though intraguild competition (Terborgh et al. 1999, Miller et al. 2012). Therefore, removal of large carnivores of a particular ecosystem results in cascading effects (Ripple et al. 2014, 2016). Declining abundance of top predators can favor an increasing of mesopredators – known as “mesopredator release” – that, in turn, change the food web structures and the ecosystems’ functions (Prugh et al. 2009). For instance, the removal of the largest Australian land predator (*Canis lupus dingo*) has been linked to the expansion of invasive mesopredators and to the reductions of small mammals preyed on by the mesopredators, and of plant biomass due to increased herbivory by kangaroos (Letnic et al. 2012). Other example of top predator importance for ecosystem function has been verified in the Yellowstone National Park (Ripple & Beschta 2012). Although the park is still in early stage of ecosystem recovery, it is notable the trophic cascade restoration 15 years after wolf (*Canis lupus*) reintroduction. Among the changes observed are the control of elk (*Cervus canadensis*) populations that, in turn, reduced its dominance and allowed the increasing of its potential competitors, such as beavers (*Caster canadensis*) and bisons (*Bison bison*). This was a possible result of the reduction of the competition with elk for food resources which increased the availability of plants such as aspen (*Populus tremuloides*), willow (*Salix* spp.), and cottonwood (*Populus* spp.). Therefore, these studies emphasize the importance of top predators in the community regulation, though pressures of predation and competition on coexisting carnivores and herbivores, with consequences on plant populations.

Studies have also supported that species of carnivores can negatively affect each other in local communities due to intraguild competition by interference or exploitation (Palomares & Caro 1999, Linnell & Strand 2000). Competition though exploitation occurs between species mostly when there is a decline of their common resource (Putman, 1994) and interference competition occurs when individuals have agonistic encounters or use territorial signals that displace individuals of the dominated species (Schoener 1983). Extreme negative effects may occur when interference causes injury or even the death of fighting competitors (Case & Gilpin 1974). Population density and viability can be strongly reduced under competition, so different carnivore species can develop strategies to avoid competition risk (Lima 1998, Linnell & Strand 2000, Palomares & Caro 1999). Hence, competition and aggressive interaction can shape patterns of spatial distribution and of temporal avoidance between carnivore species. Thus, coexistence of potential competitors may depend upon temporal and/or spatial partitioning of resources (Palomares et al. 1996, Durant 1998, Lucherini et al. 2009). The niche partitioning consider that high overlap between species in one niche component should be associated with low degree in the other components to allow their coexistence (Schoener 1974). Therefore, knowledge about overlapping niche components among carnivores is crucial to understand the factors that enable or prevent their co-occurences.

Detecting terrestrial carnivores can be a challenge due to the secretive and nocturnal behavior and low population densities of most species. Camera trapping has proved an efficient method for wildlife surveys, as it is non-invasive and provides information on cryptic and inconspicuous species (Harmsen et al. 2009, Sarmento et al. 2009, Surnato et al. 2013). Data obtained from camera trapping can be used to model the occupancy of target species, with a variety of applications such as site occupancy estimation (MacKenzie & Royle 2005, O’Connell et al. 2006, Rich et al. 2013), determining the patterns of spatial partitioning among species (Sarmento et al. 2011, Sollmann et al. 2012), to provide a general overview of the temporal interactions between species as well as determining the species daily activity partterns (Foster et al. 2013, Ridout & Linkie 2009), to evaluate effects of habitat disturbance on species interactions (Cruz et al. 2015) and to predict the effects of future land-use changes on target species (Kowalski et al. 2015). Additional uses of camera trapping include the estimation of relative densities of elusive species (MacKenzie et al. 2006, Royle et al. 2005), identification of critical habitats for threatened species as well as for predicting their population trends (McCarthy et al. 2015).

Through the use of camera trapping, in the last two decades several factors that favors coexistence have been studied for Neotropical carnivore species (Vieira & Port 2006, Di Bitetti et al. 2009, Foster et al. 2013, Bianch et al. 2016). Although the Neotropical regions harbor a strikingly rich biodiversity, carnivores do not present the richest diversity in this region and they has suffered a more significant decreased in numbers than the African carnivores (Dalerum et al. 2009). Neotropical carnivores comprise eight families and approximately 65 species. In Brazil, terrestrial carnivores comprise 26 species in four families (Felidae, Canidae, Mustelidae and Procyonidae) with 18 species recorded in the Pantanal wetland (Hannibal et al. 2015). Carnivores in this region include ecologically similar species, which should present different mechanisms of coexistence (Shostell & Ruiz-Garcia 2013). Thus, carnivores in the Pantanal are a good study system to address factors associated with coexistence (Jácomo et al. 2004; Di Bitetti et al. 2010; Foster et al. 2013; Bianchi et al. 2016).

Felidae species may coexist in different parts of the Neotropics, the top predators, jaguar (*Panthera onca*) and puma (*Puma concolor*), the medium-sized, ocelot (*Leopardus pardalis*) and the small-sized, jaguarundi (*Puma yagouaroundi*), margay (*Leopardus wiedii*), oncilla (*Leopardus tigrinus*), southern little spotted cat (*Leopardus gutullus*), guiña (*Leopardus guigna*), geoffroy's cat (*Leopardus geoffroyi*) and pampas cat (*Leopardus colocolo*) . Several studies have debated aspects enabling coexistence among jaguars, pumas and ocelots based on food preferences (Núñez et al. 2002, Foster et al. 2013, Porfirio et al. 2016), habitat use (Di Bitetti et al. 2006; Sollmann et al. 2012; Palomares et al. 2016) and temporal partitioning (Scognamillo et al. 2003, Lucherini et al. 2009, Romero-Muñoz 2010, Foster et al. 2013, Bianchi et al 2016). However, few data are available about mechanisms of coexistence among the others small-sized felid (Di Bitetti et al. 2010, Silva-Pereira et al. 2011, Nagy-Reis et al 2017). In its turn, for the Neotropical canids only four out of 10 species have studies about mechanisms of coexistence, the crab-eating fox (*Cerdocyon thous*), the pampas fox (*Pseudalopex gymnocercus*), the maned wolf (*Chrysocyon brachyurus*), and the hoary fox (*Lycalopex vetulus*) (Juarez & Marinho-Filho 2002, Jácomo et al. 2004, Vieira & Port 2006). However, like for the small felines, few studies addressed mechanisms that favor the coexistence among the others canids, as well as among Procyonidae and Mustelidae carnivores. Most studies about coexistence of carnivores include two or three species, and so only a few investigate coexistence among carnivores of different guilds (Davis et al. 2011, Kasper et al. 2015, Massara et al. 2016). Therefore, to investigate the potential competition among the carnivores and its consequences is necessary to understand the ecology of single species in its community.

In the present thesis, I address habitat selection, circadian rhythms and intraguild competition in the use of space and time by the Pantanal carnivore species. I access richness and distribution of carnivore species, estimate their occupancy rates and the factors affecting occupancy and detectability, and evaluate the spatial and temporal partitioning between the predator and mesopredator species.

As top predators exerts a strong role in maintaining the structures and dynamics of the community (Terborgh, 1990), it was expected that mesopredators present mechanisms to reduce competition effects, which might include different activity patterns and differential habitat use. Based on previously reported relationships and data on ecological requirements by carnivores, I hypothesized that:

1) Mesopredator occupancy and detection will be positively influenced by the presence of prey species and negatively by the presence of competitors or predators (jaguar, puma and ocelot);
2) Competitive species will show temporal and spatial nichi partition, such as jaguar and puma, ocelot and crab-eating fox, and top predators and mesopredators.
3) Species with higher spatial partition will be more tolerant partion, mainly with the species have similar diet.

Methods

Study region and sites

The Pantanal is a vast wetland (160.000 $km^{2,}$) in South America that covers territories of Brazil (140.000 km^2), Bolivia (15.000 km^2) and Paraguay (5.000 km^2), comprising most of the upper Paraguay basin. Climate is tropical savannic (Aw of Köppen) with the wet season from October to April and the dry season from May to September (PCBAP, 1997). Annual average temperature varies from 24 to 25 °C, and annual average precipitation is approximately 1000 mm (Zavattini 2009). The Pantanal has two distinct seasonal flood regimes, one in the northeastern part with intense and relatively fast flood pulse and other in the southwestern part with more progressive and long pulses (Penatti et al. 2015). Based on distinct flood dynamics and soil and vegetation types, the Pantanal has been divided into different subregions with diverse landscapes (Silva & Abdon 1998, Junk et al. 2006, Penatti et al. 2015) (Figure 1). In addition to the effects of seasonal floods, the Pantanal biota has been influenced by the major surrounding domains - Cerrado, Amazon Forest, Chaco and Atlantic Forest (MMA, 2010). The vegetation is mainly composed by grasslands, deciduous and semideciduous forest patches, and forested savannahs (IBGE, 1992). Due to high habitat diversity and influence of different domains, the Pantanal hosts a striking biodiversity, comprised of at least 170 species of mammals, 463 of birds, 263 of fishes, 40 of amphibians, 177 of reptiles and more than 2000 species of plants (Britski et al. 1999, Tubelis & Tomas 2003, Médri & Mourão 2004, Junk et al. 2006, Alho et al. 2011). The seasonal floods have kept the Pantanal as a large pristine region in the world, with almost 85% of its area still covered by natural vegetation (MMA, 2007). Due to the high biodiversity and conservation status of this huge floodplain, the Pantanal was classified as a Biosphere Reserve and World Heritage Site by UNESCO (Junk et al. 2006). Nonetheless, intensive fish exploitation, livestock ranching, deforestation and degradation of waterways have currently altered the ecosystem (Harris et al. 2005, MMA 2007).

The study was conducted in four sites that encompass most of the Pantanal diversity of habitats and landscapes (Figure 1). The natural reserve Eliezer Batista (18°05’25” S, 57°28’24” W) is located in the Upper Paraguay Basin in the western Brazilian Pantanal, Paraguai subregion. This region is shaped by mountains, swamps and seasonally flooded grasslands. The Sagrado Ranch (19°26’53”S 57°00’28”W), situated in the southern Pantanal, Abobral subregion, is characterised by the presence of several interspaced forest patches (0.5-5 ha) situated 1-2 m above the surrounding grasslands subjected to annual floods. The Sagrado ranch is located near the Abobral river and its riparian forest. The Cáceres Ranch (19°09’32”S, 56°49’40”W), located in the Nhecolândia subregion, is composed of a mosaic of seasonally flooded grasslands, savannas, scrub savannas, forests patches, and several permanent and temporary lakes. The Mata Grande Ranch (20°31’41”S, 56°37’33”W), in the municipality of Bodoquena, is in the edge of the Miranda subregion of Pantanal. The vegetation in this site is mainly composed by deciduous forest with portions of semideciduous forest, shrubby and arboreal savanna (Cáceres et al. 2007) (Figure 1).

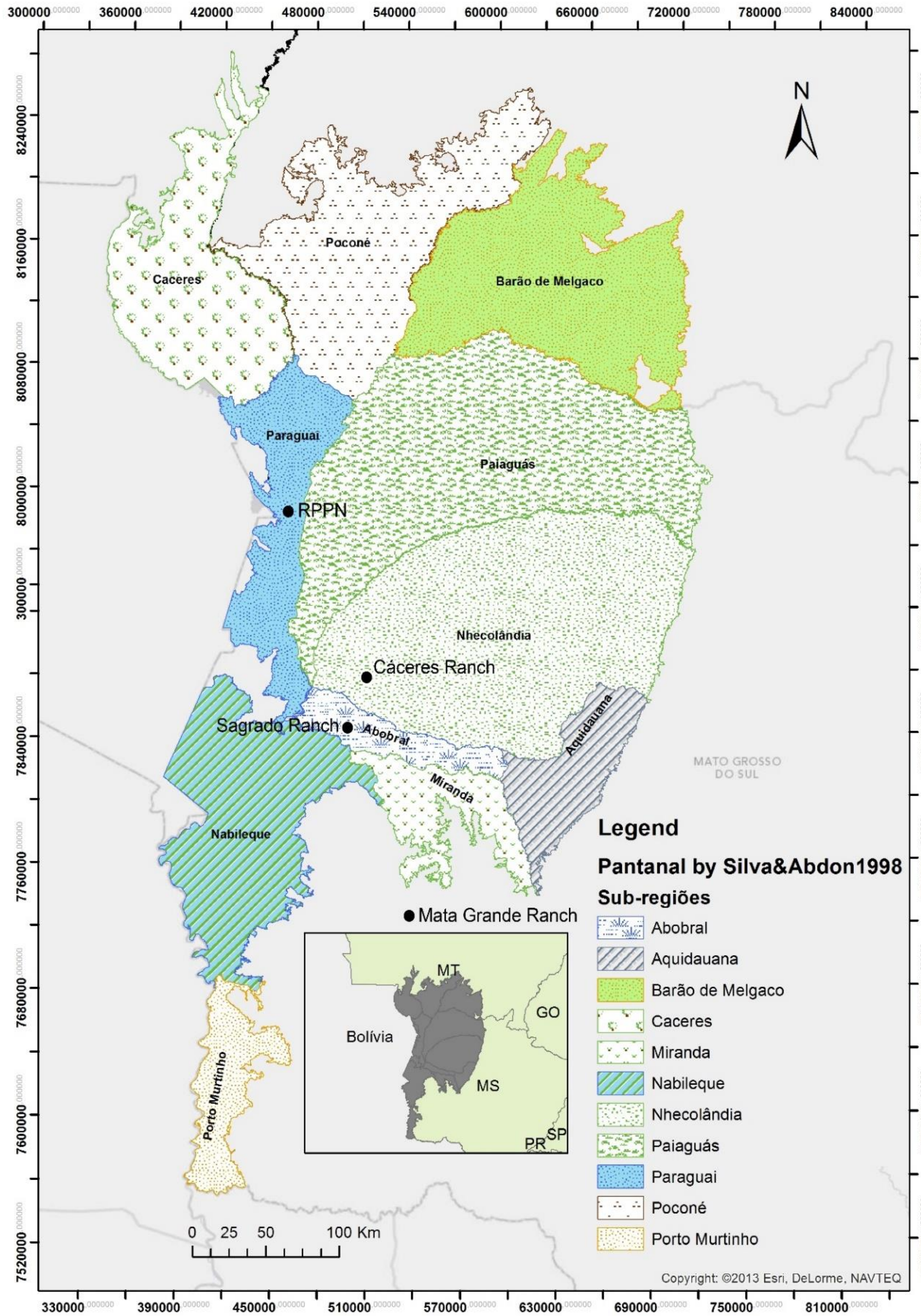

Figure 1. Brazilian Pantanal sub-regions according to Silva and Abdon (1998) and the location of each study site. Map by André Coelho.

Data collection

I surveyed carnivores using camera traps (Bushnell Trophy Cam), which varied in number among study sites and seasons (Table 1). In the four study sites, cameras were fixed to the vegetation 45-50 cm above the ground along dirt roads, river margins and in the forest, in order to encompass most of the landscape diversity. No baits were used to attract animals. All cameras were continuously active (24h/day), and programmed to take three pictures in each detection or to record a video for 10 s with date and time marks after activation by infrared movement or heat, and with delay of 5 s between records. Camera traps were checked at 20-30 days intervals for downloading pictures and changing batteries. In each study site, cameras were arranged in a grid following a habitat-stratified design with a minimum inter-camera distance of 500 m and maximum of 1500 m to achieve spatial independence among detections (Porfirio et al. 2014, Moreira-Arce et al. 2015).

Data analyses

Occupancy models

To avoid oversampling individuals (Silveira et al. 2003), for occupancy analyses, I only used pictures of the same species by each camera with more than 24 h interval (Linkie & Ridout 2011).

To investigate factors affecting the rate of occupancy (ψ) and detectability (p) of carnivores, I used five groups of explanatory variables: habitat (vegetation categoty), landscape (measures of landscape complexity and composition), prey (photographic capture rates of large, medium and small mammals), competitors (photographic capture rates of predators and mesopredators) and locality (variables related to sample efforts) (Table 2). I added the survey variable “Area” in the models to evaluate potential effect of the study areas on the carnivore occupancy and detectability. As there was no effect of “Area”, I then polled all data from the four sampling sites for subsequent modelling.

A buffer of 1000 m encircling each camera trap was created to account for the relative contribution of landscape structure to carnivore species distribution (Lyra-Jorge 2008, Jackson & Fahrig 2012). Inside each buffer area the landscape cover and landscape structure were measured using ArcGis 10.2 (ESRI 2013), a 2014 land cover map of Pantanal (SOS Pantanal & WWF-Brasil, 2015) and FRAGSTATS software at an 8-m cell resolution (McGarigal et al. 2012). The vegetation category were measured using ArcMap

10.2 (ESRI 2013). The proportions of vegetation category was calculated in defined areas enclosed in each buffer. Four classes of habitat were defined to encompass all main types of vegetation in the study sites – Grassland Savanna (GS), Forested Savana (FS), Forest Formation (loggFF) and Vegetation with Fluvial Influence (VIF) (Table 2).

The prey variable was measured as capture rate of potential preys, defined as the number of captures per camera trap location per 100 trap-days (Dillon & Kelly, 2007). Due to low availability of previous data on prey species for several carnivores, all trapped mammals (marsupials, rodents, lagomorphs and ungulates) were included as potential prey source, but divided into three size classes according Davis et al. (2011): small (< 5 kg), medium (5-15 kg) and large (> 15 kg) (Table 3). The capture rates of potential preys were measured for species and for groups. Jaguars prey on animals weighting 15 kg on average, and pumas prey on smaller ones (Sunquist & Sunquist, 2002). Medium and small carnivores, like ocelots and crab eating foxes, usually prey on animals smaller than1 kg, but can eventually do on larger ones (Konecny 1989, Abreu et al. 2008).

Continuous variables were standardized to z-scores before analyses (Royle & Nichols 2003) and some variables were log transformed to reach normality prior to be used in the models. To prevent collinearity effects, I calculated the Spearman rank correlation coefficient (r) between predictor variables and used $r > 0.6$ to indicate high collinearity (Zuur et al. 2009).

Occupancy (ψ) and detectability (p) of carnivore species were estimated using a maximum likelihood framework from our detection/non-detection data (MacKenzie et al. 2002, MacKenzie et al. 2006). Conceptually, occupancy models have been used to estimate the proportion of sites or sampled areas occupied by a target species (MacKenzie et al., 2002). Using five sampling occasions of consecutive 20 days, detection histories were constructed for each camera trap station to generate a sufficient number of captures of each target species. Data of all study sites were polled for analyses, except if a given focal species was not recorded in one the site, then this site was not incorporated. To ensure spatial independence, for occupancy and detectability I only used data from at least 1000 m interspaced cameras, which included 98 out 231 camera traps. The detection histories were coded as 1 (record of target species), 0 (no record of target species) or "." (if the site was not sampled on the occasion). The product of multinomial likelihood model was used to estimate the detection probabilities (p) and the proportion of sites occupied by a target species (ψ) using single species-single season models (MacKenzie et al. 2006). As these parameters can be influenced by site characteristics (MacKenzie et al. 2002), variables were used for construction of realistic models of occupancy (ψ) and detectability (p) of species, while accounting for imperfect detectability (MacKenzie et al. 2002, Wintle et al. 2005, MacKenzie et al. 2006, Long et al. 2010). Analyses were done in the software R 3.1.3 (R Core Development Team, 2012) using a 2-step approach (Sarmento et al. 2011) with the package unmarked (Fiske & Chandler, 2011). Firstly, I assessed the effect of the variables on detection probability keeping occupancy constant (i.e. ψ [.] p[variable]). The variables were firstly tested individually. Only those whose ß coefficient 95% confidence intervals did not overlap zero were selected to construct the models with only one variable or with additive combination of variables.

Using the best-fitting model for detection probabilities, I created models adding variables to explain patterns of occupancy. A global model was constructed contained all potential variables that can affect occupancy. The best models were ranked through Akaike Informaton Criterion corrected for small sample size (AIC_c) using the dredge function of the MuMin package (Bartón 2013). Models with Δ AIC_c values ≤ 2 compared with the most parsimonious model were considered robust, and variables included were considered as determinant on the species occurrence patterns (Burnham & Anderson, 2002). I used the Akaike weights (ω) to determine the individual importance of each variable (Burnham et al. 2010). When no single model had a $\omega_i > 0.9$, other models were considered to infer about the data by using the sum of each weight until achieved $\omega_i = 0.9$ (Burnham & Anderson, 2002). A 90% confidence model set was created by summing all ωi values until achieved 0.90. For determining significant differences among the models we used the likelihood ratio (LR) test based on deviance (-2logL) between pairs of nested models and the critical value of the Chi-square distribution (Neyman & Pearson 1928 a, b). Only models significantly different were used. Selected models allowed the average estimates of occupancy and detectability for each species.

Activity pattern

To estimate the daily activity patterns of carnivore species I only used pictures of a given camera that were obtained at least 1 h after the last record of the same species, except when possible a clear identification of distinct individuals. I pooled all records of the target species obtained in all surveys. Only carnivore species with more than 20 independent records were included in the temporal analyses (Gómez et al. 2005). The activity of these carnivores was classified into one of the six categories (cf. Gómez et al. 2005): diurnal

(<15 % of night records), mostly diurnal (15 – 35% of night records), nocturnal (> 85% of night records), mostly nocturnal (65-85% of night records), cathemeral (diurnal and nocturnal peaks), and crepuscular (> 50% of records in the until 1 h before sunrise or 1 h after sunset). I determined the exact time of sunset and sunrise using the software Moonrise 3.5 (Sidell 2002).

The overlap of daily activity periods between carnivore species was measured using the two-step approach developed by Ridout & Linkie (2009). In the first step, I estimated the activity pattern for each species separately using kernel density, which assumes pictures as random samples from an underlying continuous distribution instead of grouping them into discrete time categories (Ridout & Linkie 2009). At this step, I calculated the proportion of time active for each period by integrating the areas under the activity curve for each respective period, corresponding to the probability of observing the species during that time. In the second step, I calculated the coefficient of overlapping (Δ), which varies from 0 (no overlap) to 1 (complete overlap). Among Ridout and Linkie's (2009) estimators, I used the most suitable for small sample size (Δ_1). It is defined as $\Delta_1 = \int_0^1 min\{\hat{f}\ (t), \hat{g}\ (t)\}\, dt$, where $\hat{f}\ (t)$ and $\hat{g}\ (t)$ are the two activity functions of time t being compared. The statistical analyses were implemented in the software R 3.1.3 (R Core Development Team, 2012) using the "*overlap*" package (Meredith & Ridout 2016).

Co-occurrence

To estimate co-occurrences between carnivore species I used the pairwise co-occurrence approach (Veech, 2014). Differently from matrix-level approaches used in co-occurrence analyses, the pairwise one evaluates positive (co-occurrence), negative (exclusion), or random patterns between two species. Thus, represents all possible ways of species associations (Veech, 2013, 2014). The probabilistic model through combinatorial analyses estimates the probability of two species co-occur at an observed frequency (J_{obs}) significantly greater than (P_{gt}), significantly less than (P_{lt}) or not significantly different of the frequency expected if the two species were distributed randomly from each other (J_{exp}) among the sites (Veech, 2013). Based on values of P_{gt} and P_{lt} the species pairs were classified in positive, negative or random associations. The data was organized in a presence-absence matrix (10 row x 88 columns) where each row represented a focal species and each column represent the camera trap location. Similar to the detection history, the presence of the target species was coded as 1 and its absence coded as 0. The matrix were imported into R software and analyzed using the "*Cooccur*" package 1.3 version (Griffith et al. 2016). The model calculates the probability of two species co-occur at exactly *j* number of camera station given that each one occurs at N1 (number of stations with presence of species 1) and N2 (number of stations with presence of species 2) out of the total of N (number of stations surveyed), as follow:

$$P_j = \frac{\binom{N_1}{j} \times \binom{N-N_1}{N_2-j}}{\binom{N}{N_2}},$$

where, $\binom{N_1}{J}$ calculate the numbers of ways that *j* selected station have the species 1; $\binom{N-N_1}{N_2-j}$ calculate the numbers of ways that $N_2 - j$ selected stations have only the species 2 given that there are $N - N_1$. The result of this multiplication gives the total number of ways of select *j* station have both species. The denominator $\binom{N}{N_2}$ gives the total number of ways that N_2 can be obtained out of the *N* stations. The result of this equation is the proportion of N_2 with presence of species 1 under the condition that the two species co-occur at *j* stations (Griffith et al 2016).

Table 1. Camera-trapping surveys, and efforts in four sites of Pantanal southwestern Brazil.

Study sites	Survey periods	Survey days	Cameras (n)	Average distance between cameras (m)	Sampling effort (Camera days)
Sagrado	Feb - May 2014	99	23	1000	2277
	Oct 2014 - Jan 2015	90	23	1000	2070
Caceres	May - Sep2014	119	20	1000	2380
	Jan - May 2015	110	20	1000	2200
Mata Grande	Apr - Augu 2014	110	13	1000	1430
	Jan - May 2015	108	13	1000	1404
Eliezér Batista	Aug – Sep 2011	62	23	500	1426
	Nov 2011- Jan 2012	58	12	1500	696
	Fev-May 2012	95	20	1500	1900
	Aug-Sep 2012	30	14	500	420
	Nov 2012-May 2013	169	41	2000	6929
	Apr-Sep 2013	148	9	500	1332
Total		1198	231		24464

Table 2. Predictor variables (and used abbreviations) for investigating occupancy rates of carnivores in the Brazilian Pantanal. *Variables log transformed.

Variable	Description	Target species
HABITAT		
Grassland Savanna (GS)	Grass fields with scattered trees;	All carnivores
Forested Savanna (FS)	Tree dominance with low canopy height;	All carnivores
Forest Formation (logFF*)	Deciduous and semi-deciduous forests;	All carnivores
Vegetation with fluvial Influence (VIF)	Swamp and monodominant formations with pioneer trees influenced by water;	All carnivores
LANDSCAPE		
Shannon's diversity index (SHDI)	Measure of relative patch diversity	All carnivores
FOOD		
Medium (Med)	Trapping success of 5-15kg mammals	All carnivores
Large	Trapping success of mammals >15 kg	All carnivores
Small	Trapping success of mammals < 5 kg	All carnivores
COMPETITORS		
Puma (Puma)	Trapping p success of *Puma concolor*	All carnivores
Jaguar (Jaguar)	Trapping success of *Panthera onca*	All carnivores
Ocelot (Lpard)	Trapping success of *Leopardus pardalis*	All carnivores, except jaguar and puma
Crab-eating fox (Cthous)	Trapping success of *Cerdocyon thous*	All carnivores, except jaguar and puma
LOCALITY		
Effort (Eff)	Sample effort used as co-variable	All carnivores
Area (Area)	Sample area used as co-variable	All carnivores

Table 3. Mean capture rate (100 days/trap), weight and size class (L: large, M: medium, S: small) of mammal species included as potential prey for carnivores in four sites of Pantanal, southwestern Brazil.

			Mean capture rate (SE) per study site			
Species	Weight (kg)[a]	Size class	Sagrado	Cáceres	Mata Grande	Eliezer Batista
Alouatta caraya	3.8 - 9.0	M	0.14 (0.06)	0	0	0.08 (0.05)
Blastocerus dichotomus	150	L	0.03 (0.03)	0.25 (0.22)	0	0.02 (0.02)
Sapajus cay	1.4 - 4.8	S	0.00	0	0.35 (0.26)	0.07 (0.05)
Cuniculus paca	4 - 6.5	M	0.00	0	1.97 (1.49)	0
Cabassous tatouay	6.2	M	0.00	0	0.24 (0.09)	0
Dasyprocta azarae	1.5 - 2.8	S	5.10 (1.60)	3.31 (1.21)	2.78 (1.24)	4.21 (1.31)
Didelphis albiventris	0.5 - 2.7	S	0.04 (0.04)	0	0.10 (0.07)	0
Dasypus novemcinctus	3.2 - 4.1	S	1.13 (0.27)	0.38 (0.13)	0.79 (0.43)	0.14 (0.08)
Euphractus sexcinctus	3.2 - 6.5	M	0.85 (0.30)	1.10 (0.51)	0.11 (0.07)	0
Hdrochaeris hydrochaeris	3.5 - 6.5	M	0.17 (0.13)	0	0.04 (0.04)	0.51 (0.27)
Mazama americana	25 - 30	L	4.85 (1.06)	1.44 (0.35)	1.01 (0.28)	1.24 (0.47)
Mazama gouazoubira	17 - 23	L	4.48 (0.86)	2.42 (0.40)	1.05 (0.50)	1.65 (0.39)
Myrmecophaga tridactyla	45	L	0.69 (0.25)	1.10 (0.39)	2.26 (0.79)	0.02 (0.02)
Ozotocerus bezoarticus	30 - 40	L	0.00	0.29 (0.19)	0	
Pecari tajacu	18 - 30	L	0.89 (0.19)	11.07 (1.95)	8.63 (2.07)	0
Sylvilagus brasiliensis	1.2	S	0.00	0	1.12 (0.51)	0.53 (0.26)
Sus scrofa	50 - 350	L	0.78 (0.27)	29.87 (4.97)	0	0
Tayassu pecari	25 - 40	L	14.35 (2.62)	15.89 (2.23)	5.59 (2.03)	0
Tapirus terrestris	150 - 300	L	3.39 (1.00)	5.26 (1.26)	8.38 (2.64)	2.05 (0.81)
Tamandua tetradactyla	7	M	0.36 (0.13)	0.13 (0.06)	1.63 (0.41)	0.02 (0.02)

[a] Weights obtained from Reis et al. 2006

Results

Global results

Combining all study sites and camera trap stations, I recorded 11 carnivore species in 1109 independent records with a global capture success of 4.53 captures per 100 trap days (1 carnivore capture per 22.07 trap days) (Figure 2). Among the species recorded *Cerdocyon thous* and *Nasua nasua* had more than 300 records; four species scored between 80 and 270 records and the remaining five species, less than 20 records (Table 4). *Leopardus colocolo* (n=2), *Lycalopex vetulus* (n=16) and *Chrysocyon brachyurus* (n=2) were not incorporated in the analyses because of their low record numbers. Sagrado ranch was the richest (11 species detected) site, where all recorded carnivore species occurred (Table 4). The other study sites presented seven to eight carnivore species. Twenty non-carnivore mammal species were additionally recorded, and thus incorporated as prey variables in the occupancy models (Table 3).

Table 4. Carnivore species captured, conservations status conservations status according to the International Union for Conservation of Nature (IUCN, 2017), number and rate captures, number of camera-trapping station and study site where the species were captured (Ab: Abobral, Pa: Paraguai, All: in all for subregions) through camera-trapping surveys in the Pantanal wetland, southwestern Brazil.

Species	Status	Captures (n)	Capture rate (100 traps day^{-1})	Occupied stations (n)	Naive occupied stations (%)	Sub-regions
Chrysocyon brachyurus	NT	2	0.008	1	0.01	Ab
Cerdocyon thous	LC	317	1.29	50	0.51	All
Eira barbara	LC	67	0.27	23	0.23	All
Leopardus colocolo	NT	2	0.008	1	0.01	Ab
Leopardus pardalis	LC	185	0.75	46	0.47	All
Lycalopex vetulus	LC	16	0.065	3	0.03	Ab
Nasua nasua	LC	325	1.33	58	0.59	All
Panthera onca	NT	70	0.28	28	0.43	Ab/Pa
Procyon cancrivorus	LC	20	0.08	13	0.13	All
Puma concolor	LC	104	0.41	36	0.37	All
Puma yagouaroundi	LC	13	0.05	10	0.10	All

Figure 2. Carnivores recorded through camera-trapping in the Pantanal wetland, southwestern Brazil. Legend: A- Crab eating fox (*Cerdocyon thous*), B- Jaguarundi (*Puma yagouaroundi*), C- Pampas cat (*Leopardus colocolo*), D- Jaguar (*Panthera onca*), E- Ocelot (*Leopardus pardalis*), F- Tayra (*Eira barbara*), G- Coati (*Nasua nasua*), H- Puma (*Puma concolor*), I- Crab-eating Raccoon (*Procyon cancrivorous*), J- Maned Wolf (*Chrysocyon brachyurus*), K- Hoary Fox (*Lycalopex vetulus*).

Occupancy models

Among the eleven carnivores recorded, six presented adequate capture rates to carry out occupancy analyses (Table 5). These species exhibited a notorious variability of detection probabilities (p), with the highest value for the crab-eating fox *Cerdocyon thous* ($p = 0.50 \pm 0.06$), and the lowest one for the puma *Puma concolor* ($p = 0.18 \pm 0.04$). Regarding the probability of occupancy (ψ), the outcome varied among focal species with the highest probability of occupancy for the coati *Nasua nasua* ($\psi = 0.79 \pm 0.10$) and the lowest for the tayra *Eira barbara* ($\psi = 0.35 \pm 0.11$) (Table 5). Though the probability of occupancy was possible to generate distribution maps for each species in each study area (Figure S1 until Figure S9).

The jaguar *Panthera onca* was registered only on the Sagrado Ranch and Eliezer Batista reserve, in 28 sites out of 65 surveyed, corresponding to a naïve occupancy of 0.43. Nineteen candidate models were selected which showed a Δ $AIC_c \leq 2$ and a cumulative AIC_c weight (ω_i) of 0.9. However, only eight showed significant difference among them (Table S2). None of the best candidate models presented a $\omega_i > 0.90$, thus the final estimative for jaguar occupancy and detectability used the average of models (ψ mean = 0.65, SE = 0.12; p mean = 0.23, SE = 0.07) (Table 5).

Jaguar detection probability was positively correlated with Vegetation under Fluvial Influence (VIF; z = 0.19; P(>|z|) = 0.01) and Forest Formation (logFF; z = 0.18; (P(>|z|) = 0.10). Both variables were present in most of the best candidate models (Table S2) and their ß coefficient 95% confidence intervals did not overlap zero (Table S3). Capture rate of medium mammals (Med) and Grassland Savanna (GS) were also present in the best candidate models, with low representativeness in detection probability (Table 6). On the other hand, jaguar occupancy probability did not exhibit correlation with the tested variables. Although capture rate of small mammals (Small) and large mammals (Large) entered in the best models, they did not present significant influence as their ß coefficient 95% confidence intervals overlapped zero (Table S4). So the top-ranked model for occupancy was a constant function (Table 5; Table 7).

The puma *Puma concolor* was recorded in 36 camera trap stations (Table 4) in the four study sites with a naïve occupancy of 0.37. Our analysis obtained five top candidate models to predict puma occupancy and detectability with Δ $AIC_c \leq 2$ with a cumulative AIC_c weight of 0.9. Through the LR test only three candidate models showed significant differences among them (Table S5). Since no single model achieved a $\omega_i > 0.90$ all best candidate models were used to predict mean occupancy and detectability for puma (ψ mean = 0.44, SE = 0.09; *p* mean = 0.19, SE = 0.04) (Table 5). Its detection probability was best modelled as a constant function (p(.)) followed by the variable Vegetation under Fluvial Influence (VIF). This variable had a significant negative influence on puma detectability (z = -1.23; P(>|z|) = 0.02) (Table 5). Other variables, such as Area, also influenced puma detection, but their 95% confidence intervals of ß coefficients overlapped zero indicating a low predictive role for puma occupancy (Table S6). Occupancy, in its turn, was significantly positively affected by the capture rate of large mammals (Large; z = 2.95; P(>|z|) = 0.003) and small mammals (Small; z = 1.94; P(>|z|) = 0.05), with 95% confidence interval of ß coefficient not overlapping zero (Table 5; Table S6). The Large and Small variables entered in three best candidate models and they consequently ranked high in importance when summed the AIC_c weights of the models (Table 7).

The ocelot *Leopardus pardalis* was detected in 46 sites and in all study sites (Table 4), with a naïve occupancy of 0.47. After analysis four candidate models presented Δ AIC_c ≤ 2 and a cumulative AIC_c weight of 0.9. However, using the LR test, only two models presented significant differences between them (Table S7). Considering that none of them achieved a $\omega i>0.90$, the two models were used to calculate the average occupancy and detectability as the final estimative (Table S7).

Ocelot detection probability was best explained by Forested Savannas (FS) with a significant positive influence (z = 3.13; P(>|z|) = 0.001) (Table 5). Forested Savannas (FS) was present in all best models, supporting its high importance for predicting the ocelot detection probability (ß coefficient 95% confidence interval did not overlap zero in all models) (Table 5; Table S8). The most parsimonious model was ψ(Jaguar+Puma+GS+Small)*p*(FS) with Akaike weigh (ω_i) of 0.53, followed by ψ(Jaguar+Puma+Small)*p*(FS+GS) with Akaike weigh (ω_i) of 0.47 (Table S7). The top-ranked model for ocelot occupancy included significant positive relationship with the capture rates of *Puma concolor* (Puma; z = 2.30; P(>|z|) = 0.02) and of small mammals (Small; z = 2.17; P(>|z|) = 0.03). The variables Puma and Small entered in all best ranked models (Table 7, Table S7). Jaguar was present in the model but with no significance (z = 1.76; P(>|z|) = 0.08). Grass Savannah (GS) was negatively correlated (z = -1.94; P(>|z|) = 0.05) with ocelot occupancy. The ß coefficient 95% confidence intervals of these variables did not overlap zero (Table S9).

The crab-eating fox *Cerdocyon thous* was the second most common carnivore, being recorded in 50 camera trap stations (Table 4) in the four study sites, which corresponded to a naïve occupancy of 0.51. Thirteen models of occupancy and detectability were produced with $AIC_c \leq 2$ and cumulative AIC_c weight of 0.9. Through the LR test, only five showed, significant differences between them. No candidate models achieved AIC_c weight (ω_i) of 0.9, then they were all used for averaging occupancy and detectability (Table S10).

Crab-eating fox detectability was positively influenced by the capture rate of jaguar (Jaguar; z = 3.02; P(>|z|) = 0.002) and negatively by Vegetation under Fluvial Influence (VIF; z = - 3.04; P(>|z|)=0.002). Both variables entered in all best candidate models and their ß coefficient 95% confidence intervals did not overlap zero in all models (Table 6; Table S11). The species' occupancy was positively affected by capture rate of puma (Puma; z= 1.35; P(>|z|) = 0.18) and negatively affected by Forested Savanna (FS) and Vegetation under Fluvial Influence (VIF; z = -1.62, P(>|z|) = 0.10; z = -1.44, P(>|z|) = 0.15, respectively) (ß coefficient 95% confidence interval did not overlapped 0) (Table 5, Table S12). Through the average model it was predicted that 64 % of the study surveyed area is occupied by crab-eating fox (ψ mean = 0.56, SE = 0.14) with a mean detectability of 0.36 (*p* mean = 0.36, SE = 0.05) (Table 5).

Individuals of tayra *Eira barbara* was detected in 23 camera trap stations in the four study sites (Table 4) with a naïve occupancy of 0.23 (67 records). The Dredge analysis resulted in nine candidate models with $AIC_c \leq 2$ and cumulative AIC_c weight of 0.9. The LR test showed that two models did not differ from the nested models and were excluded. Thus, seven models were used to calculate average occupancy and detectability values (Table S13). Once no candidate models achieved AIC_c weight (ω_i) of 0.9 all the best models were used to determined occupancy and detectability as the final estimative (ψ mean = 0.34, SE = 0.10; *p* mean = 0.26, SE = 0.06) (Table 5). Detection probability of tayra was best explained by the capture rate of medium mammals (Med; z = 2.47; P(>|z|) = 0.01). Med entered in all best models and its ß coefficient 95% confidence interval did not overlapped zero (Table 6; Table S14). The capture rate of small mammals (Small) also entered in some models, but with low representativeness for detection probability (Table 6). The capture rate of puma (Puma) had a significantly positive influence (z = 2.36; P(>|z|) = 0.02) on tayra occupancy. On the other hand the Grassland Savanna (GS) had a negative influence on tayra occupancy (z = -1.94; P(>|z|) = 0.05) and its ß coefficient 95% confidence interval did not overlapped zero (Table

5; Table S15). The most parsimonious occupancy model was ψ(Puma+GS)*p*(Med), with (ω_i) = 0.21. Puma was present in all best models and ranked high in importance when summed models' AIC_c weights (Table 7). Area and Jaguar were also included in the best models, however with low representativeness compared to Puma (Table 7).

The coati *Nasua nasua* was the most recorded species, being detected in the four study sites and 58 camera trap stations (Table 4), corresponding to a naïve occupancy of 0.59. Final analysis indicated that nine models can explain its patterns of occupancy and detection (Table S16). Since no single model achieved a $\omega_i > 0.90$ the average values of the eight best ranking models were used to estimate occupancy and detectability (ψ mean = 0.79, SE = 0.10; *p* mean = 0.29, SE = 0.05) (Table 5). Coati detection probability was positively influenced by the capture rate of large mammals (z = 2.82; P(>|z|) = 0.004) and negatively affected by two habitat variables, forest formation (z = -2.80; logFF, P(>|z|) = 0.005) and vegetation under fluvial influence (VIF; z = -1.98; P(>|z|) = 0.04), as 95% interval of ß coefficient did not overlap zero (Table 5, Table S17).

The best supported model for coati occupancy was ψ(Puma+FS+VIF)*p*(Large+logFF+Med+VIF) with Akaike weight (ω_i) = 0.22, which means 22% of probability of being the best among candidate models, followed by ψ((Jaguar+Puma+FS+VIF)*p*(Large+logFF+Med+VIF) with ω_i = 0.20 (Table S16). Considering the covariates in the first best model, capture rate of puma (Puma) was positively associated, however without significance (z = 1.29; P(>|z|) = 0.19), with coati occupancy, whereas the covariate forested savanna (FS) and Vegetation under fluvial Influence (VIF) had significant negative influence with z = -2.45 and P(>|z|) = 0.01; and z = -2.22 and P(>|z|) = 0.02, respectively. Although the variable Jaguar as also included in the best model, the 95% confidence interval of ß coefficient overlapped zero, thus it was not considered a good predictor (Table S16, Table S18). The FS and VIF were present in all best candidate models and also ranked high in importance when summed the ω_i of the models that contain them (Table 7).

Table 5: Probability of detection and occupancy, with the best predictors and estimatives of beta coefficients, of carnivore species among sites surveyed through camera-trapping in the Pantanal wetland, southwestern, Brazil.

Species	Probability of Detection (*p*)		Probability of Occupancy (ψ)	
	Mean (SE)	Variable (Estimates of beta coefficients (SE))	Mean (SE)	Variable (Estimates of beta coefficients (SE))
Panthera onca	0.23 (0.07)	VIF (0.48 (0.19)) GS (-0.43 (0.19)) Med (-0.33 (0.23))	0.65 (0.12)	(.)
Puma concolor	0.19 (0.04)	(.) VIF (-0.35 (0.19))	0.44 (0.09)	Large (1.81 (0.61)) Small (0.66 (0.34))
Leopardus pardalis	0.35 (0.05)	FS (0.18 (0.11))	0.64 (0.12)	Puma (1.26 (0.80)) Small (0.63 (0.48)) GS (-2.22 (1.12))
Cerdocyon thous	0.36 (0.05)	Jaguar (1.14 (0.40)) VIF (-1.40 (0.49))	0.56 (0.14)	Puma (0.45 (0.33)) VIF (-0.80 (0.56)) FS (-0.34 (0.21))
Eira barbara	0.26 (0.06)	Med (0.42 (0.17)) Small (0.15 (0.19))	0.34 (0.10)	Puma (1.99 (0.84)) GS (-0.66 (0.34))
Nasua nasua	0.29 (0.05)	Large (0.35 (0.12)) FF (-0.33 (0.12)) VIF (-0.60 (0.30))	0.79 (0.10)	Puma (1.38 (1.07)) FS (-2.35 (0.96)) VIF (-2.33 (1.05))

Table 6. Ranking of covariates (FS – Forested Savanna, GS – Grassland Savanna, VIF – Vegetation under Influence Fluvial) based on the sum of AIC_c weight of detectability of carnivore species in the Pantanal wetland, southwestern Brazil. * Constant function.

Species	Covariate	Sum AICwt	Rank
Panthera onca	VIF	0.70	1
	logFF	0.48	2
	Med	0.46	3
	GS	0.39	4
Puma concolor	(.)	0.43	1
	VIF	0.56	2
Leopardus pardalis	FS	1.00	1
	GS	0.47	2
Cerdocyon thous	Jaguar	1.00	1
	VIF	1.00	1
Eira barbara	Med	0.99	1
	Small	0.20	2
Nasua nasua	Large	0.998	1
	logFF	0.998	1
	Med	0.792	2
	VIF	0.723	3
	Cthous	0.301	4

Table 7. Ranking of covariates (FS – Forested Savanna, GS – Grassland Savanna, VIF – Vegetation under Influence Fluvial) based on the sum of AIC_c weight of the best models of occupancy of carnivore species in the Pantanal wetland, southwestern Brazil. * Constant function.

Species	Covariate	Sum AICwt	Rank
Panthera onca	(.)**	0.72	1
	Small	0.16	2
	Large	0.12	3
Puma concolor	Large	0.99	1
	Small	0.99	1
Leopardus pardalis	Small	1.00	1
	Puma	1.00	1
	Jaguar	1.00	1
	GS	0.53	2
Cerdocyon thous	Puma	0.71	1
	VIF	0.62	2
	FS	0.54	3
	Lpard	0.31	4
	GS	0.26	5
Eira barbara	Puma	0.99	1
	GS	0.59	2
	Area	0.50	3
	Jaguar	0.31	4
Nasua nasua	FS	1.00	1
	VIF	1.00	1
	Puma	0.73	2

Activity pattern

Activity patterns differed among the eight carnivore species (Table 8). Only *Procyon cancrivorus* was completely nocturnal with one pronounced peak from early night to sunrise (1830 to 0600 h) (Figure 3). *Leopardus pardalis* and *Cerdocyon thous* were mostly nocturnal (Table 8). The ocelot exhibited a homogenous activity from early night (1900h) to sunrise (0500h), and occasional diurnal activity with some records near midday (Figure 3). The crab-eating fox presented two pronounced peaks of activity, in the night (2200h) and sunrise (0500 to 0600 h) (Figure 3). *Eira barbara*, *Puma yagouaroundi* and *Nasua nasua* were recorded throughout the day with two pronounced peaks, in the early morning after sunrise (0600 and 0800 h) and in the late afternoon (1600 and 1700 h); and presented few activity in the hottest hours (1100 and 1400 h) (Figure 3). The two top predators, *Panthera onca* and *Puma concolor*, largely overlapped their circadian activity patterns. They were cathemeral as activity occurred throughout the day and night (Table 8), with crepuscular peaks (0500 to 0600 h, and 1730 to 1900 h) and few activity in the hottest hours (Figure 3).

Temporal partitioning occurred among the carnivore species (Table 9). Some species presented high temporal segregation, with a low coefficient of overlap between tayra and ocelot ($\Delta_1 = 0.27$, CI 0.17 - 0.29) and between coati and ocelot ($\Delta_1 = 0.27$, CI 0.19 - 0.28). On the other hand, temporal overlap occurred between jaguar and puma presented low temporal segregation, with high coefficient of overlap ($\Delta_1 = 0.85$, CI 0.78 - 0.95) (Table 9).

Table 8. Classification of activity patterns and percentage of records in each part of the day for the carnivore species recorded across camera-trapping surveys carried out in the Pantanal

Species	Records (n)	Activity period (%)			Classification
		Crepuscular	Diurnal	Nocturnal	
Procyon cancrivorous	20	10%	0%	90%	Nocturnal
Leopardus pardalis	273	13%	9%	78%	Mostly nocturnal
Cerdocyon thous	494	24%	10%	66%	Mostly nocturnal
Panthera onca	99	17%	33%	50%	Cathemeral
Puma concolor	102	30%	34%	36%	Cathemeral
Eira barbara	80	25%	74%	1%	Diurnal
Nasua nasua	339	20%	77%	3%	Diurnal
Puma yagouaroundi	27	22%	78%	0%	Diurnal

Table 9. Overlap coefficients (Δ_1) and 95% confidence intervals (lower-upper) of daily activity patterns between carnivorous species in the Pantanal wetland, southwestern of Brazil.

Species	*Panthera onca*	*Cerdocyon thous*	*Eira barbara*	*Leopardus pardalis*	*Puma concolor*
Cerdocyon Thous	0.80 (0.73 - 0.88)	-	-		
Eira Barbara	0.50 (0.38 - 0.57)	0.33 (0.23 - 0.36)	-		
Leopardus Pardalis	0.74 (0.65 - 0.83)	0.86 (0.82 - 0.92)	0.27 (0.17 - 0.29)	-	
Puma Concolor	0.85 (0.78 - 0.95)	0.72 (0.62 - 0.80)	0.57 (0.47 - 0.65)	0.66 (0.54 - 0.73)	-
Nasua Nasua	0.50 (0.39 - 0.57)	0.33 (0.25 - 0.34)	0.81 (0.73 - 0.90)	0.27 (0.19 - 0.28)	0.59 (0.48 - 0.67)
Puma yagouaroundi	0.51 (0.36 - 0.60)	0.34 (0.21 - 0.39)	0.79 (0.74 - 0.99)	0.29 (0.14 - 0.32)	0.58 (0.45 - 0.68)
Procyon cancrivorous	0.64 (0.51 - 0.80)	0.76 (0.63 - 0.93)	0.20 (0.03 - 0.26)	0.80 (0.74 - 0.99)	0.54 (0.40 - 0.68)

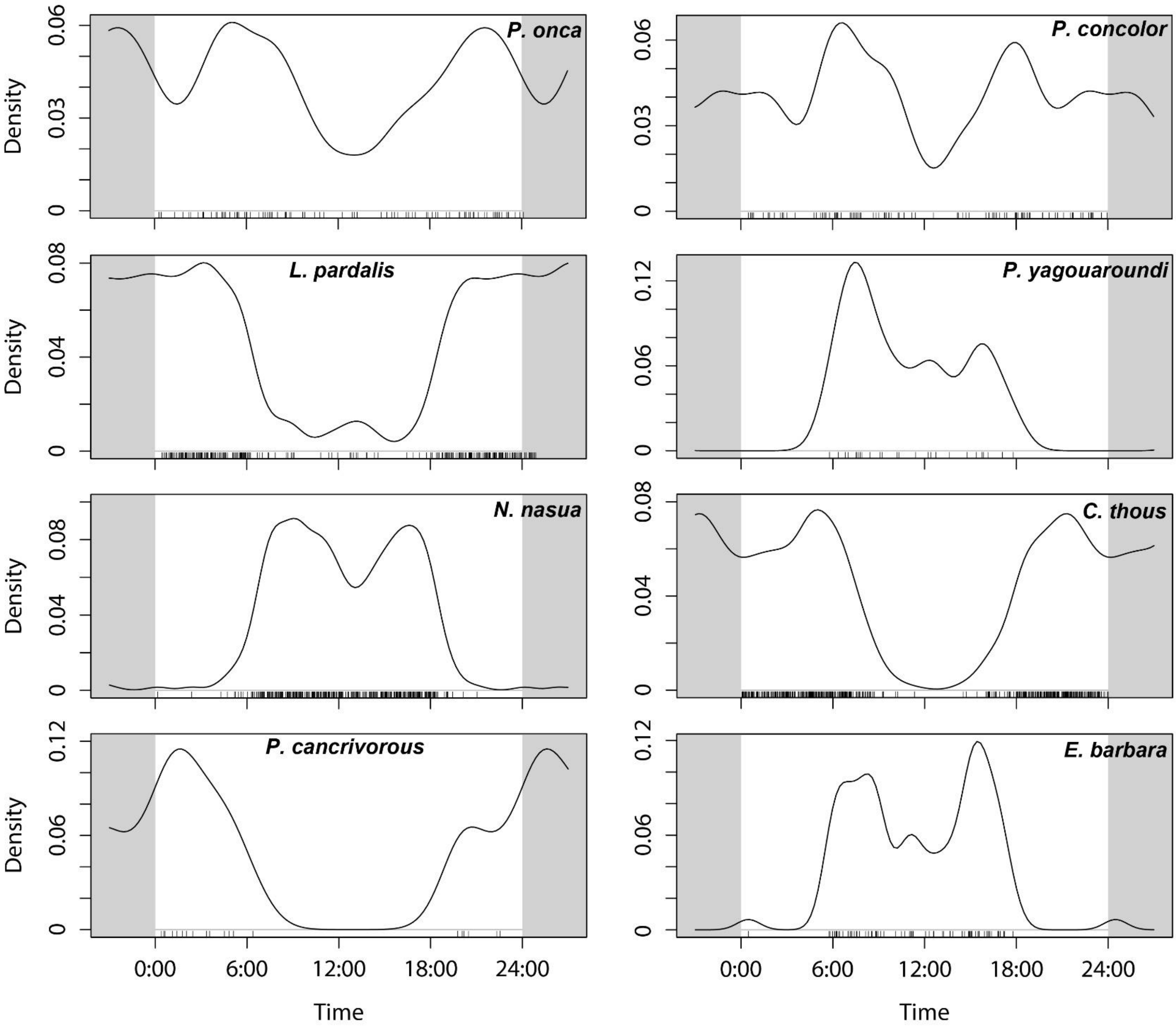

Figure 3. Kernel time-density distributions of camera trap records of eight carnivore species in the Pantanal wetland, southwestern of Brazil. Small bars above the X-axis show individual records.

Co-occurrence

The pairwise co-occurrence approach included ten carnivore species in 88 camera trap stations, and performed 45 different pairwise co-occurrences (Table 10). Among these pairs, 33 represented random associations between carnivore species and 12 were nonrandom, being nine positive and three negative associations (Table 11, Figure 4). The *Panthera onca* was present in most of the negative associations (n = 3), which occurred with *Nasua nasua*, *Cerdocyon thous* and *Eira barbara*. The *Puma concolor* showed only positive or random associations. The *Nasua nasua*, was the species with more positive associations (n = 4) and the *Leopardus pardalis* presented the highest number of random associations (n = 9) (Table. 11).

Table 10. Percentage and number of positive, negative and random associations between carnivore species in the Brazilian Pantanal wetland.

Species	Number of associations (%)		
	Positive	Negative	Random
Cerdocyon thous	4 (44)	1 (11)	4 (44)
Nasua nasua	3 (33)	1 (11)	5 (55)
Eira barbara	4 (44)	1 (11)	4 (44)
Puma concolor	4 (44)	0	5 (55)
Puma yagouaroundi	3 (33)	0	6 (66)
Panthera onca	0	3 (33)	6 (66)
Leopardus pardalis	0	0	9 (100)
Leopardus vetulus	0	0	9 (100)
Leopardus colocolo	0	0	9 (100)
Procyon cancrivorus	0	0	9 (100)

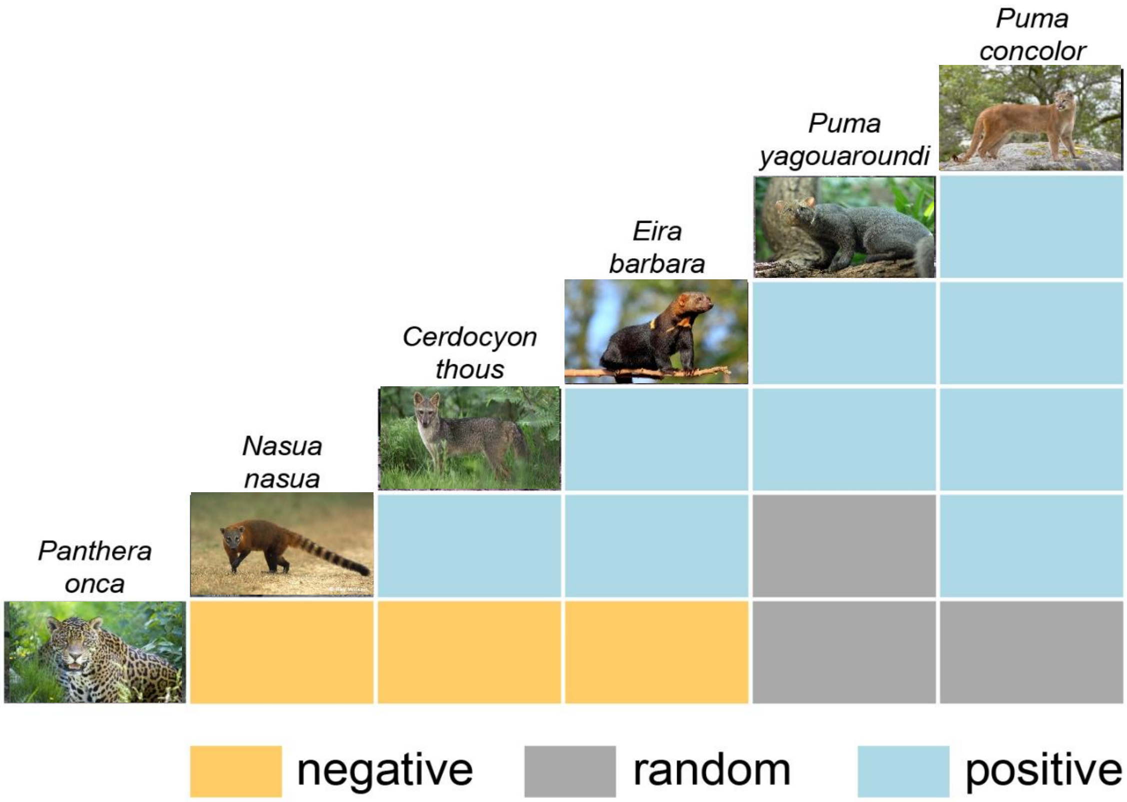

Figure 4. Species co-occurrence matrix showing positive, negative or random pairwise associations between carnivore species in the Pantanal wetland, southwestern Brazil.

Table 11. Co-occurrence parameters of 45 pairs of carnivore species in the Pantanal wetland, southwestern Brazil (p_lt and p_gt are considered *p-values* for observed negative and positive co-occurrences respectively). *Significant values.

Species pairs		Sites with sp1 (n)	Sites with sp2 (n)	Sites with both (n)	Co-occur (p)	Expected sites with both (n)	p_lt	p_gt
1	2							
C. thous	*N. nasua*	50	58	43	0.374	33	1.00	0.00*
C. thous	*P. concolor*	50	36	27	0.232	20.5	1.00	0.00*
C. thous	*L. pardalis*	50	46	27	0.297	26.1	0.72	0.44
C. thous	*P. onca*	50	29	12	0.187	16.5	0.03*	0.99
C. thous	*L. vetulus*	50	3	2	0.019	1.7	0.82	0.60
C. thous	*L. colocolo*	50	1	1	0.006	0.6	1.00	0.57
C. thous	*E. barbara*	50	23	19	0.149	13.1	1.00	0.00*
C. thous	*P. cancrivorus*	50	13	8	0.084	7.4	0.75	0.48
C. thous	*P. yagouaroundi*	50	10	9	0.065	5.7	1.00	0.02*
N. nasua	*P. concolor*	58	36	30	0.27	23.7	1.00	0.00*
N. nasua	*L. pardalis*	58	46	28	0.345	30.3	0.21	0.90
N. nasua	*P. onca*	58	29	10	0.217	19.1	0.00*	1.00
N. nasua	*L. vetulus*	58	3	3	0.022	2	1.00	0.28
N. nasua	*L. colocolo*	58	1	1	0.007	0.7	1.00	0.66
N. nasua	*E. barbara*	58	23	21	0.172	15.2	1.00	0.00*
N. nasua	*P. cancrivorus*	58	13	11	0.097	8.6	0.98	0.11
N. nasua	*P. yagouaroundi*	58	10	9	0.075	6.6	0.99	0.08
P. concolor	*L. pardalis*	36	46	22	0.214	18.8	0.95	0.12
P. concolor	*P. onca*	36	29	8	0.135	11.9	0.06	0.98
P. concolor	*L. vetulus*	36	3	0	0.014	1.2	0.20	1.00
P. concolor	*L. colocolo*	36	1	0	0.005	0.4	0.59	1.00
P. concolor	*E. barbara*	36	23	17	0.107	9.4	1.00	0.00*
P. concolor	*P. cancrivorus*	36	13	7	0.06	5.3	0.91	0.23
P. concolor	*P. yagouaroundi*	36	10	8	0.046	4.1	1.00	0.01*
L. pardalis	*P. onca*	46	29	18	0.172	15.2	0.94	0.14
L. pardalis	*L. vetulus*	46	3	1	0.018	1.6	0.47	0.90
L. pardalis	*L. colocolo*	46	1	0	0.006	0.5	0.48	1.00
L. pardalis	*E. barbara*	46	23	12	0.137	12	0.59	0.60
L. pardalis	*P. cancrivorus*	46	13	6	0.077	6.8	0.43	0.78
L. pardalis	*P. yagouaroundi*	46	10	7	0.059	5.2	0.94	0.20
P. onca	*L. vetulus*	29	3	1	0.011	1	0.75	0.70
P. onca	*L. colocolo*	29	1	1	0.004	0.3	1.00	0.33
P. onca	*E. barbara*	29	23	2	0.086	7.6	0.00*	1.00
P. onca	*P. cancrivorus*	29	13	2	0.049	4.3	0.13	0.97
P. onca	*P. yagouaroundi*	29	10	3	0.037	3.3	0.57	0.71
L. vetulus	*L. colocolo*	3	1	0	0	0	0.97	1.00
L. vetulus	*E. barbara*	3	23	1	0.009	0.8	0.83	0.60
L. vetulus	*P. cancrivorus*	3	13	0	0.005	0.4	0.62	1.00
L. vetulus	*P. yagouaroundi*	3	10	1	0.004	0.3	0.97	0.31
L. colocolo	*E. barbara*	1	23	0	0.003	0.3	0.74	1.00
L. colocolo	*P. cancrivorus*	1	13	0	0.002	0.1	0.85	1.00
L. colocolo	*P. yagouaroundi*	1	10	0	0.001	0.1	0.89	1.00
E. barbara	*P. cancrivorus*	23	13	6	0.039	3.4	0.98	0.08
E. barbara	*P. yagouaroundi*	23	10	7	0.03	2.6	1.00	0.00*
P. cancrivorus	*P. yagouaroundi*	13	10	2	0.017	1.5	0.84	0.45

Discussion

Carnivores species richness and composition in the Pantanal sub-regions

This study is one of the few focusing on species richness and habitat use of mammalian carnivores in the Pantanal wetland. Camera trapping surveys recorded 11 out of the 18 carnivore species known to inhabit the study sites (Hannibal et al. 2015), thus proving to be an efficient method to survey elusive, nocturnal and rare species. Some Pantanal carnivore species not recorded here were the bush dog *Speothos venaticus*, which is a rare species in its entire range of distribution (Jorge et al. 2013), and the semi-aquatics otters *Pteronura brasiliensis* and *Lontra longicaudis*. Absence of them in my records is likely related to distinct behavior of otters and rarity of bush dog in the study regions (Hanibbal et al. 2015). The bush dog was already recorded in the Nhecolândia Pantanal sub-region however only in the dense forests (Desbiez el al. 2010). Sometimes, the placement of the camera traps in dense vegetation was difficult since the movement while surveying the area was restrict and there places impossible to cross. Even so, estimative of species richness show a high diversity of small to large sized carnivores, and the presence of nearly all species expected for the Pantanal (Alho et al. 2011, Hanibbal et al. 2015).

The Sagrado Ranch was richer (11 species) than the other study sites (7-8 species), which is reasonable as this ranch is close to the Abobral river and presents lower deforestation and habitat degradation levels when compared to the other study sites. Sagrado ranch has some parts without management, whereas the management practices in the other study area transformed natural vegetation into planted pasture lands. Therefore, the high richness of carnivores found in the Sagrado Ranch can be due the high habitat quality, with more available preys that is a major ecological requirement of carnivores (Pierce et al. 2000).

The frequency of records of carnivore species varied according to study site, which is probably related to differences of detectability influenced by distinct behavioral patterns, differences in sampling designs and environmental factors (Bailey et al. 2004). For example, the frequency of records of the maned wolf, jaguar and jaguarundi was low when compared to that of coati and crab-eating fox. The jaguar was not record neither in the Cáceres Ranch nor Mata Grande Ranch, however in the Sagrado Ranch and Eliezer Batista reserve the jaguar presence was common. The low density and absence of this species in the other study sites are linked to the habitat fragmentation caused by human and intensification of land use in Pantanal (Cavalcanti et al. 2012). The jaguarundi was recorded in all study sites with low frequency, suggesting rarity in the Pantanal wetland. The rarity of jaguarundi can be related with the higher abundance of ocelots in the Pantanal, a potential competitors (Oliveira et al. 2010). Other species such as puma, coati and crab eating fox were frequently recorded in all study sites, due to this plasticity to use habitats with human presence and cattle ranching.

Factors influencing carnivore occupancy and detectability

The spatial analyses indicate that distinct carnivore species respond differently to variation of habitats, food and competitors, as these covariates influenced positively or negatively the occupancy estimates of particular carnivore species (Manley et al. 2005, Lesmeister 2015). In addition, I also identified species-specific patterns of variations across the entire community, highlighting their preference and avoidance trends, and habitat use segregation among the carnivore species. This was based on differences of occupancy estimates for each species (Table 29), incorporating the imperfect detection probability parameters (detection probability < 1) into the occupancy model (Royle & Nichols, 2005). It is especially important accounting for imperfect detection in occupancy models of rare and elusive species, such as the carnivore species studied here, as the bias is reduced (Royle & Nichols, 2005).

I observed that presence of top predators has the most consistent effect on the mesopredator community, with positive influence, followed by the habitat variable. Unlike expected, the predator puma was present in the occupancy models of four species - ocelot, crab-eating fox, tayra and coati - with a positive influence which can be an indicator of facilitation between them probably as a result of same habitat selection patterns. Some of these mesopredators such as coati were already present in the puma diet (Novack et al., 2005). However, the abundance of small and medium vertebrates (Table 2) potentially preyed on by puma in the Pantanal can be considered factors promoting the spatial aggregation between species. It is supported by the positive influence of the potential small-sized preys in both best models of puma and ocelots. These results indicate no spatial segregation between puma and mesopredator species in the Pantanal, likewise in western Belize where small carnivores and puma share the same areas (Davis et al. 2010). On the other hand, the jaguar was not a good predictor mesopredators occupancy and was only present in a few models with low representativeness (Table 9).

Habitat types entered in the occupancy models of mesopredator species, with positive or negative association showing that carnivore species use the available habitats differently. For example, the Vegetation under Fluvial Influence was positive for jaguar occupancy, but negative for occupancies of the mesopredators coati and crab-eating fox, an outcome that can be a behavioral mechanism to avoid encounters with large predators (Droge et al. 2017).

Among the tested variables, prey availability had the most consistent effect on the predator community with positive influence in the occupancy estimative of jaguar and pumas. These results agree with other studies supporting prey abundance as the most important driving force on felid occurrence (Pierce et al. 2000, Ramalho 2006), once jaguar and puma are considered opportunist predators, using preys relative to their abundances (Weckel et al., 2006). My results concur with Fuller & Sievert (2001) that prey abundance is the major force influencing the density and distribution of carnivores, such as the large felines. Those authors also suggested that the availability of resources largely affects the reproduction and survival of carnivores. The prey availability can also influence the coexistence between jaguar and puma, as is discussed below. Similarly, Karanth et al. (2004) found that under a wide range of ecological conditions prey density is a key determinant for distribution and abundance of tigers *Panthera tigris*.

Regarding to detectability, the results showed that the habitat categories influence, positively or negatively the detection probability of carnivore species. Estimated carnivore detection probabilities can reflect the species-specific behavioral patterns, for example, it is known the preference of jaguar from habitats dominated by water (Emmons, 1987, Crawshaw & Quigley, 1991, Sollmann et al 2012) and this habitat use was found in the present study where the jaguar detectability increased in areas with Vegetation under Fluvial Influence. On the other hand, detectability of pumas was negatively influenced by the Vegetation under Influence Fluvial, which can be interpreted as a behavioral mechanism to avoid encounters with jaguars (Sollmann et al. 2012) and/or due to a preference of pumas for dry habitats (Núñez et al. 2010).

Through the jaguar occupancy models, it was verified that the predictors used in the candidate models did not improve model precision, suggesting a low interference in jaguar distribution (Table 2). When modelling jaguars occupancy, the null model ranked as the highest among the candidate models (Table 9), however, the prey variables, capture rates of small mammals and large mammals, entered in the best models indicating a positive influence in the jaguar occurrence. Alternatively, the jaguar detectability increased with the increase of Vegetation under Fluvial Influence. The positive correlation of the jaguar with habitats dominated by water has been documented before in the Pantanal floodplain (Crawshaw & Quigley 1991) as well as in the Amazon rainforest (Emmons 1987) and Cerrado grasslands (Sollmann et al. 2012). The close association of this species with water may be explained for the fact that the species was only recorded in two of the four study sites, which present more habitats dominated by water: the Sagrado Ranch in the subregion Abobral, and the natural reserve Eliezer Batista located in the Paraguai subregion.

The puma occupancy models indicate that availability of preys has stronger effect on its occupancy than the other predictors (Habitat, Landscape and Competitors; Table 2) - which was positively correlated with the presence of small and large mammals. These results are in line with those obtained in Central Brazil where the best predictor was the prey abundance (Negrões et al. 2010). The habitat categories did not interfere in puma occupancy. In fact, pumas are considered to be super generalists in habitat use (Iriarte et al., 1990), although their detectability in the Pantanal was negatively influenced by the Vegetation under Fluvial Influence. This negative effect may decrease potential competition with jaguars. However, this negative correlation also can be a result of the difficult to movement in this habitat type and the preference, already recorded, by puma to dry habitats (Núñez et al. 2010).

The models for ocelot indicated that occupancy was positively affected by the increased capture rate of small mammals, which are potential preys, and by the presence of pumas. It is known that ocelots occupy a wide range of habitats (Murray & Gardner 1997), and it was suggested that their habitat preference may have been related to prey availability (Oliveira et al. 2010, Caso 2013), corroborating with its positive association with the presence of small mammals in the Pantanal. In the present study, ocelot not appear to have well defined habitat preferences, but Grass Savanna negatively influenced its occupancy. The negative effect of Grass Savanna was also observed in other regions, such as in the Emas National Park, Brazil (Oliveira 2010) and in Nhecolância subregion of Pantanal (Rocha 2006). Contrary to my expectation, the ocelots did not avoid areas with large predators. Puma and jaguar are present in the best model for ocelot occupancy with a positive association suggesting no spatial partitioning, nevertheless, more investigation in a fine scale is needed to confirm this pattern. Ocelots may feed on preys smaller than those of top predators (Moreno et al. 2006), thus avoiding competition with these large carnivores. In contrast, for ocelot, the detection probability seems to be higher in the areas presenting forested savannas, confirming the importance of this habitat to this species (Oliveira 2010, Bianchi et al. 2016). This association supports the need of dense vegetation cover by ocelots (Haines 2006, Horne et al. 2009).

Crab-eating fox occupancy is influenced by five predictor variables that include competitors (Puma and Ocelot) and habitats (Forested savannah, Grassland savannah and Vegetation under fluvial influence). It is known that the crab-eating fox use all available habitats in proportion to their availability being considered a habitat generalist (Jacomo et al. 2004, Juarez & Marinho-Filho 2002). Crab-eating fox are known by their flexibility in terms of habitat use, either natural, deforested or regenerating areas (Jacomo et al. 2004, Ferraz et al. 2010). Therefore, use of anthropogenic disturbed areas, such as agricultural areas, should not be interpreted as ideal habitat, but it may bring benefits to this species, providing increased foraging opportunities (Jacomo et al. 2004, Ferraz et al. 2010). Other study in the Nhecolândia subregion showed that crab-eating foxes randomly uses all habitats within their home range (Bianchi et al. 2016). In the present study, the Forested Savannah and Vegetation under Fluvial Influence had a significantly negative effect on the fox occupancy. As expected, the avoidance of these habitats can be a mechanism for coexistence with other carnivores, such as ocelots that are positively associated with Forested Savannah (Table 13). On the other hand, the presence of pumas had a significant positive influence on the occupancy of foxes, indicating no spatial partitioning between them and probably the use of similar habitats in the Pantanal. This result matches the ones of Davis et al. (2010) in Belize, where small carnivores, such as the crab-eating fox, did not avoid habitats used by large carnivores, like puma and jaguar.

This was the first study on the occupancy patterns for tayra. The averaging models indicated that tayra is mostly positively influenced by the presence of puma, thus supporting no spatial partitioning between them. However, areas mainly composed by Grassland Savannah negatively influenced tayra occupancy. Other studies also indicate that tayra avoid open areas, and occurs in dense forests along watercourses (Cáceres et al. 2007, Alves et al. 2012). Its habitat preference may be partly linked to an exploratory behavior and food habits, once tayra’s diet is majority compost with prey items found in closed habitat (Presley 2000). Although the tayra was detected in all study sites, this species was mostly recorded inside dense forests with watercourses, especially in the Mata Grande ranch, corroborating results achieved by Alves et al. (2012). More investigation is needed concerning the other factors that affect tayra occurrence, to clarify if the preference or avoidance of such habitats are linked to prey abundance or escaping from competitors.

Habitat categories and presence of pumas were the most important predictors of coati occupancy. Forested savannah and Vegetation under Fluvial Influence negatively influenced its occupancy, and other habitats presented low interference, which agrees with other studies that also found low presence of coati in habitats under fluvial influence and Forested Savannah (cerrado) (Yanoshi & Mecolli, 1992, Holt 2001, Rocha 2006). On the other hand, the presence of puma had positive influence on the occupancy of coati and the presence of jaguar did not influence coati distribution in the Pantanal, contrary to the expectations of negative effects of both top predators on it, since jaguar and puma were reported as predators of coatis (Novack et al. 2005). Absence of negative influence of top predators on coati occupancy in the Pantanal might be explained by the high abundance of potential prey species, more profitable than coatis to those predators diet, such as *Pecari tajacu*, *Myrmecophaga tridactyla*, and *Hydrochaeris hydrochaeris* (Emmons 1987, Iriarte et al. 1990, Scognamillo et al. 2003) (Table 2).

Capture rate of medium mammals (variable Med) had no effect on the occupancy of carnivore species in the Pantanal, as it was only present among the best model for tayra detectability. Medium mammals comprised species with 5 and 15 kg body mass, and included *Alouatta caraya*, *Cuniculus paca*, *Cabassous tatouay*, *Euphractus sexcinctus*, *Hydrochaeris hydrochaeris* and *Tamandua tetradactyla*. These species presented low capture rates at the study sites, which contributed to the low representativeness of medium mammals in the occupancy models.

Table 29. Negative (-), positive (+) or none (n) influence of habitat types (FS – Forested Savanna, GS – Grassland Savanna, VIF – Vegetation under Fluvial Influence and Forested Formation - FF) On the probability of occupancy and detectability of carnivore species in the Pantanal wetland, southwestern Brazil.

	Habitats							
Species	Detectability				Occupancy			
	FS	GS	VIF	FF	FS	GS	VIF	FF
Panthera onca	n	n	+	n	n	n	n	n
Puma concolor	n	n	-	n	n	n	n	n
Leopardus pardalis	+	n	n	n	n	+	n	n
Cerdocyon thous	n	n	-	n	-	n	-	n
Eira barbara	n	n	n	n	n	-	n	n
Nasua nasua	n	n	-	-	-	n	-	n

Daily activity patterns

My results on carnivore activity rhythms indicate temporal segregation among Pantanal carnivore species. The general activity patterns found in the present study resemble those reported elsewhere for most carnivore species, with crepuscular or nocturnal activity (Gómez et al. 2005, Di Bitteti et al. 2006, Bianch et al. 2016), except that tayra, coati and jaguarundi are mostly diurnal in the Pantanal.

Ocelot was the mostly nocturnal mesopredator being active throughout the night and crepuscular periods, as already reported in the Pantanal (Bianch et al. 2016). However, this crepuscular activity was not found in other regions, as in the Bosque Chiquitano in Bolivia (Maffei et al. 2002), Amazon (Gómez et al. 2005, Kolowski & Alonso 2010) and Atlantic Forest of Argentina (Di Bitteti et al. 2006) where ocelots present predominately nocturnal activity. The crepuscular behavior of ocelots in the Pantanal can be related to an increased activity of their preys in crepuscular periods rather than an effect of top predator avoidance, once no temporal segregation occurred between ocelots and jaguars or pumas (Table 19). The crab-eating fox also presented predominantly nocturnal activity, as previously reported in the Pantanal (Porfírio 2014, Bianch et al. 2016) and others regions (Maffei et al. 2002, Vieira & Port 2007, Di Bitteti et al. 2009). Circadian activity of crab-eating foxes highly overlapped with ocelots, jaguars and pumas, indicating no temporal partitioning among them. On the other hand, activity period of crab-eating fox differed from other mesopredators, such as tayra, coati and crab-eating racoon. Once these species present similar diet and habitat use, the temporal segregation among them potentially reduces competition (Silva-Pereira et al. 2011, Bianch et al. 2016).

The crab-eating raccoon was the only species completely nocturne like observed in other Pantanal region (Bianch et al. 2016). However, in the Amazon forest and in the Bosque Chiquitano of Bolivia the raccoon has presents some crepuscular activity, being classified as mostly nocturnal (Arispe et al. 2008, Goméz et al. 2005). This species presented higher activity overlap with all Pantanal carnivore species, except tayra which presented no temporal partitioning with raccoon (Table 19). In general, therefore, the results indicate that time sharing is more important among small mesopredators, which likely present a more similar diet and habitat use (Alho et al. 1987, Presley 2000, Arispe et al. 2008).

Tayra was the only species with diurnal activity in the Pantanal. This result concurs with others conducted in the Pantanal region (Alho et al. 1987) and in Medellín, Colombia (Delgado et al. 2011). However, tayra is cathemeral in the Amazon, where it also presents nocturnal activity (Gómez et al. 2005). High activity overlap was verified among tayra and large predators, thus with no temporal segregation between them. However, low circadian activity overlap between tayra and ocelot supports temporal segregation between these mesopredators. Tayra has been recorded as prey of ocelot (Bianch et al. 2010, 2014), which supports the circadian activity of tayra as a mechanism to avoid predation by ocelots (Massara et al. 2016). Likewise, diurnal habits have been observed for coatis in the Pantanal (Bianchi et al. 2016; present study) and also in the Amazon and Atlantic forests (Gómez et al. 2005, Massara et al. 2016). Therefore, time sharing might be an anti-predator mechanism between coatis and the mesopredators crab-eating fox and ocelot, both considered as predators of coatis (Bianchi et al. 2010, 2014).

My results indicate that jaguarundis are mainly active during the daylight in the Pantanal wetland, such as in the Chaco-Chiquitano of Bolivia (Maffei et al. 2002, 2007), in Atlantic Forest of Argentina (Di Bitetti et al. 2010) and in the Tamaulipan thorn scrub of Mexico (Caso 2013). Jaguarundi’s activity temporally segregates it from the others felines and medium-size predators, thus its diurnal habit would be an adaptive trait reducing intraguild competition and favoring coexistence of jaguarundi and other predators (Caso 1994, Kronfeld-Schor & Dayan 2003). In the Pantanal, daylight activity of jaguarundis can specially contribute for its co-occurrence with ocelots, as these felines are closely similar regarding to other ecological traits (Table 19).

The top predators jaguar and puma where cathemeral with similar activity patterns, being active during the night and day periods. This behavior differs from that observed in Belizean rain forests, where jaguars and pumas are predominantly nocturnal (Harmsen et al. 2009), as well as it differs from that reported in other Pantanal parts where they are mostly diurnal (Crawshaw & Quigley 1991, Foster et al. 2013). The absence of temporal partitioning between jaguars and pumas in the Pantanal has been also found in the Venezuelan llanos and in Belizean rain forests (Scognamillo et al. 2003, Harmsen et al. 2009). Studies in other regions have associated the circadian activities of these top predators with the diurnal activity of their local preys (Emmons 1987, Foster et al. 2013, Nuñez et al. 2000, Scognamillo et al. 2003, Harmsen et al. 2009), supporting that jaguars and pumas respond to prey availability rather than to each other avoidance. In the present study, although daytime activity is not a mechanism of segregation between jaguars and pumas, they present differential use of habitats, which may promote their coexistence in the Pantanal wetland.

Carnivore co-occurrences

The present study showed that carnivore species in the Pantanal wetland differently use the available habitats, with preference and avoidance trends among them. According to the pairwise co-occurrence approach, most pairs of species co-occurred more than expected by chance, an evidence of low spatial avoidance among the Pantanal carnivores. Jaguar, the largest predator of Pantanal, was the only species negatively associated with other carnivores, the mesopredators coati, crab-eating fox and tayra (Figure 4). If these mesopredators are susceptible to predation by jaguars, then the avoidance of habitats occupied by jaguars could be shaped throughout the interaction history among them in the Pantanal floodplain (Lesmeister 2015). The two top predators, jaguars and pumas, were randomly associated each other in the Pantanal, nonetheless some spatial segregation occurs based on differential occupancy of habitats, as already discussed above. The random co-occurrence between these top predators in the Pantanal could be mediated by the consumption of distinct prey species (Foster et al. 2013).

Contrasting to jaguars, pumas were positively or randomly associated with the others studied mesopredators, indicating that pumas do not affect the occurrence patterns of small carnivores in the Pantanal, as also found in western Belize by Davis et al. (2010). Likewise, ocelot occurrence does not influence the spatial distribution of smaller mesocarnivores in the Pantanal, as ocelots are randomly associated with them. It was contrary to my expectation, as a clear negative influence of ocelot on other small cats was found in the lowland neotropics, including sites from the northernmost (South Texas) and southernmost (north-eastern Argentina and southern Brazil) by Oliveira et al (2010) and in the Tamaulipan thorn scrub of Mexico by Caso (2013). Nonetheless, similarly to my results, no spatial influence of ocelots on small carnivores also occurs in the Atlantic Forest (Massara et al. 2016). Spatial overlapping with ocelots can be mediated by the behavioral plasticity of some small carnivores that adjust their circadian rhythms to avoid encounters with ocelots (Massara et al. 2016). In addition, the nocturnal mesocarnivores species in the Pantanal, crab-eating fox and crab-eating raccoon, might be unthreatened by ocelots (Massara et al. 2016).

Overall Conclusion

In the present study I assessed spatio-temporal dynamics of Pantanal carnivores, revealing their trends of habitat use, spatial pairwise association types and circadian rhythms at a large scale, incorporating the regional landscape heterogeneity. In almost all cases, distributions of taxa were best predicted by the frequency of potential preys and habitat types. It has been suggested that the spatial environmental complexity, such as that of the Pantanal, together with the trend of habitat preference and avoidance of carnivores, may facilitate the coexistence of predator and mesopredator species (Simon 1974, Sollmann et al. 2012) and contribute to the high diversity of carnivores in the Pantanal. I highlight that results indicate more avoidance than preference of certain habitats by the species, as the frequency of some types of habitat presented negative effect in their occupancy models. It suggested a mechanism against competition or predation among carnivores in the Pantanal.

Overall findings of this study support that carnivores largely use similar resources, with the share of space and/or time between few species, thus showing a low general level of niche partitioning in the Pantanal. This behavior can be associated to the abundance of preys founded in the Pantanal, facilitating the coexistence between carnivore species. However, to affirm this hypothesis specific diet studies are required. In addition, in the present study different circadian rhythms contributed more than spatial partitioning for niche segregation among carnivores. The ability of carnivore species in modifying their activity patterns to avoid predators or competitors, or to adjust to the availability of their main preys, is a feature that facilitates their coexistence.

References

Abreu KC, Moro-Rios RF, Silva-Pereira, JE, Miranda JMD, Jablonski EF & Passos FC. 2008. Feeding habits of ocelot (Leopardus pardalis) in Southern Brazil. Mammalian Bioloeach 73, 407–411.

Alho CRJ, Lacher TE, Campos JRZMS & Gonçalves HC. 1987. Mamíferos da Fazenda Nhumirim, sub-região de Nhecolândia, Pantanal do Mato Grosso do Sul. I – Levantamento preliminar das espécies. Revista Brasileira de Zoologia 4: 151-164.

Alho CJR & Sabino J. 2011. A conservation agenda for the Pantanal's biodiversity. Brazilian Journal of Biology 71(1): 327-335.

Alho CJR, Camargo G. & Fischer E. 2011. Terrestrial and aquatic mammals of the Pantanal. Brazilian Journal of Biology 71(1): 297-310.

Alves, T. R.; Fonseca, R. C. B. & Engel V. L. 2012. Mamíferos de médio e grande porte e sua relação com o mosaico de habitats na *cuesta* de Botucatu, Estado de Sao Paulo, Brasil. Iheringia, Serie Zoologia 102(2): 150-158.

Arispe R, Venegas C & Rumiz D. 2008. Abundancia y patrones de actividad del mapache (Procyon cancrivorous) en un bosque Chiquitano de Bolívia. Mastozoología Neotropical 15(2): 323–333.

Azevedo FCC & Murray DL. 2007. Spatial organization and food habits of jaguars (*Panthera onca*) in a floodplain forest. Biological Conservation 137: 391-402.

Barea-Azcón JM, Virgós E, Ballesteros-Duperón E, Moleón M & Chirosa M. 2006. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. Biodiversity Conservation 16: 1213–1230.

Bartón K. 2013. MuMIn: multi-model inference, R package version 1.9.0. Available via http://CRAN.R-project.org/package=MuMIn. (accessed 11 February 2013).

Bianchi RdC, Campos RC, Xavier-Filho NL, Olifiers N, Gompper ME & Mourão G. 2014. Intraspecific, interspecific, and seasonal differences in the diet of three mid-sized carnivores in a large neotropical wetland. Acta Theriologica 59: 13–23.

Bianchi RdC, Mendes SL &.Júnior PDM. 2010. Food habits of the ocelot, Leopardus pardalis, in two areas in southeast Brazil. Studies on Neotropical Fauna and Environment 45: 111–119.

Bianchi RdC, Olifiers N, Gompper ME & Mourão G. 2016. Niche Partitioning among Mesocarnivores in a Brazilian Wetland. PLOS ONE 11(9): e0162893. doi: 10.1371/journal.pone.0162893

Britski HA, Silimon KZS & Lopes BS. 1999. Peixes do Pantanal. Manual de identificação. Brasília: Empresa Brasileira de Pesquisa Agropecuária, Serviço de Produção de Informação (EMBRAPASPI) e Corumbá-MS: Centro de Pesquisa Agropecuária do Pantanal (EMBRAPA-CPAP).

Burnham KP & Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Burnham KP, Anderson DR & Huyvaert K. 2010. AICc model selection in ecological and behavioral science: some background, observations, and comparisons. Behavioral Ecology & Sociobiology. doi:10.1007/s00265-010-1029-6

Cáceres NC, Cherem JJ & Graipel ME. 2007. Distribuição geográfica de mamíferos terrestres na Região Sul do Brasil. Ciência Ambiental 35: 167–180.

Case TJ & Gilpin ME. 1974. Interference competition and niche theory. Proceeding of National Academy of Sciences of the United States of America **71**(8): 3073–3077.

Cavalcanti SM, Gese E. 2009. Spatial ecology and social interactions of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. Journal of Mammalogy 90: 935-45.

Cavalcanti SMC & Gese EM. 2010. Kill rates and predation patterns of jaguars (*Panthera onca*) in the southern Pantanal, Brazil. Journal of Mammalogy 91: 722–736.

Cavalcanti SMC, Azevedo FCC, Tomás WM, Boulhosa RLP & Crawshaw PG Jr. 2012. The status of the jaguar in the Pantanal. CATnews. (Special Issue 7):29-34.

Crawshaw PG & Quigley HB. 1984. A ecologia do jaguar ou onc¸a pintada no Pantanal. Relatório entregue ao Instituto Brasileiro de Desenvolvimento Florestal (IBDF)/DN (Brasilia), p. 110.

Crawshaw PGJr & Quigley HB. 1989. Notes on ocelot movement and activity in the Pantanal region, Brazil. Biotropica 21: 377–379.

Crawshaw PG & Quigley HB. 1991. Jaguar spacing, activity and habitat use in a seasonally flooded environment in Brazil. Journal of Zoology 223: 357–370.

Cruz J, Sarmento P & White P. 2015. Influence of exotic forest plantations on occupancy and co-occurrence patterns in a Mediterranean carnivore guild. Journal of Mammalogy 10: 1-13.

Dalerum F, Cameron EZ, Kunkel K & Somers M J. 2009. Diversity and depletions in continental carnivore guilds: implications for prioritizing global carnivore conservation. Biology Letters 5: 35–38.

Davis ML, Kelly MJ & Stauffer DF. 2011. Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. Animal Conservation 14: 56-65.

Desbiez ALJ, Bodmer RE & Tomas WM. 2010. Mammalian densities in a neotropical wetland subject to extreme climatic events. Biotropica 42: 372-378.

Di Bitetti MS, De Angelo CD, Di Blanco YE & Paviolo A. (2010) Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologica 36: 403–412.

Di Bitetti MS, Paviolo A, De Angelo C. 2006. Density, habitat use and activity patterns of ocelots (*Leopardus pardalis*) in the Atlantic Forest of Misiones, Argentina. Journal of Zoology 270: 153 e 163.

Di Minin E, Slotow R, Hunter LTB, Montesino Pouzols F, Toivonen T, Verburg PH, Leader-Williams N, Petracca L & Moilanen A. 2016. Global priorities for national carnivore conservation under land use change. Scientific Reports 6: 23814.

Dillon A & Kelly MJ. 2007. Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates. Oryx 41: 469–477.

Durant SM. 1998. Competition refuges and coexistence: an example from Serengeti carnivores. Journal of Animal Ecology 67: 370–386.

ESRI. 2013. ArcGIS® Version 10. Redlands (CA) ESRI

Emmons LH. 1987. Comparative feeding ecology of felids in a neotropical rainforest. Behavioral Ecology and Sociobiology 20: 271‑283.

Ferraz K, de Siqueira MF, Martin PS, Esteves CF, do Couto HTZ. 2010. Assessment of Cerdocyon thous distribution in an agricultural mosaic, southeastern Brazil. Mammalia. 74(3): 275–80.

Fiske I & Chandler R. 2011. Unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software 43(10): 1-23.

Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácomo ATA, Negrões N, Fonseca C, Silveira L. 2013. Jaguar and puma activity patterns and predator–prey interactions in four Brazilian biomes. Biotropica 45: 373-379. 10.1111/btp.12021.

Fuller TK & Sievert PR. 2001. Carnivore demography and the consequences of changes in prey availability, 163-178. In : *Carnivore conservation* . Gittleman, J.L.; Funk, S.M.; Macdonald, D. & Wayne, R.K. (Eds). Cambridge University Press

Gardner B, Reppucci J, Lucherini M & Royle JA. 2010. Spatially-explicit inference for open populations: estimating demographic parameters from camera-trap studies. Ecology 91: 3376–3383.

Gese EM. 2001. Monitoring of terrestrial carnivore populations. In: Carnivore conservation (Eds. JL Gittleman, SM Funk, DW Macdonald & KR Wayne), pp 372–396. Cambridge University Press, Ithaca, New York.

Gittleman, JL, Funk SM, MacDonald D & Wayne RK. 2001. Carnivore conservation. Cambridge University Press, Cambridge, United Kingdom

Gómez H, Wallace RB, Ayala G, Tejada R. 2005 Dry season activity periods of some Amazonian mammals. Studies of Neotropical Fauna and Environment 40: 91-95.

Griffith DM, Veech JA and Marsh CJ. 2016. Cooccur: probabilistic species cooccurrence analysis in R. Journal of Statistical Software 69 (2).

Hamilton SK. 2002. Hydrological controls of ecological structure and function in the Pantanal wetland (Brazil). In: McClain, M. (Ed.), The Ecohydrology of South American Rivers and Wetlands. Special Publication, vol. 6. International Association of Hydrological Sciences, pp. 133–158.

Hannibal W, Duarte LA & Santos CC. 2015. Mamíferos não voadores do pantanal e entorno. Campo Grande, MS: Natureza em foco, 244p.

Harmsen BJ, Foster RJ, Silver SC, Ostro LET & Doncaster CP. 2009. Spatial and temporal interactions of sympatric jaguars (*Panthera onca)* and pumas (*Puma concolor*) in a neotropical forest. Journal of Mammalian. 90: 612–620.

Harris M, Tomas WM, Mourão G, Silva CJ, Guimarães E, Somoda F & Fachim E. 2005. Desafios para proteger o Pantanal Brasileiro: ameaças e iniciativas em conservação. Megadiversidade 1(1): 156-164.

IBGE. 1992. Manual técnico da vegetação brasileira (IBGE, ed.), Rio de Janeiro. 92p.

IUCN. 2016. The IUCN Red List of Threatened Species. Version 2016-3. <www.iucnredlist.org>. Downloaded on 30 january 2017.

Jackson HB & Fahrig L. 2012. What size is a biologically relevant landscape? Landscape Ecology 27: 929–941.

Jácomo ATA, Silveira L, Diniz-Filho JAF. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. Journal of Zoology 262: 99–106.

Jorge, RPS., Beisiegel, BM., Lima, ES., Jorge, MLPS., Leite-Pitman, MRP. & Paula, RC. 2013. Avaliação do Estado de Conservação do Cachorro-Vinagre Speothos venaticus (Lund, 1842) no Brasil. Biodiversidade Brasileira 3(1): 179-190.

Juarez KM & Marinho-Filho J. 2002. Diet, habitat use, and home ranges of sympatric canids in central Brazil. Journal of Mammalogy 83(4): 925-933.

Junk WJ, Cunha CN, Wantzen KM, Petermann P, Strussmann C, Marques MI & Adis J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquatic Sciences 68: 278-309.

Kanda CZ. 2015. Ecologia do movimento e dinâmica espaço-temporal da onça-pintada (*Panthera onca*) no Pantanal sul do Brasil. Tese de mestrado. Universidade Universidade Estadual Paulista "Júlio de Mesquita Filho",Unesp, Rio Claro, Brasil. 52pp.

Karanth KU & Nichols JD. 1998. Estimating tiger (*Panthera tigris*) populations form camera-trap data using capture–recaptures. Ecology 79: 2852–2862.

Karanth, KU & SUNQUIST ME. 2000. Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarahole, India. Jounal of Zoology 250: 255-265.

Kasper C, Peters F, Christoff AU & de Freitas TRO. 2015. Trophic relationships of sympatric small carnivores in fragmented landscapes of southern Brazil: niche overlap and potential for competition. Mammalia 80(2):143-152.

Konecny MJ. 1989. Movement patterns and food habits of four sympatric carnivore species in Belize, Central America. In Advances in neotropical mammalogy: 243–264. Redford, K.H. & Eisenberg, J.F. (Eds). Gainesville: The Sandhill Crane Press Inc..

Kowalski B, Watson F, Garza C & Delgado B. 2015. Effects of landscape covariates on the distribution and detection probabilities of mammalian carnivores. Journal of Mammalian 96(3): 511-521.

Letnic M, Ritchie EG & Dickman CR. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. Biological Reviews 87: 390–413.

Lima SL. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27: 215–290.

Linkie M, Dinata Y, Nugroho A & Haidir I.A. 2007. Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation 137: 20–27.

Linkie M, Ridout MS. 2011. Assessing tiger-prey interactions in Sumatran rainforests. Journal of Zoology 284: 224-229.

Linnell JD & Strand O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distribution 6: 169–176.

Long RA, Donovan TM, MacKay P, Zielinski WJ & Buzas JS. 2010. Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. Landscape Ecology 26: 327-340.

López-Bao, JV & González-Varo JP. 2011. Frugivory and spatial patterns of seed deposition by carnivorous mammals in anthropogenic landscapes: A multi-scale approach. Plos One 6 e14569: 1–11.

Lucherini M, Reppucci JI, Walker RS, Villalba ML, Urstten A, Gallardo G, Iriarte A, Villalobos R & Perovic P. 2009. Activity pattern segregation of carnivores in the high Andes. Journal of Mammalogy 90(6): 1404–1409.

Lyra-Jorge M, Ribeiro M, Ciocheti G, Tambosi L, Pivello V. 2010. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. European Journal of Wildlife Research 56: 359–368.

MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA & Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248–2255.

MacKenzie DI & Royle JA. 2005. Designing efficient occupancy studies: general advice and tips on allocation of survey effort. Journal of Applied Ecology 42: 1105-1114.

MacKenzie DI, Nichols JD, Royle, JA, Pollock, KP, Bailey, LL & Hines, JE. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, San Diego, California, USA.

Massara RL, Paschoal AMO, Bailey LL, Doherty PF, Jr Chiarello AG. 2016; Ecological interactions between ocelots and sympatric mesocarnivores in protected areas of the Atlantic Forest, southeastern Brazil. Jounal of Mammalian 97(6): 1634-1644.

McCarthy JL, Wibisono HT, McCarthy KP, Fuller TK & Andayani N. 2015. Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. Global Ecology and Conservation 3: 210–221.

McGarigal K & Ene E. 2012. Fragstats 4.1. A spatial pattern analysis program for categorical maps.

Médri IM & Mourão G. 2004. A fauna do Pantanal. Ação Ambiental 14-17.

Meredith M & Ridout M. 2016. Overview of the overlap package. https://cran.rproject.org/web/packages/overlap/vignettes/overlap.pdf

Michalski F, Peres CA & Metzger JP. 2010. Predicting the spatial distribution of four sympatric species of mid-sized carnivores in an Amazonian deforestation frontier Chapter 6 In: Middle-Sized Carnivores in Agricultural Landscapes, Nova Science Publishers, Inc.

Miller B, Harlow HJ, Harlow T, Biggins D & Ripple WJ. 2012. Trophic cascades linking wolves (*Canis lupus*), coyotes (*Canis latrans*), and small mammals. Canadian Journal of Zoology 90: 70–78.

Mills MGL. 1991. Conservation management of large carnivores in Africa. Koedoe 34: 81–90.

Ministério do Meio Ambiente- MMA. (2007). Áreas prioritárias para a Conservação, Uso Sustentável, e Repartição de Benefícios da Biodiversidade Brasileira. Brasília: MMA. 301 pp.

Ministério do Meio Ambiente MMA. 2010. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais. Monitoramento do desmatamento nos biomas brasileiros por satélite. Monitoramento do bioma Pantanal 2002 a 2008. Brasília: MMA/IBAMA/CID. 30 p.

Moreira-Arce D, Vergara PM, Boutin S. 2015. Diurnal human activity and introduced species affect occurrence of carnivores in a human-dominated landscape. PLoS ONE 10, e0137854

Moreno RS, Kays RW, Samudio R Jr. 2006. Competitive release in diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. Journal of Mammalogy 4: 808–816.

Nagy-Reis MB, Nichols JD, Chiarello AG, Ribeiro MC & Setz EZF. 2017. Landscape Use and Co-Occurrence Patterns of Neotropical Spotted Cats. PLOS ONE 12(1): e0168441. doi: 10.1371/journal.pone.0168441

Negrões N, Sarmento P, Cruz J, Eira C, Revilla E, Fonseca C, Sollmann R, Tôrres NM, Furtado MM, Jácomo ATA & Silveira, L. 2010. Use of camera-trapping to estimate puma density and influencing factors in central Brazil. The Journal of Wildlife Management 74: 1195-1203.

Neyman J & Pearson ES. 1928a. On the use and interpretation of certain test criteria for purposes of statistical inference part I. Biometrika, 20A: 175–240.

Neyman J & Pearson ES. 1928b. On the use and interpretation of certain test criteria for purposes of statistical inference. part II. Biometrika, 20A: 263–294.

Noss RF, Quigley HB, Hornocker MG, Merrill T & Paquet PC. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10: 949–963.

Noss Roemer GW, Gompper ME & Van Valkengurgh B. 2009. The ecological role of the mammalian mesocarnivore. BioScience 59(2): 165-173.

Novack AJ, Main MB, Sunquist ME & Labisky RF. 2005. Foraging ecology of jaguar (*Panthera onca*) and puma (*Puma concolor*) in hunted and non-hunted sites within the Maya Biosphere Reserve, Guatemala. Journal of Zoology 267: 167–178.

Núñez R, Miller B & Lindzey F. 2002. Ecología del jaguar en la reserva de la biosfera Chamela-Cuixmala, Jalisco, México. pp. 107-125. *In*: Medellín, R., Equihua, A., Chetkiewics, C., Rabinowitz, C., Crawshaw, A., Rabinowitz, P., Redford, A., Robinson, K., Sanderson, J.G. & Taber, A. (Eds.). El Jaguar en el nuevo milenio. Fondo de Cultura Económica, Universidad Nacional Autónoma de México y Wildlife Conservation Society. México D.F.

Núñez R, Miller B & Lindzey F. 2000. Food habits of jaguars and pumas in Jalisco, Mexico. Journal of Zoology 252: 373-379.

O'Connell AF, Talancy NW, Bailey LL, Sauer JR, Cook R. & Gilbert AT. 2006. Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. Journal of Wildlife Management 70*(*6*):* 1625-1633.

Oliveira, T.G. *Herpailurus yagouaroundi*. Mammalian Species,1998. 578: p.1-6.

Palomares F & Caro TM. 1999. Interspecific killing among mammalian carnivores. Am. Nat., 153, 492–508.

Oliveira TG, Tortato MA, SilveiraL, Kasper CB, Mazim FD, Jácomo ATA, Lucherini M, Soares JBG, Marques RV & Sunquist M. 2010. Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. In: Macdonald, D.W., Loveridge, A. (Eds.), Biology and Conservation of Wild Felids. Oxford University Press, Oxford.

Palomares F, Fernández N, Roques S, Chávez C, Silveira L, Keller C & Adrados B. 2016. Fine-scale habitat segregation between two ecologically similar top predators. PLoS One 11: e0155626.

Palomares F, Ferreras P, Fedriani JM & Delibes M. 1996. Spatial relationships between Iberian lynx and other carnivores in an area of south-western Spain. Journal Applied in Ecology 33: 5–13.

Penatti NC, Ribeiro ATI, Ferreira LG, Arantes AE & Coe MT. 2015. Satellite-based hydrological dynamics of the world's largest continuous wetland. Remote Sensing of Environment p.1-13.

Plano de Conservação da Bacia do Alto Paraguai - PCBAP. 1997. Ministério do Meio Ambiente dos Recursos hídricos e da Amazônia legal. Brasília: Ministério do Meio Ambiente. 433 pp.

Pongsiri MJ, Roman J, Ezenwa VO, Goldberg, TL, Koren, HS, Newbold SC, Ostfeld R S, Pattanayak SK & Salkeld DJ. 2009. Biodiversity loss affects global disease ecology. BioScience 59: 945–954.

Porfirio G. 2009. Ecologia alimentar da onça-pintada (Panthera onca) na sub-região do Pantanal de Miranda, MS. Dissertação de Mestrado. Universidade Federal de Mato Grosso do Sul. 89 pp.

Porfirio G. 2014. Ecology and conservation of felids in the Brazilian Pantanal. Aveiro, Portugal, University of Aveiro.

Porfirio G, Sarmento P, Foster V & Fonseca C. 2016a. Activity patterns of jaguars and pumas and their relationship to those of their potential prey in the Brazilian Pantanal. Mammalia, 0(0), pp. -. Retrieved 30 Mar. 2017, from doi:10.1515/mammalia-2015-0175

Porfirio G, Foster VC, Fonseca C, Sarmento P. 2016b. Activity patterns of ocelots and their potential prey in the Brazilian Pantanal, Mammalian Biology - Zeitschrift für Säugetierkunde 81(5): 511-517.

Presley SJ. 2000. Eira barbara. Mammalian Species 636: 1-6

Prevosti FJ & Pereira JA. 2014. Community structure of South American carnivores in the past and present. Journal of Mammalian Evolution 21: 363–68.

Prugh LR, Stoner CJ, Epps CW, Bean WT, Ripple WJ, Laliberte AS & Brashares JS. 2009. The rise of the mesopredator. BioScience 59: 779–791.

Putman RJ. 1994. Community Ecology. London, Chapman & Hall, 178p.

Quigley HB. 1987. Ecology and conservation of the jaguar (*Panthera onca*) in the Pantana region, Mato Grosso do Sul, Brazil. Idaho Dissertation Ph.D – University of Idaho, Moscow.

Quigley H & Crawshaw PG. 1992. A conservation plan for the jaguar (*Panthera onca*) in the Pantanal region of Brazil. Biological Conservation 61: 149-157.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Ramalho EE. 2006. Uso do habitat e dieta da onça-pintada (*Pantera onca*) em uma área de várzea, Reserva de Desenvolvimento Sustentável Mamirauá, Amazônia Central, Brasil. Tese de mestrado. UFAM/INPA. 60 pp

Reis NR dos, Peracchi, AL, Pedro WA & Lima IP. 2006. (Eds.). Mamíferos do Brasil. Londrina. 437p.

Rich LN, Russell RE, Glenn E, Mitchell MS & Gude JA, Podruzny KM, Sime CA, Laudon K, Ausband DE & Nichols JD. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. Journal of Wildlife Management 77(6): 1280-1289.

Ridout MS & Linkie M. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural Biological and Environmental Statistics 14: 322-337.

Ripple WJ & Beschta RL. 2012. Trophic Cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation 145: 205-213.

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith, DW, Wallach AD & Wirsing AJ. 2014. Status and ecological effects of the world's largest carnivores. Science 343: 151–163.

Ripple WJ, Estes JA, Schmitz OJ, Constant V, Kaylor MJ, Lenz A, Motley JL, Self KE, Taylor DS, Wolf C. 2016. What is a Trophic Cascade? Trends in Ecology & Evolution 31(11): 842-849, ISSN 0169-5347

Ritchie EG & Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12: 982–98.

Rocha FL. 2006. Áreas de uso e seleção de habitats de três espécies de carnívoros de médio porte na fazenda Nhumirim e arredores, Pantanal da Nhecolândia. MSc Dissertation, Universidade Federal de Mato Grosso do Sul, Brazil.

Romero-Muñoz A, Maffei L, Cuellar E & Noss AJ. 2010. Temporal separation between jaguar and puma in the dry forests of southern Bolivia. Journal of Tropical Ecoloy 26: 303–311.

Rovero F, Collett L, Ricci S, Martin E & Spitale D. 2013. Distribution, occupancy and habitat associations of the grey-faced sengi (*Rhynchocyon udzungwensis*) as revealed by camera traps Journal of Mammalogy 94: 792–800.

Royle JA & Nichols JD. 2003. Estimating abundance from repeated presence absence data or point counts. Ecology 84: 777-790.

Royle AJ, Nichols JD & Kéry M. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110: 353-359.

Simon AL. 1974. Dispersion and Population Interactions. The American Naturalist. 108(960):207–28.

Sarmento P, Cruz J, Eira C & Fonseca C. 2009. Spatial colonization by feral domestic cats Felis catus of former wildcat *Felis silvestris silvestris* home ranges. Acta Theriologica 54(1): 31–38.

Sarmento P, Cruz J, Eira C & Fonseca C. 2011. Modelling the occupancy of sympatric carnivorans in a Mediterrenean ecosystem. European Journal of Wildlife Research 57:119–131.

Schaller GB & Vasconcelos JMC. 1978. Jaguar predation on capybara. Z Saugetierkd 43:296-301

Schoener TW. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Schoener TW. 1983 Field experiments on interspecific competition. The American Naturalist 122, 240–285.

Scognamillo D, Maxit IE, Sunquist M & Polisar J. 2003. Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. Journal of Zoology 259: 269–279.

Shostell JM & Ruiz-Garcia M. 2013. An introduction to neotropical carnivores. In: Molecular Population Genetics, Evolutionary Biology and Biological Conservation of the Neotropical Carnivores. Ruiz García M. & Shostell J.M. (Eds.), Nova Science Publishers Inc., New York, NY, 1–45.

Sidell BP. 2002. Moonrise 3.3 (32 Bit) Software. Accessed 25 November 2016

Silva JSV & Abdon MM. 1998. Delimitação do Pantanal Brasileiro e suas sub-regiões. Pesquisa Agropecuária Brasileira 33:1703-1711.

Silva-Pereira JE, Moro-Riosa RF, Bilski DR, Passos FC. 2011. Diets of three sympatric Neotropical small cats: Food niche overlap and interspecies differences in prey consumption. Mammalian Biology, 76(3): 308-312.

Silveira L. 2004. Ecologia comparada de onça pintada (*Panthera onca*) e onça-parda (*Puma concolor*) no cerrado do Brasil. PhD Thesis, Universidade de Brasília. 235 pp.

Silveira L, Jacomo ATA & Diniz-Filho JAF. 2003. Camera trap, line transect census and track surveys: A comparative evaluation. Biology Conservavtion 114: 351–355.

Soisalo MK & Cavalcanti SMC. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture–recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129: 487–496.

Sollmann R, Furtado MM, Hofer H, Jácomo ATA, Tôrres NM & Silveira L. 2012. Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. Mammalian Biology 77: 41–46.

SOS Pantanal & WWF-Brasil, 2015. Bacia do Alto Araguaia Cobertura Vegetal 2012 – 2014, Relatório Técnico Metodológico Cobertura Vegetal Bacia do Alto Paraguai. Pantanal Porção Brasileira, 66pp.

Sunarto S, Sollmann R, Mohamed A & Kelly MJ. 2013. Camera trapping for the study and conservation of tropical carnivores. Raffles Bull Zoology 28:21–42.

Sunquist M & Sunquist F. 2002. Wild cats of the world. The University of Chicago Press, Chicago, Illinois.

Terborgh J, Este J, Paquet P, Ralls K, Boyd D, Miller B & Noss R. 1999. Role of top carnivores in regulating terrestrial ecosystems. In The science of continental scale reserve design. Edited by Soulé M. & Terborgh J.. Island Press, Washington, D.C. pp. 39–64

Terborgh J & Freeley K. 2010. In Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature, Terborgh J, Estes JA, Eds. Island Press, Washington, DC pp. 125–140.

Terborgh J, Lopez L, Nunez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD & Balbas L. 2001. Ecological meltdown in predator-free forest fragments. Science 294: 1923–1926.

Tobler MW, Zúñiga Hartley A, Carrillo-Percastegui SE, Powell GVN. 2015 Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. Journal Applied of Ecology 52: 413– 421.

Trolle M. & Kéry M. 2003. Estimation of ocelot density in the Pantanal using capture–recapture analysis of camera-trapping data. Journal of Mammalogy 84:607–614.

Tubelis DP & Tomas WM. 2003. Bird species of the wetland, Brazil. Ararajuba 11: 5-37.

Veech JA. 2013. A probabilistic model for analysing species co-occurrence. Global Ecology Biogeografy 22: 252–260.

Veech JA. 2014. The pairwise approach to analysing species co-occurrence. Journal of Biogeography 41: 1029–1035.

Vieira EM & Port D. 2007. Niche overlap and resource partitioning between two sympatric fox species in southern Brazil. Journal of Zoology (Lond.) 272: 57–63.

Wintle BA, Elith J & Potts JM. 2005. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. Australian Ecology 30:719-738.

Zavattini JA. 2009. As chuvas e as massas de ar no estado de Mato Grosso do Sul. Estudo geográfico com vistas a classificação climática. São Paulo: Cultura Acadêmica.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA & Smith GM. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Supplementary Material

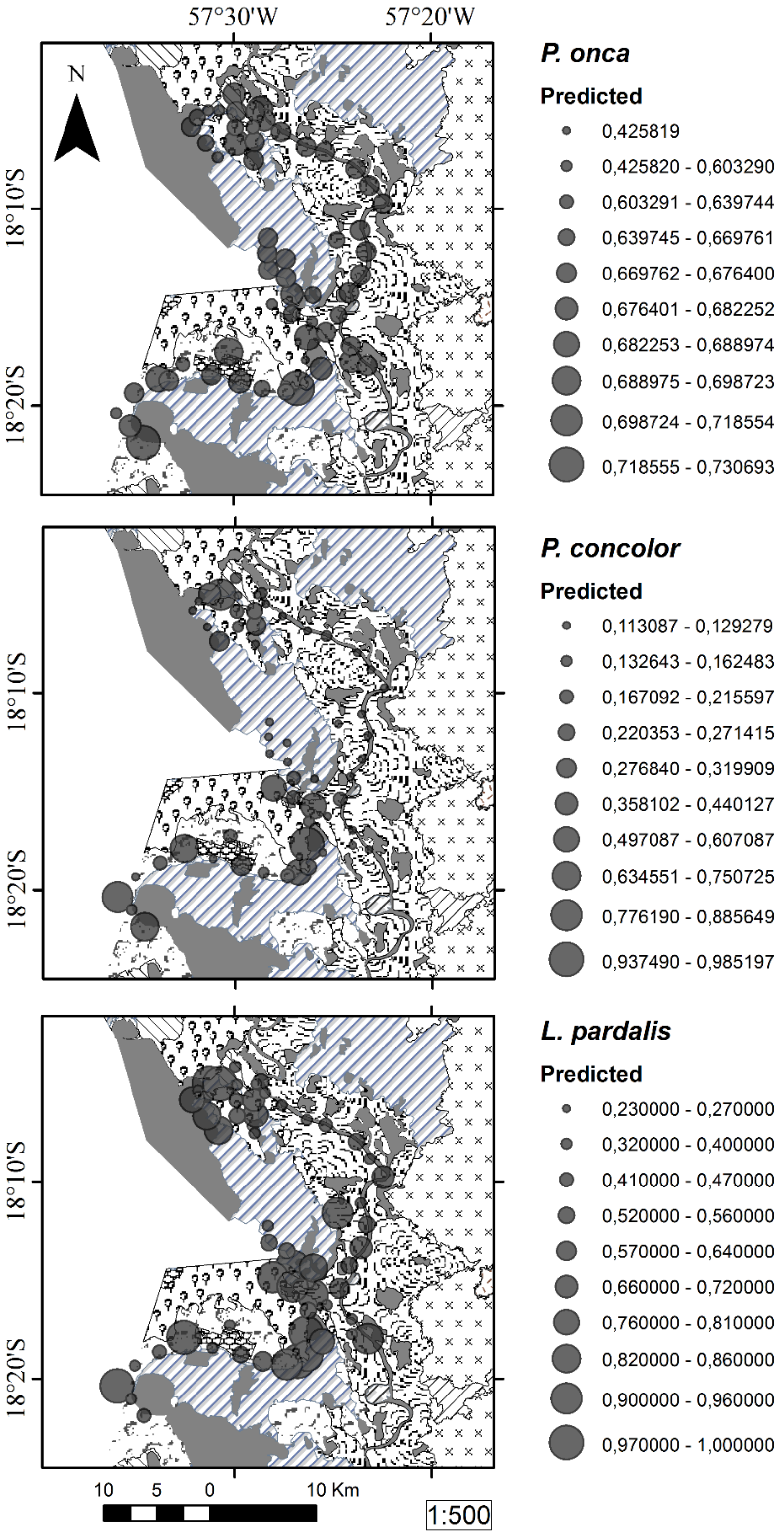

Figure S1. Maps of carnivore species occupancy estimation per site at natural reserve Eliezer Batista, in the Pantanal wetland, southwestern Brazil.

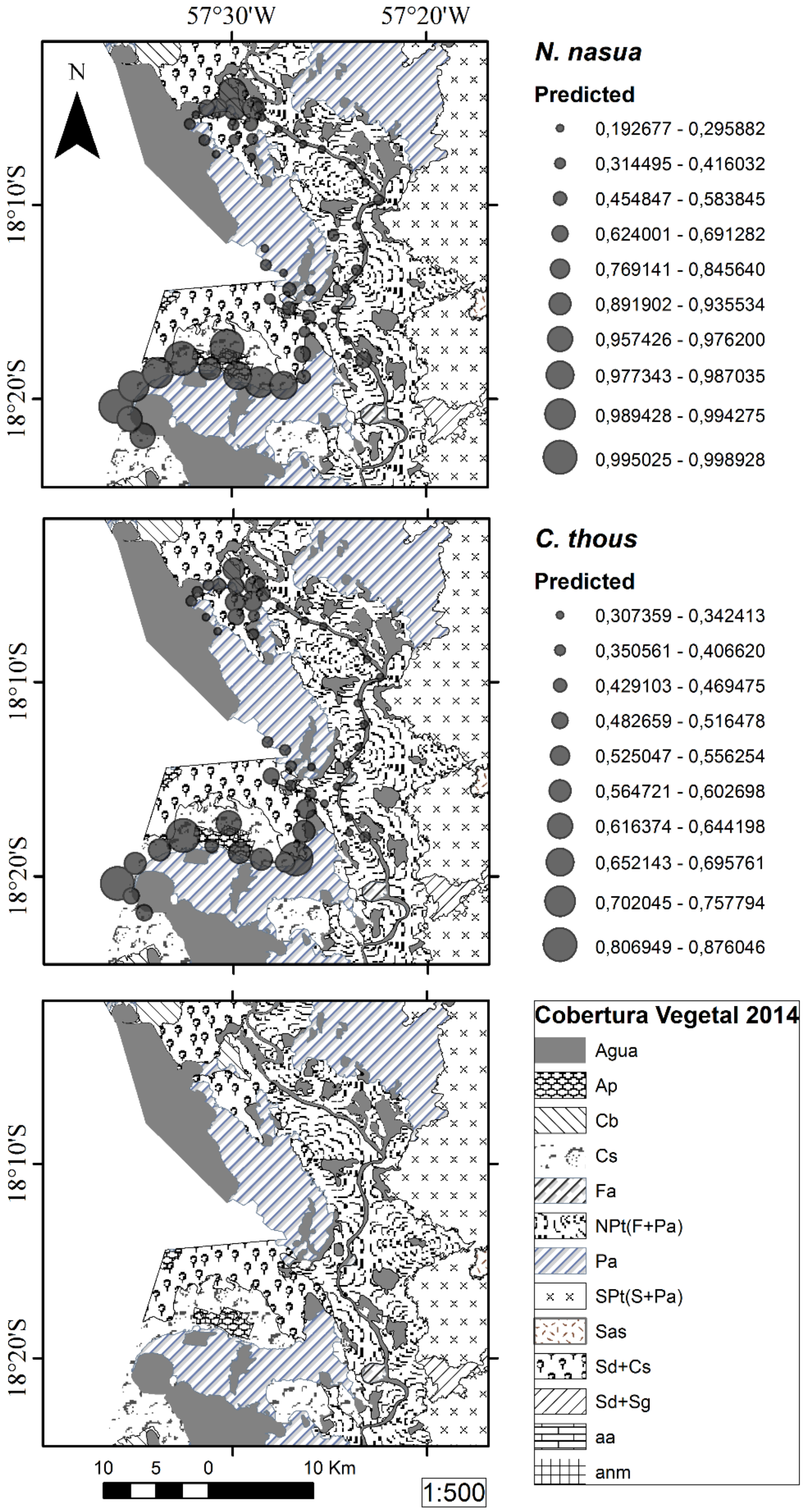

Figure S2. Continuation of Maps of carnivore species occupancy estimation per site at natural reserve Eliezer Batista, in the Pantanal wetland, southwestern Brazil.

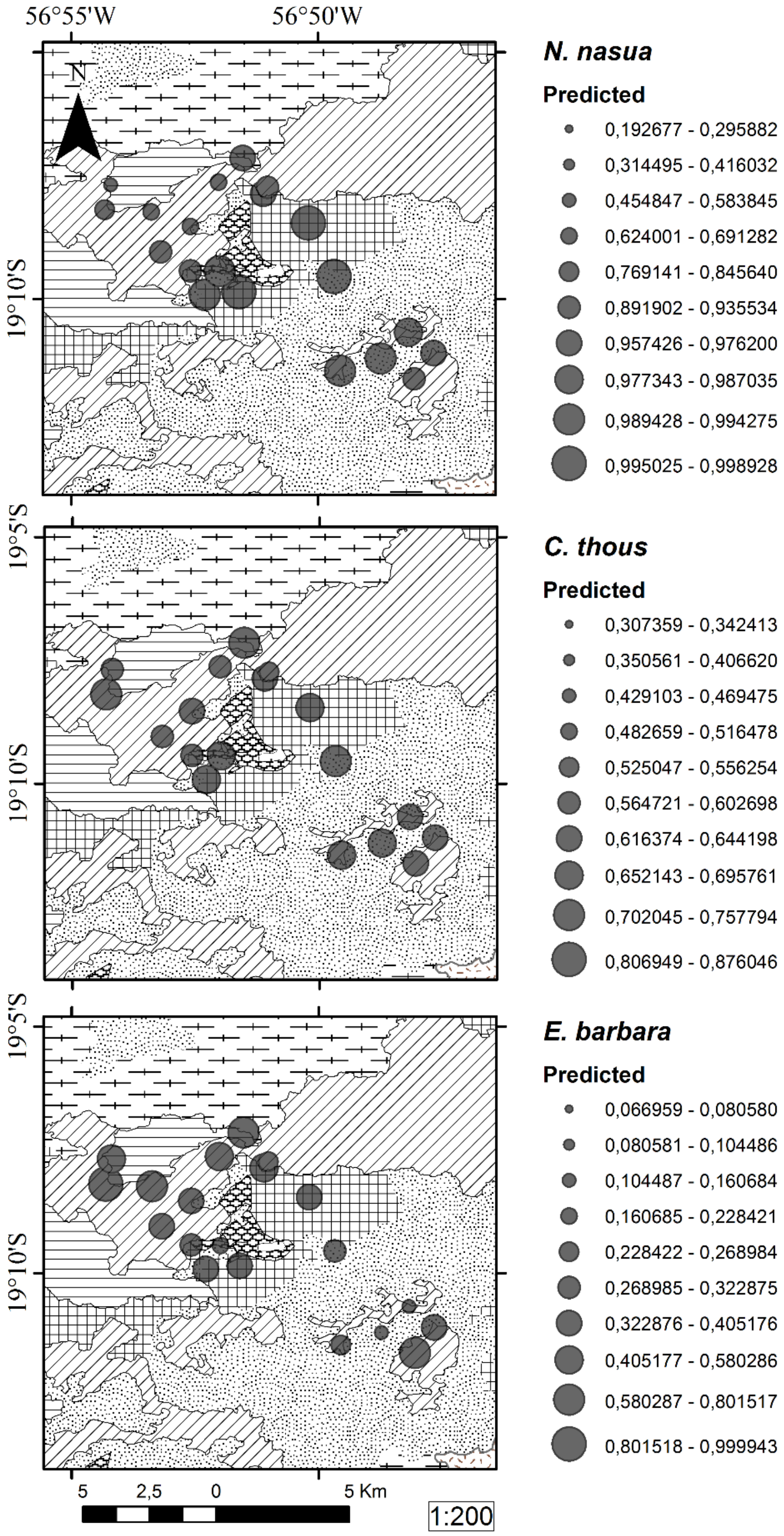

Figure S3. Maps of carnivore species occupancy estimation per site at Caceres Ranch, in the Nhecolândia subregion of the Pantanal wetland, southwestern Brazil.

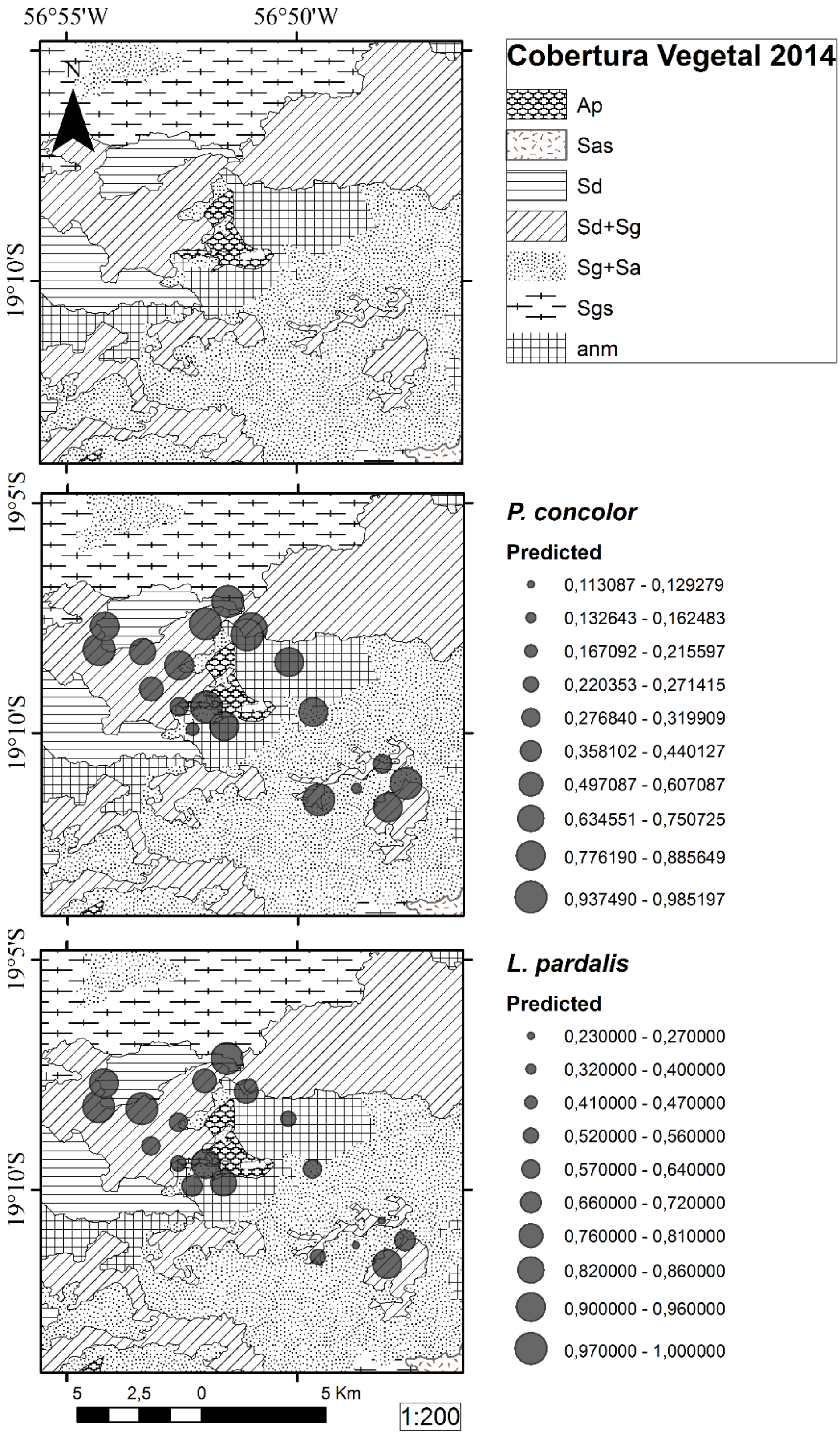

Figure S4. Continuation of Maps of carnivore species occupancy estimation per site at Caceres Ranch, in the Nhecolândia subregion of the Pantanal wetland, southwestern Brazil.

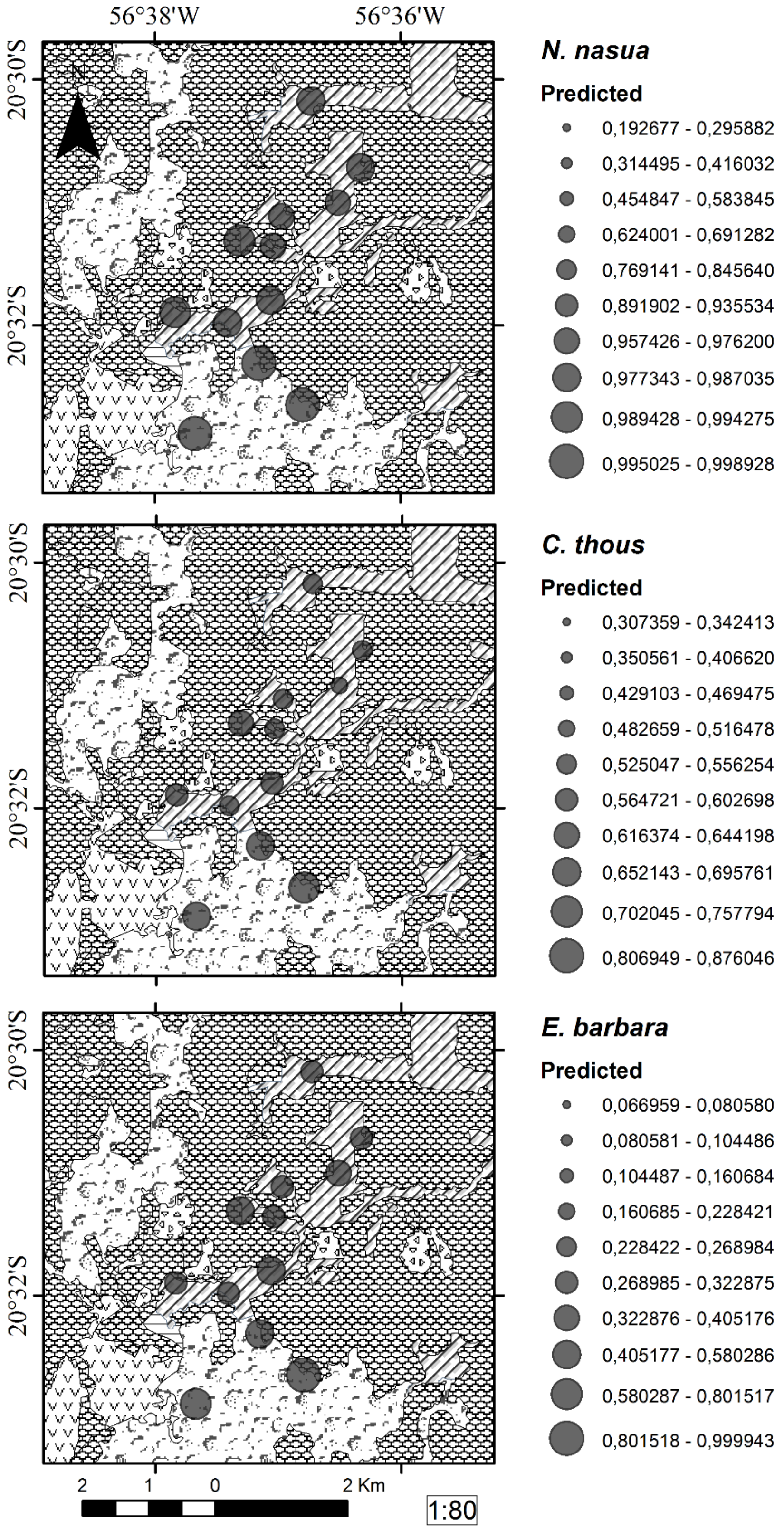

Figure S5. Maps of carnivore species occupancy estimation per site at Mata Grande Ranch, situated in the edge of the Pantanal, subregion called Miranda, southwestern Brazil.

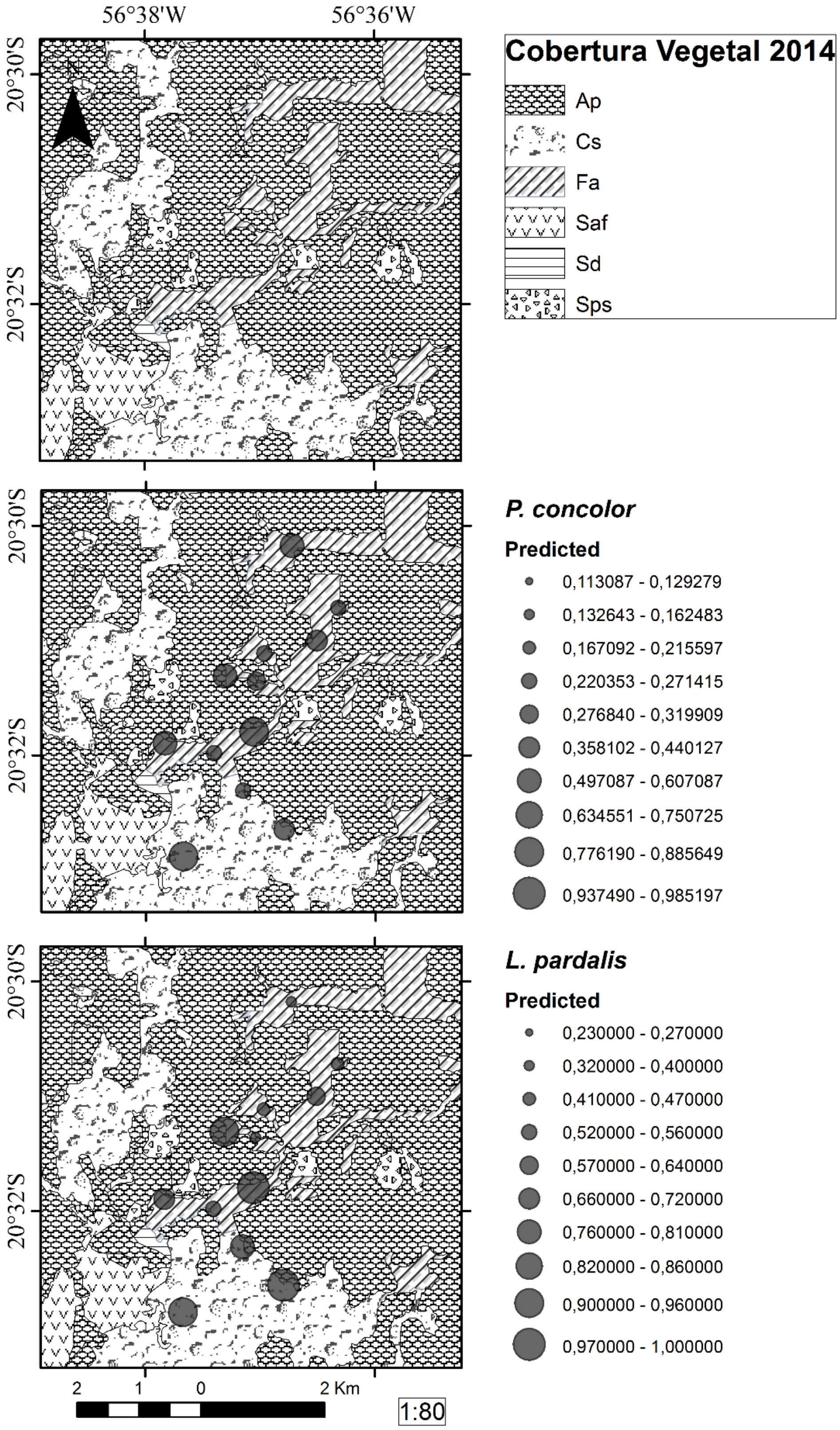

Figure S6. Continuation of the maps of carnivore species occupancy estimation per site at Mata Grande Ranch, situated in the edge of the Pantanal, subregion called Miranda, southwestern Brazil.

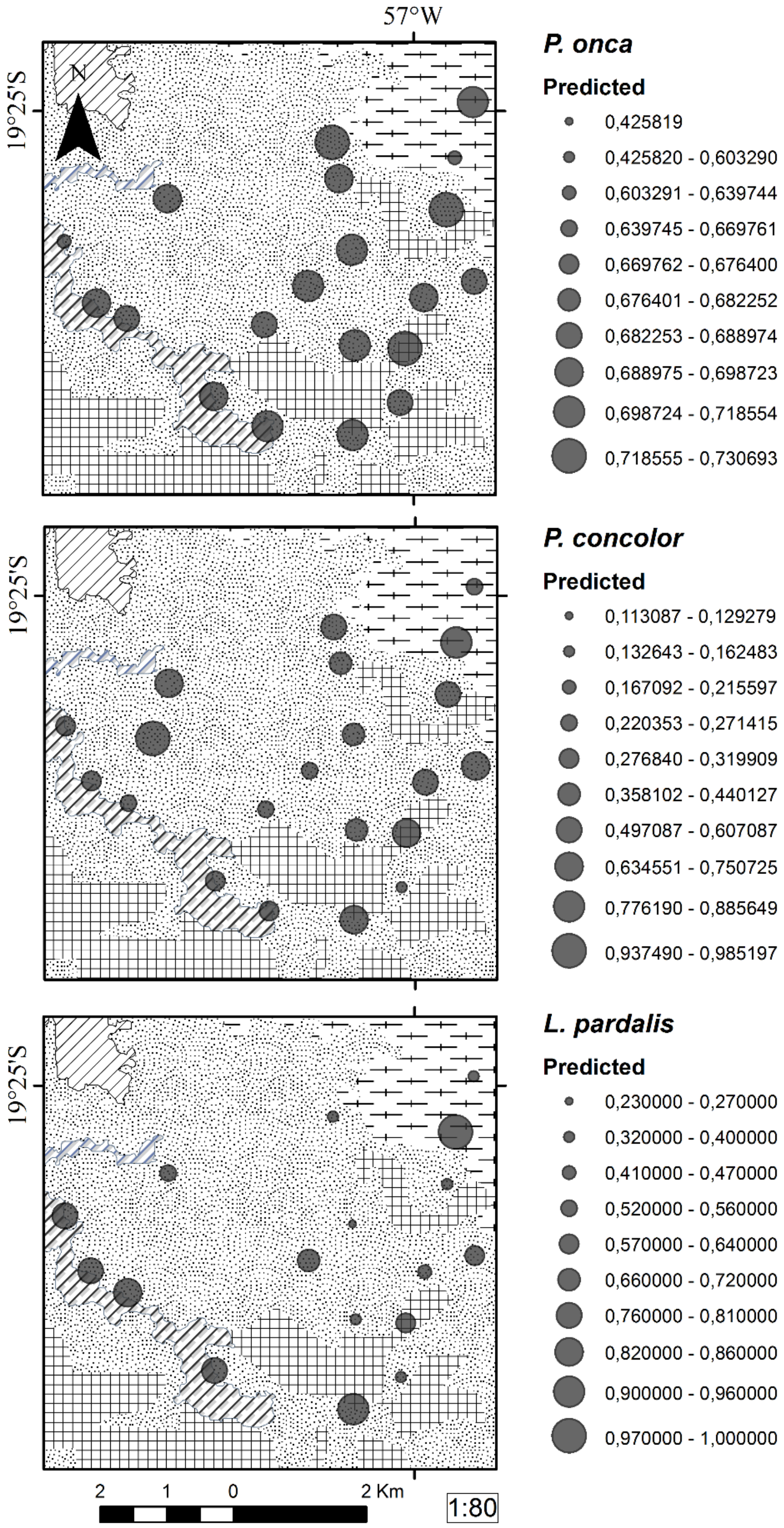

Figure S7. Maps of carnivore species occupancy estimation per site at Sagrado Ranch, subregion Abobral of the Pantanal Wetland, southwestern Brazil.

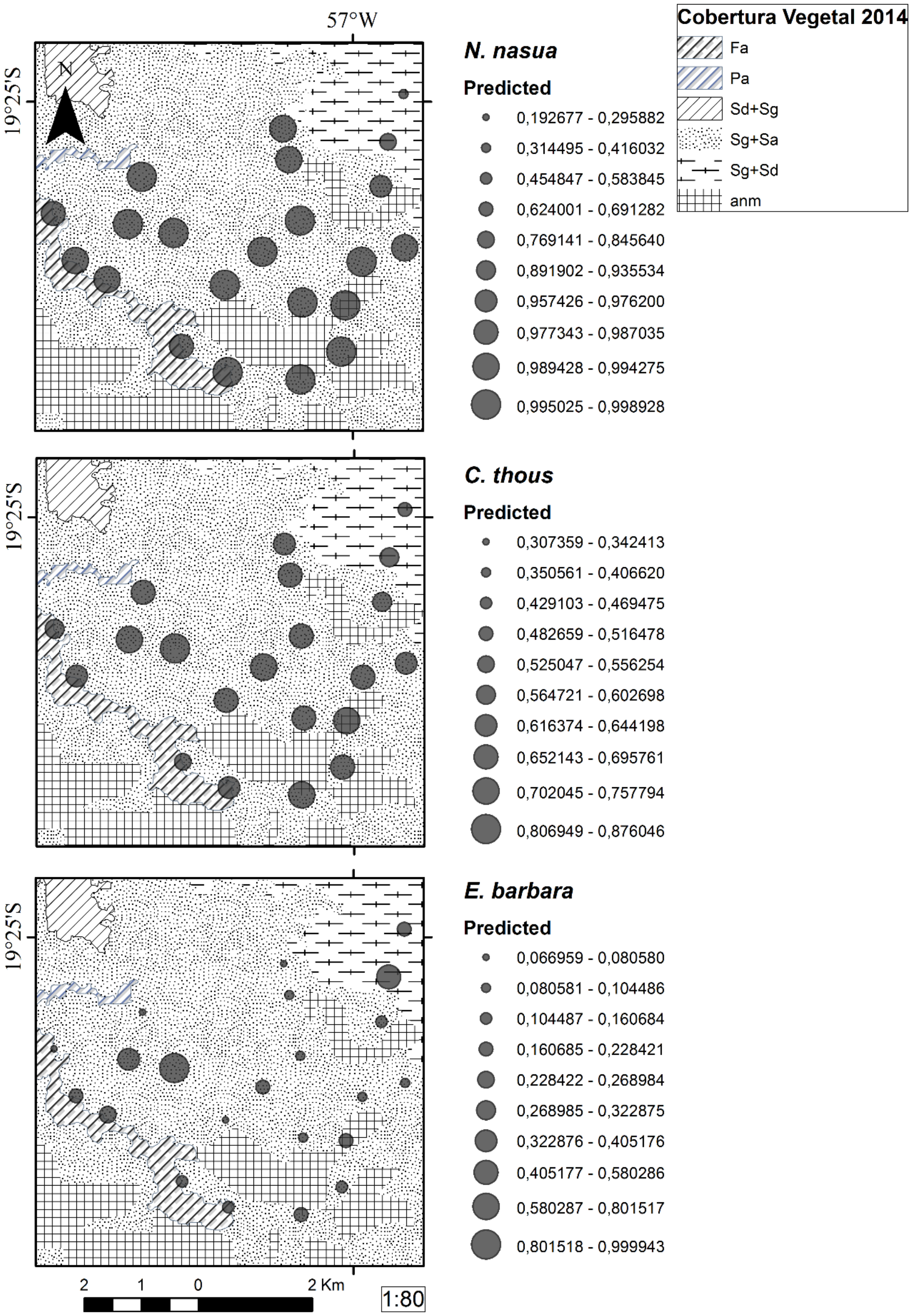

Figure S8. Continuation of the maps of carnivore species occupancy estimation per site at Sagrado Ranch, subregion Abobral of the Pantanal Wetland, southwestern Brazil.

Table S1. Probability of detection and occupancy of carnivore species among sites surveyed through camera-trapping in the Pantanal wetland, southwestern, Brazil.

Species	Mean (SE) probability of detection (*p*)	Mean (SE) probability of occupancy (ψ)
Panthera onca	0.23 (0.07)	0.65 (0.12)
Puma concolor	0.19 (0.04)	0.44 (0.09)
Leopardus pardalis	0.35 (0.05)	0.64 (0.12)
Cerdocyon thous	0.36 (0.05)	0.56 (0.14)
Eira barbara	0.26 (0.06)	0.34 (0.10)
Nasua nasua	0.29 (0.05)	0.79 (0.10)

Table S2. Best candidate models (Δ AIC$_c$ ≤ 2) for estimating the probability of occupancy and detectability of jaguar *Panthera onca* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.65 (0.12) and *p* = 0.23 (0.07).

Species	Models	nPars	AIC	ΔAIC	ω_i	Cumul ω_i
Jaguar						
JM01	ψ(.)*p*(logFF+VIF)	4	317.04	0	0.166	0.17
JM02	ψ(.)*p*(Med+VIF)	4	317.49	0.45	0.133	0.3
JM03	ψ(.)*p*(GS)	3	317.55	0.51	0.129	0.43
JM04	ψ(Large)*p*(logFF+Med+VIF)	6	317.77	0.73	0.116	0.54
JM05	ψ(.)*p*(logFF +Med+ VIF)	5	317.78	0.74	0.115	0.66
JM06	ψ(.)*p*(Med+GS)	4	318.14	1.1	0.096	0.75
JM07	ψ(.)*p*(GS+VIF)	4	318.37	1.32	0.086	0.84
JM08	ψ(Small)*p*(logFF+VIF)	5	318.44	1.4	0.082	0.92
JM09	ψ(Small)*p*(GS)	4	318.55	1.5	0.078	1.00

Table S3. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for detectability of jaguar *Panthera onca* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (*p*)	*p*(logFF)	*p*(VIF)	*p*(GS)	*p*(Med)
JM01	-1.27(0.25)	0.30(0.19)	0.48(0.19)**	NA	NA
JM02	-1.28(0.24)	NA	0.33(0.20)	NA	-0.33(0.23)
JM03	-1.18(0.24)	NA	NA	-0.43(0.19)**	NA
JM04	-1.28(0.24)	0.25(0.19)	0.40(0.20)**	NA	-0.26(0.24)
JM05	-1.23(0.24)	NA	NA	-0.31(0.21)	-0.30(0.24)
JM06	-1.43(0.22)	0.28(0.18)	0.58(0.21)**	NA	-0.34(0.23)
JM07	-1.26(0.25)	NA	0.26(0.23)	-0.27(0.24)	NA
JM08	-1.26(0.25)	0.30(0.19)	0.46(0.19)	NA	NA
JM09	-1.18(0.24)	NA	NA	-0.43(0.20)**	NA

Table S4. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for occupancy of jaguar *Panthera onca* in the Pantanal wetland, southwestern Brazil. *SFs that overlap with 0.

Models	Intercept (ψ)	ψ(Large)	ψ(Small)
JM01	0.62(0.47)	NA	NA
JM02	0.47(0.42)	NA	NA
JM03	0.63(0.45)	NA	NA
JM04	0.62(0.45)	NA	NA
JM05	0.54(0.43)	NA	NA
JM06	1.70(1.87)	1.67(2.33)*	NA
JM07	0.59(0.46)	NA	NA
JM08	0.48(0.43)	NA	-0.30(0.30)*
JM09	0.60(0.47)	NA	-0.27(0.33)*

Table S5. Best candidate models ($\Delta\ AIC_c \leq 2$ and Cumω_i of 0.9) for estimating occupancy and detectability of puma *Puma concolor* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.44 (0.09) and p = 0.19 (0.04).

Species	Models	nPars	AIC	ΔAIC	ω_i	Cumul ω_i
Puma						
PM01	ψ(Large+Small)p(.)	4	392.51	0	0.43	0.43
PM02	ψ(Large+Small)p(VIF)	5	392.91	0.4	0.35	0.79
PM03	ψ(Area+Large+Small)p(VIF)	6	393.93	1.41	0.21	1.00

Table S6. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for estimating occupancy and detectability of puma *Puma concolor* in the Pantanal wetland, southwestern Brazil. *SFs that overlap with 0; ** Significant values.

Models	Intercept (ψ)	psi(Large)	psi(Small)	psi(Area)	Intercept (*p*)	*p*(VIF)
PM01	-0.11 (0.44)	1.81 (0.61)**	0.66 (0.34)**	NA	-1.37 (0.20)	NA
PM02	-0.15 (0.42)	1.47 (0.66)**	0.68 (0.36)	NA	-1.50 (0.23)	-0.35 (0.28)
PM03	-0.77 (0.70)	1.37 (0.67)	0.71 (0.36)**	0.27 (0.28)*	-1.51 (0.23)	-0.38 (0.29)

Table S7. Best candidate models (Δ AIC$_c$ ≤ 2 and Cumω_i of 0.9) for estimating occupancy and detection of ocelot *Leopardus pardalis* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.64 (0.12) and p = 0.35 (0.05)

Species	Models	nPars	AIC	ΔAIC	ω_i	Cumω
Ocelot						
OM01	ψ(Jaguar+Puma+GS+Small)p(FS)	7	607.01	0	0.53	0.53
OM02	ψ(Jaguar+Puma+Small)p(FS+GS)	7	607.22	0.21	0.47	1.00

Table S8. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for estimating detectability of ocelot *Leopardus pardalis* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (*p*)	FS	SG
OM01	-0.50 (0.11)	0.18 (0.11)**	NA
OM02	-0.76 (0.13)	0.19 (0.12)**	0.45 (0.11)**

Table S9. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for estimating occupancy of ocelot *Leopardus pardalis* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (ψ)	Jaguar	Puma	GS	Small
OM01	1.90 (0.83)	-0.25 (0.22)	1.26 (0.80)**	2.22 (1.12)**	0.63 (0.48)**
OM02	1.51 (0.50)	-0.53 (0.29)	1.03 (0.94)**	NA	1.26 (0.92)**

Table S10. Best candidate models (Δ AIC$_c$ ≤ 2 and Cumω_i of 0.9) for estimating the probability of occupancy and detectability of crab-eating fox *Cerdocyon thous* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.56 (0.14) and p = 0.36 (0.05).

Species	Models	nPars	AIC	ΔAIC	ω_i	Cumul ω_i
CFM01	ψ(Puma+SF+VIF)p(Jaguar+VIF)	7	533.25	0	0.305	0.3
CFM02	ψ (Lpard+Puma+SF+VIF)p(Jaguar+VIF)	8	533.81	0.55	0.231	0.54
CFM03	ψ (.)p(Jaguar+VIF)	4	534.03	0.77	0.207	0.74
CFM04	ψ (Puma+SG)p(Jaguar+VIF)	6	534.37	1.12	0.174	0.92
CFM05	ψ (Lpard+SG+VIF)p(Jaguar+VIF)	7	535.88	2.62	0.082	1.00

Table S11. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for detection of crab-eating fox *Cerdocyon thous* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (*p*)	*p*(Jaguar)	*p*(VIF)
CFM01	-0.74 (0.28)	1.14 (0.40)**	-1.40 (0.49)**
CFM02	-0.96 (0.20)	1.34 (0.36)**	-1.80 (0.34)**
CFM03	-0.82 (0.29)	1.23 (0.41)**	-1.54 (0.51)**
CFM04	-1.04 (0.19)	1.42 (0.36)**	-1.93 (0.32)**
CFM05	-0.76 (0.29)	1.18 (0.41)**	-1.44 (0.51)**

Table S12. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for occupancy of crab-eating fox *Cerdocyon thous* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (ψ)	ψ (Lpard)	ψ(GS)	ψ(VIF)	ψ(Puma)	ψ(FS)
CFM01	0.14 (0.40)	NA	NA	-0.80 (0.56)	0.45 (0.33)	-0.34 (0.21)
CFM02	0.04 (0.38)	0.36 (0.31)	NA	-1.01 (0.57)	0.26 (0.33)	-0.43 (0.23)**
CFM03	0.57 (0.24)	NA	NA	NA	NA	NA
CFM04	0.45 (0.25)	NA	0.21 (0.22)	NA	0.46 (0.33)	NA
CFM05	0.04 (0.35)	0.35 (0.26)	0.21 (0.23)	-0.78 (0.52)	NA	NA

Table S13. Best candidate models (Δ $AIC_c \leq 2$ and Cumω_i of 0.9) for estimating the probability of occupancy and detectability of tayra *Eira barbara* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.34 (0.10) and *p* = 0.26 (0.05).

Species	Models	nPars	AIC	ΔAIC	ω_i	Cumul ω_i
TM01	ψ (Puma+GS)p(Med)	5	227.99	0	0.208	0.21
TM02	ψ(Jaguar+Puma+GS)p(Med)	6	228.26	0.27	0.182	0.39
TM03	ψ(Puma+Area)p(Med)	5	228.27	0.28	0.181	0.57
TM04	ψ(Area+Jaguar+Puma)p(Med)	6	228.97	0.98	0.127	0.70
TM05	ψ(Puma+GS)p(Med+Small)	6	229.35	1.37	0.105	0.80
TM06	ψ(Area+Puma)p(Med+Small)	6	229.47	1.48	0.099	0.90
TM07	ψ(Area+Puma+GS)p(Med)	6	229.53	1.54	0.096	1.00

Table S14. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for detection of tayra *Eira barbara* in the Pantanal wetland, southwestern Brazil. ** Significant values

Models	Intercept (*p*)	p(Med)	p(Small)
TM01	-1.07(0.27)	0.42(0.17)**	NA
TM02	-1.09(0.28)	0.41(0.17)**	NA
TM03	-1.08(0.27)	0.41(0.17)**	NA
TM04	-1.09(0.28)	0.41(0.17)**	NA
TM05	-1.12(0.28)	0.39(0.16)**	0.15(0.19)
TM06	-1.14(0.29)	0.39(0.16)**	0.17(0.19)
TM07	-1.08(0.27)	0.42(0.17)**	NA

Table S15. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for occupancy of tayra *Eira barbara* in the Pantanal wetland, southwestern Brazil. **Significant values

Models	Intercept (ψ)	ψ(Puma)	ψ(GS)	ψ(Area)	ψ(Jaguar)
TM01	-0.63(0.39)	1.99(0.84)**	-0.66(0.34)**	NA	NA
TM02	-0.68(0.42)	2.03(0.88)**	-0.52(0.35)	NA	-0.64(0.63)
TM03	-1.80(0.78)	1.88(0.86)**	NA	0.50(0.26)	NA
TM04	-1.50(0.82)	1.95(0.89)**	NA	0.35(0.29)	-0.63(0.70)
TM05	-0.61(0.40)	1.94(0.84)**	-0.67(0.34)**	NA	NA
TM06	-1.83(0.77)	1.83(0.86)**	NA	0.52(0.27)**	NA
TM07	-1.24(0.99)	1.94(0.87)**	-0.42(0.49)	0.25(0.38)	NA

Table S16. Best candidate models (Δ AIC$_c$ ≤ 2) for estimating occupancy and detection of coati *Nasua nasua* in the Pantanal wetland, southwestern Brazil. Models average (SE): ψ = 0.79 (0.10) and *p* = 0.29 (0.05).

Model		nPars	AICc	ΔAICc	ω_i	Cumω
CM01	ψ(Puma+FS+VIF)*p*(Large+logFF+Med+VIF)	9	651.43	0	0.224	0.22
CM02	ψ(Jaguar+Puma+FS+VIF)*p*(Large+logFF+Med+VIF)	10	651.62	0.18	0.204	0.43
CM03	ψ(Jaguar+Puma+FS+VIF)*p*(Cthous+Large+logFF+Med+VIF)	11	652.41	0.97	0.137	0.57
CM04	ψ(Puma+FS+VIF)*p*(Cthous+Large+logFF+Med+VIF)	9	653.18	1.75	0.093	0.66
CM05	ψ(FS+VIF)*p*(Cthous+Large+logFF)	7	653.72	2.29	0.071	0.73
CM06	ψ(Puma+FS+VIF)*p*(Large+logFF)	7	653.75	2.31	0.07	0.8
CM07	ψ(FS+VIF)*p*(Large+logFF+Med)	7	653.78	2.35	0.069	0.87
CM08	ψ(Jaguar+FS+VIF)*p*(Large+logFF)	7	653.89	2.46	0.065	0.94
CM09	ψ(FS)*p*(Large+logFF+Med+VIF)	7	653.91	2.48	0.065	1.00

Table S17. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for estimating detection of coati *Nasua nasua* in the Pantanal wetland, southwestern Brazil.

Models	Intercept (*p*)	Large	*p*(logFF)	*p*(Med)	*p*(VIF)	*p*(Cthous)
CM01	-1.15 (0.18)	0.35 (0.12)**	-0.33 (0.12)**	0.17 (0.09)	-0.60 (0.30)**	NA
CM02	-1.11 (0.16)	0.36 (0.12)**	-0.33 (0.12)**	0.16 (0.09)	-0.52 (0.27)**	NA
CM03	-1.10 (0.16)	0.38 (0.13)**	-0.32 (0.12)	0.16 (0.09)	-0.44 (0.28)	0.10 (0.09)
CM04	-1.13 (0.17)	0.37 (0.13)**	-0.32 (0.12)**	0.16 (0.09)	-0.52 (0.31)	0.10 (0.09)
CM05	-0.90 (0.12)	0.50 (0.11)**	-0.31 (0.12)**	NA	NA	0.14 (0.09)
CM06	-0.87 (0.12)	0.49 (0.11)**	-0.32 (0.12)**	NA	NA	NA
CM07	-0.89 (0.12)	0.46 (0.11)**	-0.35 (0.12)**	0.14 (0.09)	NA	NA
CM08	-0.87 (0.12)	0.49 (0.12)**	-0.32 (0.12)**	NA	NA	NA
CM09	-1.33 (0.13)	0.35 (0.12)**	-0.31 (0.12)**	0.19 (0.09)**	-0.87 (0.20)**	NA

Table S18. Estimates of beta coefficients and standard error (SE) for all covariates contained in the best candidate models for estimating occupancy of coati *Nasua nasua* in the Pantanal wetland, southwestern Brazil. *SE that overlap with 0.

Models	Intercept (ψ)	Puma	FS	VIF	Jaguar
CM01	3.58 (1.42)	1.38 (1.07)	-2.35 (0.96)	-2.33 (1.05)	NA
CM02	3.44 (1.35)	1.18 (0.88)	-2.36 (0.92)	-2.88 (1.02)**	0.76 (0.77)*
CM03	3.47 (1.38)	1.15 (0.87)	-2.38 (0.95)	-2.94 (1.03)**	0.75 (0.76)*
CM04	3.59 (1.46)	1.33 (1.04)	-2.37 (0.99)**	-2.41 (1.06)**	NA
CM05	2.58 (1.35)	NA	-1.75 (0.93)	-2.61 (0.91)	NA
CM06	2.73 (1.31)	0.97 (0.75)	-1.99 (0.93)**	-2.60 (0.87)**	NA
CM07	2.45 (1.21)	NA	-1.68 (0.84)**	-2.58 (0.83)**	NA
CM08	2.38 (1.08)	NA	-1.69 (0.75)**	-2.88 (0.81)**	0.50 (0.43)
CM09	4.16 (1.71)	NA	-1.64 (0.82)**	NA	NA