UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

Ecospatial Insights into the Jaguar: Unraveling Movement Ecology, Predator-Prey Interactions, and Habitat Selection Patterns among Brazilian Cats

VANESA FABIOLA BEJARANO ALEGRE

Rio Claro – SP
2023

UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

Ecospatial Insights into the Jaguar: Unraveling Movement Ecology, Predator-Prey Interactions, and Habitat Selection Patterns among Brazilian Cats

VANESA FABIOLA BEJARANO ALEGRE

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia, Evolução e Biodiversidade.

Orientador: Prof. Dr. Milton Cezar Ribeiro

Co-orientador: Dr. Ronaldo Gonçalves Morato

Rio Claro – SP
2023

A366e

Alegre, Vanesa Fabiola Bejarano
Ecospatial insights into the jaguar: unraveling movement ecology, predator-prey interactions, and habitat selection patterns among brazilian cats / Vanesa Fabiola Bejarano Alegre. -- Rio Claro, 2023
111 p.

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientador: Milton Cezar Ribeiro
Coorientador: Ronaldo Gonçalves Morato

1. Movement ecology. 2. Landscape ecology. 3. carnivores. 4. GPS. 5. Camera Trap. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

Essa ficha não pode ser modificada.

CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: Ecospatial Insights into the Jaguar: Unraveling Movement Ecology, Predator-Prey Interactions, and Habitat Selection Patterns among Brazilian Cats

AUTORA: VANESA FABIOLA BEJARANO ALEGRE

ORIENTADOR: MILTON CEZAR RIBEIRO

Aprovada como parte das exigências para obtenção do Título de Doutora em Ecologia, Evolução e Biodiversidade, área: Biodiversidade pela Comissão Examinadora:

Prof. Dr. MILTON CEZAR RIBEIRO (Participaçao Presencial)
Departamento de Biodiversidade / Unesp - IB Rio Claro

Profa. Dra. MIRIAM LUCIA LAGES PERILLI (Participaçao Virtual)
Instituto de Pesquisas Ecológicas / IPE

Prof. Dr. FERNANDO SILVA LIMA (Participaçao Virtual)
Departamento de Biodiversidade / Unesp - IB Rio Claro

Rio Claro, 30 de agosto de 2023

Título alterado para: "Ecospatial Insights into the Jaguar: Unraveling Movement Ecology, Predator-Prey Interactions, and Habitat Selection Patterns among Brazilian Cats"

Ao meu pai José Arturo Bejarano Dominguez, terminei esse doutorado com uma dor reprimida no peito pela sua perda, mas você sempre esteve no meu coração e me fez continuar.

Agradecimentos

A todas as mulheres que abriram caminhos na ciência e cujas conquistas foram injustamente esquecidas.

Esta tese não teria sido possível sem a Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; processo número 2018/13037-3) agradeço profundamente. Além a Fundação de Amparo à Pesquisa do Estado de São Paulo me outorgou a Bolsa Estágio de Pesquisa no Exterior (BEPE) (FAPESP; processo número 2020/07586-4) o que me permitiu fazer meu estágio e me desenvolver melhor como pesquisadora. Gostaria de agradecer profundamente pelo seu apoio financeiro, pois foi o principal impulsionador deste sucesso.

Sou muito grata à minha família na Bolívia, que me viu viajar para o exterior e me apoiou em todos os momentos. Ao meu querido pai que sempre teve orgulho de mim (sim! sei que sou a sua filha favorita!) e à minha mãe Beatriz Alegre que luta para manter a família unida e ser minha melhor amiga. Aos meus amigos que se lembraram de mim apesar de toda a distância a minha Tia Josefina por todo o carinho e conversa. Ao meu Prof. Dr. Jaime Alcazar que me deu "o pontapé inicial" para que eu pudesse me aventurar pelo mundo para continuar estudando... obrigada professor por me ceder seu tempo livre e me ensinar mais!

Agradeço fortemente de coração ao meu orientador Milton Cezar Ribeiro “Miltinho”, por confiar em mim, por me apoiar, por me acolher com um abraço no Brasil, por me ensinar além da ciência, mas também na vida. Quero agradecer também ao meu orientador de mestrado Alex Jahn... “Sou eternamente grata por me ajudar em tudo e estar sempre presente”. Quero agradecer ao meu co-orientador Dr. Ronaldo G. Morato por todo apoio e ajuda. Também ao meu co-orientador Prof. Dr. Luca Börger por me ajudar, me dar todo o apoio e me proporcionar a melhor experiência profissional no Swansea Laboratory for Animal Movement (SLAM).

Às pessoas que me apoiaram e deram sua amizade e fortalecimento na minha formação, Zaida Ortega, Érika Garcez, Claudia Kanda, Milene Alves, Raissa Sepulvida carrego vocês sempre comigo... obrigada, obrigada, obrigada, obrigada!

A todos do Laboratório de Ecologia e Conservação Espacial (LEEC) e associados pelo excelente ambiente de trabalho que me proporcionaram, pelo carinho e confiança. Com carinho especial para Claudinha Kanda, “Fofinha, obrigada por toda ajuda que você me deu sem pedir nada em troca, você está no meu coração para sempre!”, para Julia Oshima, obrigada por toda ajuda!!, Milene Alves, Julia Assis, Paula Montagnana, Urucum, Natalia Stefanini e muitos que tal vez não citei aqui, mas que me proporcionaram um excelente período de laboratório. Ao Luis Miguel Senzano Castro, por me dar a melhor companhia, ajuda e carinho, obrigada pelos nove anos. Ao Paul Gadd por juntar as peças e caminhar agora comigo.

A todos os professores e administradores da Universidade Estadual Paulista – UNESP em Rio Claro, que me acolheram e me proporcionaram a melhor experiência!

A você ...muito obrigada!

Resumo

A seleção de habitat desempenha um papel crucial na sobrevivência de carnívoros, pois está diretamente relacionada à capacidade de defender território e garantir os recursos necessários para atender às suas necessidades fisiológicas. No entanto, a perda e fragmentação de habitat representam ameaças significativas para esses animais, que já são sensíveis devido às suas amplas áreas de vida, baixa abundância e taxas de reprodução reduzidas. A Onça-pintada (*Panthera onca*), um dos maiores carnívoros das Américas, enfrenta declínios populacionais devido a diversos fatores, como a diminuição da densidade de suas presas em áreas naturais, fragmentação do habitat, caça ilegal e conflitos com a expansão humana. Além disso, outros felinos enfrentam ameaças semelhantes. Para aprofundar nossa compreensão das necessidades e desafios ambientais em uma ampla distribuição de espécies felinas, propomos um projeto de doutorado com quatro objetivos principais: 1) Compreender como a estrutura da paisagem influencia a seleção de habitat em relação ao sexo da Onça-pintada, adotando uma abordagem de múltiplas escalas. Este estudo fornecerá insights valiosos sobre como a percepção em escala de paisagem afeta a escolha de recursos pelas Onças-pintadas. 2) Investigar como a estrutura da paisagem afeta os padrões de movimentação e os locais de revisitação central das Onças-pintadas. Isso permitirá a geração de dados essenciais relacionados à influência da estrutura da paisagem nos comportamentos de movimento e revisitação das Onças-pintadas. 3) Explorar como as interações entre a Onça-pintada e o Queixada (*Tayassu pecari*) são afetadas pela estrutura da paisagem no Pantanal. Este estudo fornecerá informações valiosas sobre as dinâmicas de movimentação tanto do predador quanto da presa. 4) Compreender a seleção de habitat de nove felinos no Brasil, este estudo fornecerá informações sobre a percepção da paisagem por esses felinos que habitam o Brasil. Os resultados deste estudo forneceram informações decisivas sobre como os aspectos da estrutura da paisagem desempenham um papel fundamental nas necessidades vitais da Onça-pintada e de outros felinos em um contexto amplo. Esses dados serão usados para desenvolver ferramentas mais eficazes de manejo e conservação desses felinos magníficos.

Palavras-chave: seleção de habitat, ponto de mudança de comportamento, interações predador-presa, biomas, Onça-pintada, Queixada, Leopardus, Puma.

Abstract

Habitat selection plays a crucial role in the survival of carnivores as it is directly related to their ability to defend territory and secure the necessary resources to meet their physiological needs. However, habitat loss and fragmentation pose significant threats to these animals, which are already sensitive due to their extensive home ranges, low abundance, and reduced reproduction rates. The Jaguar (*Panthera onca*), one of the largest carnivores in the Americas, faces population declines due to various factors such as the decrease in prey density in natural areas, habitat fragmentation, illegal hunting, and conflicts with human expansion. Additionally, other feline species face similar threats. To deepen our understanding of the environmental needs and challenges across a wide range of feline species, we propose a doctoral project with four main objectives: 1) To understand how landscape structure influences habitat selection in relation to the sex of the Jaguar, using a multi-scale approach. This study will provide valuable insights into how landscape-scale perception affects the choice of resources by Jaguars. 2) To investigate how landscape structure affects movement patterns and central revisitation sites of Jaguars. This will allow the generation of essential data related to the influence of landscape structure on Jaguar movement and revisitation behaviors. 3) To explore how interactions between Jaguars and Peccaries (*Tayassu pecari*) are affected by landscape structure in the Pantanal. This study will provide valuable information about the movement dynamics of both predators and prey. 4) To understand the habitat selection of nine feline species in Brazil, providing insights into the landscape perception of these felines inhabiting Brazil. The results of this study will provide decisive information on how aspects of landscape structure play a fundamental role in the vital needs of Jaguars and other feline species in a broad context. This data will be used to develop more effective management and conservation tools for these magnificent felines.

Keywords: habitat selection, behavior change point, predator-prey interactions, biomes, Jaguar, Peccary, Leopardus, Puma.

Table of Contents

Introduction

Habitat selection acquire a vital influence for an organism because individual fitness condition is as a result of habitat-related factors like availability of food resources (Gittleman and Harvey 1982; Manly et al. 2007; Benhaiem et al. 2008), habitat suitability (Mysterud and Østbye, 1999; Rabinowitz and Zeller, 2010), intraspecific and interspecific dynamic interactions (Fortin et al. 2005; Bitetti et al. 2010) and species-specific life-history traits (Allen et al. 2014). All of these ecological interactions and mechanisms must also operate, to some extent, separately under different spatial and temporal scales (Dussault et al. 2005; Boyce, 2006). In the case of large carnivores, these spatial use and temporal scales must be large enough, because it must satisfy the metabolic energy requirements that large-bodied species usually demand (Gittleman and Harvey 1982) while attempting to meet their needs for growth, survival, and reproduction (Noss et al. 1996; Milner et al. 2007).

However, loss and fragmentation of natural habitats have increased in the last decades (Hanski, 2011), which is one of the principal causes in the worldwide decline of biodiversity (McKinney, 2002; Haag et al. 2010). Large carnivores are especially sensitive to habitat loss and fragmentation because of their large home range requirements, low abundance and low birth rates (Woodroffe, 2000; Croock, 2002 Milner et al. 2007). Changes in the landscape structure usually driven by anthropogenic activities (e.g., deforestation), agricultural expansion and artificial barriers (Ito et al. 2013) have mainly influenced most of these losses and fragmentation. With the corresponding changes in the landscape structure, animals should adopt different habitat selection (or avoidance) patterns that allow them to cope with detrimental factors that otherwise would limit individual fitness (Woodroffe, 2000; Dussault et al. 2005). For example, animals tend to move and spend time differently in areas under scarce natural shelters where the risk of hunting/predation is higher when compared to undisturbed regions (Blumstein and Daniel 2002; Benhaiem et al. 2008), even in contrasting food resource areas (Manly et al. 2007; Allen et al. 2014).

From a perspective of predator-prey interaction, the predator's movement is led by the hunting mode, while the prey can follow a predator-avoidance strategy (Blumstein and Daniel, 2002; Creel et al. 2005; Fortin et al. 2005). Since the distribution of prey influences the predator distribution

(Pontes and Chivers 2007; Fortin et al. 2013), the predator's movement will likely reflect its relationship with the prey. Thus, the habitat selection of each species will be influenced by those of the other (Mitchell and Lima 2002; Sih, 2005; Kauffman et al. 2007). Likewise, it emphasises that preys can also face similar pressures related to habitat loss, resulting in the reduction of prey density, displacement to other areas or even prey local extinction (Harrison, 1991; Sutherland and Anderson, 1993), thus forcing carnivores to enter into anthropogenic areas when searching for food (see Bateman and Fleming 2012). In the light of these aspects, changes in the landscape structure will be reflected in the animal's movement patterns, delivering critical signals of the habitat suitability status (Winker et al. 1995). Indeed, due to their role as top predators, as well as their sensibility to habitat fragmentation (Crooks, 2002), carnivores have been used as keystone indicator species for the suitability assessment of entire ecosystems (Noss et al. 1996).

The jaguar (*Panthera onca*) is the largest felid in the Neotropics (Silver et al. 2004), and as big carnivores, it is also facing severe declines in their population (Altrichter et al. 2006; Paviolo et al. 2008; Haag et al. 2010; Galetti et al. 2013; Morato et al. 2016). With a natural range distribution that covers from south of the United States, throughout Central and South America to Argentina (Eizirik et al. 2001; Morato et al. 2018), today their distributional range decreased to 45% (de la Torre et al. 2018). Therefore, the Jaguar classification is like as a vulnerable species in Brazil (Morato et al. 2013) and near threatened to the IUCN (Quigley et al. 2017). Its population decline is associated with factors like decline density of preys in their natural areas (Salom-Pérez et al. 2007), fragmentation (Haag et al. 2010), poaching (Paviolo et al. 2008), human conflict (Zimmermann et al. 2005) and habitat shrink or loss by human expansion (Michalski et al. 2006; Galetti et al. 2013). Different approaches have been used for designing conservation strategies for the species like defining corridors (Rabinowitz and Zeller 2010; Morato et al. 2014), reserve areas (Crawshaw, 1992), and potential units for conservation (Rodrígues-Soto et al. 2011).

Although the existence of a vast literature focused on the jaguar's biology and conservation (see Thornton et al. 2015), with some exceptions, most of the studies have been conducted under a more local (or regional) jaguar's population approach –exception is Morato et al. (2016) who evaluated space use and home-range size for 44 individuals within several regions of Brazil. Interestingly, variations in the home range size (Astete et al. 2008), the effectiveness of corridors

in conservation (Thornton et al. 2015) or Jaguars' body size (Iriarte et al. 1990) has been reported to vary across different habitats, suggesting that resource availability and requirements vary across different biomes. In part because, not only seasonality may influence jaguars' fitness (Morato et al. 2004; Guilder et al. 2015), but also the density of resources (Carrillo et al. 2009; Michalski et al. 2006) and the degree of human impact across each habitat type (Santos et al. 2008). Besides that, differential spatial and feature habitat requirements may also vary by gender (Cavalcanti and Gese, 2009) and season (Pontes and Chivers, 2007). Here we propose to improve our understanding of how human alterations on, and within, the natural landscape could alter the Jaguars' habitat selection, and thus recognize if there is an adaptability behaviour that can be detected on movement or not. Furthermore, it is critical to understand the movement patterns in response to habitat structure, in order to have a better knowledge of what features of habitat composition and configuration it is selecting more, and that others try to avoid (or spend less time). Finally, to understand the predator-prey interaction, we first explore the overlapping habitat between the Jaguar and White-lipped peccary; then, we analyse the distance throughout the time and space between both of them; and finally, we will analyse how jaguar presence influences peccary movement in the Pantanal. All these integrative approaches is necessary because 1) it facilitates a comprehensive understanding of the environmental requirements and challenges that a jaguar might face; 2) it highlights critical insights about how jaguars cope with changes in the habitat structure or food resources; and 3), it provides new knowledge to develop efficient jaguar management tools based on the specific requirements for jaguar's conservation.

The main aim of this work is to understand how the landscape structure and predator-prey interactions affect the movement patterns and resource selection within the jaguar habitat. This understanding will allow us to identify key landscape structures to the jaguar's habitat conservation management. The first chapter will be destined to understand how landscape structure affects the sex-related habitat selection of Jaguar under a multi-scale approach. This chapter will provide insights related to which landscape scale the jaguar responds to different resource selection will vary under a different time scale. In the second chapter, we aim to understand how landscape structure affects the movement patterns and core revisitation sites of jaguars. This chapter will generate important data related to how much landscape structure

influences the jaguar space use. Finally, the third chapter will be focused on predator-prey interactions, by use of both the Jaguar and White Lipped Peccary (*Tayassu pecari*) interaction of movement in the landscape structure in dry season. However, an additional fourth chapter was made exploring the habitat selection of all Brazilian cats, with the intention of understanding what the trends and information gaps were. This PhD generated important knowledge on how key landscape structures are used by both species and it is an important component to determine the degree of how these structures shape that interaction.

References

Allen, A. M., Månsson, J., Jarnemo, A., & Bunnefeld, N. (2014). The impacts of landscape structure on the winter movements and habitat selection of female red deer. European journal of wildlife research, 60(3), 411-421.

Altrichter, M., Boaglio, G. & Perovic, P. (2006). The decline of jaguars Panthera onca in the Argentine Chaco. Oryx, 40(3), 302-309.

Astete, S., Sollmann, R. &Silveira, L. (2008). Comparative ecology of Jaguars in Brazil. CAT News, 4, 9-14.

Bateman, P. W. & Fleming, P. A. (2012). Big city life: carnivores in urban environments. Journal of Zoology, 287, 1-23.

Benhaiem, S., Delon, M., Louetet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. J. M., Morellet, N. & Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. Animal Behaviour, 76(3), 611-618.

Blumstein, D. T. & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. Behavioral Ecology 13(5), 657-663.

Boyce, M. S. (2006). Scale for resource selection functions. Diversity and Distributions, 12(3), 269-276.

Carrillo, E., Fuller, T. K. & Saenz, J. C. (2009). Jaguar (Panthera onca) hunting activity: effects of prey distribution and availability. Journal of Tropical Ecology, 25, 563-567.

Cavalcanti, S. M. C. & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (Panthera onca) in the southern Pantanal, Brazil. Journal of Mammology, 90(4), 935-945.

Crawshaw, H. B. 1992. A conservation plan for the Jaguar Panthera onca in the Pantanal region of Brazil. Biological Conservation, 61, 149-157.

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology, 16(2), 488-502.

De la Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar Panthera onca. Oryx, 1-16.

Dussault, C., Ouellet, J., Courtois, R., Hout, J., Breton, L., Jolicoeur, H. & Kelt, D. (2005). Linking moose habitat selection to limiting factors. Ecography, 28(5), 619-628.

Eizirik, E., Kim, J., Menotti-Raymond, M., Crawshaw, P. G., O'Brien, S. J. & Johnson, W. E. (2001). Phylogeography, population history and conservation genetics of jaguars (Panthera onca, Mammalia, Felidae). Molecular Ecology, 10, 64-79.

Foster, V. C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A. T., Negrões, N., ... & Silveira, L. (2013). Jaguar and Puma activity patterns and predator-prey interactions in four Brazilian Biomes. Biotropica, 45(3), 373-379.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology, 86(5), 1320-1330.

Galetti, M., Eizirik, E., Beisiegel, B., Ferraz, K., Cavalcanti, S., Srbek-Araujo, A. C., ... & Marinho-Filho, J. (2013). Atlantic rainforest's jaguars in decline. Science, 342(6161), 930-930.

Gittleman, J. L., & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs, and ecology. Behavioral Ecology and Sociobiology, 10(1), 57-63.

Guilder, J., Barca, B., Arroyo-Arce, S., Gramajo, R. & Salom-Pérez, R. (2015). Jaguars (Panthera onca) increase kill utilization rates and share prey in response to seasonal fluctuations in nesting

green turtle (Chelonia mydas mydas) abundance in Tortuguero National Park, Costa Rica. Mammalian Biology, 80, 65-72.

Gurarie, E., Bracis, C., Delgado, M., Meckley, T. D., Kojola, I., & Wagner, C. M. (2016). What is the animal doing? Tools for exploring behavioural structure in animal movements. Journal of Animal Ecology, 85(1), 69-84.

Haag, T., Santos, A. S., Sana, D. A., Morato, R. G., Cullen Jr, L., CrawshawJr, P. G., De Angelo C., Di Bitetti, M.S., Salzano, F. M. & Eizirik, E. (2010). The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (Panthera onca). Molecular Ecology, 19(22), 4906-4921.

Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. A Journal of the Human Environment 40(3), 248-255.

Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. Metapopulation Dynamics: Empirical and Theoretical Investigations, 73-88.

Ito, T. Y., Lhagvasuren, B., Tsunekawa, A., Shinoda, M., Takatsuki, S., Buuveibaatar, B., & Chimeddorj, B. (2013). Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. PLoS One, 8(2), e56995.

Iriarte, J. A., Franklin, W. L., Johnson, W. E. & Redford. (1990). Biogeographic variation of food habits and body size of the America puma. Oecologia, 85, 185-190.

Kauffman, M. J., Varley, N., Smith, D. W., Stahler, D. R., MacNulty, D. R. & Boyce, M. S. (2007). Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters, 10, 690-700.

Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience, 52, 883–890.

Michalski, F., Boulhosa, R. L. P. & Peres, C. A. (2006). Human–wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation onLivestock. Animal Conservation, 9, 179-188.

Milner, J. M., Nilsen, E. B. & Andreassen. (2007). Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology, 21(1), 36-47.

Mitchell, A. & Lima, S. L. (2002). Predator-prey shell games: large-scale movement and its implications for decision-making by prey. Oikos, 99(2), 249-259.

Morato, R. G., Thompson, J. J., Paviolo, A. , La Torre, J. A., Lima, F. , McBride, R. T., Paula, R. C., Cullen, L. , Silveira, L. , Kantek, D. L., Ramalho, E. E., Maranhão, L. , Haberfeld, M. , Sana, D. A., Medellin, R. A., Carrillo, E. , Montalvo, V. , Monroy-Vilchis, O. , Cruz, P. , Jacomo, A. T., Torres, N. M., Alves, G. B., Cassaigne, I. , Thompson, R. , Saens-Bolanos, C. , Cruz, J. C., Alfaro, L. D., Hagnauer, I. , Silva, X. M., Vogliotti, A. , Moraes, M. F., Miyazaki, S. S., Pereira, T. D., Araujo, G. R., Silva, L. C., Leuzinger, L. , Carvalho, M. M., Rampin, L. , Sartorello, L. , Quigley, H. , Tortato, F. , Hoogesteijn, R. , Crawshaw, P. G., Devlin, A. L., May, J. A., Azevedo, F. C., Concone, H. V., Quiroga, V. A., Costa, S. A., Arrabal, J. P., Vanderhoeven, E. , Blanco, Y. E., Lopes, A. M., Widmer, C. E. and Ribeiro, M. C. (2018), Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. Ecology, 99: 1691-1691. doi:10.1002/ecy.2379

Morato, R. G., Stabach, J. A., Fleming, C. H., Calabrese, J. M., De Paula, R. C., Ferraz, K. M., ... & Paviolo, A. (2016). Space use and movement of a Neotropical top predator: the endangered jaguar. PloSone, 11(12), e0168176.

Morato, R. G., de Barros, K. M. P. M., de Paula, R. C., & de Campos, C. B. (2014). Identification of priority conservation areas and potential corridors for jaguars in the Caatinga biome, Brazil. PloSone, 9(4), e92950.

Morato, R., Verreschi, L. T. N., Guimarães, M., Cassaro, K., Pessuti, C. & Barnabe, R. C. (2004). Seasonal variation in the endocrine–testicular function of captive jaguars (Panthera onca). Theriogenology, 61(7-8), 1273-1281.

Mysterud, A. & Østbye, E. (1999). Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin, 27(2), 385-394.

Noss, R. F., Quigley, H. B., Hornocker, M. G., Merrill, T. & Paquet, P. C. (1996). Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology, 10(4), 949-963.

Paviolo, A., Angelo, C. D., Blanco, Y. E. & Bitetti, M. S. (2008). Jaguar Panthera onca population decline in the Upper Paraná Atlantic Forest of Argentina and Brazil. Oryx, 42(4), 554-561.

Pontes, A. R. M. & Chivers, D. J. (2007). Peccary movements as determinants of the movements of large cats in Brazilian Amazonia. Journal of Zoology, 273(3), 257-265.

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. In (Pearl M. C. eds) Research techniques in animal ecology: controversies and consequences, 1, 476.

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biological Conservation, 143(4), 939-945.

Rodrígues-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J. C., Briones, M. Á, Núñez, R., Rosas-Rosas, O., Ceballos, G. & Falcucci, A. (2011). Predicting potential distribution of the jaguar (Panthera onca) in Mexico: identification of priority areas for conservation. Diversity and Distributions, 1-12.

Salom-Pérez, R., Carrillo, E., Sáenz, J. & Mora, J. M. (2007). Critical condition of the jaguar Panthera onca population in Corcovado National Park, Costa Rica. Oryx, 41(1), 51-56.

Santos, F. R., Jácomo, A. T. & Silveira, L. (2008). Humans and jaguars in five Brazilian Biomes: same country, different perceptions. CAT News, 4, 21-25.

Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioral response race. In: (Barbosa, P. & Castellanos, I. eds). Ecology of predator-pray interactions. Oxford University Press.

Schmitz, O. J., Miller, J. R., Trainor, A. M., & Abrahms, B. (2017). Toward a community ecology of landscapes: predicting multiple predator-prey interactions across geographic space. Ecology, 98: 2281-2292.

Silver, S. C., Ostro, L. E. T., Marsh, L. K., Maffei, L., Noss, A. J., Kelly, M. J., Wallace, R. B., Gómez, H. & Ayala, G. (2004). The use of camera traps for estimating jaguar Pantheraonca abundance and density using capture/recapture analysis. Oryx, 38(2), 148-154.

Sutherland, W. J. & Anderson, C. W. (1993). Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. Journal of Theoretical Biology, 160(2), 223-230.

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., Rabinowitz, A. & Quigley, H. (2015). Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications, 26(4), 1112-1124.

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. Movement ecology, 2(1), 4.

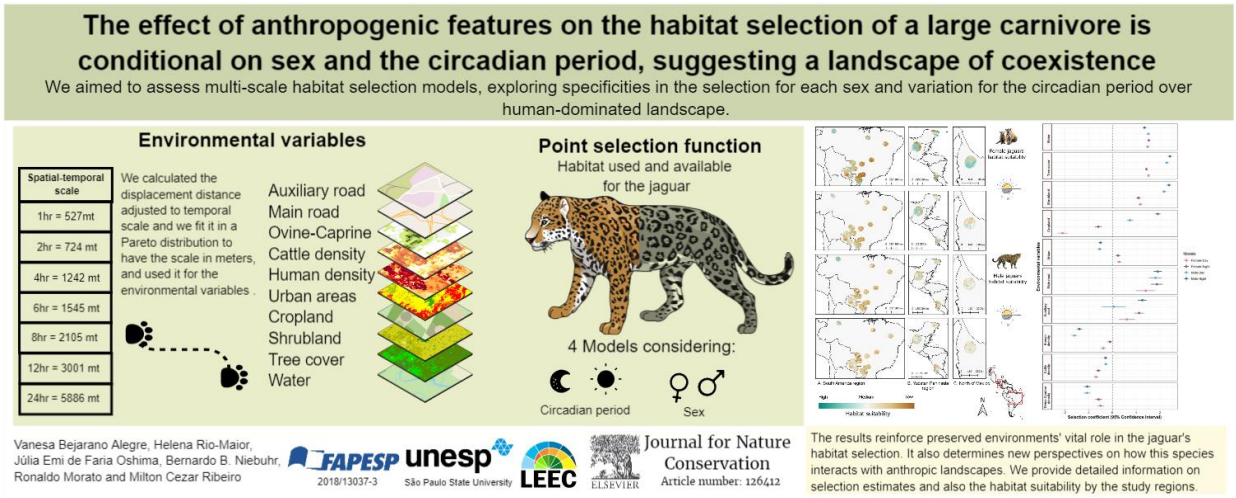
Winker, K., Rappole, J. H. & Ramos, M. A. (1995). The use of movement data as an assay of habitat quality. Oecologia, 101, 211-216.

Woodroffe, R. (2000). Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3, 165-173.

Zimmermann, A., Walpole, M. J. & Leader-Willians, N. (2005). Cattle rancher's attitudes to conflicts with jaguar Panthera onca in the Pantanal of Brazil. Oryx, 39(4), 406-412.

Chapter # 1:

The effect of anthropogenic features on the habitat selection of a large carnivore is conditional on sex and circadian period, suggesting a landscape of coexistence



https://doi.org/10.1016/j.jnc.2023.126412

Abstract

Human-carnivores coexistence is one of the major requirements for large predator survival, especially in the Neotropics, where retaliatory conflicts are still frequent. This problem was increased due to the human expansion, and the loss of natural habitats. Therefore, we aimed to assess multi-scale habitat selection models, exploring specificities in the selection for each sex and variation for the circadian period over human-dominated landscape. We found that jaguars live in real landscapes of fear with high human and livestock density, where the perception of risk related to humans governed the selection of their resources. However, depending on the sex of individuals and the circadian period, jaguars positively selected some anthropic structures, such as areas of crops and human settlements. This selection suggested an aptitude to use various human-dominated structures and indicated jaguars could locally perceive risks in different ways, depending of the sex and day period. Unexpectedly, jaguars presented attraction to roads, sexual or circadian related, regardless of the natural environments. In addition, we conclude that the knowledge of the habitat selection for jaguars is a crucial component to the structure of the landscape of coexistence of this species and can give us efficient guidance to better comprehend the behavior through different scales of selection and through different periods of the day. Finally, our results show fundamental observations on the movement plasticity of this species for the construction of conservation plans focusing on the coexistence in different landscapes of the Neotropics dominated by humans.

Keywords: Panthera onca, resource selection, roads, croplands, livestock, landscape of fear

1. Introduction

The increase in road networks, urban and agricultural areas has reduced the availability of natural habitats for large carnivores. These changes raise human-carnivore conflicts, one of the most significant obstacles to the conservation of carnivores (Treves and Karanth, 2003). These conflicts threaten carnivores, increasing the chance of these species being killed by retaliation, either due to livestock predation or fear of attack on humans, which could lead to carnivores population reductions in the short term (Castaño-Uribe et al., 2016; Loveridge et al. 2010; Marchini and MacDonald 2012). Besides that, large carnivores need large areas to search for their prey. Thus, reducing their natural habitat raises the risk of being run over or hunted while traveling through roads and settlements (Espinosa et al., 2018; Treves and Karanth, 2003). Therefore, a keystone for their successful conservation is improving our understanding of the spatio-temporal dynamics of human-carnivore coexistence (Bateman and Fleming, 2012). Consequently, it is crucial to recognize when and what resources are selected by carnivores in human-dominated landscapes and in what spatial and temporal scales this selection occurs.

In this context, the landscape of coexistence framework helps to understand how the carnivores interact with human-dominated landscapes. Landscapes of coexistence are rooted in the ecology of fear, in which the human presence is assumed to alter animal behavioral aspects due to their perception of risks (Oriol-Cotterill et al., 2015). The aim of designing landscapes of coexistence is to identify areas where the chance of human-caused mortality is low enough or tolerable in space and time to sustain large carnivores and the ecological processes they require (Oriol-Cotterill et al., 2015). Therefore, it emerges from the interaction among the type and intensity of anthropic level disturbances, the carnivore behavior, and the landscapes' environmental attributes (Gehr et al., 2017; Oriol-Cotterill et al., 2015). Based on understanding these relationships, this approach minimizes contact or/and interaction between humans and wildlife by accommodating habitat use behavior and reducing conservation obstacles related to carnivores.

Jaguars (*Panthera onca*) are not outsiders to this conservation obstacle; this species is subject to conflicts throughout their range, especially in livestock areas (Castaño-Uribe et al., 2016). In addition, roads are widespread across the jaguar distribution range and threaten their populations and prey (Abra et al., 2021; Espinosa et al., 2018; Cerqueira et al., 2021). The original

jaguar distribution range was reduced by around 48% (de la Torre et al.,2018) and is classified as "Near threatened" by the IUCN (Quigley et al., 2017). However, in many countries, such as Brazil, Argentina, Paraguay, Bolivia, and Mexico, jaguars are threatened by extinction (de la Torre et al., 2018).

Generally, jaguars prefer dense tree cover or suitable quality habitat (Conde et al., 2010; Cullen et al., 2005; Morato et al., 2018), and habitat selection varies according to sex since females have smaller home ranges and stay in more natural areas than males (Conde et al., 2010; Kanda et al., 2019; Thompson et al. 2021). In contrast, males have more extensive home ranges and venture into anthropized regions with low human and agricultural density. The impact of roads has been studied recently, showing mixed results. At the same time, different studies reported that roads negatively affect jaguar occurrence (Conde et al., 2010; Espinosa et al., 2018; Cerqueira et al., 2021); others did not find any effect on jaguar movement patterns (Morato et al., 2018). Consequently, based on the mixed results with various scales and regions studied, there remain questions about jaguar tolerance of anthropic matrix and their road use in human-dominated landscapes in which they coexist. That information might help better decision-making for managing natural areas close to anthropic areas.

Throughout the jaguar distribution, most studies related to habitat selection are local (Alvarenga et al., 2021; Cullen et al., 2005; 2013; except Morato et al., 2018). Thus, our interest was determining jaguar habitat selection by prioritizing circadian cycles and exploring if jaguars were restricted to natural structures for their use and movement in different human domain landscapes in a broad perspective of its distribution range. Therefore, our main objective was to build a model that could provide a scale of jaguar habitat selection determined by the distance of movement within 24 hours. Thus, guide the conservation plans of the species based on the components of the human-jaguar interaction of the coexistence landscape throughout its entire range of distribution. This model allows us to determine which landscape structures are selected or avoided along the circadian cycle (day-night) for both male and female jaguars. We hypothesized that jaguar habitat selection would respond to anthropogenic modifications and ecological processes at the broader scale of our study (scale determined at 24-h jaguar

displacement), as observed in similar studies with large carnivores. (Alvarenga et al., 2021; Zeller et al., 2014). In addition, we expected that the selection of natural environments would be positive in jaguars of both sexes. According to our findings, we contribute results for a better understanding of the main components of a landscape of coexistence, helping decision-makers in species conservation by giving insights for management actions and directions for future studies.

1. Methods

The landscape of coexistence is determined by predictions of the behavioral effects of human-caused mortality risk on large carnivores. Therefore, in a spatial-temporal context, carnivores will have distinct responses in their habitat use due to the presence or activity of humans (Oriol-Cotterill et al., 2015). Also, the spatial-temporal scale is crucial to adjusting risk variation over time (Brown and Kotler, 2004). Hence, we use resource selection functions based on points in a multi-scale approach (multi-scale in space and time, *sensu* MacGarigal et al. 2016). The key to this analysis is a 'used' versus 'available' design, where 'preferred' habitats are used in proportions higher than their availability (Manly et al., 2002).

1.1. Jaguar data and environmental variables

We selected the jaguar data of different studies throughout its distribution range from an open resource available jaguar GPS database (Morato et al., 2018a). We used data from 117 jaguars (62 females and 55 males) distributed in different ecoregions (Figure 1). Some regions reported less data than others because they are based on short-term studies (e.g., Brazilian Caatinga data from Morato et al., 2016, 2018b). This reported is common for large carnivores due to their low population density and rugged terrain in which they can inhabit, leading to fewer capture and collaring opportunities (e.g., Cavalcanti and Gese, 2009; Cullen et al., 2013; Nuñez-Perez and Miller, 2019; Rio-Maior et al., 2019; Zeller et al., 2014).

Initially, we selected 14 environmental variables for our habitat selection modeling approach (Table 1). The selection of these variables was related to its homogeneous distribution in all the areas from which our jaguar data were taken to have the broad-range response habitat selection.

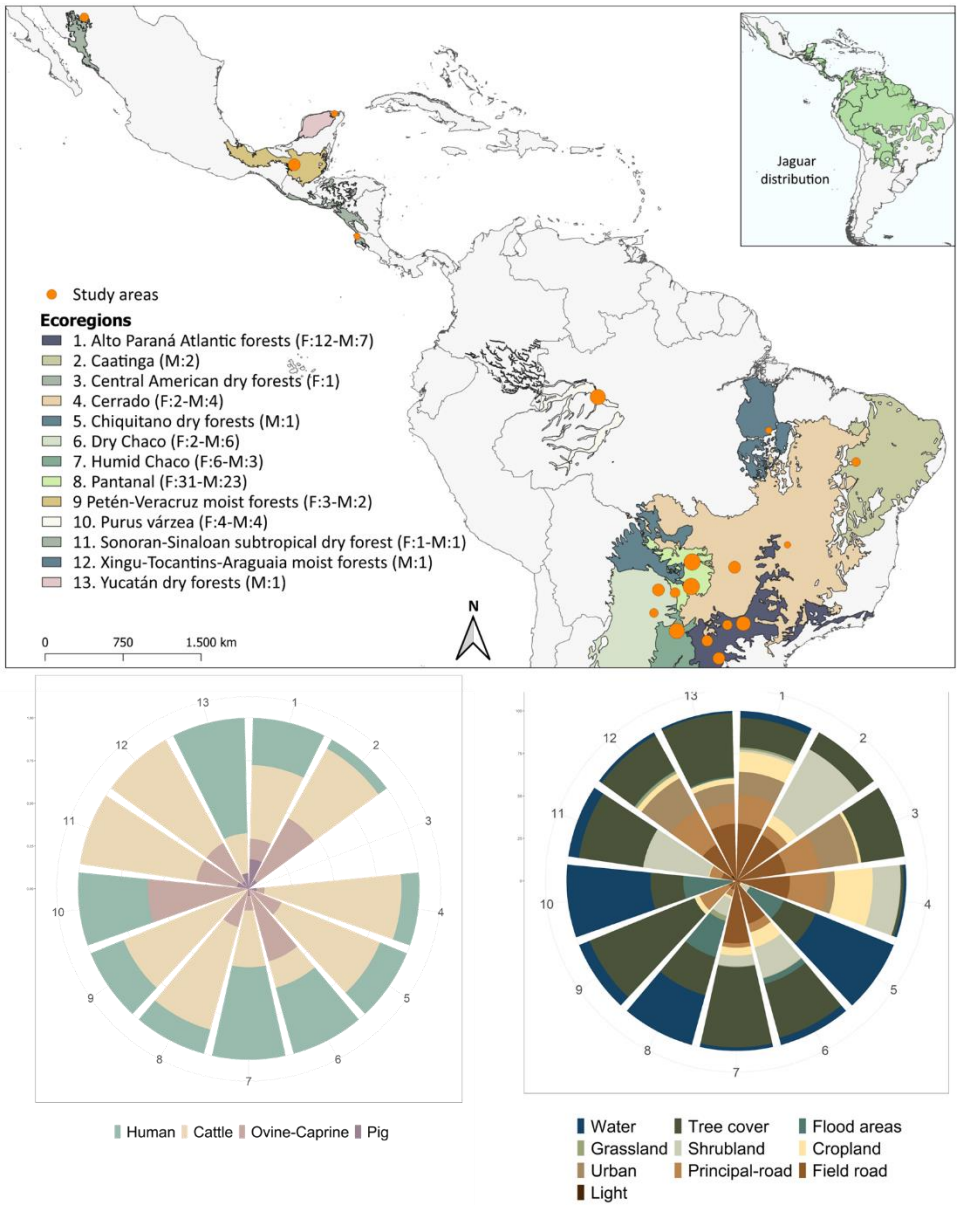


Figure 1. A) Jaguar data distribution in this study. The number of females and males are in parenthesis. The distribution of the variables in each study area is on the bottom, divided by ecoregions (in numbers) for better visualization: B) Distribution of the human, bovine, ovine-goat, and porcine density variables per ecoregion (median of the scaled data). C) Distribution of the land cover, road, and light variables per ecoregion (percentage of the data). For the raw data review, see Table A1 and A2 from Supplementary Material.

Also was associated with the human presence and disturbance, the density of livestock, and some ecological variables which are known or expected to influence the jaguar's landscape suitability and permeability and are essential to designing the landscape of coexistence (Oriol-Cotterill et al., 2015; Thompson et al. 2021). We converted categorical variables such as land cover classes and road presence into binary variables based on the essential categories hypothesized to influence jaguar habitat selection (Table B1, Supplementary material). Also, we standardized and transformed the variables to reduce the influence of extreme values on density covariates. We converted each variable into a logarithmic value (Legendre and Legendre, 1998; e.g., Rio-Maior et al., 2019) and normalized it to zero mean and unit variance to enhance comparability effect sizes (e.g., Rio-Maior et al., 2019). We worked with all the rasters using a resolution of 30 m. For all raster processing, we have used the QGIS 3.10.7-A Coruña (QGIS Development Team, 2020).

1.2. The multi-scale point selection function

For the habitat selection analysis, we used the approach proposed by Zeller et al. (2014, 2016) following the ecological neighborhood approach (Addicott et al., 1987) to determine the scale of the effect of the environmental variables. First, we calculated the displacement distance - straight-line - for all the jaguars' datasets that presented GPS schedules adjusted to seven different temporal scales: 1, 2, 4, 6, 8, 12, and 24 hours. Then, we fit a Pareto distribution using the *POT* package (Ribatet and Dutang, 2019) with the 97.5 percentile as a threshold (Zeller et al., 2014). We used the Pareto distributions' population mean as the final scale to avoid extreme data (Table C1, supplementary material). The last step was to fit Gaussian kernels using the seven spatial scales obtained, corresponding to the temporal scales above (Zeller et al., 2014, 2016). We used the scales obtained with the Pareto distribution on each jaguar location point. We then calculated their intensities based on the environmental variables and converted them to proportions using the *smoothie* package (Gilleland, 2013). All these operations we performed within the R software environment (R Core Team, 2021).

We performed the Point Selection Function (PSF) to determine the habitat selection due to the differences and some of them discontinuous in data collection of the jaguars. For each point, we

designated the "used" habitat as a 30 m fixed-width buffer around the pixel, taking the mean value; we did this to avoid minor data collection errors and consider the surrounding habitat.

Table 1.

Information type and description of the variables considered in this study. Flooded areas, grassland, night-time lights and pig density were eliminated for the final model.

#	Variables	Information type	Description	Reference
1	Water	Natural	Frequency	Feng et al., 2015
2	Tree cover	Natural	Binary classification	ESA/UCLouvain, 2017
3	Flooded area *	Natural	Binary classification	ESA/UCLouvain, 2017
4	Grassland **	Natural	Binary classification	ESA/UCLouvain, 2017
5	Shrubland	Natural	Binary classification	ESA/UCLouvain, 2017
6	Cropland	Anthropic	Binary classification	ESA/UCLouvain, 2017
7	Urban areas	Anthropic	Binary classification	Cattaneo et al. 2021
8	Main road	Anthropic	Binary classification	OpenStreetMap 2015
9	Auxiliary road	Anthropic	Binary classification	OpenStreetMap 2015
10	Night-time lights**	Anthropic	Equal quantile bins	Venter et al., 2016
11	Human density	Anthropic	Human population density per 1 km^2	CIESIN 2018
12	Cattle density	Anthropic	Cattle head densities per 1 km^2	Robinson et al., 2014
13	Ovine density	Anthropic	Sheep-Goat head densities per 1 km^2	Robinson et al., 2014
14	Pig density **	Anthropic	Pig head densities per 1 km2	Robinson et al., 2014

Variables removed from analysis: * VIF >3, ** Scarse

Then we used the values of the points in the different spatial scales (Zeller et al., 2014, 2016), as explained before, to determine the "available" habitat. Next, we constructed multivariate mixed-effect conditional logistics models at each scale with the *Survival* package (Thernau, 2021) with the jaguar individual identification as a random effect (Elliot et al., 2014). Then we used model selection based on Akaike's Information Criterion (AICc) to identify the best-supported scale for each variable (Burnham and Anderson, 2002; Zuur et al., 2009). All the selection analysis was made separately by circadian period (day-night) because previous research has shown that the human presence at different circadian periods could affect the choice of landscape structures (Oriol-Cotterill et al.,2015; Rio-Maior et al., 2019). To reduce collinearity, we removed variables

whose Pearson correlation was > 0.7 (See Table D1 supplementary material) and used the variance inflation factor (VIF) to exclude variables with VIF > 3 (Table 1; Zuur et al., 2009) using the *usdm* package (Naimi, 2015). If any variable presented a correlation, we would select, in our criteria, the variable that humans most use. We carried out the final multivariate conditional logistic models separately by sex and circadian cycle, creating a group "stratum" (e.g., Cushman et al., 2011; Rio-Maior et al., 2019) with their respective selected variables scales.

Finally, we calculated the predictions of the selection models using the "predict" function of the *raster* package (Hijmans, 2021), which were then projected in the studied regions. A 100 km buffer was considered for each data point for each area. Thus, larger regions are created due to the number of individuals recorded (e.g., the Pantanal and the Dry Chaco). We used the Boyce index to assess how much the model differed from random expectations using presence-only data for the model validation. Boyce index values range from -1 to 1, with negative values indicating counter-prediction, zero values indicating randomness, and near 1 values indicating a highly accurate prediction (Hirzel et al., 2006). We used the *ecospat* package in the R program (Di Cola et al., 2016).

2. Results

The scales obtained from the Pareto distribution were 527, 724, 1242, 1545, 2105, 3001, and 5886 meters for periods 1, 2, 4, 6, 8, 12, and 24 hours, respectively. We analyzed the 14 variables (Table 1), and the final models had variables mostly of 5886 m which was the most likely according to Akaike's Information Criterion. We removed the flooded land variable for presenting a VIF > 3, and the variables representing night-time lights, grassland, and pig density, which were not homogeneous in many of the studied regions (Figure 1, Table A1 and A2 supplementary material), causing extreme values for selection coefficients. The final models retained eleven significant environmental variables ($p < 0.001$) and presented high predictive ability. Using the Boyce index with independent retention data determined that the model for females during the day was f = 0.81, and at night f = 0.87. For males, the selective model during the day was f = 0.89, and at night f = 0.87.

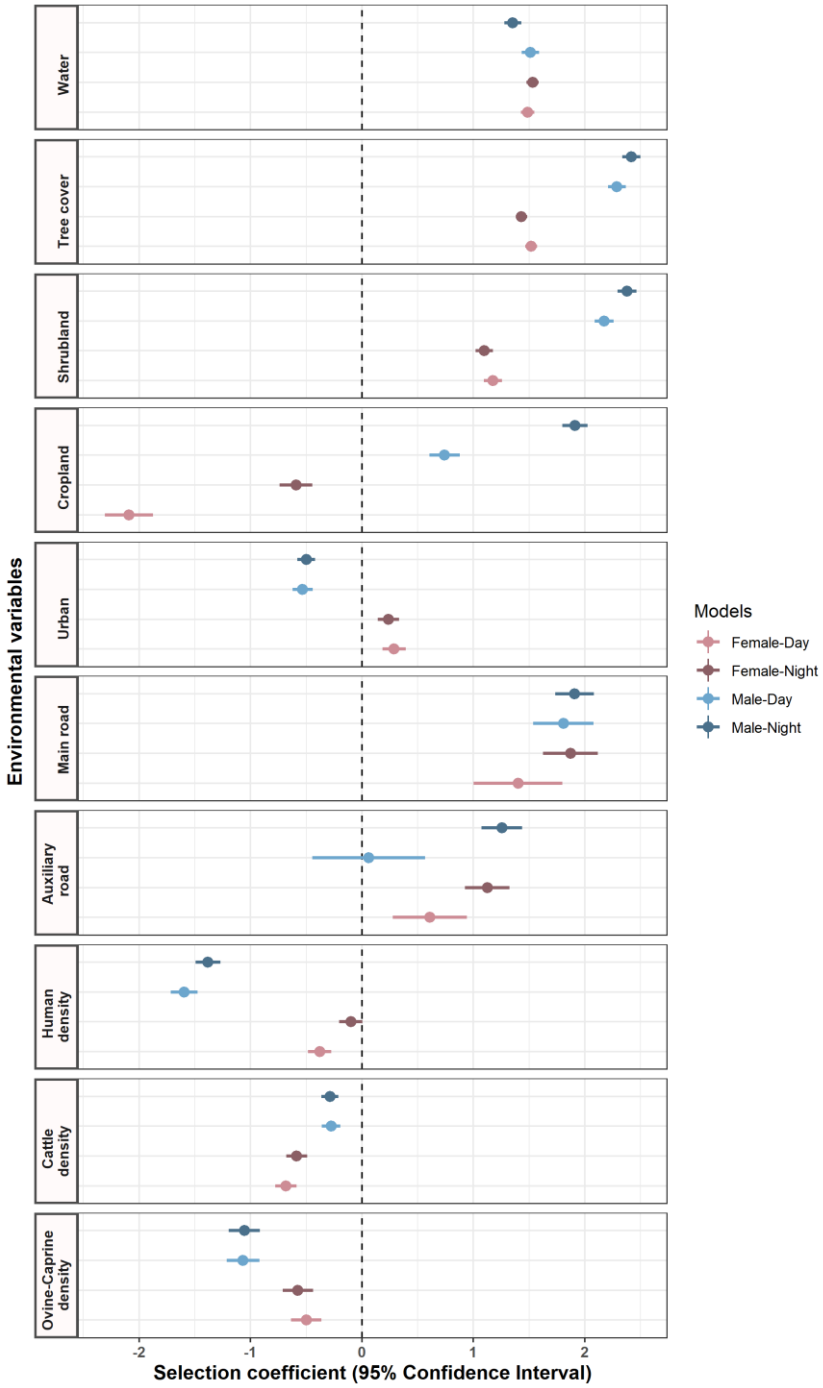


FIGURE 2. Jaguar (*Panthera onca*) estimated selection coefficients by sex and circadian period for each standardized environmental variable. Values above 0 represent selection and values below 0 represent avoidance.

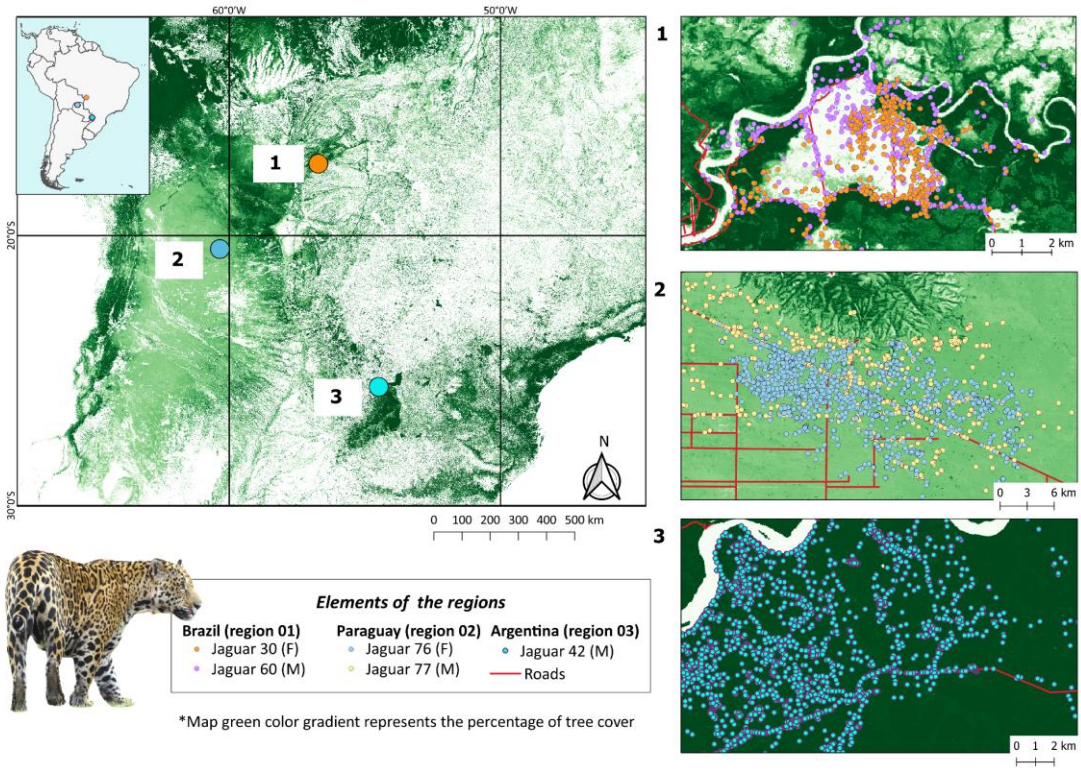


FIGURE 3. Example of the predominance of road use in jaguars, in three different regions. 1) In Brazil, two jaguars are monitored using different roads in an agricultural area in the ecoregion Pantanal. The central area has low tree cover and surrounding areas with high tree cover. 2) In Paraguay, the main road is frequently used and crossed by two jaguars; trees cover ~ 50%. 3) Region of Argentina, with a tree cover of 100%, an individual is frequently observed using the main road. Jaguar photo by Eduardo Fragoso.

Habitat selection

Regardless of sex and circadian period, jaguars' presented a high probability of selecting areas with high tree cover, shrubland, and areas with water (Figure 2, Table E1 supplementary material). Females avoided crop areas while males actively selected crops, especially at night. Although males avoided urban, females occurred in such places, with no major differences between circadian periods. Females and males used the main roads (Figures 2 and 3), with no large differences along the circadian period. Also, males and females selected auxiliary roads, even though males used them according to their availability during the day. However, males and females avoided areas with higher cattle, sheep, goat, and human density without circadian period differences. The avoidance effect of human density is larger on males than on females.

Our results showed that the selection of the variables tested was very similar between males and females; however, the selection coefficients of each choice differed (Figure 2).

According to the environmental variables studied here, many habitats where jaguars are distributed do not meet high suitability. According to the predictions map, females have a better perception of the resources than male during the day (Figure 4). In South America, habitats are very suitable in the Purus Varzea ecoregion for both sex and Paraguayan Chaco for females during the day. However, Pantanal, Cerrado, and Atlantic Forest regions show low suitability. The study areas of the Yucatan Peninsula are suitable for both sex, especially females during the day, as is in northern Mexico. In all areas, rivers and riverside forests are remarkably suitable for using the jaguar.

3. Discussion

Our study is the first to explore range-wide habitat selection across multi-scales and circadian periods for jaguars to contribute to the landscape of coexistence. The results reinforce preserved environments' vital role in the jaguar's habitat selection. It also determines new perspectives on how this species interacts with anthropic landscapes. For example, roads are the artificial structures most commonly used by the species, despite their high mortality risk. On the other hand, the species mainly avoid areas with a high density of humans and livestock. These results contribute globally to the particular aspects of this species' habitat selection, highlighting the anthropic structures we must better manage to ensure the maintenance of the species.

Our results showed that jaguars selected resources over broad scales of available habitat in a consistent pattern. Other large carnivores such as pumas (Zeller et al., 2014), lions (Elliot et al., 2014), and bears (Cushman and Lewis, 2010) also selected their resource on a broad scale. Furthermore, another study showed that broad effect scales better-explained jaguar habitat use (see Alvarenga et al., 2021). For this reason, the multi-scale habitat selection studies (McGarigal et al., 2016) for carnivore species provided essential insights into their specific resource and area requirements.

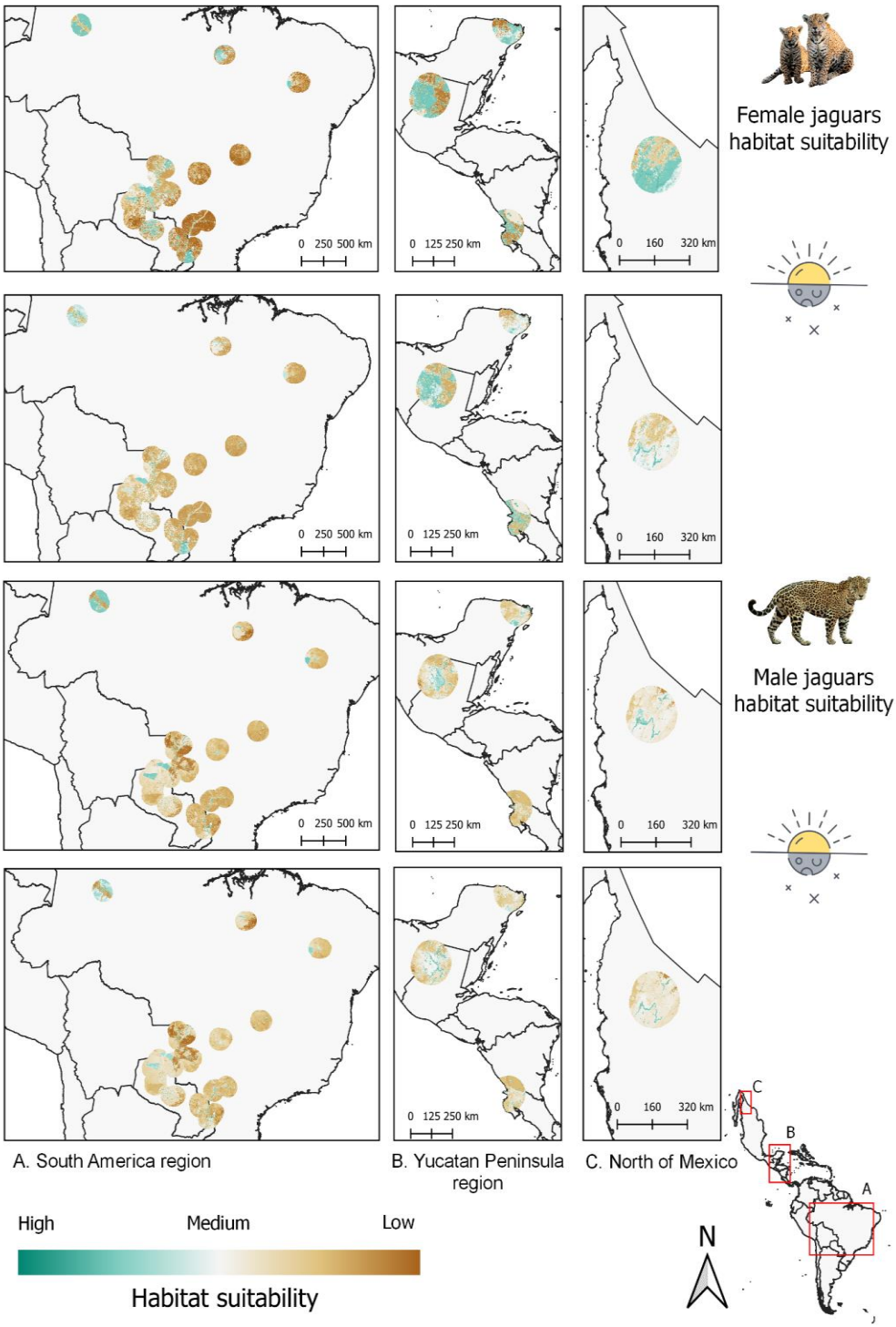


FIGURE 4. The habitat suitability by the study regions, and the habitat is inferred using the models' predictions for each sex and circadian period. The resolution is 30 m. Jaguar photos by Eduardo Fragoso.

We found a positive selection for natural land cover in our global model of the jaguar-resource selection. As predicted, this feline selected areas with higher tree cover and water availability (Alveranga et al., 2021; Conde et al., 2010; Morato et al., 2018). Many studies highlighted the importance of these structures for maintaining their habitat suitability (de Angelo et al., 2013; Conde et al.,2010; Morato et al., 2014; 2018). Other natural habitats, such as shrubs, also had a higher probability of use by the species. Similar responses are described at the Pantanal (Alvarenga et al., 2021). In addition, our results comparing the selection for artificial and natural structures separately show that this tendency is more relevant in males than in females, regardless of the time of the day. Since these natural land cover areas serve as foraging and resting grounds, they are crucial to the species' survival (Fontes et al., 2021).

In human-dominated areas, females avoided cropland with greater intensity during the day. However, males used these areas with higher intensity at night. In other studies, similar results were found, combining agriculture information with cattle distribution (Conde et al., 2010). The sex differences observed could be related to males having territories that are more extensively explored in search of prey, females, and avoidance of other males (Cavalcanti and Gese, 2009; Kanda et al., 2019; Morato et al., 2016). Males occupied more extensive home ranges than females (Cavalcanti and Gese, 2009; Morato et al., 2016; Thompson et al., 2021), which tend to be part of these environments. In addition, this species entered the agricultural matrix in the Pantanal but no deeper than 650 meters, indicating that it uses this structure to cross areas between nearby patches (Alegre et al., in preparation). The difference in selection intensity of croplands between the circadian periods could be due to the avoidance of high human activity periods, as was already reported for other mammal species (Gaynor et al., 2018).

Human-related risks to jaguars are mainly highlighted by avoiding areas with higher livestock density. Our results showed that females and males did not preferentially select areas with a high density of cattle, sheep, or goats. This result is unclear in other investigations (Conde et al., 2010; Morato et al., 2018) and contradictory in regional reports on livestock predation by jaguars (Castaño-Uribe et al., 2016). The jaguar's tendency to kill cattle may reflect the variation in the abundance availability of other wild prey species and not a preferential use of cattle ranching

areas (De Azevedo, 2008; Cavalcanti and Gese, 2010). Furthermore, it suggests that jaguars preferentially use and hunt in forested areas. They may forage in grazing areas near forest edges but not necessarily where the highest livestock densities are located. Likewise, there are records of lower predation rates on farms with better livestock and pen management (Castaño-Uribe et al., 2016). Regions like the Pantanal present a continuous conflict with the jaguar due to the predation of domestic animals. Thus, to prevent jaguar entry into ranching areas, compensation should be with natural areas with high proportions of wild jaguar prey and good livestock management. In addition, our result suggests that jaguars do not preferentially use areas with high cattle densities; instead, jaguars select areas with a high density of tree cover and water availability.

The jaguar avoided areas of high human density, and those areas were previously reported as having a negative impact on many regions (Conde et al., 2010; Colchero et al., 2011; De Angelo et al., 2011; Morato et al., 2014; 2016; Alvarenga et al.,2021). We found that males, more than females, avoided regions with higher human density. Also, we found that females decreased this avoidance behavior during the night. This selection might be explained because females positively selected urban. However, males did not use urban areas in any period. This result could be related to the fact that the jaguars monitored selected areas near intermediate cities of 500,000 inhabitants or less. Nevertheless, all jaguars avoided areas with higher human density, indicating that this species may have certain plasticity to live in rural or peri-urban environments with low human density (Conde et al., 2010; Rabinowitz and Zeller, 2010; Colchero et al., 2011; De Angelo et al., 2013; Morato et al., 2014; 2016;2018b).

The anthropic structures most used by the jaguar were the main and auxiliary roads, all significantly selected on a scale of ~6 km, except for auxiliary roads by males during the day. In other studies, the selection of this structure is unclear (Conde et al., 2010; Morato et al., 2018). However, the roads, especially paved roads, significantly decrease wildlife populations (Abra et al., 2021; Espinosa et al.,2018). Other felines, such as the Puma, use these areas mainly for hunting because their prey uses them as an antipredatory behavior (Ditmer et al., 2021). Also, many carnivores use these structures to "traveling" in day times when they are less used by

humans (Kautz et al., 2021). Therefore, the jaguar does not avoid roads entirely, as it may contain valuable resources for traveling or foraging, so avoiding it would result in higher energetic costs for movement. Then we can conclude that jaguars positively select the roads and present a high probability of coexistence if these structures present management and control for the passage of fauna.

Our predictive maps present many unsuitable areas for the jaguar, such as the Cerrado, Atlantic Forest, and Pantanal. This is mentioned in other studies within these ecoregions due to the loss of natural habitats due to the expansion of livestock and urban areas and the depletion of natural prey for the jaguar (De Angelo et al., 2013; Diniz et al., 2018; Morato et al., 2016). The Cerrado is one of the ecoregions with few suitable areas for the jaguar and few protected areas that can shelter the species (Portugal et al., 2020). In the Atlantic Forest, the jaguar population has almost completely disappeared (around 90%) due to the lack of connectivity of the few remnants found in these areas (Beisiegel et al., 2012; De Angelo et al., 2013). Our results also show that the Pantanal has low habitat suitability for the jaguar; this contradicts other studies (Cavalcanti et al., 2012; Alvarenga et al., 2021). However, it should be noted that flooded natural areas within this ecoregion, were not integrated into our model, but the species frequently use. Nevertheless, the Pantanal presents priority conservation areas unsuitable for jaguars (see Alvarenga et al., 2021).

The area studied in Purus Varzea is a suitable habitat for the species; this region is the Mamiraua Sustainable Use Reserve, in which a Jaguar density of 10/100km2 has previously been reported (de Oliveira et al., 2012; Ramalho, 2008). This Amazon region is highly preserved compared to others, such as Bolivia and Colombia (de Oliveira et al., 2012). The areas of the Paraguayan Chaco origin of our data show a more significant presence of human densities, which also has a high percentage of forest cover (See tables A1 and A2 in supplementary material), attractive structures for females, according to our model. On the other hand, the areas with the greatest suitable habitat for both sexes were the regions studied in northern Mexico and the regions of the Yucatan peninsula since the landscape presents natural structures.

4. Conservation implications and conclusions

The jaguar is a charismatic and umbrella species for nature conservation (Rabinowitz and Zeller, 2010). In addition, the jaguar is one of the large carnivore species with significant human conflict throughout its distribution (Treves and Karanth, 2003). Our study demonstrated the resource preferences of the species over a wide range of land cover and human-built environments. In addition, jaguars are living in landscapes of fear throughout almost their entire distribution range, where the selection of their resources and habitat is governed by the risk perception related to humans. Landscapes within most ecoregions have high human and livestock density; however, jaguars explore altered human areas: males use crop areas, especially at night, and females use intermediary cities settlements positively. This species' responses suggested an aptitude to use various human-dominated structures and land covers.

Although the species explores various Human-dominated structures at different times during the day, little can be said about the type of use of these structures. For males, cropland areas are not an immediate death risk like roads (Abra et al., 2021), and these places could be used to expand their territory further (Conde et al., 2010; Thompson et al., 2021). However, for females, the proximity to cities must be reflected in the search for food as observed in other carnivores (e.g., Ditmer et al., 2021), but this is not clear, and more studies of the species must be carried out to understand this behavior. Despite everything, the probability of encountering humans remains a conflict and a risk for the jaguar in regions where the species is seen as a threat (Castaño-Uribe et al., 2016; Treves and Karanth, 2003). Therefore, identifying conflict zones helps to promote conservation efforts with the community and involve them in the management and policies of the species, raising awareness and education about the species.

Moreover, jaguars may adopt compensatory mechanisms to survive in these environments even more if human-dominated landscapes present strategies targeting species conservation, such as ecotourism. The natural environments of the jaguar habitat, such as the availability of forests, shrubs, and water, have an important refuge and feeding role. These structures are generally less permeable for humans to cross in an invasive way (Oriol-Cotterill et al., 2015). Therefore we

strengthen that native vegetation patches and access to water areas are crucial elements within the landscape of coexistence with this species.

On the other hand, roads, especially auxiliary roads in remote and rural areas, are attractive sinks (De Angelo et al., 2013), mainly for species displacement, and could lead to population declines (Espinosa et al., 2018). Few studies have focused on the impact of wildlife crossing structures on carnivores due to the economic and political implications that this reflects in many areas of South America (Barger et al., 2015). However, it has been observed that the jaguar uses this wildlife crossing, such as wildlife underpasses (Gonzales-Gallina et al., 2018). Therefore, these crossings of wild fauna should be considered in specific conservation management to reduce the mortality risks of the species in areas with greater reporting or the probability of being run over. For this, it is indispensable to understand the primary function of roads for the species, the landscape context, and local features, which can vary between regions, types of roads, and vehicular traffic density.

Finally, our study contributes to planning landscapes of coexistence for the species using a multi-scale approach. It provides results that can be used to interpret the species' selective behavior using information from various landscapes in different ecoregions of the species range distribution. Our predictive landscapes showed that more than the natural components of the landscape, such as tree cover, water, and shrubs, is needed to design coexistence landscapes for the species in an anthropic environment. However, the social, agricultural, and structural management of these environments is also essential to sustain our coexistence with the species. Our results demonstrate that some anthropic structures can be significantly effect more than others in different day periods. These results are essential for decision-making on conserving the species globally without neglecting the continuous study on a regional basis.

5. References

Abra, F. D., Huijser, M. P., Magioli, M., Bovo, A. A. A., and de Barros, K. M. P. M., 2021. An estimate of wild mammal roadkill in São Paulo state, Brazil. Heliyon, 7(1), e06015. https://doi.org/10.1016/j.heliyon.2021.e06015

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., and Soluk, D. A., 1987. Ecological neighborhoods: scaling environmental patterns. Oikos, 340-346. https://doi.org/10.2307/3565770

Alvarenga, G. C., Chiaverini, L., Cushman, S. A., Dröge, E., Macdonald, D. W., Kantek, D. L. Z., ... and Kaszta, Ż., 2021. Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. Biological Conservation, 253, 108900. https://doi.org/10.1016/j.biocon.2020.108900

Bager, A., Borghi, C. E., & Secco, H. (2015). The influence of economics, politics, and environment on road ecology in South America. *Handbook of road ecology*, 407-413.

Beisiegel, B., Sana, D. A., & Moraes, E. 2012. The jaguar in the Atlantic Forest. Cat News Spec, (2012).

Brown, J. S., and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology letters*, *7*(10), 999-1014.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed). Ecol. Model. https://doi.org/10.1016/j.ecolmodel.2003.11.004

Castaño-Uribe, C., C. A. Lasso, R. Hoogesteijn, A. Diaz-Pulido y E. Payán (Editores). 2016. II. Conflictos entre felinos y humanos en América Latina. Serie Editorial Fauna Silvestre Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá, D. C., Colombia. 489 pp.

Cattaneo, A., Nelson, A., & McMenomy, T. (2021). Global mapping of urban–rural catchment areas reveals unequal access to services. Proceedings of the National Academy of Sciences, 118(2), e2011990118.

Cavalcanti, S. M., Gese, E. M., 2009. Spatial ecology and social interactions of jaguars (Panthera onca) in the southern Pantanal, Brazil. Journal of Mammalogy, 90(4), 935-945. https://doi.org/10.1644/08-MAMM-A-188.1

Cavalcanti, S. M., and Gese, E. M. (2010). Kill rates and predation patterns of jaguars (Panthera onca) in the southern Pantanal, Brazil. Journal of Mammalogy, 91(3), 722-736.

Cavalcanti, S. M., Azevedo, F. D., Tomás, W. M., Boulhosa, R. L., & Crawshaw Jr, P. G. (2012). The status of the jaguar in the Pantanal. Cat News, 7, 29-34.

Center for International Earth Science Information Network - CIESIN - Columbia University, and Information Technology Outreach Services - ITOS - University of Georgia. 2013. Global Roads Open Access Data Set, Version 1 (gROADSv1). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). http://dx.doi.org/10.7927/H4VD6WCT. Accessed 2018.

Cerqueira, R. C., de Rivera, O. R., Jaeger, J. A., & Grilo, C. (2021). Direct and indirect effects of roads on space use by jaguars in Brazil. *Scientific reports*, *11*(1), 1-9.

Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., and Ceballos, G. (2011). Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. Animal Conservation, 14(2), 158-166.

Conde, D. A., Colchero, F., Zarza, H., Christensen Jr, N. L., Sexton, J. O., Manterola, C., ... and Ceballos, G., 2010. Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation, 143(9), 1980-1988. https://doi.org/10.1016/j.biocon.2010.04.049

Cullen Jr, L., Abreu, K. C., Sana, D., and Nava, A. F. D., 2005. Jaguars as landscape detectives for the upper Paraná River corridor, Brazil. Natureza e Conservação, 3(1), 124-146.

Cullen Junior, L., Sana, D. A., Lima, F., Abreu, K. C. D., Uezu, A., 2013. Selection of habitat by the jaguar, Panthera onca (Carnivora: Felidae), in the upper Paraná River, Brazil. *Zoologia (Curitiba)*, *30*(4), 379-387. https://doi.org/10.1590/S1984-46702013000400003

Cushman, S.A., Lewis, J.S., 2010. Movement behavior explains genetic differentiation in American black bears. Landsc. Ecol. 25, 1613–1625. https://doi.org/10.1007/s10980-010-9534-6

Cushman SA, Raphael MG, Ruggiero LF, Shirk AS, Wasserman TN, O'Doherty EC. 2011. Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landscape Ecol 26:1137–1149

De Angelo, C., Paviolo, A., Wiegand, T., Kanagaraj, R., and Di Bitetti, M. S. (2013). Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest. Biological conservation, 159, 422-433.

De Azevedo, F. C. C. (2008). Food habits and livestock depredation of sympatric jaguars and pumas in the Iguacu National Park area, south Brazil. Biotropica, 40(4), 494-500.

De la Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., Medellín, R. A., 2017. The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar Panthera onca. Oryx, 1-16.

de Oliveira, T. G., Ramalho, E. E., & de Paula, R. C. 2012. Red List assessment of the jaguar in Brazilian Amazonia. Cat News, 7, 8-13.

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., d'Amen, M., Randin, C., ... & Guisan, A. (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*(6), 774-787.

Diniz, M. F., Machado, R. B., Bispo, A. A., & Brito, D. 2018. Identifying key sites for connecting jaguar populations in the Brazilian Atlantic Forest. Animal conservation, 21(3), 201-210.

Ditmer, M. A., Stoner, D. C., Francis, C. D., Barber, J. R., Forester, J. D., Choate, D. M., ... and Carter, N. H. (2021). Artificial nightlight alters the predator-prey dynamics of an apex carnivore. Ecography, 44(2), 149-161.

Elliot, N., Cushman, S., Macdonald, D.W., Loveridge, A., 2014. The devil is in the dispersers: the metrics of landscape connectivity change with demography. J. Appl. Ecol. 51, 1169–1178. https://doi.org/10.1111/1365-2664.12282.

Espinosa, S., Celis, G., and Branch, L. C. (2018). When roads appear, jaguars decline: Increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PloS one, 13(1), e0189740.

ESA/UCLouvain - European Space Agency Climate Change Initiative, Land Cover project. 2017. 300m Annual Global Land Cover Time Series from 1992 to 2015. Retrieved from http://maps.elie.ucl.ac.be/CCI/viewer/.

Feng, Min, Joseph O. Sexton, Saurabh Channan, and John R. Townshend. 2015. "A Global, High-Resolution (30-M) Inland Water Body Dataset for 2000: First Results of a Topographic-Spectral Classification Algorithm." International Journal of Digital Earth. doi:10.1080/17538947.2015.1026420.

Fontes, G., S., Morato, G., R., Stanzani, S. L., and Pizzigatti Corrêa, P. L. (2021). Jaguar movement behavior: using trajectories and association rule mining algorithms to unveil behavioral states and social interactions. Plos one, 16(2), e0246233.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232-1235.

Gehr, B., Hofer, E. J., Muff, S., Ryser, A., Vimercati, E., Vogt, K., and Keller, L. F., 2017. A landscape of coexistence for a large predator in a human-dominated landscape. Oikos, 126(10), 1389-1399.

Gilleland E., 2013. "Two-dimensional kernel smoothing: Using the R package smoothie." NCAR Technical Note, TN-502+STR, 17pp. Doi: 10.5065/D61834G2.

González-Gallina, A., Hidalgo-Mihart, M. G., & Castelazo-Calva, V. (2018). Conservation implications for jaguars and other neotropical mammals using highway underpasses. PLoS One, 13(11), e0206614.

Hijmans J. Robert (2021). raster: Geographic Data Analysis and Modeling. R package version 3.4-13. https://CRAN.R-project.org/package=raster

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences.Ecol. Model. 199, 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

ICMBio/MMA, 2018 Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume II – Mamíferos / – 1. ed. -- Brasília, DF

Inskip, C., Zimmermann, A., 2009. Human-felid conflict: a review of patterns and priorities worldwide. Oryx, 43(1), 18-34. doi:10.1017/S003060530899030X

Kanda, C. Z., Oliveira-Santos, L. G. R., Morato, R. G., De Paula, R. C., Rampim, L. E., Sartorello, L., ... and Cezar Ribeiro, M. (2019). Spatiotemporal dynamics of conspecific movement explain a solitary carnivore's space use. Journal of Zoology, 308(1), 66-74.

Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Svoboda, N. J., and Belant, J. L. (2021). Large carnivore response to human road use suggests a landscape of coexistence. Global Ecology and Conservation, 30, e01772.

Legendre P. and Legendre L. 1998. Numerical Ecology, 2nd English ed. Amsterdam: Elsevier.

Loveridge, A. J. S. W., Wang, S. W., Frank, L., Seidensticker, J., 2010. People and wild felids: conservation of cats and management of conflicts. Biology and conservation of wild felids.

Manly BF, McDonald L, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. KluwerAcademic Publishers, Dordrecht

Marchini, S., & Macdonald, D. W. 2012. Predicting ranchers' intention to kill jaguars: case studies in Amazonia and Pantanal. *Biological Conservation*, *147*(1), 213-221.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., and Cushman, S. A. (2016). Multi-scale habitat selection modeling: a review and outlook. Landscape ecology, 31(6), 1161-1175.

Michalski, F., Boulhosa, R. L. P., Faria, A., Peres, C. A., 2006. Human-wildlife conflicts in a fragmented Amazonian forest landscape: determinants of large felid depredation on livestock. Animal Conservation, 9(2), 179-188. https://doi.org/10.1111/j.1469-1795.2006.00025.x

Morato, R. G., Ferraz, K. M. P. M. D. B., de Paula, R. C., and Campos, C. B. D. (2014). Identification of priority conservation areas and potential corridors for jaguars in the Caatinga biome, Brazil. PloS one, 9(4), e92950.

Morato, R.G., Stabach, J.A., Fleming, C.H., Calabrese, J.M., De Paula, R.C., Ferraz, K.M. P.M., Kantek, D.L.Z., Miyazaki, S.S., Pereira, T.D.C., Araujo, G.R., Paviolo, A., De Angelo, C., Di Bitetti, M.S., Cruz, P., Lima, F., Cullen, L., Sana, D.A., Ramalho, E.E., Carvalho, M.M., Soares, F.H.S., Zimbres, B., Silva, M.X., Moraes, M.D.F., Vogliotti, A., May, J.A., Haberfeld, M., Rampim, L., Sartorello, L., Ribeiro, M.C., Leimgruber, P., 2016. Space use and movement of a neotropical top predator: the endangered jaguar. PLoS One 11, 1–17. https://doi.org/10.1371/journal.pone.0168176

Morato, R.G., Thompson, J.J., Paviolo, A., La Torre, J.A., Lima, F., McBride, R.T., Paula, R.C., Cullen, L., Silveira, L., Kantek, D.L.Z., Ramalho, E.E., Maranhao, ˜ L., Haberfeld, M., Sana, D.A., Medellin, R.A., Carrillo, E., Montalvo, V., MonroyVilchis, O., Cruz, P., Jacomo, A.T., Torres, N.M., Alves, G.B., Cassaigne, I., Thompson, R., Saens-Bolanos, C., Cruz, J.C., Alfaro, L.D., Hagnauer, I., Silva, X.M., Vogliotti, A., Moraes, M.F.D., Miyazaki, S.S., Pereira, T.D.C., Araujo, G.R., Silva, L. C., Leuzinger, L., Carvalho, M.M., Rampin, L., Sartorello, L., Quigley, H., Tortato, F., Hoogesteijn, R., Crawshaw, P.G., Devlin, A.L., May, J.A., Azevedo, F.C.C., Concone, H.V.B., Quiroga, V.A., Costa, S.A., Arrabal, J.P., Vanderhoeven, E., Blanco, Y.E., Lopes, A.M.C., Widmer, C.E., Ribeiro, M.C., 2018a. Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. Ecology 99, 1691. https://doi.org/10.1002/ecy.2379.

Morato, R.G., Connette, G.M., Stabach, J.A., De Paula, R.C., Ferraz, K.M.P.M., Kantek, D. L.Z., Miyazaki, S.S., Pereira, T.D.C., Silva, L.C., Paviolo, A., De Angelo, C., Di Bitetti, M.S., Cruz, P., Lima, F., Cullen, L., Sana, D.A., Ramalho, E.E., Carvalho, M. M., da Silva, M.X., Moraes, M.D.F., Vogliotti, A., May, J.A., Haberfeld, M., Rampim, L., Sartorello, L., Araujo, G.R., Wittemyer, G., Ribeiro, M.C., Leimgruber, P., 2018b. Resource selection in an apex predator and variation in response to local landscape characteristics. Biol. Conserv. 228, 233–240. https://doi.org/10.1016/j.biocon.2018.10.022

Naimi B. 2015. usdm: Uncertainty analysis for species distribution models. R package version 1.1-15. Retrieved from https://cran.r-project.org/ package=usdm

Nuñez-Perez, R., Miller, B., 2019. Movements and home range of jaguars (Panthera onca) and mountain lions (Puma concolor) in a tropical dry forest of western Mexico. In Movement Ecology of Neotropical Forest Mammals (pp. 243-262). Springer, Cham. https://doi.org/10.1007/978-3-030-03463-4_14

OpenStreetMap-Shapefiles (2019). http://download.geofabrik.de. Accessed 2020.

Oriol-Cotterill, A., Valeix, M., Frank, L. G., Riginos, C., Macdonald, D. W., 2015. Landscapes of coexistence for terrestrial carnivores: the ecological consequences of being downgraded from

ultimate to penultimate predator by humans. Oikos, *124*(10), 1263-1273. https://doi.org/10.1111/oik.02224

Portugal, M. P., Morato, R. G., de Barros, K. M. P. M., Rodrigues, F. H. G., & Jacobi, C. M. 2020. Priority areas for jaguar Panthera onca conservation in the Cerrado. Oryx, 54(6), 854-865.

QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Quigley H, Foster R, Petracca L, Payan E, Salom R, Harmsen B (2017) Panthera onca. The IUCN Red List of Threatened Species. T15953A50658693.en. [errata version published in 2018]

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ramalho, E. E. 2008. Jaguar population dynamics in the varzea floodplain forests of Mamirauá. Report to WCS Jaguar Conservation Program.

Rabinowitz, A., Zeller, K.A., 2010. A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biol. Conserv. 143, 939–945.

Ribatet, M. and Dutang, C., 2019. POT: Generalized Pareto Distribution and Peaks Over Threshold. R package version 1.1-7

Rio-Maior, H., Nakamura, M., Álvares, F., Beja, P. (2019). Designing the landscape of coexistence: integrating risk avoidance, habitat selection, and functional connectivity to inform large carnivore conservation. Biological Conservation, *235*, 178-188. https://doi.org/10.1016/j.biocon.2019.04.021

Ripple, W.J., Estes, J., Beschta, R.L., Wilmers, C.C., Ritchie, E.G, Hebblewhite, M., Berger, J., et al., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. DOI: 10.1126/science.1241484

Robinson T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I and Gilbert, M. (2014) Mapping the global distribution of livestock. PLoS ONE 9(5):e96084. doi:10.1371/journal.pone.0096084

Therneau T, 2021. *A Package for Survival Analysis in R*. R package version 3.2-11, https://CRAN.R-project.org/package=survival.

Thompson, J. J., Morato, R. G., Niebuhr, B. B., Alegre, V. B., Oshima, J. E. F., de Barros, A. E., ... & Ribeiro, M. C. (2021). *Environmental and anthropogenic factors synergistically affect space use of jaguars.* Current Biology, 31(15), 3457-3466.

Treves, A., and Karanth, K. U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation biology, 17(6), 1491-1499.

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., ... & Watson, J. E. (2016). Global terrestrial human footprint maps for 1993 and 2009. Sci. Data 3, 160067. DOI: 10.1038/sdata.2016.67

Weber, W., Rabinowitz, A.,1996. A global perspective on large carnivore conservation. Conservation Biology, *10*(4), 1046-1054.

Woodroffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3, 165-173. https://doi.org/10.1111/j.1469-1795.2000.tb00241.x

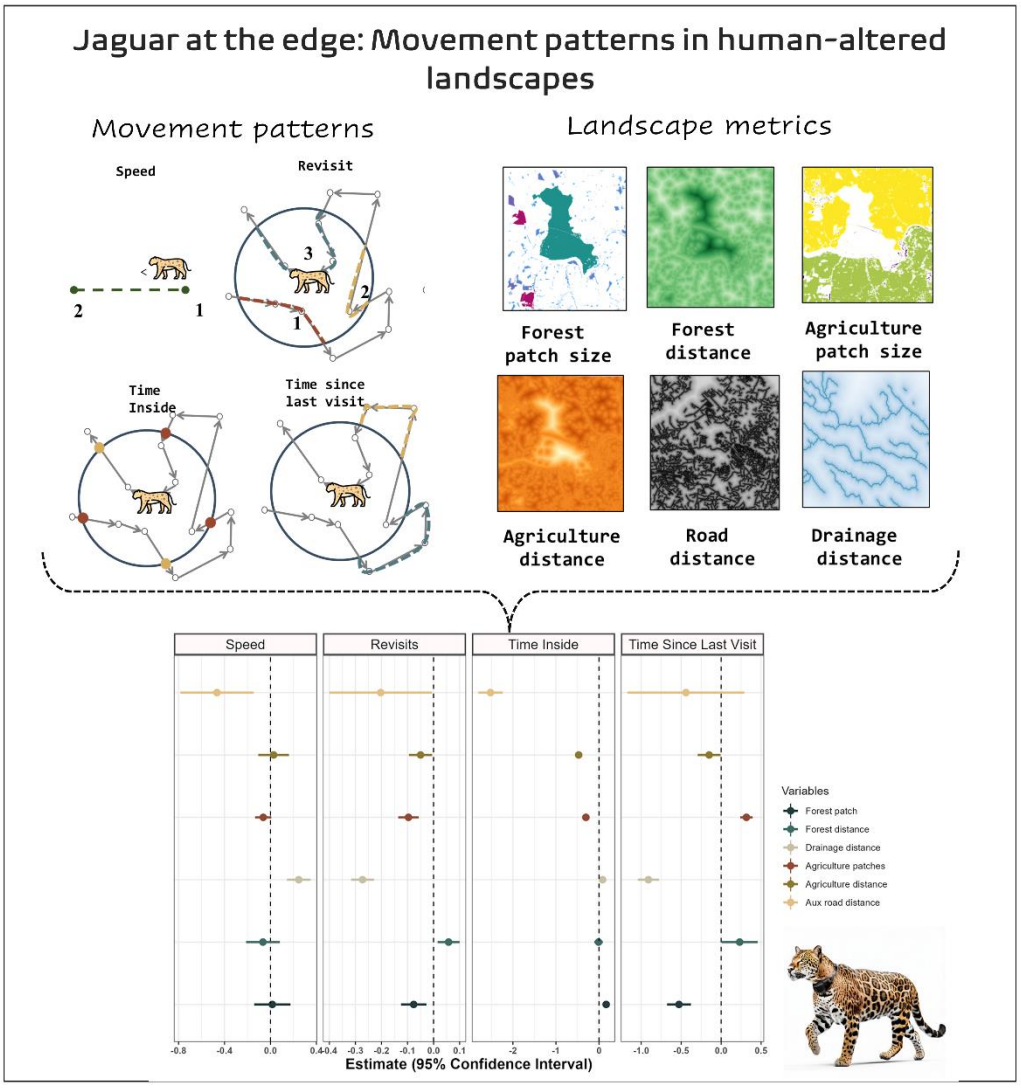
Zeller, K.A., McGarigal, K., Beier, P., Cushman, S.A., Vickers, T.W., Boyce, W.M., 2014. Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landsc. Ecol. 29, 541–557. https://doi.org/10.1007/s10980-014-9991-4.

Zimmermann, A., McQuinn, B., Macdonald, D. W., 2020. Levels of conflict over wildlife: Understanding and addressing the right problem. Conservation Science and Practice, 2(10), e259. DOI: 10.1111/csp2.259

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed-effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6.

Chapter # 2:

Jaguar at the edge: Movement patterns in human-altered landscapes



Abstract

Due to expansion and anthropic activity, carnivores' habitats have been modified and reduced. Connections between large natural expanses have been lost, making it difficult for them movement in search of food, shelter, or interaction with other individuals without the risk of mortality from being run over or hunted. Therefore our main objective is to determine the movement patterns of the jaguar inside and outside forest fragments and areas near roads and drainage. We considered movement patterns such as visit, time spent, time of the last visit, and speed as response variables within our models. Our results revealed that the jaguar revisits the edges of forests, agricultural areas, drainages, and roads. However, they spend more time within larger forest fragments than small ones. They take longer to visit larger patches of agricultural areas and the minimal distance of roads and drainage. Our results lead that the large forest patches remain an essential refuge for the jaguar but only meet some of the requirements for the maintenance of the species. Therefore, they are forced to visit the edge frequency of these landscapes. One of the probabilities may be the absence of prey within the natural habitats because they are hunted or moving to more urban areas for shelter and food. Our results indicate aspects to be considered within the landscape structure for conserving this species and future directions to consider when managing the species.

Keywords: Panthera onca, jaguar, human-domain landscape, movement patterns.

Introduction

The natural habitat continuity of terrestrial mammals is being lost due to the expansion of human activities (Crooks & Sanyan, 2006). The loss of connectivity due to the fragmentation of these biological structures threatens different mammal populations (Crooks et al., 2011; Crooks & Sanyan, 2006; Tucker et al., 2018; Woodroffe & Ginsberg, 1998). Carnivore populations are susceptible to habitat loss and fragmentation due to intrinsic biological characteristics, including large body sizes and an extensive home range to move around and find sufficient food and shelter (Crooks, 2002; Thompson et al., 2021). In addition, these species have a much higher chance of becoming extinct regionally in fragmented habitats due to human encounters or persecution (Woodroffe & Ginsberg, 1998; Woodroffe, 2000). Since carnivores have low densities and slow growth rates, it is difficult to recover losses in their population (Stier et al., 2016; Woodroffe, 2000). Therefore, it is essential to identify how fragmentation affects the movement patterns of carnivores in their habitat and understand the species' adaptability and the dangers they may face.

Understanding the movement patterns of carnivores provides us with knowledge of their ecological and evolutionary processes (Kays et al.,2015; Nathan et al., 2008). These patterns can give us clues as to how carnivores adapt to their habitat, which structures within the landscape these species benefit from, and which ones they avoid. It also provides behavioral and interaction information about the species, which is beneficial for defining population connectivity and developing conservation corridors (Kays et al.,2015). Movement studies with large carnivores indicate how vital the continuity of habitat coverage is (Kramer-Schadt et al., 2011). Also, these species translocate great distances since they have an extensive home range (Thompson et al., 2021). However, carnivores, sensitive to human presence, are forced to explore for food in anthropic areas due to habitat reduction (Dobson et al., 2006; Mortelliti & Boitani, 2008). This behavior promotes the carnivore-human conflict and, consequently, the persecution and death by a reprisal of these populations (Woodroffe, 2000).

The jaguar (*Panthera onca*) is one of the large carnivores in the Neotropics; that has the most significant conflict with humans in almost their entire distribution (Castaño-Uribe et al., 2016;

Zimmermann et al., 2021). This conflict is noticeable in habitat that suffers fragmentation and conversion to agricultural areas, also causing a reduction in their current distribution (de la Torre et al., 2018; Cullen et al., 2016; Haag et al., 2010; Zimmermann et al., 2021). Although jaguars prefer natural areas (Alveranga et al., 2021; Conde et al., 2010; Morato et al., 2018), they also prey on livestock in certain circumstances (Zimmermann et al., 2021), which means they use agricultural areas, peri-urban areas, and roads (Colchero et al., 2011; Cerqueira et al., 2021; Morato et al., 2018). Also, road mortality rates can be exceptionally high in fragmented habitats, as jaguars are more likely to cross roads due to reduced habitat areas (Cullen et al., 2016). However, we must be aware of how the fragmentation of natural regions impacts Jaguar movement patterns. For instance, determine if Jaguar uses agricultural patches frequently or if it only serves as a mechanism for displacement. By examining this information, we might be able to determine what level of landscape structure can impact the species and how much it can tolerate.

For this reason, our interest is to establish knowledge about the movement behavior in fragmented areas of the Jaguar, a top predator in Central and South America with a near-threatened category by the IUCN (Quigley et al., 2017). Our main objective is to determine the movement patterns of the Jaguar inside and outside forest fragments and areas near roads and drainage. We considered movement patterns such as visit, time spent, time of the last visit, and speed as response variables within our models. In addition to determining at what depth it enters agricultural and forest fragments. We predict that the Jaguar will avoid anthropic structures in all movement patterns due to populations generally remaining stable in heavily forested areas (De Angelo et al., 2013; De Angelo et al., 2011). For example, we expect that visits will not be recurrent in larger agricultural patches and will spend more time in large forested patches. Our results will be relevant to understanding the effect of these structures' size and distance on jaguar habitat and how fragmentation affects populations, in addition to providing tools to identify the appropriate level of forest management to maintain the permeability of the landscape for wildlife.

Methods

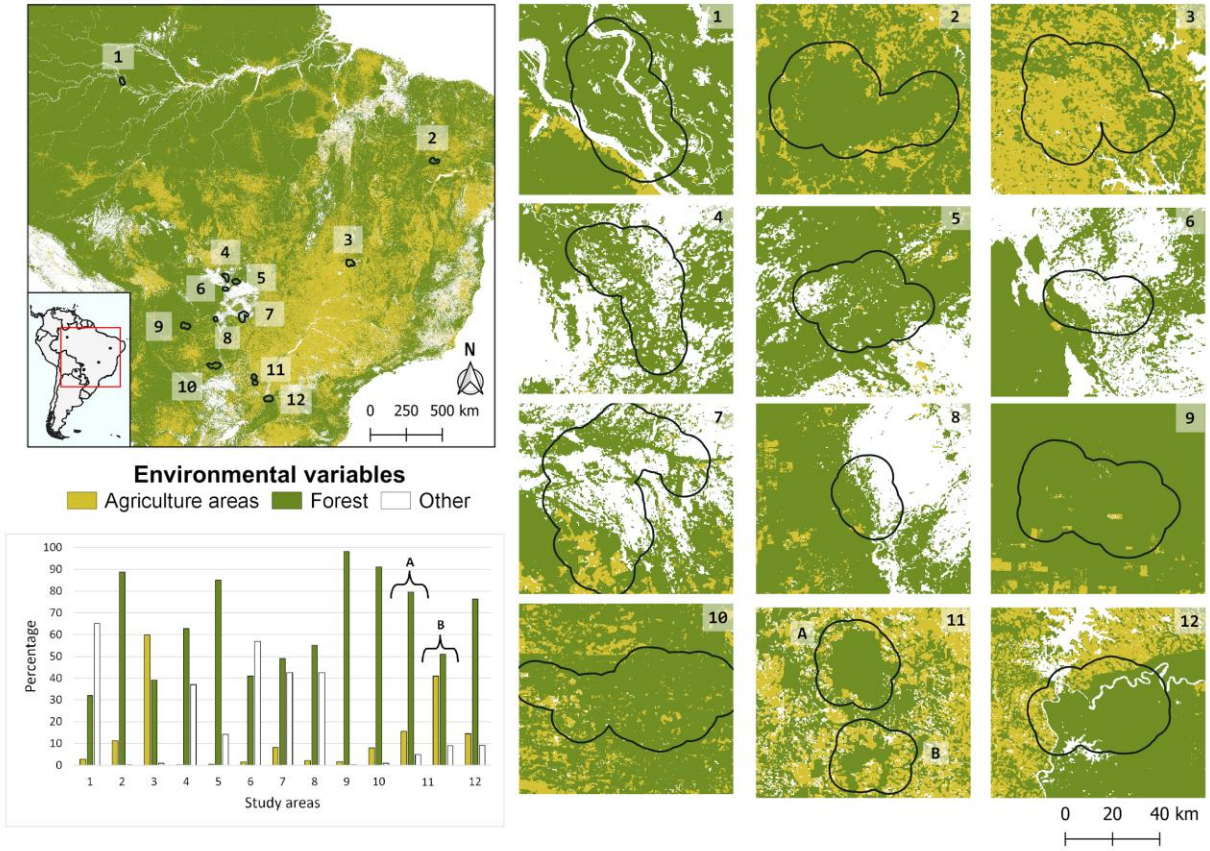


Figure 1. Jaguar distribution in this study. The numbers indicate the different regions in South America, wich availability of forest and agricultural areas differ in percentages.

Jaguar data and movement patterns

We selected 54 individuals from the Jaguar GPS open database (Morato et al., 2018b) distributed in the Neotropics (Figure 1). The selection criteria were: 1) regularity of the data, 2) samples or can be resampled every 4 hours (see Table A in Supplementary material). For movement patterns, we resample every 4 hours and analyze the speed of each individual with *amt* package (Signer et al., 2011). We calculator the metrics with the *recurse* package (Bracis et al., 2018), which takes the radius circle 250 meters and moves it along the trajectory. The 250-meter radius was calculated using the mean population distance traveled in 4 hours(see also Table A in Supplementary material). The number of trajectory segments entering and leaving the circle is counted at each location to determine the number of revisits. Also, it calculated the spend time

for each visit and the time since the last visit (Figure 2). All the packages were from the R program (R Core Team, 2022).

Environmental data and landscape metrics

We selected eight landscape metrics (Table 1) based on forest, agricultural areas, drainage, and roads. We converted the variables to raster (Drainage and road specifically), and we used QGIS 3.10.7-A Coruña program (QGIS Development Team, 2020) to do the conversion. The base data of agricultural and forest areas, we used the landcover base (see Table 1 and Figure 2), to obtain binarized raster. Then we measured patch size and distance using LandScape Metrics (LSMetrics; Niebuhr et al., In preparation). Then, to avoid collinearity, we analyze the correlation and variance inflation factor (VIF) between the environmental variables generated with the *vifcor* function from *usdm* package (Naimi, 2015) with a threshold of 0.7. This function removes variables with a correlation > 0.7 and shows the VIF values, so we also remove variables with VIF > 3 (Table 1; Zuur et al., 2009).

Models and diagnostics

We executed generalized linear mixed models using individuals and regions as random variables; our models were performed with the glmmTMB an R-package (Brooks et al., 2017) because it fixes generalized mixed models with various extensions, including zero inflation. The response variables that led each model were: revisit, time spent, time of the last visit, and speed. The models were diagnosed with KS-test, Dispersion test, and Outlier test within the DHARMa in the R-program (Hartig, 2022).

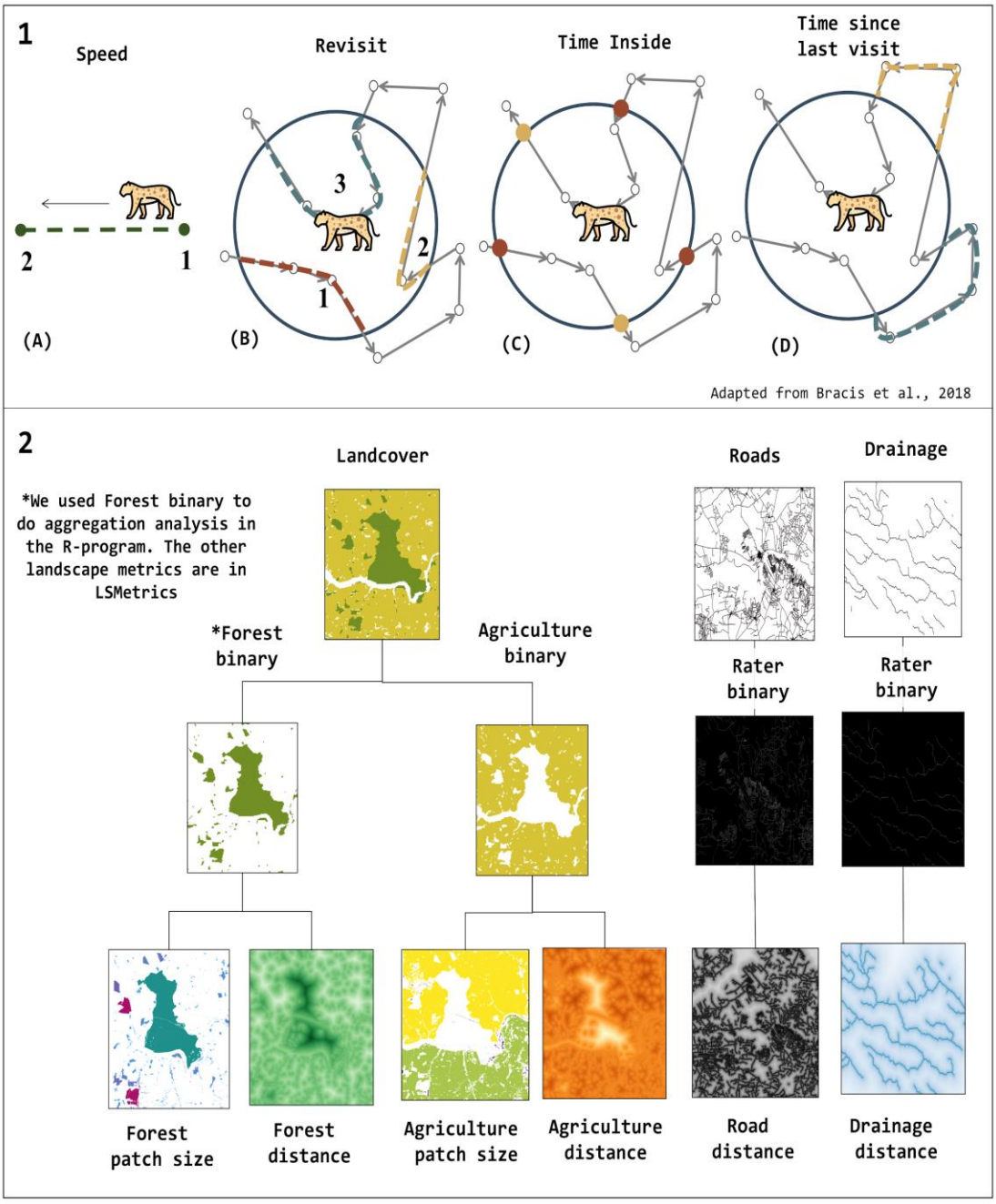


Figure 2. Methods were carried out in this study. 1) Movement patterns, a) we measured speed from one point to another, b) Visit the number of trajectories made within a radius of 250 meters. c) The time spent on each visit, considering entry and exit time, and d) the time spent to return to the 250-meter radius. 2) Analysis of the environmental variables was crossed from 3 base variables transformed in binary (landcover) and vector at Raster in the case of drainage and roads. The rest of the metrics were performed through binary maps.

Table 1. The variables informations considered in this study. Forest aggregation and main road distance were eliminated for the final model because it presented collinearity

#	Variables	Description	Landscape Metrics tools (Reference)	Pixel resolution (m)	Original range values	Binarizarion ranges	Reference resource
1	Forest patch size	Clasification of patch size in Hectares	LS metrics	300	10 -220 Categories	50 to 170	ESA/UCLouvain, 2015
2	Forest distance	The distance of this pixel to the nearest edge. Inside of forest negative value, outside positive values	LS metrics	300	10-220 Categories	50 to 170	ESA/UCLouvain, 2015
3	Forest aggregation	Clumpiness index (Aggregation metric)	landscapemetrics -R package	300	10 -220 Categories	50 to 170	ESA/UCLouvain, 2015
4	Agriculture patch	Clasification of patch size in Hectares	LS metrics	300	10 -220 Categories	10 to 40	ESA/UCLouvain, 2015
5	Agriculture distance	The distance of this pixel to the nearest edge. Inside of cropland negative value, outside positive values	LS metrics	300	10-220 Categories	10 to 40	ESA/UCLouvain, 2015
6	Drainage distance	The distance of this pixel to the nearest edge.	LS metrics	30	Vector line	0-1	Lehner and Grill, 2013
7	Auxiliary road distance	The distance of this pixel to the nearest edge.	LS metrics	30	Multiple line structure descriptions	Cycleway, cable path, service/road, track, footway, bridleway	OpenStreetMap 2015
8	Main road distance	The distance of this pixel to the nearest edge.	LS metrics	30	Multiple line structure descriptions	Motorway, trunk, primary, secondary, tertiary, residential, living street, pedestrian, raceway, railwa	OpenStreetMap 2015

Results

In the collinearity analysis, the main road variable was removed due to a correlation > 0.7 with auxiliary roads; we decided to remove this variable because also it is absent in one study area. We removed forest aggregation because it presents a VIF > 3. All models met the statistical assumptions for analysis of generalized linear mixed models (See Appendix A in Supplementary Material). Jaguars enter an average of 534.54 meters within agricultural areas, managing to enter a maximum of 2977.142 meters. Within forest areas, an average of 986.53 meters and a maximum of 14,987.8 meters enter (Table 2).

Table 2. Descriptive data of movement patterns of agricultural and forest areas

Agriculture areas				
Movement patterns	**Minimum**	**Mean**	**Maximum**	**Standart Desviation**
Distance inside (meters)	292.515	534.539	2977.142	486.422
Distance ouside (meters)	292.515	3709.126	16923.38	3011.74
Speed inside (m/4h)	0	834.0307	8943.171	1369.4571
Revisitation	1	7.0181	66	10.8507
Time inside (h)	0.004408558	11.5547	700.8034	19.8628
Time since last visit (h)	0	477.3922	24389.78	1986.104
Forest				
Movement patterns	**Minimum**	**Mean**	**Maximum**	**Standart Desviation**
Distance inside (meters)	292.086	986.533	14987.8	1259.103
Distance ouside (meters)	292.086	888.318	9544.676	1367.45
Speed inside (m/4h)	0	511.8582	11351.86	845.4485
Revisitation	1	6.7055	67	8.561
Time inside (h)	0.000188767	14.2185	1736.625	22.7695
Time since last visit (h)	0	442.3369	25074.88	1709.041

Speed models based on our variables did not provide conclusive results (Figure 3, Table B in Supplementary material). However, we determined that the mean speed within agricultural areas is higher than in the forest (Table 2). For revisit models, it is observed that the jaguar visits areas near the edges of all the variables with greater frequency (Figure 4) and does not remain in the

core of the forest; it revisits mostly the smaller patches of forests as well as in agricultural areas. The mean of the visits in agriculture areas is 7.02, and in the forest is 6.71 (Table 2). The time spent within larger agricultural patches is less than in larger forest patches (Figure A and Table B in Supplementary material). Also, it does not remain close to the drains for an extended period. Jaguars take time to visit areas close to auxiliary roads, drainage, and agricultural areas. However, the time elapsed since the last visit is less for larger forest patches (Figure 3).

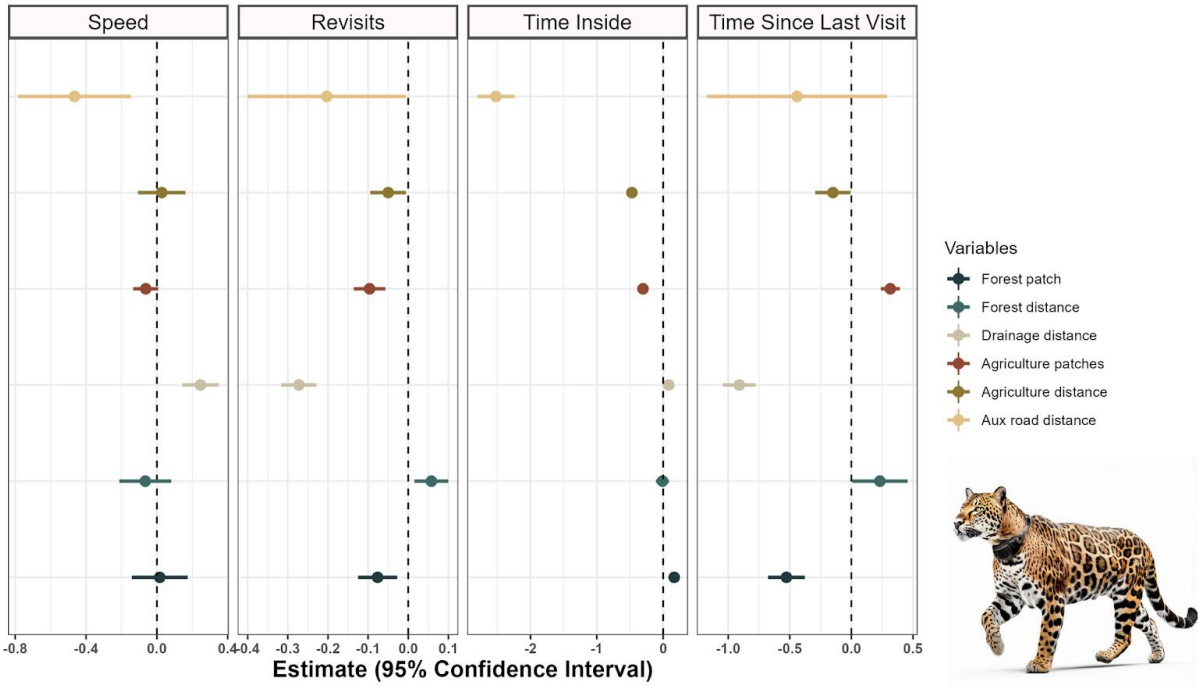


Figure 3. Estimates of the four developed models for the Jaguar (*Panthera onca*) revisitation metrics (speed, revisits, time inside, and time since last visit) and trajectory speed with the different environmental variables. Values above 0 represent the positive effect of the environmental variables analyzed for each movement pattern, and values below 0 are negative relations.

Discussion

Our study is the first to explore Jaguar movement patterns at different patch sizes and agricultural and forest distances. In addition, we examined how they interacted with distances of drainages and roads. The results show that the species frequently visit the edges of forests, agricultural

areas, roads, and drainage. However, the time between revisits varies according to the size of both agricultural and forest patches. Our results determine new perspectives on species' behavior in fragmented habitats. It also contributes to what structural aspects within the habitat must be considered as a focus for managing natural habitats in the entire species distribution.

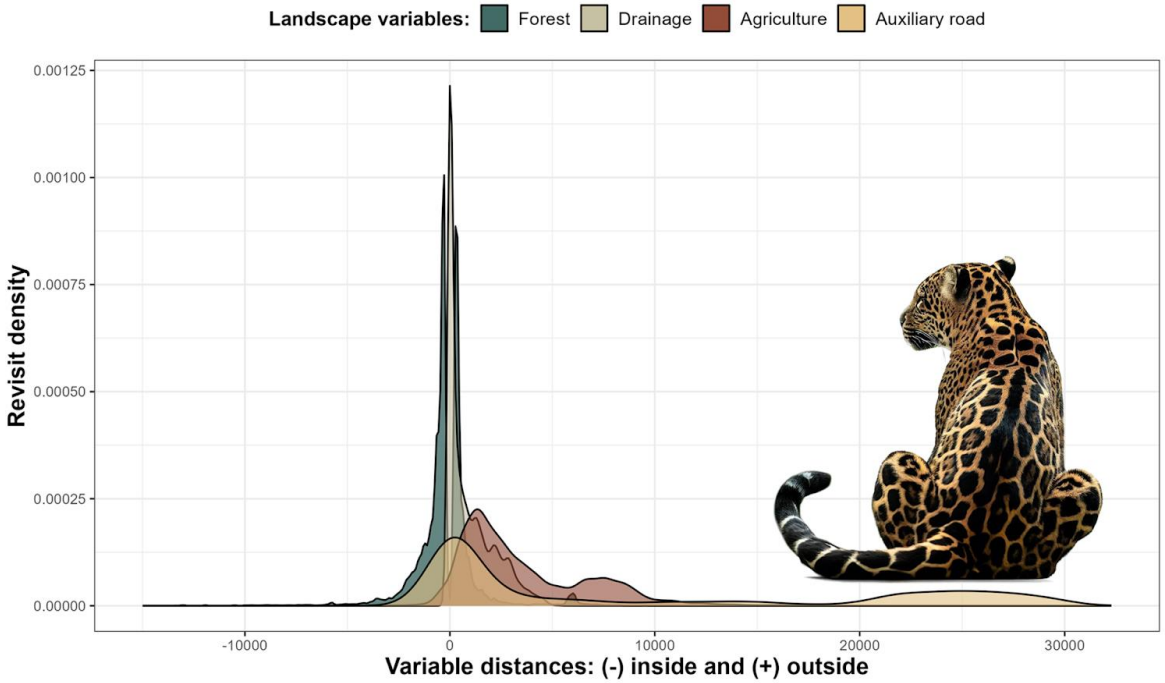


Figure 4. The number of visits across different distances of four land cover variables. Negative values indicate the distance within the variable, 0 is the edge, and positive values indicate the distance outside the variables.

Jaguars are considered one of the most important species for conserving natural habitats because they are closely associated with forested areas (Cullen Jr. et al., 2013; Thornton et al., 2015; Morato et al., 2018a). In addition, the jaguar is one of the large species, and for their maintenance, they require large areas with abundant natural prey (Cavalvanti et al., 2009; de la Torre et al., 2017; Thompson et al., 2021). Our results showed that the jaguar revisits the edge areas; this could suggest the lack of prey within forested areas or the ease of hunting that the species may have in this area (Esparza-Carlos et al., 2018). Different species respond differently to forest edges (Pfeifer et al., 2017); where species that benefit solely from the forest tend to be

endangered, those more widespread and adaptive to human presence benefit greatly (Pfeifer et al., 2017; Esparza-Carlos et al., 2018). For example, ungulate species were reported with frequent visits to the forest's edge in different patch sizes (Norris et al., 2008). It may be due to landscape configuration (Ries et al., 2004; Norris et al., 2008), resource distribution (Ries et al., 2004), or predator avoidance strategy (Winnie & Creel, 2017; Gaynor et al., 2021; Kautz et al., 2022). Since only predators perceive humans as dangerous, their spatiotemporal avoidance of humans may provide refuge for prey (Berger, 2007). This avoidance strategy forces carnivores to visit anthropic areas to obtain prey (Berger, 2007; Murphy et al., 2021). The visits cause a high chance of conflict with humans (one of the main problems for all carnivores; see Treves & Karanth, 2003; Castaño-Uribe et al., 2016), and in the long run, the extinction of the species.

On the other hand, we observed that the jaguar spent time within large patches of forested areas is greater than in smaller patches; this shows that the forest continues to be a safe area for the species. Just as it is observed that the time is extended to return to small forest patches, it indicates clear evidence that the use of small forest patches as agricultural areas are resources that the species uses additionally for maintenance. Similar responses were seen with the puma, which spends more time in larger patches and less in areas where its prey is concentrated (Laundré, 2010). In addition, in human-presence areas, predator-prey interactions are influenced mainly by the impact of anthropic structures (Murphy et al., 2021). Some studies indicate that many generalist species are more resilient in small forest patches due to a small home range and a frugivore-granivore diet (Norris et al., 2008). Also, many species use agricultural areas to benefit from them (Fitzgibbon, 1997; Dijak et al., 2000) and migrate to more urban areas to benefit from urban waste, domestic animals (as prey), or artificial habitats (Bateman & Fleming, 2012; Ditmer et al., 2021). For example, one of the jaguar's prey, the white-lipped peccary, its population is drastically reduced in much of its distribution. This reduction is due to the conflict in many agricultural areas since they feed on crops on the forest's edge and are hunted or poisoned by farmers (Lima et al., 2019). As mentioned above, this example is clear evidence that human structures, directly and indirectly (Berger, 2007; Murphy et al., 2021), modify the interaction between predator and prey (Patten et al.,2019). As well as demonstrates that prey can benefit

from forest edges in different ways and that these can bring about conflicts with the agricultural area through the reduction of populations, thus resulting in empty forests.

Likewise, Jaguars revisit the edge of the natural drainage. The drainage areas are, in many cases, resources for the hydration of the species. As well as for food, the jaguar could find prey in these areas as the capybaras and caiman (Azevedeo & Murray, 2007; Azevedo & Verdade, 2012). Our results also indicated that the jaguar frequently revisits the edge of the roads. Recent studies show that the jaguar is not affected by roads directly (Cerqueira et al., 2021); they use the road positively as a resource (Alegre in revision). Similar studies with large carnivores demonstrate the use of roads according to traffic intensity (Kautz et al., 2021); this behavior suggests that carnivores adjusted their behaviors concerning the road's proximity and dynamic change for the capture of prey (Colchero et al., 2010; Patten et al., 2019; Ditmer et al.,2021; Kautz et al., 2021). On the other hand, roads are a danger to reducing species and their prey due to car collisions that can perform high death among wildlife populations (Espinosa et al., 2018).

Conservation implications and conclusions

The jaguar is a threatened species throughout its distribution range, mainly due to human conflicts (Castaño-Uribe et al., 2016). Our results could be one key to explaining one of this conflict's consequences. Our results demonstrate the jaguar revisited of forest edge areas, agriculture, and even roads and their permanence in larger forest fragments. It suggests that the landscape's configuration and structure influence the jaguars' movement. Despite its presence in anthropic structures, the large patches of forest remain a safe place for the species. Studies show that in addition to landscape structure and patch size, the abundance of food resources determines the movement of carnivores in fragmented landscapes (Mortelliti & Boitani, 2008). Therefore, for decision-making on managing and conserving the species, we must focus on habitat connections as ecological corridors and consider the insertion of species that can maintain the ecological chain within them. It is also essential to consider the composition of shrubs and vegetation within them to allow optimal foraging conditions and shelter for large carnivores' prey.

Establishing a single jaguar movement pattern for landscape structures may become difficult, as prey dispersal may influence them. However, monitoring the diverse populations' dispersal strategies that depend on the landscape could help to understand how these populations respond to natural connections or corridors. Future studies must focus on predator-prey dynamics on landscape response because they may give us additional insight into the components that drive these occupational strategies within a habitat structure.

References

Alvarenga, G. C., Chiaverini, L., Cushman, S. A., Dröge, E., Macdonald, D. W., Kantek, D. L. Z., ... & Kaszta, Ż., (2021). Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. Biological Conservation, 253, 108900. https://doi.org/10.1016/j.biocon.2020.108900

de Azevedo, F. C. C., & Murray, D. L. (2007). Spatial organization and food habits of jaguars (Panthera onca) in a floodplain forest. *Biological conservation*, *137*(3), 391-402.https://doi.org/10.1016/j.biocon.2007.02.022

Azevedo, F. C. C. D., & Verdade, L. M. (2012). Predator–prey interactions: jaguar predation on caiman in a floodplain forest. *Journal of Zoology*, *286*(3), 200-207.https://doi.org/10.1111/j.1469-7998.2011.00867.x

Bateman, P. W., & Fleming, P. A. (2012). Big city life: carnivores in urban environments. *Journal of Zoology*, *287*(1), 1-23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology letters*, *3*(6), 620-623. https://doi.org/10.1098/rsbl.2007.0415

Bracis C, Bildstein K, Mueller T (2018). “Revisitation analysis uncovers spatio-temporal patterns in animal movement data.” _Ecography_. doi:10.1111/ecog.03618

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*, *9*(2), 378-400. doi: 10.32614/RJ-2017-066

Castaño-Uribe, C., C. A. Lasso, R. Hoogesteijn, A. Diaz-Pulido y E. Payán (Editores). 2016. II. Conflictos entre felinos y humanos en América Latina. Serie Editorial Fauna Silvestre Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Bogotá, D. C., Colombia. 489 pp.

Cavalcanti, S. M., & Gese, E. M. (2009). Spatial ecology and social interactions of jaguars (Panthera onca) in the southern Pantanal, Brazil. *Journal of Mammalogy*, *90*(4), 935-945. https://doi.org/10.1644/08-MAMM-A-188.1

Cerqueira, R. C., de Rivera, O. R., Jaeger, J. A., & Grilo, C. (2021). Direct and indirect effects of roads on space use by jaguars in Brazil. *Scientific reports*, *11*(1), 1-9. https://doi.org/10.1038/s41598-021-01936-6

Colchero, F., Conde, D. A., Manterola, C., Chávez, C., Rivera, A., & Ceballos, G. (2011). Jaguars on the move: modeling movement to mitigate fragmentation from road expansion in the Mayan Forest. *Animal Conservation*, *14*(2), 158-166. https://doi.org/10.1111/j.1469-1795.2010.00406.x

Conde, D. A., Colchero, F., Zarza, H., Christensen Jr, N. L., Sexton, J. O., Manterola, C., ... & Ceballos, G., (2010). Sex matters: Modeling male and female habitat differences for jaguar conservation. Biological Conservation, 143(9), 1980-1988. https://doi.org/10.1016/j.biocon.2010.04.049

Crooks, K. R. (2002). Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation biology*, *16*(2), 488–502. https://doi.org/10.1046/j.1523-1739.2002.00386.x

Crooks, K. R., & Sanjayan, M. (2006). Connectivity conservation: maintaining connections for nature. K.R. Crooks, M. Sanjayan (Eds.), Connectivity Conservation, Cambridge University Press (2006), pp. 1-19

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1578), 2642-2651.https://doi.org/10.1098/rstb.2011.0120

Cullen Junior, L., Sana, D. A., Lima, F., Abreu, K. C. D., & Uezu, A. (2013). Selection of habitat by the jaguar, Panthera onca (Carnivora: Felidae), in the upper Paraná River, Brazil. Zoologia (curitiba), 30, 379-387. https://doi.org/10.1590/S1984-46702013000400003

Cullen Jr, L., Stanton, J. C., Lima, F., Uezu, A., Perilli, M. L., & Akçakaya, H. R. (2016). Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic forest, Brazil. *PLoS One*, *11*(12), e0167372. https://doi.org/10.1371/journal.pone.0167372

De Angelo, C., Paviolo, A., & Di Bitetti, M. (2011). Differential impact of landscape transformation on pumas (Puma concolor) and jaguars (Panthera onca) in the Upper Paraná Atlantic Forest. Diversity and Distributions, 17(3), 422-436. https://doi.org/10.1111/j.1472-4642.2011.00746.x

De Angelo, C., Paviolo, A., Wiegand, T., Kanagaraj, R., & Di Bitetti, M. S. (2013). Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest. *Biological conservation*, *159*, 422-433. https://doi.org/10.1016/j.biocon.2012.12.021

De La Torre, J. A., Núñez, J. M., & Medellín, R. A. (2017). Spatial requirements of jaguars and pumas in Southern Mexico. *Mammalian Biology*, *84*, 52-60. https://doi.org/10.1111/mam.12081

De La Torre, J. A., González-Maya, J. F., Zarza, H., Ceballos, G., & Medellín, R. A. (2018). The jaguar's spots are darker than they appear: assessing the global conservation status of the jaguar Panthera onca. *Oryx*, *52*(2), 300-315.https://doi.org/10.1017/S0030605316001046

Dijak, W. D., & Thompson III, F. R. (2000). Landscape and edge effects on the distribution of mammalian predators in Missouri. *The Journal of wildlife management*, 209-216.https://doi.org/10.2307/3802992

Ditmer, M. A., Stoner, D. C., Francis, C. D., Barber, J. R., Forester, J. D., Choate, D. M., ... & Carter, N. H. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore. *Ecography*, *44*(2), 149-161.https://doi.org/10.1111/ecog.05251

Dobson, A., Lodge, D., Alder, J., Cumming, G. S., Keymer, J., McGlade, J., ... & Xenopoulos, M. A. (2006). Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology*, *87*(8), 1915-1924. https://doi.org/10.1890/0012-9658(2006)87[1915:HLTCAT]2.0.CO;2

Esparza-Carlos, J. P., Íñiguez-Dávalos, L. I., & Laundré, J. (2018). Microhabitat and presence of top predators affect prey apprehension in a subtropical mountain forest. *Journal of Mammalogy*, *99*(3), 596-607. https://doi.org/10.1093/jmammal/gyy046

Espinosa S, Celis G, Branch LC (2018) When roads appear jaguars decline: Increased access to an Amazonian wilderness area reduces potential for jaguar conservation. PLoS ONE 13(1): e0189740. https://doi.org/10.1371/journal.pone.0189740

Fitzgibbon, C. D. (1997). Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology, 530-539.https://doi.org/10.2307/2404895

Gaynor, K. M., Cherry, M. J., Gilbert, S. L., Kohl, M. T., Larson, C. L., Newsome, T. M., ... & Smith, J. A. (2021). An applied ecology of fear framework: linking theory to conservation practice. *Animal Conservation*, *24*(3), 308-321. https://doi.org/10.1111/acv.12629

Haag, T., Santos, A. S., Sana, D. A., Morato, R. G., Cullen Jr, L., Crawshaw Jr, P. G., ... & Eizirik, E. (2010). The effect of habitat fragmentation on the genetic structure of a top predator: loss of diversity and high differentiation among remnant populations of Atlantic Forest jaguars (Panthera onca). *Molecular Ecology*, *19*(22), 4906–4921. https://doi.org/10.1111/j.1365-294X.2010.04856.x

Hartig F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Duquette, J. F., & Belant, J. L. (2022). White-tailed deer exploit temporal refuge from multi-predator and human risks on roads. *Ecology and Evolution*, *12*(7), e9125. https://doi.org/10.1002/ece3.9125

Kramer-Schadt, S., S Kaiser, T., Frank, K., & Wiegand, T. (2011). Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape ecology*, *26*(4), 501-513. https://doi.org/10.1007/s10980-011-9576-4

Laundré, J. W. (2010). Behavioral response races, predator–prey shell games, ecology of fear, and patch use of pumas and their ungulate prey. *Ecology*, *91*(10), 2995-3007. https://doi.org/10.1890/08-2345.1

Lehner, B., Grill G. (2013). Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. Hydrological Processes, 27(15): 2171–2186. https://doi.org/10.1002/hyp.9740

Lima, M., Peres, C. A., Abrahams, M. I., da Silva Junior, C. A., de Medeiros Costa, G., & Dos Santos, R. C. (2019). The paradoxical situation of the white-lipped peccary (Tayassu pecari) in the state of Mato Grosso, Brazil. *Perspectives in Ecology and Conservation*, *17*(1), 36-39.https://doi.org/10.1016/j.pecon.2018.12.001

Morato, R. G., Connette, G. M., Stabach, J. A., De Paula, R. C., Ferraz, K. M. P. M. D., Kantek, D. L. Z., ... & Leimgruber, P. (2018a). Resource selection in an apex predator and variation in response

to local landscape characteristics. *Biological Conservation*, *228*, 233-240. https://doi.org/10.1016/j.biocon.2018.10.022

Morato, R. G., Thompson, J. J., Paviolo, A., de La Torre, J. A., Lima, F., McBride Jr, R. T., ... & Ribeiro, M. C. (2018b). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. https://doi.org/10.1002/ecy.2379

Mortelliti, A., & Boitani, L. (2008). Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. *Landscape Ecology*, *23*(3), https://doi.org/10.1007/s10980-007-9182-7

Murphy, A., Diefenbach, D. R., Ternent, M., Lovallo, M., & Miller, D. (2021). Threading the needle: How humans influence predator–prey spatiotemporal interactions in a multiple-predator system. *Journal of Animal Ecology*, *90*(10), 2377-2390. https://doi.org/10.1111/1365-2656.13548

Naimi B. 2015. usdm: Uncertainty analysis for species distribution models. R package version 1.1-15. Retrieved from https://cran.r-project.org/ package=usdm

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059. https://doi.org/10.1073/pnas.0800375105

Niebuhr, B. B. S.; Martello, F.; Ribeiro, J. W.; Vancine, M. H.; Muylaert, R. L.; Campos, V. E. W.; Santos, J. S.; Tonetti, V. R.; Ribeiro, M. C. Landscape Metrics (LSMetrics): a spatially explicit tool for calculating connectivity and other ecologically-scaled landscape metrics. *In preparation*. https://github.com/LEEClab/LS_METRICS/wiki

Patten MA, Burger JC, Mitrovich M (2019) The Intersection of Human Disturbance and Diel Activity, with Potential Consequences on Trophic Interactions. PLoS ONE 14(12): e0226418. https://doi.org/10.1371/journal.pone.0226418

Pfeifer, M., Lefebvre, V., Peres, C. A., Banks-Leite, C., Wearn, O. R., Marsh, C. J., ... & Ewers, R. M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature*, *551*(7679), 187-191. https://doi.org/10.1038/nature24457

QGIS Development Team, 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Quigley, H., Foster, R., Petracca, L., Payan, E., Salom, R. & Harmsen, B. (2017). Panthera onca (errata version published in 2018). The IUCN Red List of Threatened Species 2017: e.T15953A123791436. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T15953A50658693.en. Accessed on 24 January 2023.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ries, L., Fletcher Jr, R. J., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu. Rev. Ecol. Evol. Syst.*, *35*, 491-522. https://doi.org/10.1146/annurev.ecolsys.35.112202.130148

Signer J., Fieberg J., Avgar T. (2011). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution, 2019 9, 880-890. URL https://doi.org/10.1002/ece3.4823.

Stier, A. C., Samhouri, J. F., Novak, M., Marshall, K. N., Ward, E. J., Holt, R. D., & Levin, P. S. (2016). Ecosystem context and historical contingency in apex predator recoveries. *Science Advances*, *2*(5), e1501769.https://doi.org/10.1126/sciadv.1501769

Thompson, J. J., Morato, R. G., Niebuhr, B. B., Alegre, V. B., Oshima, J. E. F., de Barros, A. E., ... & Ribeiro, M. C. (2021). Environmental and anthropogenic factors synergistically affect space use of jaguars. *Current Biology*, *31*(15), 3457-3466.https://doi.org/10.1016/j.cub.2021.06.029

Thornton, D., Zeller, K., Rondinini, C., Boitani, L., Crooks, K., Burdett, C., ... & Quigley, H. (2016). Assessing the umbrella value of a range-wide conservation network for jaguars (Panthera onca). Ecological Applications, 26(4), 1112-1124. https://doi.org/10.1890/15-0602

Treves, A., & Karanth, K. U. (2003). Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation biology*, *17*(6), 1491-1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., ... & Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466-469.https://doi.org/10.1126/science.aam9712

Winnie Jr, J., & Creel, S. (2017). The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs*, *12*, 88-94.

Woodroffe, R., & Ginsberg, J. R. (1998). Edge effects and the extinction of populations inside protected areas. Science, 280(5372), 2126-2128. https://doi.org/10.1126/science.280.5372.21

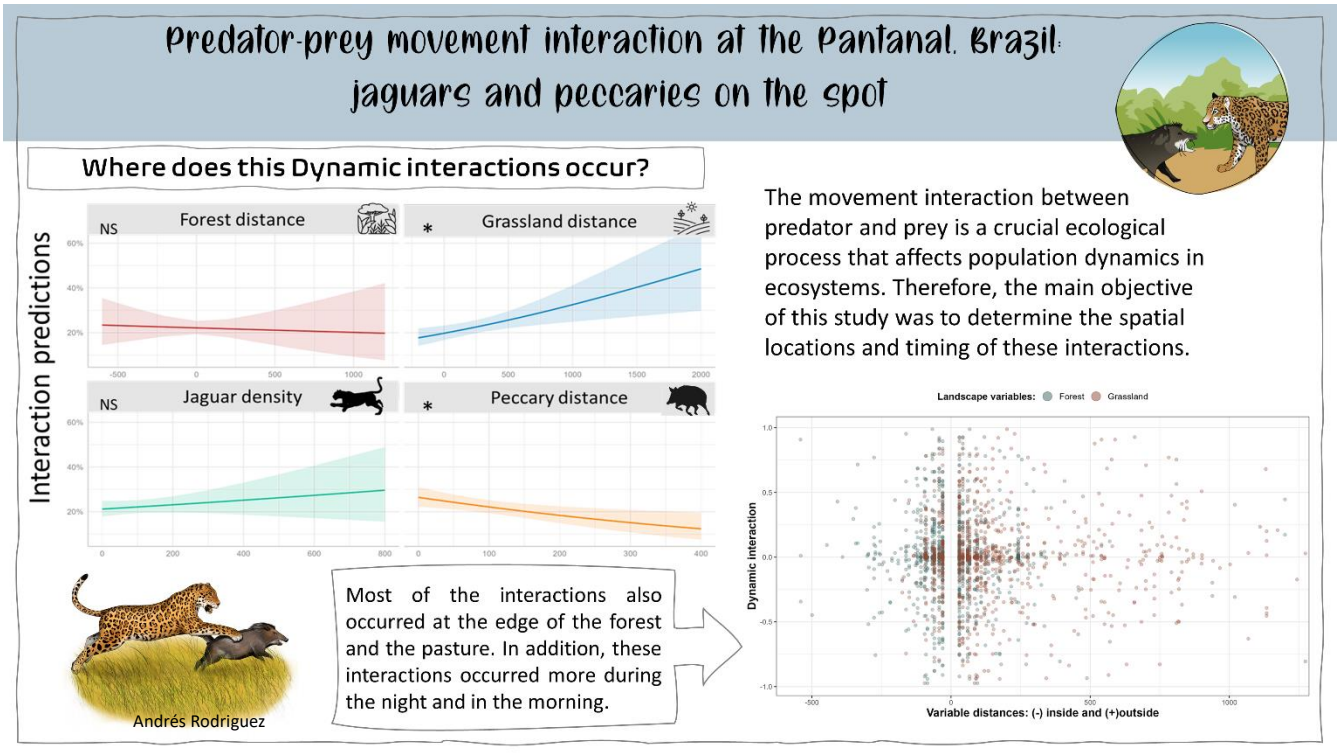
Woodroffe, R. (2000, May). Predators and people: using human densities to interpret declines of large carnivores. In *Animal conservation forum* (Vol. 3, No. 2, pp. 165-173). Cambridge University https://doi.org/10.1111/j.1469-1795.2000.tb00241.x.

Zimmermann, A., Johnson, P., de Barros, A. E., Inskip, C., Amit, R., Soto, E. C., ... & Macdonald, D. W. (2021). Every case is different: Cautionary insights about generalisations in human-wildlife conflict from a range-wide study of people and jaguars. *Biological Conservation*, *260*, 109185. https://doi.org/10.1016/j.biocon.2021.109185

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed-effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6.

Chapter # 3:

Predator-Prey movement interactions: Jaguars and peccaries on the spot



Abstract

Understanding the movement interactions between predators and prey is crucial for elucidating the ecological dynamics of ecosystems. This study investigated the movement interactions between jaguars (*Panthera onca*) and white-lipped peccaries (*Tayassu pecari*) in the Pantanal during the dry season. By analyzing the movement data of three jaguars and five peccaries, we identified and examined six recorded interactions over 44 days. Our findings revealed diverse dynamics in the movement interactions, with these encounters predominantly occurring during the morning and night. While close contacts within 700 meters were infrequent, contacts within a range of 3 to 5 kilometers were more prevalent. Moreover, our analysis highlighted that these interactions primarily occurred at the forest edge, with a greater probability of interaction occurring at greater distances from grassland areas. Additionally, lower peccary density increased the likelihood of interaction between jaguars and peccaries. This study holds significant importance in several aspects. Firstly, it contributes to our understanding of predator-prey dynamics in the Pantanal ecosystem, providing valuable insights into the spatial and temporal patterns of movement interactions between jaguars and white-lipped peccaries. Such insights are crucial for comprehending the ecological roles of these species and their impacts on population dynamics. Furthermore, this study provides valuable information for developing conservation strategies in the Pantanal. By identifying the specific areas and conditions that facilitate jaguar-peccary interactions, conservation efforts can be targeted toward preserving these crucial habitats. Understanding the factors that influence these interactions, such as habitat structure and prey density, enables us to manage better and protect the delicate balance between predators and prey in the ecosystem. Overall, this study enhances our knowledge of predator-prey interactions in the Pantanal and highlights the importance of considering movement interactions when designing effective conservation measures. The findings underscore the significance of maintaining intact habitats, preserving natural habitat edges, and ensuring the conservation of both jaguars and white-lipped peccaries to sustain the ecological integrity of the Pantanal ecosystem.

Keywords: panthera, white-lipped peccary, dynamic interactions, landscapes

Introduction

The movement interaction between predator and prey is an essential ecological process that influences population dynamics within an ecosystem (Schmitz, 2005; Creel & Christianson, 2008). The landscape structure is crucial in facilitating these interactions, providing opportunities for successful hunting for large carnivores and predator avoidance strategies for the prey (Schmitz et al., 2017; Smith et al., 2019; Suraci et al., 2022). The diverse list of prey available to these carnivores is intricately connected to the landscape's characteristics, such as vegetation cover, topography, and availability of suitable habitats (Middleton et al., 2021). By understanding how the landscape structure influences the distribution and behavior of predators and prey, we can gain insights into the spatial dynamics of their interactions and the factors that shape their population dynamics. This information is a cornerstone in the design of conservation programs (Creel & Christianson, 2008).

Large tropical carnivores, whose habitats are reduced or altered, present a varied list of prey according to their environment (Fernández-Sepúlveda & Martín, 2022; Middleton et al., 2021). As a result, they employ various interaction strategies with their prey, such as stalking, capture, and avoidance, which are influenced by the type of prey and the landscape structures that facilitate them (Gaynor et al., 2019; Smith et al., 2019). Furthermore, these interactions are influenced by various factors that are challenging to measure, such as scent, vision, and traces, which both predator and prey employ as part of their survival strategies (Gaynor et al., 2019; Smith & Ruxton, 2020). Investigating behavioral interactions poses challenges due to the hierarchical nature of predation sequences, which are challenging to document due to species-specific variations (Suraci et al., 2022). In studies of predator-prey interactions in large vertebrates in tropical regions, researchers primarily rely on patterns of temporal activity recorded by cameras and, in some cases, the spatial overlap of their home ranges (Caravaggi et al., 2018; Foster et al., 2013; Schmitz et al., 2017; Suraci et al., 2022). However, obtaining movement data exhibiting spatial and temporal overlap is a major challenge.

In the Pantanal, being an eco-region with abundant biodiversity and richness of vertebrates, there are many diverse and parallel studies on the movement of carnivores such as the Jaguar and

ungulates such as the white-lipped peccary from interaction information can be extracted (Morato et al., 2018; Oshima, 2019). The jaguar is a carnivore with various items in their diet based on the opportunities of their environment (e.g., marine turtles in Costa Rica; Carillo et al., 2009; Middleton et al., 2021); therefore, it is one of the Neotropical cats with the greatest problem of conflicts with humans that domestic animals can be found in their diet (Castaño-Uribe et al., 2016). Within the Pantanal, this conflict is continuous due to being an ecoregion that has many cattle ranches (Zimmermann et al., 2005). In the Pantanal, the jaguars present three of its most frequent prey items: cattle, caiman, and peccary (Cavalacanti et al., 2010; Perilli et al., 2016). The white-lipped peccary, a frugivorous ungulate, inhabits a wide range, with a southern range limit in Argentina, a large core population in Amazonia, and a northern range extent in Central America and southern Mexico (Altrichter et al., 2011). During the wet season, the peccary forms large herds of approximately 100-200 individuals, taking advantage of the abundance of fruits and aiding in caring for their offspring (Fragoso, 1998). However, these groups fragment into smaller herds for food during the dry season (30-40 individuals, Fragoso, 1998; Keuroghlian et al., 2004). The white-lipped peccary is listed as a threatened species by the IUCN due to habitat loss and hunting due to conflicts with agriculture and food sources (Keuroghlian et al., 2013). Weighing between 30- 40kg., they are considered one of the jaguar's bigger natural prey.

Interactions between jaguars and white-lipped peccaries in the Pantanal involve predation by the jaguar and mobbing and attacks on individual jaguars by peccary herds (Rampim et al., 2020). However, there needs to be more relevant data on where and when these interactions occur. Therefore, the main objective of this study was to determine the spatial locations and timing of these interactions. In this case, by "predator-prey interaction," we refer to the dynamic interactions and the number of contacts. Dynamic interactions are reflected in the direction and speed of both species' movements within the same spatial area and during the same period. Contacts refer to the distance between the two species found within the same spatial site and during the same period. As the first study in this context, our questions are exploratory: What are the patterns of movement interaction between jaguars and peccaries, and when do they occur? How are their contacts determined, and during which periods do they occur? Finally, we are interested in the spatial context of the interaction dynamics between predator and prey. This

study fulfilled the objective of shedding light on the dynamics of jaguar-peccary interactions in the Pantanal and providing insights for conservation strategies to preserve this delicate balance.

Methods

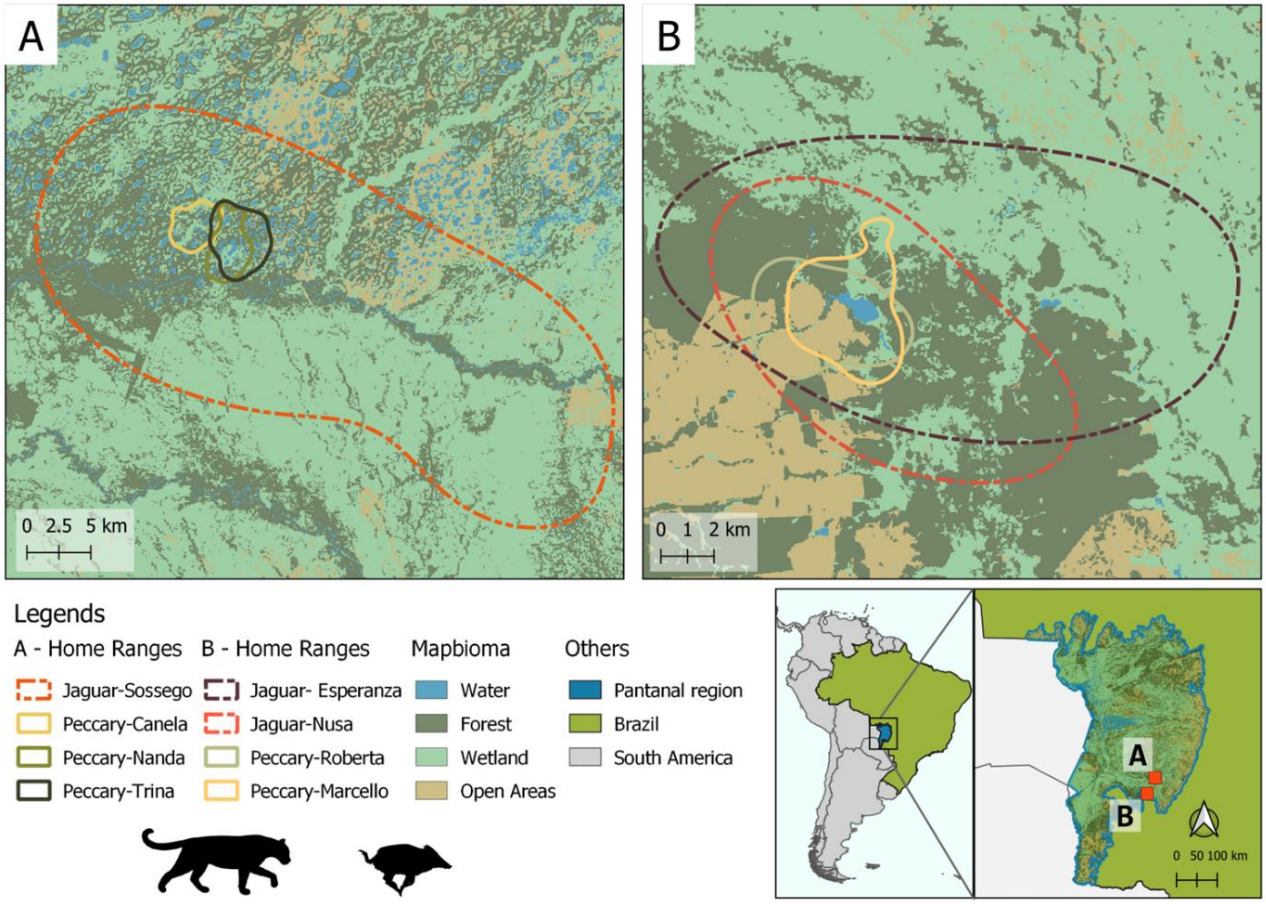


Figure 1: Study area where the interactions took place. Region A, Fazenda Barranco Alto, cattle ranch with the interaction of 1 jaguar and three peccaries. Region B Caiman Ecological Refuge ecotourism farm with two jaguars and two peccaries. Both regions part of the Brazilian Pantanal

Movement data and environmental bases

We obtained movement data for three jaguars within the Pantanal from the GPS jaguar database (Morato et al., 2018), specifically from Refugio Ecologico Caiman and Fazenda Barranco Alto. We utilized the dataset from project Oshima, 2019, for peccary data, selecting five peccaries from

the same data area. The dataset covered the period from August 17th, 2015, to September 30th, 2015, and included 525 locations focused on interactions (Table 1; Figure 1).

Table 1: Predator-prey interactions, with date information in which temporal and spatial overlap existed.

Region	Interactions	Date	# Locations	# Interactions
A	Sossego-Canela	22/Ago/2015 to 25/Sept/2015	89	21 (23.6%)
A	Sossego-Nanda	22/Ago/2015 to 25/Sept/2015	103	21 (20.4%)
A	Sossego-Trina	22/Ago/2015 to 25/Sept/2015	103	15 (14.6%)
B	Esperanza-Marcello	17/Ago/2015 to 30/Sept/2015	108	52 (48.1%)
B	Nusa-Marcello	17/Ago/2015 to 25/Sept/2015	65	15 (23.1%)
B	Nusa-Roberta	18/Ago/2015 to 25/Sept/2015	57	20 (35.1%)

Environmental variables for the study were obtained from the Mapbioma platform for the year 2015. Distance metrics were computed using the LsMetric program (Niebuhr et al., 2020). Negative values indicated distances within the variables, while positive values indicated distances outside. To estimate density, we performed a kernel density analysis using QGIS 3.10.7-A Coruña (QGIS Development Team, 2020) on the complete datasets of all individuals in the available database (Table A Supplementary material).

Interaction análisis

To investigate the interaction between jaguars and peccaries, we considered two contexts. Firstly, we used the global index of interaction dynamics proposed by Long and Nelson (2013) to determine individual interaction dynamics. The index classified attraction when the direction and speed were positive and above a threshold of 0.4, while avoidance was identified when the direction and speed were negative (less than -0.4). Random movement, exhibited by both species, was considered when the direction and speed were not synchronized (values between 0.4 and -0.4).

Secondly, we examined the contact between the species, which can influence their distance during specific periods. We used the recorded approximate travel distances of jaguars within 1 hour (500 m), 2 hours (700 m), 6 hours (1500 m), and 12 hours (3000 m) as reference values (Alegre et al., 2023). These analyses were conducted using the WildlifeDI package (Long et al., 2022) within the R program (R Core Team, 2022).

Landscape structures model and diagnostics

For our analysis, we categorized the attraction and avoidance data as positive interaction observations, assigning them a value of 1. Random data was assigned a value of 0. We then performed generalized linear mixed models using interactions as random variables. To carry out these models, we utilized the glmmTMB package in R (Brooks et al., 2017), which is well-suited for handling generalized mixed models with various extensions, including zero inflation. To assess the performance and validity of the models, we conducted diagnostic tests, including the KS, Dispersion, and Outlier tests, using the DHARMa package in R (Hartig, 2022). These tests provided essential insights into the accuracy and reliability of our models.

Results

In our study area, we investigated movement interactions between three jaguars (Esperança, Nusa, and Sossego) and five peccaries (Marcello, Roberta, Canela, Nanda, and Trina) with different home ranges (Figure 1). Over 44 days, we observed six interactions between these individuals (Table 1), in which attractions and avoidances were recorded. The study was conducted during the dry season in the Pantanal.

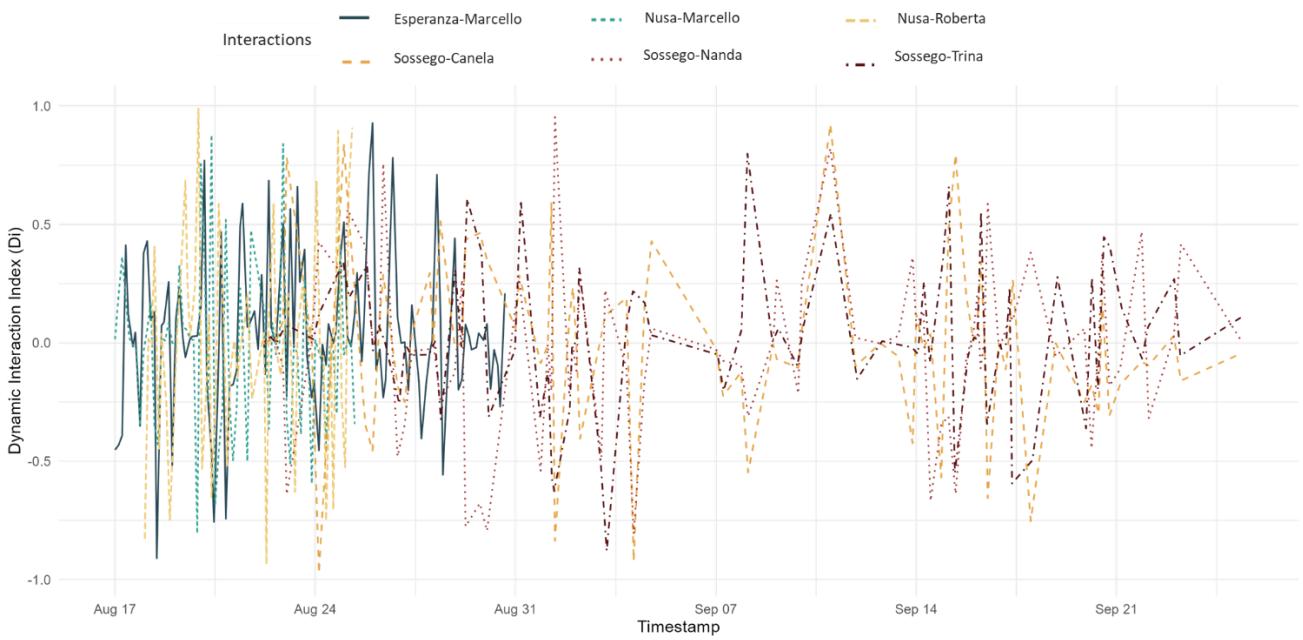


Figure 2: Dynamics of interaction between predator and prey at the time of the study.

Movement interactions

The observed movement interactions were diverse. 144 dynamic interactions were recorded between August 17th, 2015, and September 30th, 2015 (Figure 2 and Table 1). In study area A, Sossego, and Canela accounted for 23.6% of the interactions, most occurring during morning and night. In study area B, Nusa and Roberta had a higher interaction rate of 48.2%. Contacts within a distance of less than 700 meters were not frequent and were not observed in most individuals, totaling only 28 contacts (Figure 3). Specifically, Sossego and Nanda had five contacts, Nusa and Roberta had two contacts, and Nusa and Marcello had seven contacts within this distance range. These close contacts were predominantly observed during the night and early morning. The largest contacts were observed between distances of 3,000 to 5,000 meters.

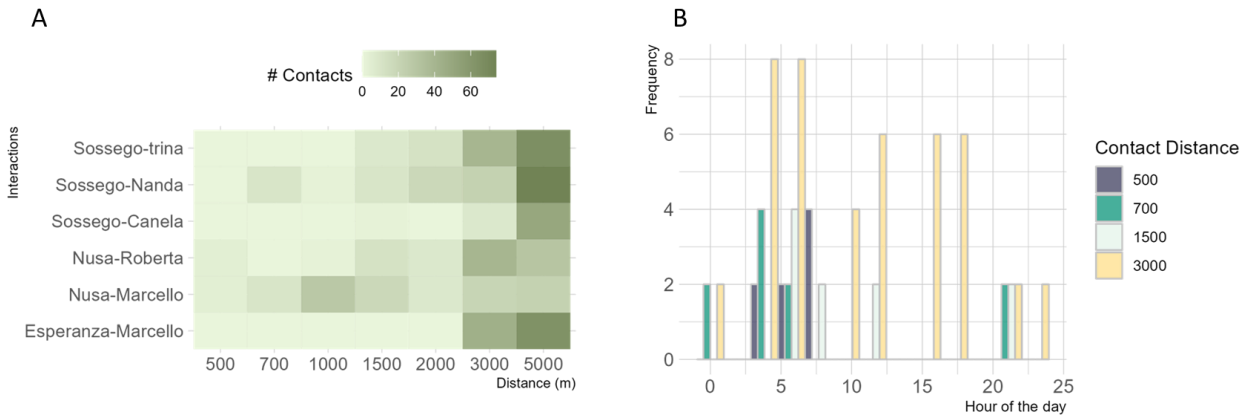


Figure 3: A) Number of contacts by interactions in the different distances and B) time of day in which the contact is made.

How the interaction arises in the landscape

Additionally, our analysis of the interaction model revealed the significance of two variables: the distance from grassland areas and the density of peccaries (Table 2). The results indicate that a greater distance from grassland areas increases the probability of interaction, while lower peccary density also increases the probability of interaction (Figure 4). The forest distance variable did not show significant importance in our model. Although jaguar density was not statistically significant, a trend suggested that higher densities correlate with increased interaction. We also observed that these interactions primarily occurred at the edges of forests and grasslands (Figure 5). Our interaction model passed all diagnostic tests (Figure A Supplementary material). By providing a more comprehensive understanding of the movement interactions and the factors influencing them, our study contributes to the knowledge of jaguar and peccary dynamics in the Pantanal during the dry season.

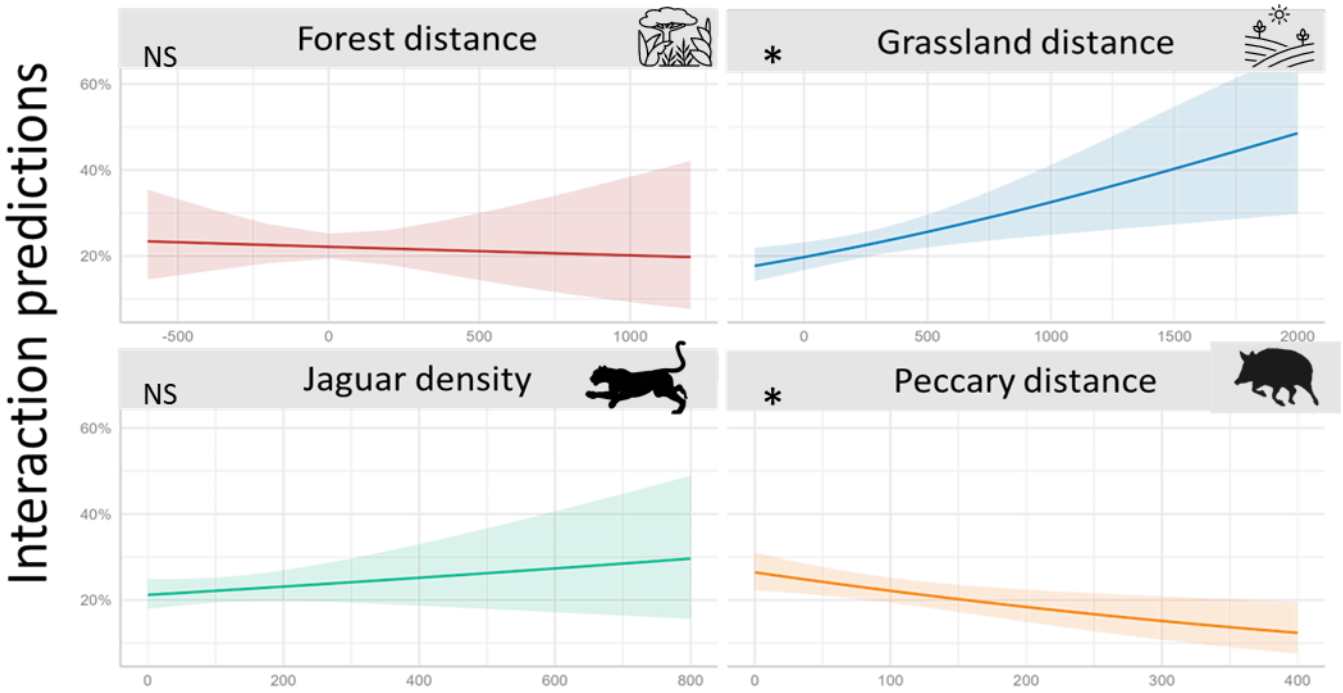


Figure 4: Prediction of the predator-prey interaction in the four variables explored. Forest distance and jaguar density were non-significant variables within the model.

Discussion

This study is the first to explore the movement interactions between a Neotropical predator and one of its prey species. Our data demonstrated attraction and avoidance behaviors between both species. These interactions varied among individuals and were mainly observed in the morning and night. Although close proximity contacts were minimal, they were prevalent within Jaguar's daily movement distances. These interactions primarily took place at the forest edge and far from grassland and were more commonly observed in regions with lower peccary density. This information is crucial for identifying essential areas to balance these interactions.

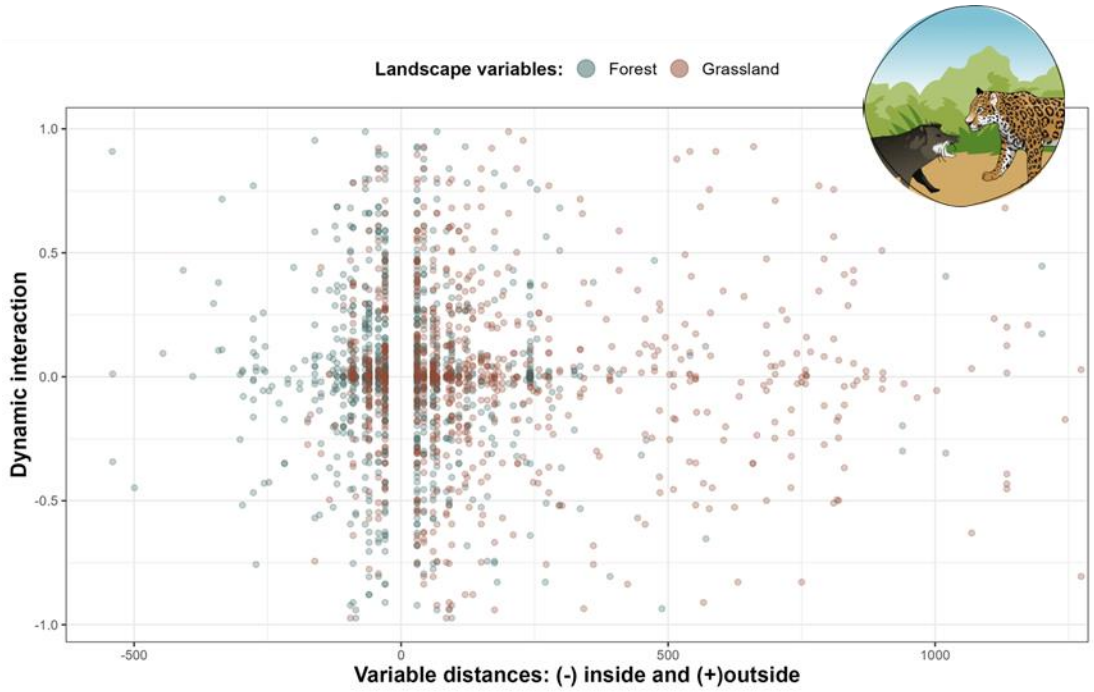


Figure 5: Distance of the studied landscape structures and the interaction dynamics obtained between predators and prey

Our results showed diverse but infrequent interactions, indicating that while the peccary is one of the main prey species in the jaguar's Pantanal diet, it is not the exclusive prey. In the Pantanal, the Jaguar has a varied prey selection depending on availability, including peccaries, caimans, capybaras, and even domestic animals like cattle (Cavalacanti et al., 2010; Perilli et al., 2016). Our data were predominantly collected during the dry season. During this period, peccaries form small (Fragoso, 1998; Keuroghlian et al., 2004), accessible groups for Jaguar hunting, as records show that white-lipped peccaries display aggressive behavior toward jaguars (Rampim et al., 2020).

Close contacts within 700 meters between these species are uncommon, possibly due to the jaguar's avoidance of large peccary herds. However, our data revealed contacts within 3 to 5 km, and previous studies have highlighted the Jaguar's heightened perception within a 5 km range (Alegre et al., 2023). Interactions between both species were primarily observed during the night

and morning, likely due to the Pantanal's afternoon heat peaks, which lead to different refuge areas for each species (Peterson et al., 2021).

Predator-prey interactions predominantly occur at forest edges and grasslands, with a higher likelihood in areas farther from the grasslands. White-lipped peccaries prefer open areas for movement and foraging (Oshima, 2019). These animals often face conflicts in agricultural regions, resulting in a significant population reduction due to hunting and poisoning (Lima et al., 2019). Our data demonstrated that white-lipped peccary and jaguar density can influence these interactions. While peccaries can display aggressive behavior and attack other predators, they become easy prey for Jaguars when solitary or in small reduced groups (Rampim et al., 2020).

The predator-prey interaction is a fundamental process for populations, and in tropical regions, many predators have multiple prey options, allowing them to control prey populations naturally. Our study highlighted the vital role of natural habitat edges in facilitating these interactions. While natural grassland areas are relevant for peccary populations, the habitat's natural heterogeneity is equally essential since these species can shift their ecological niche depending on the season and temperature. Our findings emphasized that Jaguars act as natural population regulators for peccaries without causing their extinction, making them one of the most important species for population control of many species in the Pantanal.

References

Alegre, V. B., Rio-Maior, H., de Faria Oshima, J. E., Niebuhr, B. B., Morato, R. G., & Ribeiro, M. C. (2023). The effect of anthropogenic features on the habitat selection of a large carnivore is conditional on sex and circadian period, suggesting a landscape of coexistence. Journal for Nature Conservation, 73, 126412. https://doi.org/10.1016/j.jnc.2023.126412

Altrichter, M., Taber, A., Beck, H., Reyna-Hurtado, R., Lizarraga, L., Keuroghlian, A., & Sanderson, E. W. (2012). Range-wide declines of a key Neotropical ecosystem architect, the Near Threatened white-lipped peccary Tayassu pecari. Oryx, 46(1), 87-98. https://doi.org/10.1017/S0030605311000421

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal, 9(2), 378-400. https://doi.org/10.32614/RJ-2017-066

Castaño-Uribe, C., Hoogesteijn, A., López, C. A., Núñez, R., Rosas-Rosas, O., Febles, J. L., ... & Cepeda-Beltrán, M. A. (2016). II. Conflictos entre felinos y humanos en América Latina. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Carrillo, E., Fuller, T. K., & Saenz, J. C. (2009). Jaguar (Panthera onca) hunting activity: effects of prey distribution and availability. Journal of tropical ecology, 25(5), 563-567. https://doi.org/10.1017/S0266467409990137

Cavalcanti, S. M., & Gese, E. M. (2010). Kill rates and predation patterns of jaguars (Panthera onca) in the southern Pantanal, Brazil. Journal of Mammalogy, 91(3), 722-736. https://doi.org/10.1644/09-MAMM-A-171.1

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in ecology & evolution*, *23*(4), 194-201. https://doi.org/10.1016/j.tree.2007.12.004

Fernández-Sepúlveda, J., & Martín, C. A. (2022). Conservation status of the world's carnivorous mammals (order Carnivora). Mammalian Biology, 102(5-6), 1911-1925. https://doi.org/10.1007/s42991-022-00305-8

Foster, V. C., Sarmento, P., Sollmann, R., Tôrres, N., Jácomo, A. T., Negrões, N., ... & Silveira, L. (2013). Jaguar and puma activity patterns and predator-prey interactions in four Brazilian biomes. Biotropica, 45(3), 373-379. https://doi.org/10.1111/btp.12021

Fragoso, J. M. (1998). Home Range and Movement Patterns of White-lipped Peccary (Tayassu pecari) Herds in the Northern Brazilian Amazon 1. Biotropica, 30(3), 458-469. https://doi.org/10.1111/j.1744-7429.1998.tb00080.x

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E., & Brashares, J. S. (2019). Landscapes of fear: spatial patterns of risk perception and response. Trends in ecology & evolution, 34(4), 355-368. https://doi.org/10.1016/j.tree.2019.01.004

Hartig F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Keuroghlian, A., Eaton, D. P., & Longland, W. S. (2004). Area use by white-lipped and collared peccaries (Tayassu pecari and Tayassu tajacu) in a tropical forest fragment. Biological Conservation, 120(3), 411-425. https://doi.org/10.1016/j.biocon.2004.03.016

Keuroghlian, A., Desbiez, A., Reyna-Hurtado, R., Altrichter, M., Beck, H., Taber, A. & Fragoso, J.M.V. 2013. Tayassu pecari. The IUCN Red List of Threatened Species 2013: e.T41778A44051115. https://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T41778A44051115.en. Accessed on 01 July 2023.

Lima, M., Peres, C. A., Abrahams, M. I., da Silva Junior, C. A., de Medeiros Costa, G., & Dos Santos, R. C. (2019). The paradoxical situation of the white-lipped peccary (Tayassu pecari) in the stateof Mato Grosso, Brazil. Perspectives in Ecology and Conservation, 17(1), 36-39.https://doi.org/10.1016/j.pecon.2018.12.001

Long, J.A., Nelson, T.A. (2013) Measuring dynamic interaction in movement data. Transactions in GIS. 17(1): 62-77. https://doi.org/10.1111/j.1467-9671.2012.01353.x

Long J, Webb S, Harju S, Gee K (2022). "Analyzing Contacts and Behavior from High Frequency Tracking Data Using the wildlifeDI R Package." Geographical Analysis, 54, 648–663. https://doi.org/10.1111/gean.12303

MapBiomas Project - Collection 2015 of the Annual Land Use Land Cover Maps of Brazil, accessed on January 2015

Middleton, O., Svensson, H., Scharlemann, J. P., Faurby, S., & Sandom, C. (2021). CarniDIET 1.0: A database of terrestrial carnivorous mammal diets. Global Ecology and Biogeography, 30(6), 1175-1182. https://doi.org/10.1111/geb.13296

Morato, R. G., Thompson, J. J., Paviolo, A., de La Torre, J. A., Lima, F., McBride Jr, R. T., ... & Ribeiro, M. C. (2018). Jaguar movement database: a GPS-based movement dataset of an apex predator in the Neotropics. https://doi.org/10.1002/ecy.2379

Niebuhr, B. B., Martello, F., Ribeiro, J. W., Vancine, M. H., Muylaert, R. L., Campos, V. E. W., ... Ribeiro, M. C. (2020). Landscape Metrics (LSMetrics): A tool for calculating landscape connectivity and other ecologically scaled landscape metrics (Version v0.91). Zenodo. http://doi.org/10.5281/zenodo.3736444

Oshima, J. E. D. F. (2019). Movement ecology and spatial distribution of Tayassu pecari in heterogeneous tropical landscapes. PhD. Thesis. Repositorio.unesp.br

Peterson, M., Jorge, M. L. S., Jain, A., Keuroghlian, A., Oshima, J. E. F., Richard-Hansen, C., ... & Eaton, D. (2021). Temperature induces activity reduction in a Neotropical ungulate. Journal of Mammalogy, 102(6), 1514-1524. https://doi.org/10.1093/jmammal/gyab092

Perilli, M. L., Lima, F., Rodrigues, F. H., & Cavalcanti, S. M. (2016). Can scat analysis describe the feeding habits of big cats? A case study with jaguars (Panthera onca) in Southern Pantanal, Brazil. Plos one, 11(3), e0151814. https://doi.org/10.1371/journal.pone.0151814

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Rampim, L. E., Sartorello, L. R., Fragoso, C. E., Haberfeld, M., & Devlin, A. L. (2020). Antagonistic interactions between predator and prey: mobbing of jaguars (Panthera onca) by white-lipped peccaries (Tayassu pecari). acta ethologica, 23(1), 45-48. https://doi.org/10.1007/s10211-020-00335-w

Schmitz, O. J. (2005). Prey and Links with Population-Level Processes. By: Barbosa, P., & Castellanos, I. (Eds.). Book: *Ecology of predator-prey interactions*. Oxford University Press.

Schmitz, O. J., Miller, J. R., Trainor, A. M., & Abrahms, B. (2017). Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. Ecology, 98(9), 2281-2292. https://doi/10.1002/ecy.1916

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., & Middleton, A. D. (2019). Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. Oecologia, 189, 883-890. https://doi.org/10.1007/s00442-019-04381-5

Smith, P. M. Q., & Ruxton, G. D. (2020). Camouflage in predators. *Biological Reviews*, *95*(5), 1325-1340. https://doi.org/10.1111/brv.12612

Suraci, J. P., Smith, J. A., Chamaillé-Jammes, S., Gaynor, K. M., Jones, M., Luttbeg, B., ... & Sih, A. (2022). Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. Oikos, 2022(8), e09004. https://doi.org/0.1111/oik.09004

Zimmermann, A., Walpole, M. J., & Leader-Williams, N. (2005). Cattle ranchers' attitudes to conflicts with jaguar Panthera onca in the Pantanal of Brazil. Oryx, 39(4), 406-412. https://doi.org/10.1017/S0030605305000992

Chapter # 4:

Brazilian cat habitat selection: Trends and gaps

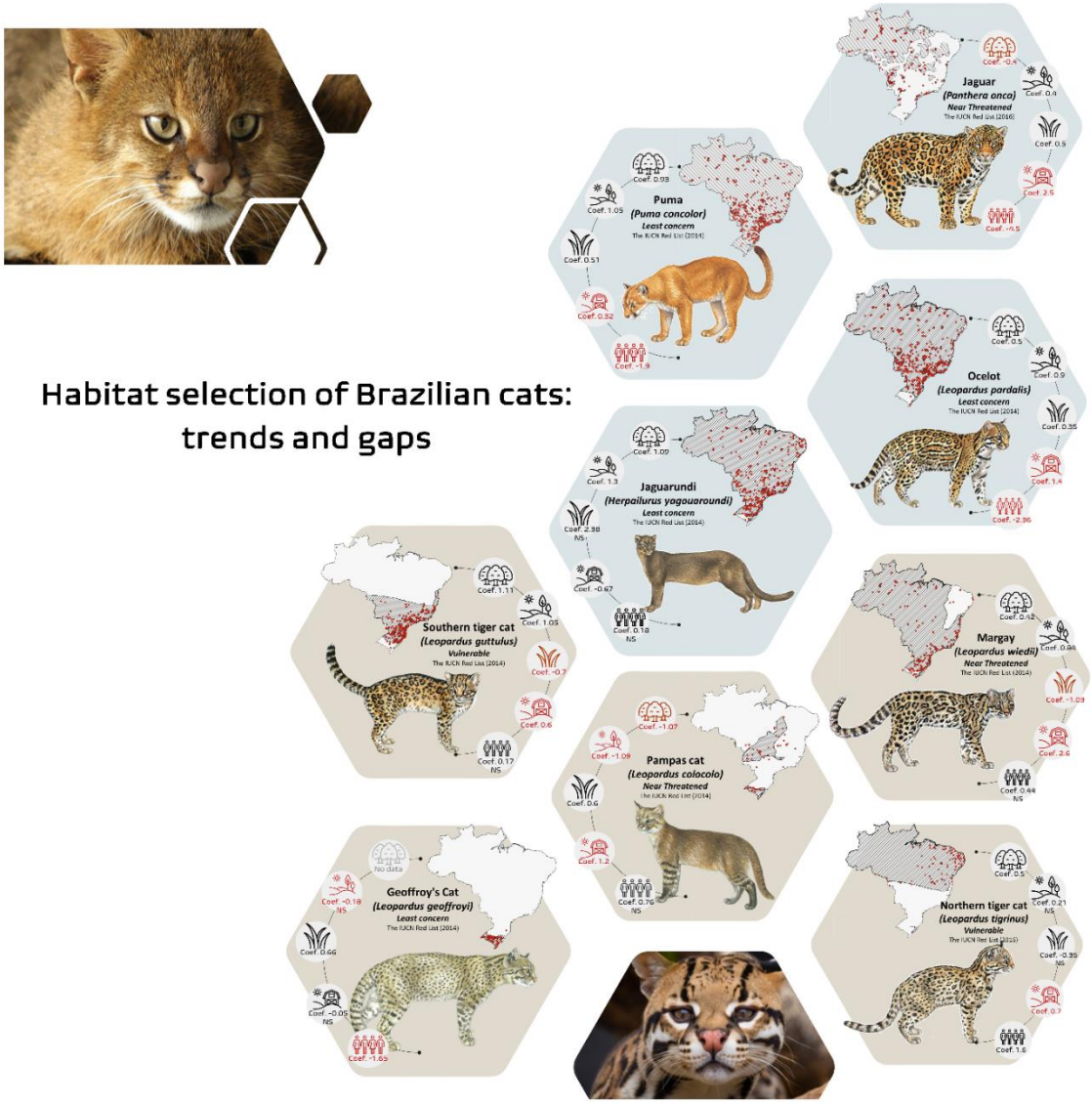


Illustration from Hunter, L. (2015) Wildcats of the world. Bloomsburry Publishing

Abstract

Eight of the nine cats in Brazil are in some category of threatened species within the region. Its main threat is the loss of habitat due to the advance of human activities. However, there is still little knowledge about how these species respond to agricultural advancement and human overpopulation. To this end, we set out to model the habitat selection of the nine cats recorded in Brazil, considering natural structures such as grasslands, forest edge and core, and anthropic structures such as distance from agricultural areas and human density. Our central hypothesis is that these species of carnivores will be limited only to natural areas and that they will not use anthropized sites. Our results show that all species selected at least one proposed natural variable; however, the jaguar was unfavorable to the use of the forest core, which we did not expect for a big cat. The ocelot, puma, and jaguar were the only species not used high human density areas or near agriculture. Small cats selected at least one anthropic structure. The jaguarundi and Geoffroy's cat were favorable to the proximity of the agricultural regions. On the other hand, the jaguarundi, pampas cat, margay, southern and northern tiger cat used areas of high human density. These results reveal the life history of some little-studied species and new findings of habitat selection in well-studied species such as the jaguar. The different selection coefficients can help characterize the use of these species in regions where these environmental structures predominate.

Keywords: *Panthera onca, Puma concolor, Leopardus, Jaguarundi, forest edge, forest core, agriculture, human density.*

Introduction

As human populations and agricultural expansion increase, landscape transformation continues forcing carnivore populations to confine themselves to small natural areas or adapt and persist in natural and human-altered mosaic habitats (Azevedo et al., 2021; Medan et al. 2011). Cat species, which require extensive habitat due to their low population density and territoriality (Oliveira et al.,2010), hence are more sensitive to changes and alterations in their habitat. However, many species benefit from the matrix, and others are more sensitive to minor disturbances (Días et al., 2019). Therefore, understanding how cats select habitat structures is fundamental for structuring their conservation and managing such populations. In addition, this information can be helpful to identify aspects within the habitat that will help the persistence of the species (Manly et al., 2007; Morato et al., 2018).

In Brazil, there are nine species of cats. Eight of them are on the list of threatened species at the national level (as Vulnerable: the jaguar - *Panthera onca*, the puma - *Puma concolor*, the jaguarundi - *Herpailurus yagouaroundi*, the margay - *Leopardus wiedii*, the Geoffroy's cat - *Leopardus geoffroyi*, the Pampas cat - *Leopardus colocola* and Southern Tiger Cat - *Leopardus guttulus*; and Northern Tiger Cat - *Leopardus tigrinus,* as Endangered), the only species not included was the ocelot (*Leopardus pardalis*; ICMBio/MMA, 2018). Due to the trophic niche and interspecific competition, these cats are recorded in different habitats (Oliveira et al., 2010). Large cats tend to use natural areas and avoid human presence and activities (Azevedo et al., 2021; Morato et al., 2018). Likewise, the ocelot, margay, and northern tiger cat are specific to forest habitats and galleries (Oliveira et al., 2010). On the other hand, species such as jaguarundi, the southern tiger cat, have been reported in a wide variety of natural and anthropic environments, not venturing deep into the matrix (Días et al., 2019; Oliveira et al., 2016). Cats from open habitats, such as Geoffroy's cat and the Pampas cat, were also recorded in intervened habitats (Castro-Pastene et al., 2021; Oliveira 1994). However, many of these records were in specific locations (excepted Morato et al., 2018), with few studies focusing on the aspect of habitat selection.

Habitat selections acquire a vital influence for an organism because habitat-related factors highly condition individual fitness. Some of these factors are the availability of food resources (Manly et al., 2007; Ditmer et al., 2021), habitat suitability (Rabinowitz and Zeller 2010), intra- and interspecific dynamic interactions (Bitetti et al., 2010), and species-specific life-history traits (Allen et al., 2014). For this reason, knowledge of the selection made by the species in landscape structures helps to understand its ecology and develop better conservation strategies at the national level (Manly et al., 2007).

Therefore, our main objective is to elaborate a habitat selection model for the nine species in Brazil. We considered natural structures such as forest, forest edge, grassland, and anthropic structures such as human density and distance from agricultural areas. Our central hypothesis is that larger and medium cats (jaguar, puma, and ocelot) will select natural structures from the environment, avoiding anthropic ones. Minor cat species will select at least one natural structure, and there will be different responses to anthropic structures.

Methods

The location data used in this study results from records by numerous scientists distributed in the Neotropical region (Nagy-Reis et al. 2020). We select the data that we found within Brazil and that are data taken from the year 1999. We worked with a total of 12409-point locations of the nine felines dispersed mainly in their distribution areas within Brazil (Figure 1 left margin of each column). All these locations were recorded by different methods, which varied between species. (Figure 1 right margin of each column); however, the camera trap method was the most prevalent. We used a total of five environmental variables with a resolution of 30 x 30 meters; the natural variables of forests, grasslands, and agriculture we extracted from a land-use map built by Mapbiomas (Souza et al., 2020). We differentiated the forest edge variable with a 200 m distance from the forest core. The variable distance to agricultural areas represents the Euclidean distance from each cell to the edge of the matrix of the closest agricultural areas. We extracted the human density variable from the Brazilian Institute of Geography and Statistics (IBGE 2012). All continuous variables were scaled.

We applied a resource selection function to determine the 'used' resources to test which resources are used or avoided by cats (Fieberg et al., 2018). The random points selected the 'available' resources in a 5 km buffer by points of location. We checked for multicollinearity across the variables, first with Pearson's correlation index (Dormann et al., 2013), excluding highly correlated variables ($|r| > 0.7$). Also, we used Variance Inflation Factor (VIF) retaining variables with VIF < 3 (Zuur et al., 2009). Finally, we incorporated by cats a generalized linear model with multiple variables.

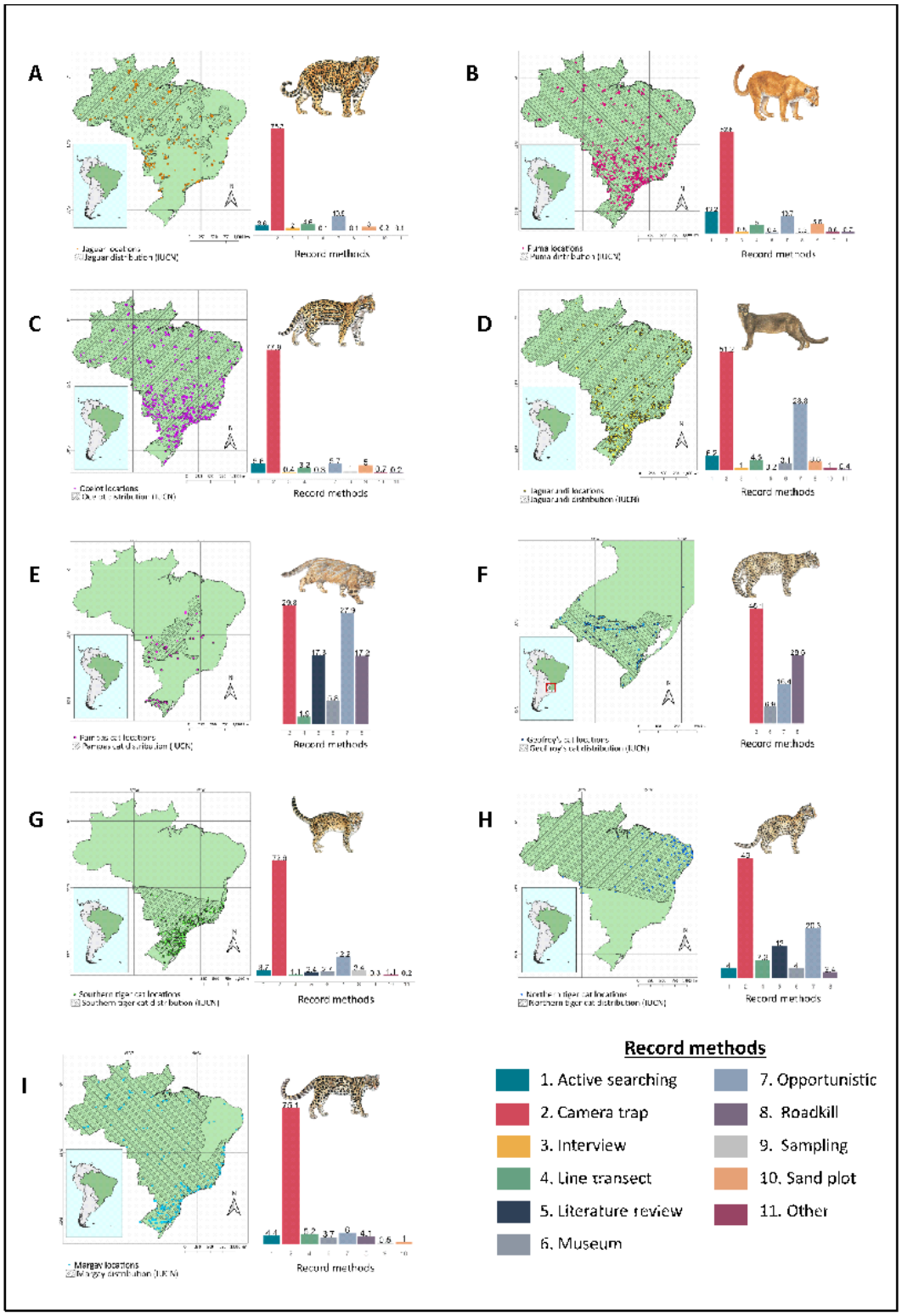


Figure 1. Distribution of the location points for each species (left margin of each column), accompanied by the proportion of data recording methods (right margin of each column). A) jaguar, B) puma, C) ocelot, D) jaguarundi, E) pampas cat, F) Geoffroy's cat, G) south tiger cat, H) north tiger cat, and I) margay.

Results

Our data showed that the jaguar selects grasslands, forest edges but avoids the forest core. The puma, ocelot, and jaguarundi established grassland, the core and edge of the forest (Figure 2). The northern and southern tiger cat, the margay, chose the edge and core of the forest areas; however, they avoided grasslands. Geoffroy's cat selected the grassland; however, we discarded in their model the forest because it was not chosen at all and was scarce within the landscape of this species. The pampas cat avoided the forest core and edge and selected the grasslands (Figure 3).

The jaguar, puma, ocelot, and Geoffroy's cat not selected anthropic variables. On the other hand, the jaguarundi chooses areas close to agriculture and not significantly low human density. The margay, the pampas cat, the north and south tiger cat selected areas away from agriculture but inhabit areas with high human density, being the northern tiger cat with significant results (Figures 2 and 3).

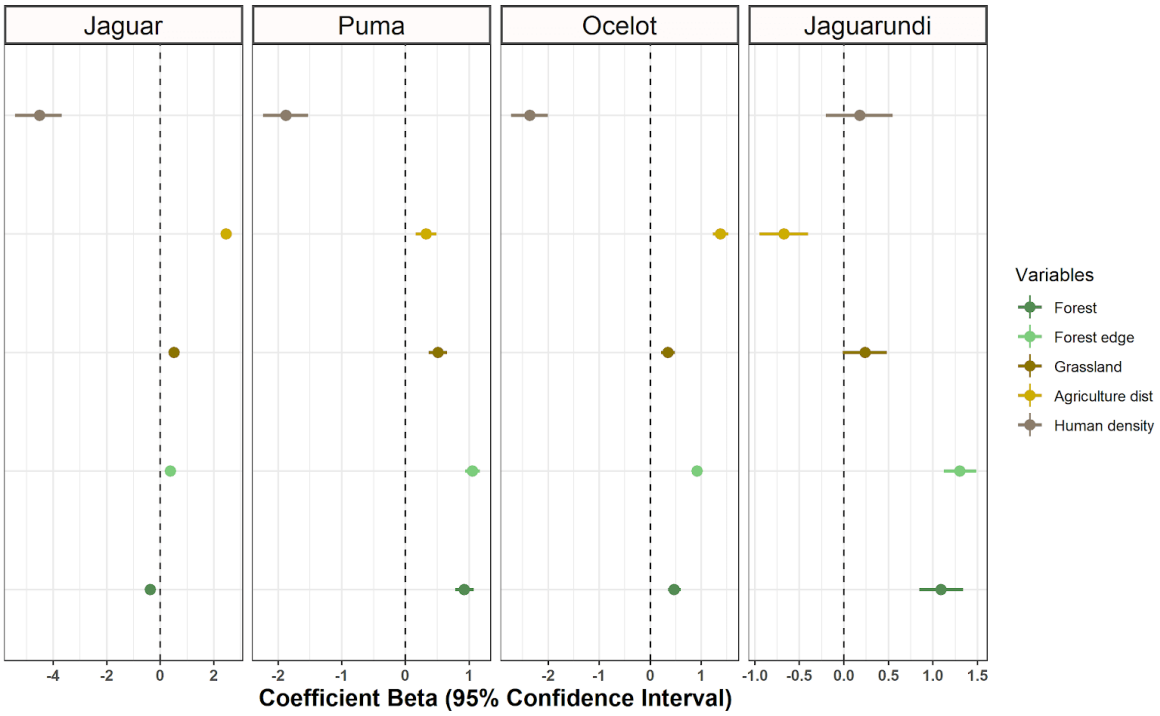


Figure 2. The selection response of the jaguar, puma, ocelot, and jaguarundi of the variables: forest core, forest edge, grasslands, agricultural distance, and human density.

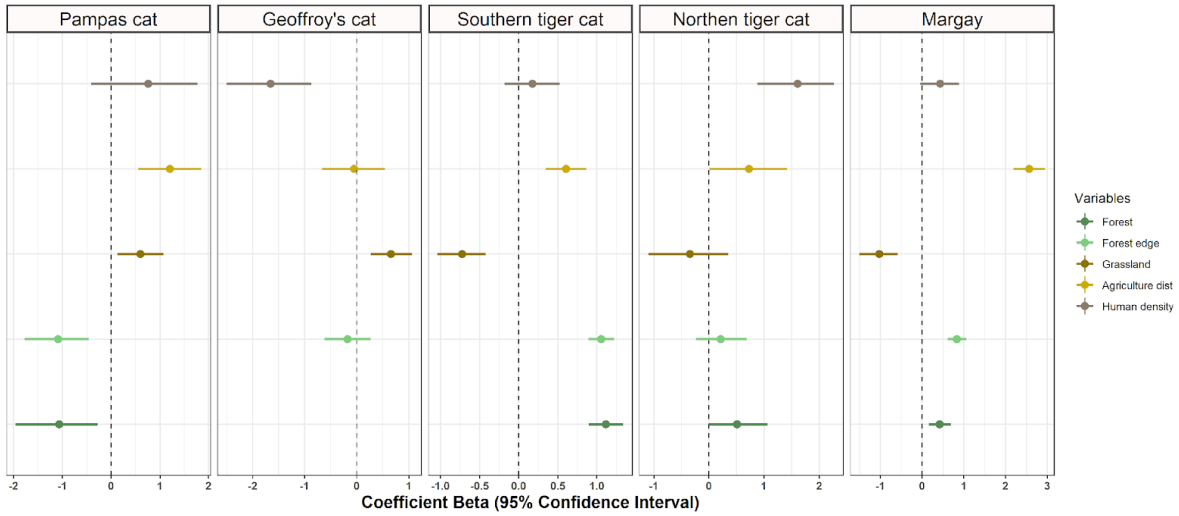


Figure 3. The selection response of the pampas cat, Geoffroy's cat, southern tiger cat, northern tiger cat, and margay of the variables: forest core, forest edge, grasslands, agricultural distance, and human density.

Discussion

This study demonstrated the different responses of cats to environmental structures such as forest core and edge, grasslands, human density, and agriculture. It is the first habitat selection study for many of the small cat species. The older and medium cats such as the Jaguar, Puma, and Ocelot selected natural structures. Small cats such as jaguarundi, pampas cat, margay, southern and northern tiger cat favorably set areas with human density, the latter being a species with a significant response. The jaguarundi also positively selected sites close to agriculture. Our findings concern the study of the life history of these species, the answers to their environmental environment, and the structures of conservation plans.

The jaguar, puma, and ocelot use natural environments favorably, avoiding the proximity of agricultural areas and high human density, a response recorded in other studies for these species (Azevedo et al., 2021; Cruz et al., 2018; Morato et al., 2018). However, the jaguar did not select the forest core and only used the edge of the forest. No study regarding the different scales of jaguar use within the forest; however, this selection may be due to the dynamics of interaction

between the predator-prey. Prey, such as deer, usually uses the forest edge as an antipredatory behavior (Ditmer et al., 2021), forcing the puma to use areas near the urban perimeter or anthropic areas for hunting their prey.

The jaguarundi uses all the natural structures and the proximity to agricultural areas with a tendency to greater human density. Descriptive studies for this species described refuge in trees with human presence (Oliveira 1994) and the jaguarundi using agricultural areas in proportion to their availability (Oliveira et al. 2008; Oliveira et al. 2010). Therefore, this species was considered a generalist capable of adapting to different types of vegetation and impacts in the Atlantic forest (Días et al., 2019). Geoffroy's cat has effective use of grassland also showed a tendency to use nearby agricultural areas; however, our data is not significant. On the other side, the male's home range of this species selected agricultural regions (Manfredi et al., 2012). Although there are no studies on the conclusive response to human density, our study indicates that this species avoids using regions with high human density.

The margay, the northern and southern tiger cat, only used forest edge and core structure and avoided grasslands, as these species are wooded habitats (Oliveira 1994). However, studies indicate that these species can move distance up to 30 km outside the forest (Cruz et al., 2018). Also, these species use other types of anthropic environments since they were not affected by human density. In the same way, the pampas cat tends to use areas with high human density, avoiding the proximity of agricultural regions; recent records indicate that this species uses both natural and intervened habitats (Castro-Pastene et al., 2021).

This study demonstrated the responses of the environmental structures of cats in the Brazilian region. We provide selection coefficients that can help determine critical areas for the conservation of these species. Finally, we facilitate the understanding within Brazil of the life history of these species on a broader scale within their distribution. On the other hand, it is essential to emphasize that we must focus on the future if there is a selection difference sex-related, especially for species whose confidence intervals were greater. As well as if the cats

selected areas with high human density in periods not very active for humans, this will help understand the actual anthropic effect within the habitat of cats in Brazil.

References

Allen, A. M., Månsson, J., Jarnemo, A., & Bunnefeld, N. (2014). The impacts of landscape structure on the winter movements and habitat selection of female red deer. European journal of wildlife research, 60(3), 411-421.

Azevedo, F. C., Lemos, F. G., Freitas-Junior, M. C., Arrais, R. C., Morato, R. G., and Azevedo, F. C. C. (2021). The importance of forests for an apex predator: spatial ecology and habitat selection by pumas in an agroecosystem. *Animal Conservation*, *24*(3), 499-509.

Bitteti, M. S. D., Angelo, C. D. D., Blanco, Y. E. D. & Paviolo, A. (2010). Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecologia, 36, 403-412.

Castro-Pastene, C., González, C., Carrasco, H., and Soto-Gamboa, M. (2021). Records of different habitats used by the Colo-Colo (Leopardus colocola colocola) Molina 1782, in Central Chile. *Gayana*, *85*(1), 84-89.

Cruz, P., De Angelo, C., Martínez Pardo, J., Iezzi, M. E., Varela, D., Di Bitetti, M. S., and Paviolo, A. (2019). Cats under cover: Habitat models indicate a high dependency on woodlands by Atlantic Forest felids. Biotropica, 51(2), 266-278.

Dias, D. D. M., Almeida, M. D. O. S., Piovezan, T. G. D. A., and Dantas, J. O. (2019). Habitat selection by mammals in an isolated fragment of Brazilian Atlantic Forest. Ecotropia, VOL. 21: 201903

Ditmer, M. A., Stoner, D. C., Francis, C. D., Barber, J. R., Forester, J. D., Choate, D. M., ... and Carter, N. H. (2021). Artificial nightlight alters the predator–prey dynamics of an apex carnivore. Ecography, 44(2), 149-161.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carr´ e, G., Marqu´ez, J.R.G., Gruber, B., Lafourcade, B., Leitao, ˜ P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schroder, ¨ B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography (Cop.). 36, 27–46. https://doi.org/10.1111/j.1600- 0587.2012.07348.x

Fieberg J, Bohrer G, Davidson SC, Kays R (2018). Short course on analyzing animal tracking data. Presented at the North Carolina Museum of Natural Sciences, Raleigh, NC, USA. May 21–23, 2018. https://movebankworkshopraleighnc.netlify.com/index.html

IBGE – INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA. Censo Brasileiro de 2010. Rio de Janeiro: IBGE, 2012. https://www.ibge.gov.br/geociencias/cartas-e-mapas/sociedade-e-economia/15955-densidade-demografica.html?=&t=acesso-ao-produto

Manly, B. F. L., McDonald, L., Thomas, D. L., McDonald, T. L., and Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Medan, D., Torretta, J. P., Hodara, K., Elba, B., and Montaldo, N. H. (2011). Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodiversity and Conservation*, *20*(13), 3077-3100.

Nagy-Reis, M., Oshima, J. E. F., Kanda, C. Z., Palmeira, F. B. L., de Melo, F. R., Morato, R. G., et al. 2020. NEOTROPICAL CARNIVORES: a data set on carnivore distribution in the Neotropics. Ecology 101(11):e03128. 10.1002/ecy.3128

ICMBio/MMA, 2018 Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume II – Mamíferos / --
1. ed. -- Brasília, DF

Morato, R. G., Connette, G. M., Stabach, J. A., De Paula, R. C., Ferraz, K. M. P. M., Kantek, D. L. Z., ... and Leimgruber, P. (2018). Resource selection in an apex predator and variation in response to local landscape characteristics. *Biological Conservation*, *228*, 233-240.

Morris, D. W. (2003). How can we apply theories of habitat selection to wildlife conservation and management?. Wildlife Research, 30(4), 303-319.

Oliveira, T. G. de (1994) Neotropical Cats: Ecology and Conservation. EDUFMA, São Luis, Brazil.

Oliveira, T. G. de, Kasper, C. B., Tortato, M. A., Marques, R. V., Mazim, F. D., and Soares, J. B. G. (2008) Aspectos ecologicos de Leopardus tigrinus e outros felinos de pequeno-medio porte no Brasil. In T. G. de Oliveira (ed.), Plano de ação para conservação de Leopardus tigrinus no Brasil. Instituto Pro-Carnivoros/Fundo Nacional do Meio Ambiente, Atibaia, Brazil

Oliveira TG, Tortato MA, Silveira L, Kasper CB, Mazim FD, Lucherini M, Jacomo AT, Soares JBC, Marques RV, Sunquist ME (2010) Ocelot ecology and its effect on the small-felid guild in the lowland Neotropics. In: Macdonald DW, Loveridge AJ (eds) *Biology and Conservation of Wild Felids*, 563–574. Oxford University Press, Oxford, UK

Oliveira, T., Trigo, T., Tortato, M., Paviolo, A. and Bianchi, R. and Leite-Pitman, M.R.P. (2016). Leopardus guttulus. The IUCN Red List of Threatened Species 2016: e.T54010476A54010576. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T54010476A54010576.en

Rabinowitz, A., & Zeller, K. A. (2010). A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. *Biological Conservation*, 143(4), 939-945.

Souza, C. M., Z Shimbo, J., Rosa, M. R., Parente, L. L., A Alencar, A., Rudorff, B. F., ... and Azevedo, T. (2020). Reconstructing three decades of land use and land cover changes in brazilian biomes with landsat archive and earth engine. *Remote Sensing*, *12*(17), 2735.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York. https://doi.org/10.1007/978-0-387-87458-6.

Principais conclusões

Capítulo # 1: O efeito de características antropogênicas na seleção de habitat de um grande carnívoro é condicional ao sexo e ao período circadiano, sugerindo um cenário de coexistência

Em conclusão, este capítulo fornece valiosos insights sobre a seleção de habitat e conservação de onças-pintadas. O estudo enfatiza a importância de compreender a seleção de habitat das onças-pintadas para sua conservação. Foi constatado que as onças-pintadas vivem em paisagens com alta densidade de seres humanos e gado, onde a percepção de risco relacionada aos humanos influencia sua seleção de recursos. No entanto, dependendo do sexo das onças-pintadas e da hora do dia, elas também podem selecionar certas estruturas antropogênicas, como áreas de cultivo e assentamentos humanos.

O estudo destaca a importância da preservação de habitats naturais para as onças-pintadas e da gestão de paisagens antropogênicas para garantir sua sobrevivência. Sugere que o comportamento das onças-pintadas pode variar em diferentes paisagens e períodos, e, portanto, os esforços de conservação devem levar em consideração essas variações. O estudo também enfatiza a necessidade de uma gestão eficiente e controle de estradas, como cercas e passagens de fauna, para promover a coexistência com as onças-pintadas e mitigar os efeitos negativos das estradas em suas populações. Além disso, o estudo discute o impacto de estruturas antropogênicas, particularmente estradas, nas onças-pintadas.

Embora as onças-pintadas possam usar estradas para viajar e procurar alimento, estradas pavimentadas podem fragmentar seus habitats e limitar seu movimento. Isso pode ter consequências negativas para sua conservação. O estudo enfatiza a importância de identificar locais-chave para a conexão das populações de onças-pintadas e implementar medidas como passagens de fauna para mitigar os efeitos negativos das estradas nas onças-pintadas.

No geral, este capítulo destaca a importância de entender a seleção de habitat das onças-pintadas e implementar estratégias eficazes de conservação. Ele ressalta a necessidade de preservar habitats naturais, gerenciar paisagens antropogênicas e abordar o impacto das estradas nas

onças-pintadas. Ao considerar esses fatores, podemos trabalhar para garantir a sobrevivência a longo prazo e a coexistência das onças-pintadas com as populações humanas.

Capítulo # 2: Onça-pintada na borda: Padrões de movimento em paisagens alteradas pelo ser humano

O destaque deste estudo é que ele enfatiza a importância de considerar a configuração da paisagem e a estrutura do habitat na gestão e conservação das populações de onças-pintadas. Os resultados indicam que as onças-pintadas frequentemente revisitam áreas de borda de floresta, áreas agrícolas e estradas, sugerindo que essas características da paisagem influenciam seus padrões de movimento. No entanto, fragmentos de floresta maiores foram identificados como áreas seguras importantes para a espécie. O estudo também destaca a importância de manter corredores ecológicos e condições ideais de forrageamento e abrigo tanto para as onças-pintadas quanto para suas presas. Compreender a dinâmica predador-presa e a influência da conectividade da paisagem nas estratégias de dispersão pode contribuir para esforços eficazes de conservação das onças-pintadas.

Em conclusão, este estudo fornece insights valiosos sobre os padrões de movimento e uso de habitat das onças-pintadas em paisagens fragmentadas. Os resultados demonstram que a configuração da paisagem e a estrutura do habitat desempenham um papel crucial na moldagem do comportamento e movimento das onças-pintadas. Foi constatado que as onças-pintadas revisitam características específicas da paisagem, como bordas de floresta, áreas agrícolas e estradas, indicando sua influência nos padrões de movimento das onças-pintadas. No entanto, fragmentos de floresta maiores foram identificados como áreas seguras importantes para a espécie, destacando a importância de manter habitats florestais intactos. O estudo enfatiza a importância de estabelecer corredores ecológicos e manter condições ideais de forrageamento e abrigo tanto para as onças-pintadas quanto para suas presas. Esses achados têm importantes implicações para a gestão e conservação das populações de onças-pintadas, enfatizando a necessidade de considerar a conectividade da paisagem e a estrutura do habitat no planejamento de conservação. Pesquisas adicionais são necessárias para aprofundar nossa compreensão dos

fatores que influenciam a ocupação das onças-pintadas em diferentes estruturas de habitat e para aprimorar nosso conhecimento da dinâmica predador-presa em paisagens fragmentadas.

Capítulo # 3: Interações de Movimento Predador-Presa: Onças-pintadas e queixadas na mira.

Em conclusão, este estudo fornece insights valiosos sobre as interações de movimento entre onças-pintadas e queixadas no Pantanal durante a estação seca. Os resultados revelam comportamentos de atração e evitação entre as espécies predadoras e suas presas, que variaram entre indivíduos e foram principalmente observados pela manhã e à noite. Embora os contatos em proximidade próxima fossem mínimos, eles ocorreram dentro das distâncias de movimento diário das onças-pintadas, principalmente nas bordas das florestas e longe das áreas de gramíneas. Essas interações foram mais comuns em regiões com menor densidade de queixadas. O estudo destaca a importância de identificar áreas essenciais para equilibrar essas interações e enfatiza o papel das onças-pintadas como reguladores naturais das populações de queixadas e outras espécies no Pantanal.

O estudo utilizou um índice para classificar o movimento de atração, evitação e aleatório entre onças-pintadas e queixadas com base na direção e na velocidade. A análise das interações de movimento revelou interações diversas, mas pouco frequentes, com um total de 144 interações dinâmicas registradas durante o período do estudo. Os contatos a uma distância inferior a 700 metros não foram frequentes, e a maioria dos contatos próximos ocorreu durante a noite e a manhã.

A análise das estruturas da paisagem indicou que a distância das áreas de gramíneas e a densidade de queixadas influenciaram significativamente a probabilidade de interação entre onças-pintadas e queixadas. Maiores distâncias das áreas de gramíneas aumentaram a probabilidade de interação, enquanto uma menor densidade de queixadas também aumentou a probabilidade de interação. A variável de distância da floresta não mostrou importância significativa no modelo. Embora não seja estatisticamente significativo, houve uma tendência

sugerindo que densidades mais altas de onças-pintadas correlacionaram-se com um aumento da interação.

No geral, este estudo contribui para nossa compreensão das interações de movimento e dos fatores que as influenciam entre onças-pintadas e queixadas no Pantanal. Os resultados destacam a importância das bordas de habitats naturais e o papel das onças-pintadas como reguladores naturais de populações. Essas informações são cruciais para esforços de conservação e para identificar áreas essenciais para manter o equilíbrio nas interações entre predadores e presas no ecossistema do Pantanal.

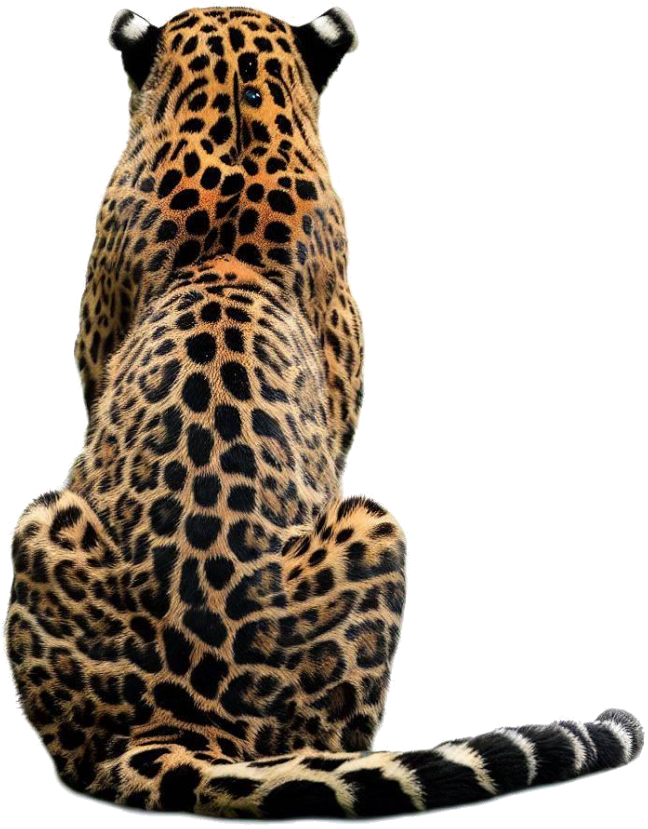
Capítulo # 4: Seleção de Habitat de Felinos Brasileiros: Tendências e Lacunas

Em conclusão, este estudo examinou os padrões de seleção de habitat de várias espécies de felinos no Brasil, incluindo a onça-pintada, puma, jaguatirica, gato-maracajá, gato-do-mato-pequeno, gato-maracajá-dos-pampas, gato-do-mato-grande-do-sul, gato-do-mato-grande-do-norte e gato-maracajá-pequeno. Os resultados revelaram que felinos maiores, como a onça-pintada, puma e jaguatirica, preferiam ambientes naturais, evitando áreas agrícolas e densamente povoadas. Por outro lado, felinos menores, como o gato-maracajá, gato-maracajá-dos-pampas, gato-maracajá-pequeno, gato-do-mato-grande-do-sul e gato-do-mato-grande-do-norte, mostraram preferência por áreas com maior densidade populacional, com o gato-do-mato-grande-do-norte exibindo uma resposta significativa. O gato-maracajá também selecionou locais próximos à agricultura. O gato-maracajá-dos-pampas demonstrou um uso eficaz de áreas de pastagens e mostrou uma tendência a utilizar áreas agrícolas próximas. O gato-maracajá-pequeno, gato-do-mato-grande-do-norte e gato-do-mato-grande-do-sul utilizaram principalmente estruturas de borda e núcleo de florestas, evitando áreas de pastagens. O gato-maracajá-dos-pampas tendeu a usar áreas com alta densidade populacional, evitando regiões agrícolas.

Essas descobertas fornecem insights valiosos sobre as preferências de habitat e respostas de diferentes espécies de felinos às estruturas ambientais no Brasil. Elas contribuem para nossa

compreensão da história de vida dessas espécies e podem informar planos de conservação. É importante considerar possíveis diferenças relacionadas ao sexo na seleção de habitat e o impacto da atividade humana nos habitats dos felinos em estudos futuros. Ao identificar áreas críticas para conservação, esta pesquisa auxilia na compreensão mais ampla da distribuição das espécies de felinos e de suas necessidades de conservação no Brasil.

Material suplementar para todos os capítulos



Supplementary material of

The effect of anthropogenic features on the habitat selection of a large carnivore is conditional on sex and the circadian period, suggesting a landscape of coexistence.

TABLES

Table A1: Percentage of the environmental variables (presence of binary and discrete data by groups of individuals of each study area) found in the distinct ecoregions

Group	Ecoregions	Total area (Km2)	Tree cover (%)	Cropland %	Shrubland %	Grassland %	Flooded areas %	Water %	Urban rural %	Light %	Principal Road %	Field road %
A	SONORA	2512.051	49.18	0.70	49.96	0.00	0.12	8.02	0.00	0.03	0.09	0.11
B	YUCATAN	1595.379	81.55	6.87	0.32	0.49	1.70	2.74	24.31	0.00	0.27	0.73
C	PETEN	2665.593	94.87	4.45	0.01	0.05	0.08	9.43	0.00	0.46	0.26	0.07
D	CENTRAL	858.559	71.08	4.88	0.02	0.10	0.16	0.33	63.83	0.00	0.26	0.56
E	PURUS	1792.558	31.87	2.83	0.17	0.00	48.42	82.27	0.29	0.47	0.00	0.00
F	TOCANTINS	1484.452	79.45	10.29	0.81	5.01	1.49	6.30	71.72	12.76	0.77	0.69
G	CAATINGA	2327.979	18.20	11.26	70.48	0.06	0.00	0.00	0.00	0.10	0.10	0.49
H	CERRADO	2553.281	0.78	59.87	38.34	0.31	0.07	6.76	0.00	7.39	0.87	1.22
I	CERRADO	4236.75	7.85	50.19	40.92	0.94	0.00	0.62	22.07	0.76	0.20	0.25
J	PANTANAL	2005.902	24.32	0.19	38.39	2.33	24.37	80.92	0.00	0.00	0.00	0.00
K	PANTANAL	1816.985	56.83	0.58	28.26	0.29	13.20	30.76	0.00	0.00	0.08	0.11
L	PANTANAL & CHIQUITANO	1054.005	32.81	1.53	8.21	0.15	34.55	80.23	0.00	0.00	0.00	0.04
M	PANTANAL	2345.707	11.86	1.50	10.94	0.02	75.56	40.86	6.58	0.00	0.10	0.07
N	PANTANAL	3842.69	39.38	8.25	9.69	0.35	41.86	29.87	0.00	0.30	0.06	0.25
O	PANTANAL	881.176	53.35	2.26	1.77	23.80	17.60	21.47	0.00	0.00	0.09	0.04
P	DRYCHACO	1391.327	58.45	2.80	15.51	0.15	20.73	26.12	0.00	0.00	0.01	0.25
Q	DRYCHACO	4035.447	67.06	5.14	26.48	1.26	0.06	0.00	0.00	0.00	0.07	0.30
R	DRYCHACO	2680.743	49.56	1.71	48.49	0.07	0.08	0.11	0.00	0.00	0.12	0.17
S	DRYCHACO	5324.053	27.51	47.17	24.76	0.50	0.03	0.71	0.00	0.00	0.12	0.89
T	ATLANTIC	1849.33	22.96	69.56	0.27	1.88	0.36	17.11	54.96	3.76	0.53	1.74
U	ATLANTIC	2398.311	29.27	44.36	15.34	2.96	1.54	25.34	12.42	0.00	0.45	0.40
V	HUMIDCHACO	3395.94	80.27	8.04	10.74	0.71	0.24	3.61	0.00	0.00	0.04	0.63
W	ATLANTIC	1319.141	77.97	15.52	1.54	4.97	0.00	1.34	21.56	0.00	0.18	1.02
X	ATLANTIC	1262.816	65.39	29.41	1.84	3.22	0.00	1.92	56.74	6.42	0.46	0.74
Y	ATLANTIC	2468.079	74.51	14.48	1.79	0.71	1.35	25.92	68.82	9.69	1.33	1.61
Z	ATLANTIC	1116.794	46.33	40.75	4.30	8.60	0.01	4.07	34.01	0.00	0.19	1.42

Table A2: Median of human and livestock variables(continuous data by groups of individuals of each study area) found in the ecoregions. Some ecoregions present more than one study.

Group	Ecoregions	Total Area (Km2)	Human density (median)	Pig density (median)	Cattle density (median)	Ovine - Caprine density (median)
A	SONORA	2512.051	0.00	0.04	0.40	0.14
B	YUCATAN	1595.379	0.58	0.08	0.20	0.00
C	PETEN	2665.593	0.05	0.00	0.19	0.00
D	CENTRAL	858.559	0.00	0.00	0.00	0.00
E	PURUS	1792.558	0.09	0.00	0.00	0.13
F	TOCANTINS	1484.452	0.00	0.04	0.54	0.20
G	CAATINGA	2327.979	0.07	0.07	0.54	0.48
H	CERRADO	2553.281	0.11	0.08	0.64	0.09
I	CERRADO	4236.75	0.07	0.01	0.73	0.00
J	PANTANAL	2005.902	0.09	0.00	0.82	0.38
K	PANTANAL	1816.985	0.08	0.00	0.80	0.22
L	PANTANAL & CHIQUITANO	1054.005	0.22	0.00	0.81	0.27
M	PANTANAL	2345.707	0.59	0.03	0.79	0.22
N	PANTANAL	3842.69	0.01	0.00	0.34	0.24
O	PANTANAL	881.176	0.04	0.00	0.77	0.23
P	DRYCHACO	1391.327	1.00	0.00	0.82	0.42
Q	DRYCHACO	4035.447	0.00	0.00	0.00	0.56
R	DRYCHACO	2680.743	0.00	0.00	0.00	0.70
S	DRYCHACO	5324.053	1.00	0.01	0.00	0.50
T	ATLANTIC	1849.33	0.13	0.07	0.80	0.15
U	ATLANTIC	2398.311	0.07	0.05	0.85	0.15
V	HUMIDCHACO	3395.94	1.00	0.08	0.61	0.16
W	ATLANTIC	1319.141	0.61	0.29	0.21	0.09

X	ATLANTIC	1262.816	0.21	0.27	0.00	0.00
Y	ATLANTIC	2468.079	0.40	0.00	0.53	0.02
Z	ATLANTIC	1116.794	0.40	0.50	0.44	0.36

Table B1: Description of the environmental variables, pixel resolution, and values of the original raster considered as 1 for their binarization.

#	Variables	Source raster	Original pixel resolution	Final pixel resolution	Original raster range values	Binarization ranges
1	Water	Water frequency	30m	30m	0-100	No binarization
2	Tree cover	Landcover	300m	30m	0 -220 Categories	50 to 100
3	Flood areas	Landcover	300m	30m	0 -220 Categories	160 to180
4	Grassland	Landcover	300m	30m	0 -220 Categories	130
5	Shrubland	Landcover	300m	30m	0 -220 Categories	110 to122
6	Cropland	Landcover	300m	30m	0 -220 Categories	10 to 40
7	Urban -Rural areas	Landcover	1km	30m	1-30 Categories	0-10 (from large city to <1 hour to intermediate city)
8	Main roads	GoogleStreetMap	vector	30m	Multiple line structure descriptions	Motorway, trunk, primary, secondary, tertiary, residential, living street, pedestrian, raceway, railway
9	Auxiliary roads	GoogleStreetMap	vector	30m	Multiple line structure descriptions	Cycleway, cable path, service/road, track, footway, bridleway
10	Human density	Human density	1km	30m	0 - 125407	No binarization
11	Cattle density	Cattle density	1km	30m	0 - 2046800	No binarization
12	Ovine - Caprine density	Ovine - Caprine density	1km	30m	0 - 201525	No binarization
13	Pig density	Pig density	1km	30m	0 - 59042.9	No binarization
14	Night-time lights	Human Footprint	1km	30m	0 - 10	No binarization

Table C1: Results obtained from the Pareto distribution of the jaguars GPS data considering each individual fix schedule.

ID	ORIGINAL REVIEW SCHEDULE	TIME SCALE USED (in hours)	1H	2H	4H	6H	8H	12H	24H
43.1	6	6,12,24				988.739		1608.153	3030.362
43.2	3	3,6,12,24				2119.716		3775.433	7239.926
64	3	3,6,12,24				2564.143		4587.586	8839.274
49	2	2,4,6,8,10,12,24		1341.681	1990.561	2631.262	3307.894	4541.356	8644.415
26	2	2,4,6,8,10,12,24		659.7369	1024.423	1354.129	1616.853	2212.34	4404.289
93	6	6,12,24				1305.874		1991.258	3488.872
94	6	6,12,24				1623.527		2480.779	4604.305
95	2	2,4,6,8,10,12,24		2084.632	3136.171	3908.952	5142.056	7475.773	13333.46
96	6	6,12,24				683.6805		995.7634	1596.483
97	6	6,12,24				1105.376		1679.53	3010.911
99	2	2,4,6,8,10,12,24		490.7387	698.1052	871.9805	1050.675	1413.579	2668.316
24	4	4,8,12,24			1059.161		1986.57	3071.509	6156.242
20	1	1,2,3,4,5,6,7,8,10,12,24	444.7143	724.3607	1077.585	1369.892	1692.292	2313.975	4711.337
50	1	1,2,3,4,5,6,7,8,10,12,24	356.5914	602.4913	938.1446	1252.887	1529.775	2037.802	3896.303
89.1	1	1,2,3,4,5,6,7,8,10,12,24	970.7749	1619.156	2526.393	3581.499	4609.646	6963.288	14006.58
12	1	1,2,3,4,5,6,7,8,10,12,24	413.1163	681.7078	989.6241	1199.472	1485.097	1980.833	3965.703
13	1	1,2,3,4,5,6,7,8,10,12,24	506.6872	749.8953	989.6979	1041.192	1277.94	1816.276	3591.177
18	1	1,2,3,4,5,6,7,8,10,12,24	532.5792	820.9907	1141.736	1360.742	1581.723	2199.522	4284.884
22	1	1,2,3,4,5,6,7,8,10,12,24	434.6084	613.1155	643.6739	921.6389	995.4871	1263.607	2557.405
23	1	1,2,3,4,5,6,7,8,10,12,24	294.8763	422.1464	566.3906	635.168	803.383	991.8985	1827.453
41	1	1,2,3,4,5,6,7,8,10,12,24	293.1564	442.2624	567.7538	706.5782	721.8927	1053.383	2150.937
52	1	1,2,3,4,5,6,7,8,10,12,24	287.7351	454.1078	540.8764	683.5246	745.5054	1036.022	2028.315
81.1	1	1,2,3,4,5,6,7,8,10,12,24	345.8338	482.8206	600.836	688.1849	716.9707	1216.184	2510.074
81.2	2	2,4,6,8,10,12,24		622.5215	839.0901	1032.428	1173.693	1531.069	2680.764
88.1	1	1,2,3,4,5,6,7,8,10,12,24	398.3877	653.1419	1029.642	1387.741	1771.62	2591.866	5194.994

88.2	2	2,4,6,8,10,12,24		508.7211	658.4548	878.0188	1101.996	2106.65	3058.214
91	6	6,12,24				1055.178		1999.06	4091.138
92	6	6,12,24				1724.249		2943	5885.586
116	1	1,2,3,4,5,6,7,8,10,12,24	509.2597	743.8475	971.0485	1098.37	1197.503	1627.824	3334.966
117	1	1,2,3,4,5,6,7,8,10,12,24	365.9139	509.1872	714.6226	836.5347	1004.554	1336.677	2907.507
27	4	4,8,12,24			789.679		1344.295	1885.121	3699.391
31	4	4,8,12,24			1221.197		1986.44	2915.828	5658.501
32	4	4,8,12,24			2140.741		4031.835	6091.248	12341.42
33	4	4,8,12,24			1476.539		2692.733	3926.619	7836.551
53	4	4,8,12,24			1759.003		3023.647	4503.811	8662.67
55	4	4,8,12,24			2158.103		3837.201	5334.862	10391.11
59	4	4,8,12,24			2337.802		4298.631	6405.251	12623.61
60	4	4,8,12,24			1676.078		3122.848	4688.253	9332.429
61	4	4,8,12,24			1864.757		3137.681	4365.583	8086.555
28	4	4,8,12,24			1014.866		1719.404	2450.621	4563.793
29	4	4,8,12,24			1740.019		3002.357	3924.518	7621.071
54	4	4,8,12,24			774.7886		1093.598	1379.358	2141.197
56	4	4,8,12,24			1441.447		2629.362	3819.664	7582.536
105	3	3,6,12,24				1748.193		3146.559	6041.572
106	3	3,6,12,24				3646.915		7104.555	14408.41
107	3	3,6,12,24				1410.602		2518.615	4641.838
108	3	3,6,12,24				2685.16		5051.615	9960.256
109	3	3,6,12,24				2912.945		5296.367	10427.52
110	3	3,6,12,24				3850.522		7080.417	14581.35
111	3	3,6,12,24				1015.368		1741.179	3347.918
112	3	3,6,12,24				1269.581		1898.29	3708.63
113	3	3,6,12,24				1480.542		2655.805	5153.986
114	3	3,6,12,24				1578.66		2621.863	4964.875
115	3	3,6,12,24				1552.371		2626.365	5108.632
15.1	1	1,2,3,4,5,6,7,8,10,12,24	860.335	1314.33	2148.097	3012.494	3917.975	5765.85	11436.64
15.2	2	2,4,6,8,10,12,24		558.788	823.3719	1024.203	1304.004	1689.782	3499.918

19	1	1,2,3,4,5,6,7,8,10,12,24	526.776	835.1344	1413.007	1989.449	2654.029	4007.905	8118.127
25.1	1	1,2,3,4,5,6,7,8,10,12,24	865.5318	1330.777	2138.858	3017.528	3845.967	5590.428	11159.87
25.2	2	2,4,6,8,10,12,24		509.6687	679.9816	855.6051	1068.243	1384.043	2843.11
68.1	1	1,2,3,4,5,6,7,8,10,12,24	791.6873	1202.394	1929.038	2586.194	2868.401	4310.989	8947.789
68.2	0.5	0.5,1,1.5,2,3,4,5,6,7,8,10,12,24	918.8903	1436.983	2513.129	3660.865	4917.388	7407.695	15131.84
69.1	1	1,2,3,4,5,6,7,8,10,12,24	1003.568	1484.662	1965.161	2473.921	3075.537	4476.224	9106.166
69.2	2	2,4,6,8,10,12,24		495.4229	758.5014	969.6885	1182.7	1538.7	3004.203
79.1	1	1,2,3,4,5,6,7,8,10,12,24	566.5493	812.9232	1166.714	1537.391	1879.424	2729.502	5485.49
79.2	2	2,4,6,8,10,12,24		492.3736	738.1284	870.1305	1027.988	1717.006	2967.298
84.1	1	1,2,3,4,5,6,7,8,10,12,24	598.6197	835.0371	1339.442	1707.438	2109.353	2982.298	5938.583
84.2	2	2,4,6,8,10,12,24		412.6528	651.3793	851.4689	959.0565	1279.871	2509.84
86.1	1	1,2,3,4,5,6,7,8,10,12,24	770.4017	1109.578	2190.484	2689.381	3555.231	5048.109	9930.689
86.2	2	2,4,6,8,10,12,24		439.7214	530.754	643.8765	777.6305	924.1797	1673.488
87.1	1	1,2,3,4,5,6,7,8,10,12,24	549.5923	712.7001	827.5833	887.5536	943.152	1168.99	2417.837
87.2	2	2,4,6,8,10,12,24		1341.301	1923.211	1462.859	2510.293	3876.962	8123.515
102	4	4,8,12,24			1429.357		2300.732	3392.298	6848.662
74	4	4,8,12,24			1031.606		1598.696	2182.525	3724.693
75	4	4,8,12,24			860.1583		1313.307	1807.987	3235.479
51	3	3,6,12,24				2638.739		4645.297	9162.635
71	2	2,4,6,8,10,12,24		1453.299	2496.07	3554.575	4598.204	6713.383	13024.4
72	2	2,4,6,8,10,12,24		1522.036	2463.064	3461.638	4542.492	6721.21	13350.84
73	2	2,4,6,8,10,12,24		1520.024	2348.084	3079.633	3791.957	5563.303	10836.61
76	4	4,8,12,24			1251.825		2092.963	2870.01	5442.023
77	4	4,8,12,24			2340.121		3817.202	5472.111	10588.81
16	3	3,6,12,24				2259.678		3817.955	7320.321
70	2	2,4,6,8,10,12,24		2723.897	4817.032	7025.016	9273.043	13895.31	27845.46
34	24	24							1247.245
37	24	24							1621.495
58	24	24							2878.724
62	12	12,24						4171.46	7611.977
39	8	8,24					1803.666		4489.703

40	8	8,24					1787.924		4090.506
63	6	6,12,24				2500.886		4667.247	8925.51
1	4	4,8,12,24			1786.606		2953.585	4016.807	7944.53
3	4	4,8,12,24			2536.592		4597.799	6768.957	13596.94
4	3	3,6,12,24				2405.272		4341.078	8840.295
5	4	4,8,12,24			723.9768		1058.948	1427.56	2601.201
6	3	3,6,12,24				1701.981		2951.018	5628.387
7	3	3,6,12,24				1832.14		3264.973	6224.888
9	2	2,4,6,8,10,12,24		417.0676	810.9624	1108.754	1376.086	2060.044	4170.676
10	2	2,4,6,8,10,12,24		714.7159	1232.723	1720.467	2252.643	3321.694	6728.866
11	2	2,4,6,8,10,12,24		577.5632	1206.025	1640.397	2100.81	2983.425	5929.428
2	4	4,8,12,24			2830.188		5501.911	8354.952	17098.73
8	4	4,8,12,24			1571.683		2722.673	3994.174	8054.221
21	4	4,8,12,24			1564.709		2788.571	3980.094	7992.921
78	4	4,8,12,24			1148.116		2114.491	3018.664	5966.348
83	4	4,8,12,24			1550.129		2358.469	3294.476	6666.819
42	0.5	0.5,1,1.5,2,3,4,5,6,7,8,10,12,24	907.5804	1206.263	1963.054	3004.617	4044.511	6114.146	12360.17
66	2	2,4,6,8,10,12,24		3225.884	5911.933	9116	12311.13	18203.96	34235.19
80	1.5	1.5,3,6,12,24				1158.363		2374.941	4887.319
90	2	2,4,6,8,10,12,24		1965.529	3457.73	5076.607	6823.487	10304.62	20958.57

Table D1. Summary of mixed-effects conditional logistic regression models relating jaguar habitat use versus availability to environmental variables. Individual jaguars were included as random effects. Separate models were built for females and males, and two circadian periods (day and night). For each model, we provided the variables included in the best models, with the corresponding coefficient estimates, importance, and 95% confidence intervals (95% CI). Variables whose 95% CI did not intersect zero were considered significant.

Day

VARIABLES	FEMALE			MALE		
	COEFFICIENT	IMPORTANCE	95% CI	COEFFICIENT	IMPORTANCE	95% CI
Water	1.48658	1	(1.428; 1.546)	1.51197	1	(1.435; 1.589)
Tree cover	1.51977	1	(1.467; 1.572)	2.28746	1	(2.208; 2.367)
Shrubland	1.1768	1	(1.096; 1.258)	2.17377	1	(2.088; 2.260)
Cropland	-2.09042	1	(-2.306; -1.875)	0.74163	1	(0.604; 0.879)
Urban-rural	0.28824	1	(0.185; 0.392)	-0.53211	1	(-0.622; -0.442)
Main road	1.40129	1	(1.003; 1.799)	1.80842	1	(1.537; 2.080)
Auxiliary road	0.60919	1	(0.278; 0.941)	0.05971	1	(-0.447; 0.566)
Human density	-0.37902	1	(-0.484; -0.274)	-1.59459	1	(-1.715; -1.475)
Cattle density	-0.68401	1	(-0.780; -0.589)	-0.27686	1	(-0.359; -0.195)
Ovine density	-0.49867	1	(-0.635; -0.363)	-1.06737	1	(-1.214; -0.921)

Night

VARIABLES	FEMALE			MALE		
	COEFFICIENT	IMPORTANCE	95% CI	COEFFICIENT	IMPORTANCE	95% CI
Water	1.53121	1	(1.477; 1.586)	1.35355	1	(1.278; 1.429)
Tree cover	1.43064	1	(1.379; 1.482)	2.4173	1	(2.337; 2.498)
Shrubland	1.09669	1	(1.018; 1.175)	2.37951	1	(2.294; 2.465)
Cropland	-0.59202	1	(-0.738; -0.446)	1.91171	1	(1.799; 2.024)
Urban-rural	0.23734	1	(0.141; 0.334)	-0.49956	1	(-0.580; -0.419)
Main road	1.87101	1	(1.624; 2.118)	1.90815	1	(1.735; 2.081)
Auxiliary road	1.12439	1	(0.925; 1.324)	1.25622	1	(1.074; 1.439)
Human density	-0.09969	1	(-0.205; 0.006)	-1.38192	1	(-1.494; -1.270)
Cattle density	-0.58623	1	(-0.680; -0.493)	-0.28731	1	(-0.364; -0.210)
Ovine density	-0.57551	1	(-0.711; -0.440)	-1.05469	1	(-1.194; -0.915)

Supplementary material of

Jaguar at the edge of empty forests: A consequence of fragmentation

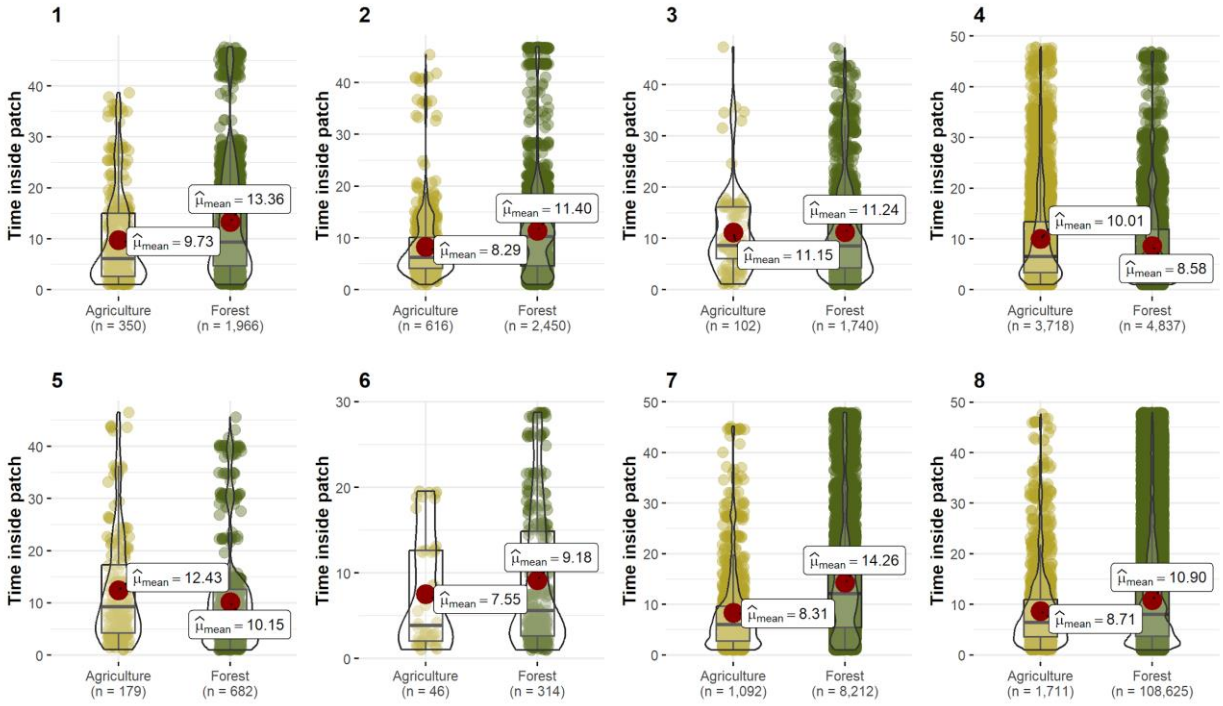


Figure A. Mean time inside the forest and agricultural patches. 1= 10-40 hectares (Ha.), 2= 40-70 Ha., 3= 70-100 Ha., 4= 100-400 Ha., 5= 400 - 1000 Ha., 6= 1000-5000 Ha. , 7= 5000-10000 Ha. and 8 >10000 Ha.

Table A. Data of the individuals used for this study. The planned schedule was expected according to the information from the source database; the planned schedule is observed according to our analysis and cleaning of the data.

STUDY AREA	ID	SEX	COUNTRY	PLANNED SCHEDULE EXPECTED	PLANNED SCHEDULE OBSERVED	ECO-REGION	DIST. MEAN (m/s)	DIST MEAN 4HRS
1	95	Male	Brazil	2h	2	Purus_varzea	0.014085	202.824
1	99	Female	Brazil	2h	2	Purus_varzea	0.0197986	285.09984
2	20	Male	Brazil	1h	1	Caatinga	0.0424848	611.78112
2	50	Male	Brazil	1h	1	Caatinga	0.0383171	551.76624
3	89	Male	Brazil	6h	1 h and then 3.5	Cerrado	0.0717394	1033.04736
4	12	Female	Brazil	1h	1	Pantanal	0.0312143	449.48592
4	13	Male	Brazil	1h	1	Pantanal	0.0287704	414.29376
4	18	Male	Brazil	1h	1	Pantanal	0.0327811	472.04784
4	22	Male	Brazil	1h	1	Pantanal	0.0194613	280.24272
4	23	Male	Brazil	1h	1	Pantanal	0.0159339	229.44816
4	41	Female	Brazil	1h	1	Pantanal	0.0161789	232.97616
4	52	Female	Brazil	1h	1	Pantanal	0.0156858	225.87552
4	81	Male	Brazil	2h	1 from 00 to 16 & 2 from 16 to 00	Pantanal	0.0205964	296.58816
4	88	Female	Brazil	2h	1 from 00 to 16 & 2 from 16 to 00	Pantanal	0.0181844	261.85536
4	116	Male	Brazil	1h	1	Pantanal	0.0256106	368.79264
4	117	Female	Brazil	1h	1	Pantanal	0.023184	333.8496
5	27	Female	Brazil	4h	4	Pantanal	0.0226485	326.1384
5	31	Female	Brazil	4h	4	Pantanal	0.0152802	220.03488
5	32	Female	Brazil	4h	4	Pantanal	0.0467522	673.23168
5	33	Female	Brazil	4h	4	Pantanal	0.0363508	523.45152
5	53	Male	Brazil	4h	4	Pantanal	0.0458811	660.68784
5	55	Male	Brazil	4h	4	Pantanal	0.0310671	447.36624
5	59	Male	Brazil	4h	4	Pantanal	0.0456065	656.7336
5	60	Male	Brazil	4h	4	Pantanal	0.0551971	794.83824
5	61	Male	Brazil	4h	4	Pantanal	0.027507	396.1008
6	28	Female	Brazil	4h	4	Pantanal	0.0241576	347.86944
6	54	Male	Brazil	4h	4	Pantanal	0.0103012	148.33728
6	56	Male	Brazil	4h	4	Pantanal	0.026361	379.5984
6	57	Male	Brazil	4h	4	Pantanal	0.0027558	39.68352

7	14	Male	Brazil	1h	1 from 22 to 9 & 2 from 9 to 21	Pantanal	0.0453233	652.65552
7	15	Male	Brazil	1h	1 from22 to 13 & 2 from 13 to 21	Pantanal	0.0695551	1001.59344
7	19	Female	Brazil	1h	30 min from 08 to 14 & then tried to be 1h	Pantanal	0.0505004	727.20576
7	25	Female	Brazil	1h	1 from 1 to 13 & 2 from 13 to 23	Pantanal	0.0348272	501.51168
7	68	Male	Brazil	1h	30 min from 08 to 14 & 1 from 14 to 08	Pantanal	0.073023	1051.5312
7	69	Female	Brazil	1h	1 from 01 to 13 & 2 from 13 to 01	Pantanal	0.0516261	743.41584
7	79	Female	Brazil	1h	1 from 01 to 13 & 2 from 13 to 01	Pantanal	0.039015	561.816
7	84	Female	Brazil	1h	1 from 01 to 13 & 2 from 13 to 01	Pantanal	0.0337678	486.25632
7	86	Female	Brazil	1h	1 from 01 to 13 & 2 from 13 to 01	Pantanal	0.0571749	823.31856
7	87	Female	Brazil	1h	1 from 21 to 09 & 2 from 09 to 21	Pantanal	0.0241954	348.41376
7	102	Female	Brazil	6h	4	Pantanal	0.035521	511.5024
8	74	Female	Paraguay	4 h	4	Pantanal	0.0341311	491.48784

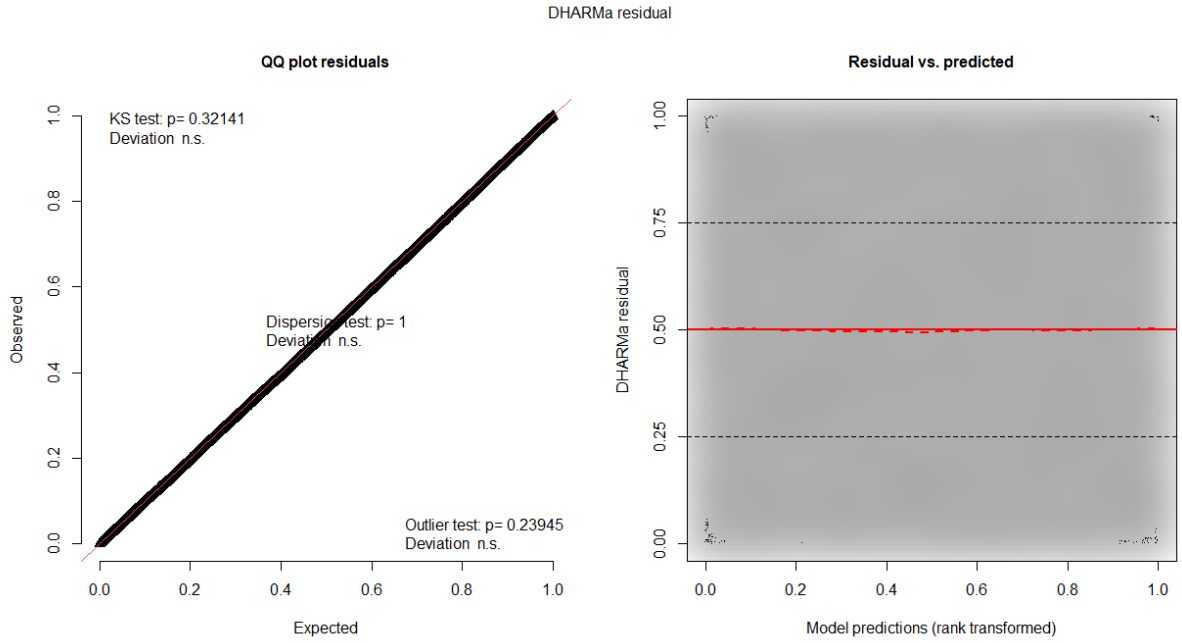
8	75	Female	Paraguay	4 h	4	Pantanal	0.0318693	458.91792
9	76	Female	Paraguay	4 h	4	Dry_Chaco	0.0478111	688.47984
9	77	Male	Paraguay	4 h	4	Dry_Chaco	0.0998819	1438.29936
10	1	Female	Paraguay	4 h	4	Humid_Chaco	0.0288281	415.12464
10	3	Male	Paraguay	4 h	4	Humid_Chaco	0.073549	1059.1056
10	5	Female	Paraguay	4 h	4	Humid_Chaco	0.0242731	349.53264
10	9	Female	Paraguay	2 h from 1800 to 0600 h	2 from 22 to 10	Humid_Chaco	0.0220631	317.70864
10	10	Female	Paraguay	2 h from 1800 to 0600 h	2 from 22 to 10	Humid_Chaco	0.0377947	544.24368
10	11	Female	Paraguay	2 h from 1800 to 0600 h	2 from 22 to 10	Humid_Chaco	0.016946	244.0224
11	8	Male	Paraguay	4 h	4	Atlantic Forest	0.0302824	436.06656
11	78	Female	Paraguay	4 h	4	Atlantic Forest	0.0318279	458.32176
12	42	Male	Argentina	0.5	0.5 or 30 min	Atlantic Forest	0.0860987	1239.82128
12	90	Female	Argentina	2h	2	Atlantic Forest	0.0375942	541.35648
							TOTAL	517.699173

Table B. Summary of mixed-effects generalized lineal models relating jaguar movement patterns versus environmental variables. Individual jaguars were included as random effects and also regions. Separate models were built for visits, speed, time inside and time since last visit. For each model, we provided the variables included in the best models, with the corresponding coefficient estimates, importance, and 95% confidence intervals (95% CI). Variables whose 95% CI did not intersect zero were considered significant.

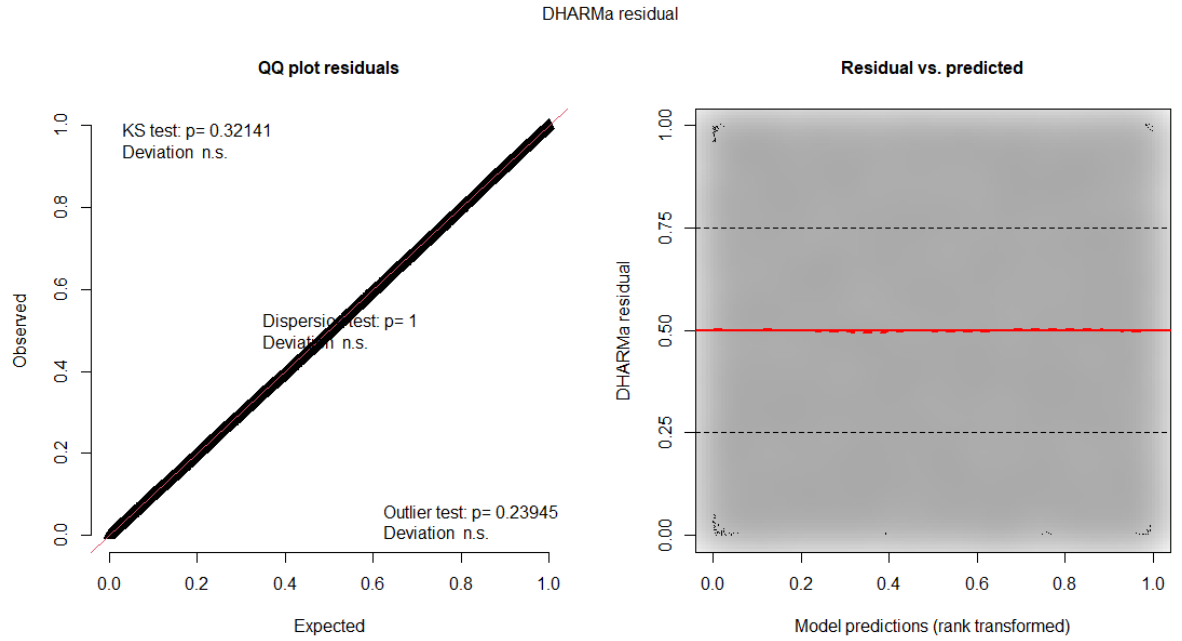
Model= Speed ~ Agro_patch + Agro_dist + Forest_patch + Forest_dist + Drainage_dist + Aux_dist			
Variables	**Estimate**	**CI_min**	**CI_max**
Agriculture patches	-0.7773366	-1.61885	0.06417
Agriculture distances	0.49956369	-0.113	1.11213
Forest patches	-0.34888282	-1.29682	0.59906
Forest distances	0.20127671	-0.56253	0.96508
Drainage distances	-0.06630454	-0.49339	0.36079
Auxiliar road distances	1.38104901	-0.56936	3.33146
Model= Visits~ Agro_patch + Agro_dist + Forest_patch + Forest_dist + Drainage_dist + Aux_dist			
Variables	**Estimate**	**CI_min**	**CI_max**
Agriculture patches	-0.096241	-0.13541571	-0.057066284
Agriculture distances	-0.04994487	-0.09432822	-0.005561516
Forest patches	-0.07632885	-0.12504253	-0.027615165
Forest distances	0.05761128	0.01547541	0.099747147
Drainage distances	-0.27242474	-0.31615989	-0.228689583
Auxiliar road distances	-0.20290071	-0.39987303	-0.005928385
Model= TimeInside ~ Agro_patch + Agro_dist + Forest_patch + Forest_dist + Drainage_dist + Aux_dist			
Variables	**Estimate**	**CI_min**	**CI_max**
Agriculture patches	-0.3038207	-0.32994786	-0.27769354
Agriculture distances	-0.47174717	-0.52929784	-0.4141965
Forest patches	0.16642795	0.11040562	0.22245028
Forest distances	-0.01001363	-0.10951174	0.08948448
Drainage distances	0.08472098	0.03587402	0.13356793
Auxiliar road distances	-2.51992847	-2.80162858	-2.23822836
Model= TimeSinceLastVisist ~ Agro_patch + Agro_dist + Forest_patch + Forest_dist + Drainage_dist + Aux_dist			
Variables	**Estimate**	**CI_min**	**CI_max**
Agriculture patches	0.3167814	0.239373713	0.394189095
Agriculture distances	-0.150001	-0.293340413	-0.006661551
Forest patches	-0.5272994	-0.676574336	-0.378024527
Forest distances	0.2321577	0.007991073	0.456324389
Drainage distances	-0.9097272	-1.041925139	-0.777529174
Auxiliar road distances	-0.441047	-1.172847029	0.290753114

APPENDIX A: Diagnosis plots of our models with the DHARMa package.

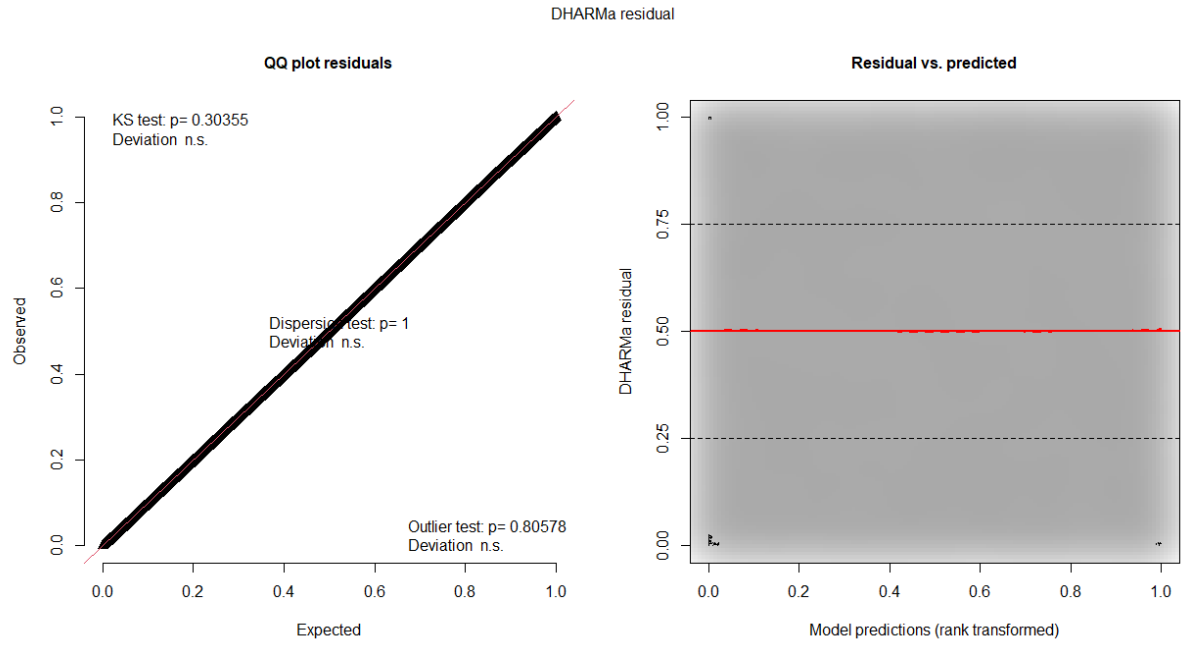
Speed model



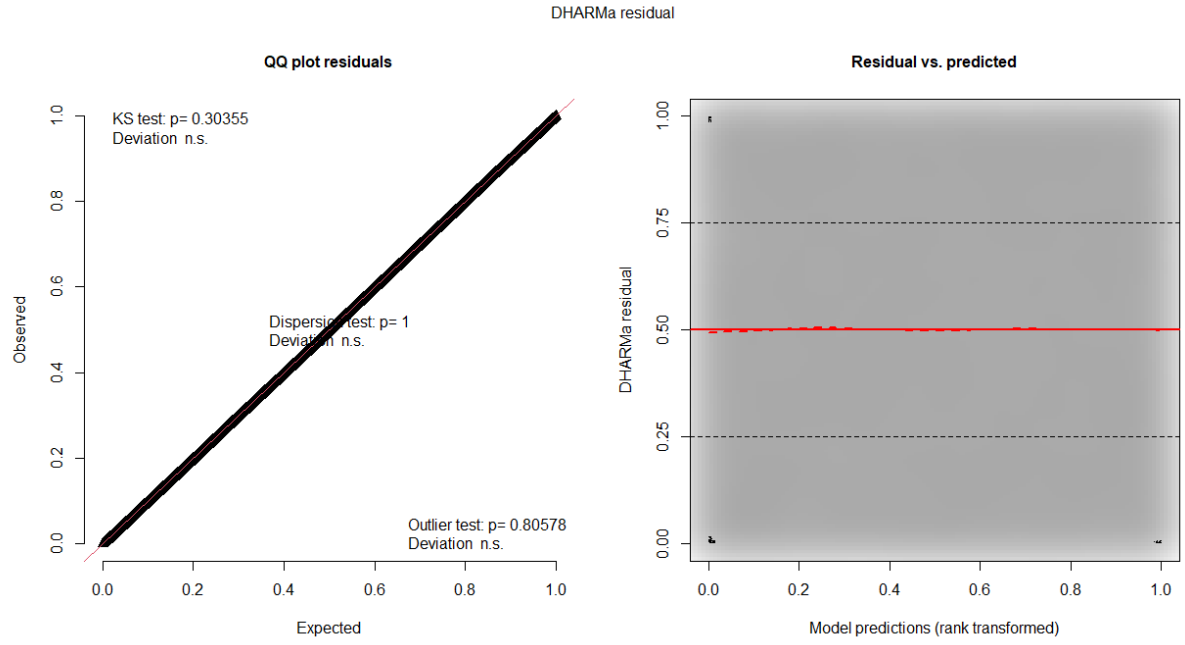
Visit model



Time Inside model



Time Since Last visit model



Supplementary material of

Predator-Prey movement interaction at Pantanal

Table A: Information on the environmental variables used in our model.

Variables	Origin	Program - Process	Source
Forest distance	Forest	LsMetric - Eucladian distance	Mapbiomas Project Collection 2015
Grassland distance	Grassland	LsMetric - Eucladian distance	Mapbiomas Project Collection 2015
Jaguar density	Inds. Brazuca (14), Esperança (25), Natureza (69), Nusa (79), Teorema (84), Vida (87), Carol (102), Copa (103) and Sossego (104)	QGIS 3.10.7-A Coruña - Kernel density	Morato et al., 2018
Peccary density	Inds. Marcello, Roberta, Canela, Nanda, Lucas, Ge and Trina	QGIS 3.10.7-A Coruña - Kernel density	Oshima 2019

Figure A: Diagnosis plots of our model with the DHARMa package.