

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA – INPA  
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

**EFEITO DE VARIÁVEIS AMBIENTAIS E ANTRÓPICAS NA SELEÇÃO DE  
HABITAT POR MACHOS E FÊMEAS DE ONÇA-PINTADA (*PANTHERA  
ONCA*) EM UMA ÁREA DE VÁRZEA DO MÉDIO SOLIMÕES**

ANELISE MONTANARIN

Manaus, Amazonas

Março, 2020

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Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requerimentos para obtenção do título de Mestre em Biologia (Ecologia).

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**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

**ATA DA DEFESA PÚBLICA DA  
DISSERTAÇÃO DE MESTRADO DO  
PROGRAMA DE PÓS-GRADUAÇÃO EM  
ECOLOGIA DO INSTITUTO NACIONAL  
DE PESQUISAS DA AMAZÔNIA.**

Aos 31 dias do mês de março do ano de 2020, às 09h00min, realizada por videoconferência. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Marcelo Gordo**, da Universidade Federal do Amazonas- UFAM, o(a) Prof(a). Dr(a). **Paulo Estefano Dineli Bobrowiec**, do Instituto Nacional de Pesquisa da Amazônia- INPA, e o(a) Prof(a). Dr(a). **Cintia Cornelius Frische**, da Universidade Federal do Amazonas- UFAM, tendo como suplentes o(a) Prof(a). Dr(a). **Igor Luis Kaefer**, do Instituto Nacional de Pesquisas da Amazônia – INPA, sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de DISSERTAÇÃO DE MESTRADO de **ANELISE MONTANARIN**, intitulado: "EFEITO DAS VARIÁVEIS AMBIENTAIS E ANTRÓPICAS NA SELEÇÃO DE HABITAT POR MACHOS E FÊMEAS DE ONÇA-PINTADA (PANTHERA ONCA) EM UMA ÁREA DE VÁRZEA DO MÉDIO SOLIMÕES", orientado(a) pelo(a) Prof(a). **William Ernest Magnusson**, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientado(a) pelo(a) Prof(a). **Fabrizio Beggiato Baccaro**, da Universidade Federal do Amazonas- UFAM e **Emiliano Esterci Ramalho**, do Instituto para a Conservação dos Carnívoros Neotropicais – Pró-Carnívoros.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

APROVADO(A)       REPROVADO(A)

POR UNANIMIDADE       POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

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### Sinopse

Este trabalho investigou se os machos e as fêmeas de onças-pintadas respondem de forma diferente ao uso dos tipos de vegetação (chavascal, várzea baixa e várzea alta), distância de corpos d'água e a distância da comunidade humana mais próxima em área de várzea da Reserva de Desenvolvimento Sustentável Mamirauá.

Palavras-Chave: onça-pintada, sexo, seleção de habitat, várzea.

***Dedico ao meu tio, por desde  
criança me incitar a curiosidade  
pelo mundo dos bichos.***

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*“Cada um é herdeiro de si”*

Joanna de Ângelis



## Resumo

A compreensão dos padrões espaciais, no uso de habitat por carnívoros, em paisagens naturais e dominadas por humanos, é fundamental para a elaboração de planos de ação e de políticas de conservação. Além disso, as ações de conservação devem levar em consideração a história natural e o comportamento das espécies relacionadas às diferenças entre sexos. No entanto, a maioria das conclusões relacionadas às diferenças sexuais, no uso de habitat por carnívoros, é baseada em estudos com poucos indivíduos, baixo esforço amostral e análises que não levaram em consideração a não independência das observações para medidas repetidas do mesmo indivíduo. Neste estudo, investigamos o uso espacial da onça-pintada (*Panthera onca*), em floresta sazonalmente inundada por águas barrentas na Amazônia (várzea), na Reserva de Desenvolvimento Sustentável Mamirauá (RDSM), com base em monitoramentos de longo prazo com armadilhas fotográficas, realizados no decurso de seis anos. Esse conjunto de dados permitiu uma reavaliação dos padrões reportados previamente e uma avaliação mais detalhada dos vieses sexuais na seleção de habitats. Nós usamos modelos hierárquicos para avaliar as diferenças entre sexos na probabilidade de ocorrência da onça-pintada relacionada a fatores ambientais, enquanto consideramos a autocorrelação individual e espacial. Especificamente, nós testamos se há diferença na probabilidade de ocorrência, entre machos e fêmeas de onças-pintadas, em resposta a diferentes tipos de habitat, distância do curso de água e distância de áreas de comunidade humana. Nossos resultados não sustentam conclusões anteriores relacionadas às diferenças entre os sexos nas preferências de qualquer uma das variáveis ambientais ou antropogênicas que testamos. Algumas das diferenças entre este e outros estudos podem ser devido a intensidade da amostragem e outros devido às características únicas das florestas inundadas da Amazônia central. Nossos dados indicam que as onças-pintadas da várzea são generalistas em termos de macro-ambientes, usando todos na proporção em que estão disponíveis.

## **Abstract**

### **Sex does not matter: Habitat selection by male and female jaguars in Amazonian seasonally flooded forest**

Understanding spatial patterns of carnivore habitat use in natural and human-dominated landscapes is critical for the development of efficient conservation policies. In addition, conservation actions should account for species natural history and behavior related to differences between sexes. However, most of the conclusions related to sexual differences in habitat use of carnivores were based on studies with few individuals, low sampling effort and analyses that did not take into consideration non-independence of observations from the same individual. In this study, we investigated space use by jaguar (*Panthera onca*) in the Varzea seasonally flooded forest of Amazonia, in the Mamirauá Sustainable Development Reserve (MSDR), using data from camera-trap surveys undertaken over six years. This comprehensive dataset allowed a reevaluation of reported patterns and a more detailed assessment of sex biases in habitat selection. We used hierarchical modeling to assess sex differences in occurrence probability related to environmental factors, while accounting for individual- and spatial autocorrelation. Specifically, we tested whether male and female jaguars responded differently to habitat type, distance to watercourses and distance to human settlements. Our results do not support previous conclusions related to differences between sexes and we indicate that in MSDR, jaguars are generalists, exploring all environments with similar probability, at least during the low-water season. Human settlements apparently have little effect on space use by jaguars in the varzea, which may lead to more intense conflict with humans, especially if the density of settlements increases.

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## **Introdução geral**

O habitat de uma espécie é composto por múltiplas dimensões (Beyer et al. 2010) e tem sido definido como um conjunto de fatores ambientais e recursos que permitem um organismo sobreviver e reproduzir (Block & Brennan 1993). Essa combinação reflete em heterogeneidade espacial e pode influenciar nas respostas comportamentais dos indivíduos (Jonzén 2008). Assim, a seleção de um elemento do habitat ocorre como um processo pelo qual um animal escolhe, de modo não aleatório, quais elementos usar, em detrimento de outros que também estejam disponíveis (Johnson 1980). Conseqüentemente, uma vez que animais conseguem distinguir entre os vários componentes do ambiente (Phillips et al. 2004), buscam maximizar o uso de recursos que melhor atendam suas necessidades (Guo et al. 2017). Portanto, o uso é tido como seletivo se um elemento for utilizado desproporcionalmente em relação a sua disponibilidade (Johnson 1980), e o uso desproporcional de espaços físicos é interpretado como seleção de habitat (Block & Brennan 1993).

A seleção de habitat tem um importante papel na determinação da distribuição dos organismos em ambientes heterogêneos (Jonzen 2008) e permite a compreensão dos fatores que afetam as escolhas dos indivíduos e suas interações (Morrison et al. 2006; Candolin et al. 2012). Nesse sentido, a compreensão dos padrões espaciais do uso de habitat por carnívoros em paisagens naturais e dominadas por humanos é fundamental para determinar políticas de conservação. Os carnívoros ajustam suas estratégias comportamentais e ecológicas para viver sob diferentes condições ambientais (Du Preez et al. 2015; Svoboda et al. 2019) e em paisagens modificadas pelo homem (Cavalcanti 2002; Ramesh et al. 2016; Evans et al. 2018). Estudos recentes mostraram que, em escalas global e local, o uso de habitat por carnívoros está associado principalmente à disponibilidade de presas (Rich et al. 2017; Valeix et al. 2009). No entanto, em escalas locais, também pode estar relacionado a variáveis ambientais e antropogênicas, dependendo da região estudada (Simcharoen et al. 2008; Rich et al. 2017).

A maioria dos estudos de seleção de habitat não consideraram possíveis diferenças entre sexos e tenderem a tirar conclusões com base em indivíduos

do sexo mais frequentemente observado (Conde et al. 2010). No entanto, as fêmeas podem ter requisitos ecológicos e comportamentais diferentes dos machos (Sandell 1989; Conde et al. 2010; Colchero et al. 2011; Oliveira et al. 2018). Por razões provavelmente relacionadas ao cuidado parental, em geral, as fêmeas se movem menos e têm áreas de vida menores que os machos (Schaller e Crawshaw 1980; Cavalcanti e Gese 2009; Sollmann et al. 2011; Aronsson et al. 2016; Gonzalez- Borrajo et al. 2017; Morato et al. 2016; McBride e Thompson 2018) e, conseqüentemente, têm menor probabilidade de detecção (Sollmann et al. 2011; Tobler et al. 2013).

Áreas sujeitas a distúrbios humanos têm sido comumente reportadas como ambientes menos tolerados por fêmeas do que por machos (Conde et al. 2010; Pallares et al. 2015), e esse comportamento pode levar os machos a taxas de mortalidade mais altas do que as fêmeas, em áreas de conflito (Conde et al. 2010; Ramalho 2012; Moss et al. 2016). As fêmeas tendem a evitar estradas e áreas próximas de ocupação humana (Colchero et al. 2010) que podem causar diferenças sexuais na escolha do habitat. O tipo de vegetação é outra característica que é percebida de forma diferente entre machos e fêmeas (Broomhall et al. 2003; Conde et al. 2010; Rich et al. 2017; Little et al. 2018). Contudo, a maioria das conclusões relacionadas às diferenças entre sexo no uso de habitat por carnívoros foi baseada em estudos com poucos indivíduos, baixo esforço amostral e análises que não levaram em consideração a não independência das observações para medidas repetidas do mesmo indivíduo.

A onça-pintada (*Panthera onca*) é o maior felino dos Neotrópicos e sua distribuição inclui vários biomas, diferentes tipos de vegetação e graus de pressão humana (Quigley et al. 2018; Morato et al. 2016; Morato et al. 2018). Portanto, existem grandes variações na ecologia e no comportamento da espécie relacionadas aos gradientes ambientais em que se encontra (Quigley 1987; Astete et al. 2008; Morato et al. 2018). Embora as onças-pintadas exibam diferentes padrões na seleção de recursos ao longo de sua distribuição geográfica, geralmente exibem uma preferência geral pela densa cobertura vegetal (Morato et al. 2018) e áreas próximas aos cursos de água (Crawshaw e Quigley 1991; Quigley e Crawshaw 1992; Hatten et al. 2005; Sunquist e Sunquist 2014), onde são capazes de encontrar suas principais presas aquáticas

(Emmons 1987). Além disso, é provável que as paisagens modificadas pelo homem tenham forte influência nos padrões de seleção de recursos e no uso do espaço pelas onças-pintadas (Cavalcanti & Gese 2009; Colchero et al. 2011; Morato et al. 2016). Embora as onças-pintadas mostrem plasticidade comportamental (Rabinowitz e Nottingham 1986; Sanderson et al. 2002; Astete et al. 2008; De La Torre et al. 2017) e uma ampla distribuição geográfica (Sanderson et al. 2002; De La Torre et al. 2018) elas são marcadamente menos estudados do que outros felinos do gênero (Brodie 2009; Tensen 2018).

A bacia amazônica possui a maior densidade de onças-pintadas das Américas (Sanderson et al. 2002; Sollmann et al. 2008; Tobler et al. 2013; De La Torre et al. 2018; Jędrzejewski et al. 2018) e é uma área crucial para estratégias de conservação da espécie em longo prazo (Sollmann et al. 2008; Torres et al. 2008; Oliveira et al. 2012; Tobler et al. 2013; Jędrzejewski et al. 2018), porém, pouco se sabe sobre a ecologia e comportamento da onça-pintada no bioma amazônico (Astete et al. 2008), especialmente em ecossistemas de várzea. As florestas inundadas por rios carregados de sedimentos (várzea) ocupam cerca de 3% da bacia amazônica (Ayres 1993; Junk 1997). Devido ao pulso de inundação sazonal, a várzea apresenta um processo biológico altamente dinâmico (Junk 1989). A várzea tem três tipos principais de vegetação: várzea alta, várzea baixa, e chavascal, que são geralmente associadas a diferentes níveis de inundação (Ayres 1993; Paim et al. 2018). A Reserva de Desenvolvimento Sustentável Mamirauá (RDSM) abrange uma área de floresta de várzea habitada por comunidades humanas, cujo modo de vida é baseado em sistemas sustentáveis de exploração de recursos naturais (Queiroz 2005; Ramalho 2012). Por abrigar uma baixa densidade populacional e contar com um monitoramento participativo de longa data, o RDSM é um local excelente para estudar a seleção de habitat de onças-pintadas em florestas de várzea.

As onças-pintadas alcançam altas densidades na RDSM, provavelmente devido à grande disponibilidade de presas (Ramalho 2012). Estudos preliminares na RDSM indicaram que as onças-pintadas são mais frequentemente encontradas nas áreas mais baixas da reserva (Ramalho & Magnusson 2008; Alvarenga et al. 2018) e que a abundância de presas arbóreas determina a ocupação da onça-pintada (Rabelo et al. 2019). No entanto, nenhum



dos estudos anteriores na RDSM discriminou o uso do habitat da onça-pintada entre os sexos. Ramalho (2012) estimou diferentes taxas de mortalidade entre machos e fêmeas na reserva com base em dados de conflitos, mas não há estudos que abranjam uma área ampla que permitam avaliar a relação entre o uso do habitat da onça-pintada e o nível de distúrbio antropogênico, que é presumivelmente maior perto das comunidades.

Neste estudo, investigamos o uso espacial da onça-pintada, com base em estudos de armadilhas fotográficas, realizados ao longo de seis anos na RDSM. Esse conjunto abrangente de dados permitiu uma reavaliação dos padrões previamente reportados e uma avaliação mais detalhada da variação em seleção de habitat entre sexos. Além disso, nos propiciou usar modelos hierárquicos para avaliar diferenças na resposta da probabilidade de ocorrência a fatores ambientais (tipo de vegetação, distância dos cursos de água e distâncias até a comunidade humana mais próxima) entre sexos, e contabilizar a autocorrelação individual e local.

Presumindo que as fêmeas adotariam estratégias para proteger seus filhotes dos efeitos de inundação, maximizando o período em uma paisagem seca, nós levantamos as hipóteses de que (1) as fêmeas demonstrariam preferência pela várzea alta, a área mais alta e a última a inundar; por esse motivo (2) as fêmeas permaneceriam a uma distância maior dos corpos da água do que os machos; e assumindo que os machos sejam mais tolerantes a presença humana, (3) supomos que as áreas mais distantes das comunidades teriam maior probabilidade de ocorrência das fêmeas, enquanto os machos seriam indiferentes à distância de comunidades humanas.

## Objetivos

### Objetivo geral

Determinar como os machos e as fêmeas de onças-pintadas respondem a diferentes variáveis ambientais e antrópicas na área de várzea da Reserva de Desenvolvimento Sustentável Mamirauá (RDSM).

### Objetivos específicos

- Determinar se machos e fêmeas usam de forma diferente os tipos de vegetação (chavascal, várzea baixa e várzea alta) da RDSM.
- Identificar se existe diferenças entre a probabilidade de ocorrência entre machos e fêmeas em relação a distância de corpos d'água.
- Investigar se existe relação entre o número de ocorrências de machos e fêmeas e a distância da comunidade humana mais próxima.

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## **Sex does not matter: Habitat selection by male and female jaguars in Amazonian seasonally flooded forest**

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### **Abstract**

Understanding spatial patterns of carnivore habitat use in natural and human-dominated landscapes is critical for the development of efficient conservation policies. In addition, conservation actions should account for species natural history and behavior related to differences between sexes. However, most of the conclusions related to sexual differences in habitat use of carnivores were based on studies with few individuals, low sampling effort and analyses that did not take into consideration non-independence of observations from the same individual. In this study, we investigated space use by jaguar (*Panthera onca*) in the Varzea seasonally flooded forest of Amazonia, in the Mamirauá Sustainable Development Reserve (MSDR), using data from camera-trap surveys undertaken over six years. This comprehensive dataset allowed a reevaluation of reported patterns and a more detailed assessment of sex biases in habitat selection. We used hierarchical modeling to assess sex differences in occurrence probability related to environmental factors, while accounting for individual- and spatial autocorrelation. Specifically, we tested whether male and female jaguars responded differently to habitat type, distance to watercourses and distance to human settlements. Our results do not support previous conclusions related to differences between sexes and we indicate that in MSDR, jaguars are generalists, exploring all environments with similar probability, at least during the low-water season. Human settlements apparently have little effect on space use by jaguars in the varzea, which may lead to more intense conflict with humans, especially if the density of settlements increases.

**Key-words:** *Panthera onca*; sex; habitat selection; human settlement; varzea forest; generalized linear mixed model.

## 1. Introduction

Habitat selection has an important role in determining the distribution of organisms (Jonzén 2008) and allows comprehension of factors affecting individual choice (Morrison et al. 2006; Candolin and Wong 2012). Carnivores adjust behavioral and ecological strategies to live under different environmental conditions (Du Preez et al. 2015; Svoboda et al. 2019) and in human-modified landscapes (Cavalcanti 2002; Ramesh et al. 2017; Evans et al. 2019). Therefore, understanding how carnivores use habitats is critical to better plan conservation actions and policies (Jędrzejewski et al. 2017).

At global and local scales, carnivores have been observed to use habitat according to prey availability (Rich et al. 2017; Valeix et al. 2009). However, at a local scale, patterns may also be related to other environmental and anthropogenic factors (Simcharoen et al. 2008; Rich et al. 2017). Most carnivore habitat-selection studies do not consider sex differences and tend to draw conclusions based on few individuals of the most frequently observed sex, usually males (Conde et al. 2010). This may cause important bias results, as females may have different ecological and behavioral requirements (Sandell 1989; Conde et al. 2010; Colchero et al. 2011; Oliveira et al. 2018). Females move less and have smaller home ranges than males (Schaller and Crawshaw 1980; Cavalcanti and Gese 2009; Aronsson et al. 2016; Gonzalez-Borrajo et al. 2017; Morato et al. 2016; McBride and Thompson 2018), and consequently tend to have lower probability of detection (Sollmann et al. 2011; Tobler et al. 2013). Males tend to be more tolerant to human disturbance (Conde et al. 2010; Colchero et al. 2011; Pallares et al. 2015), and this behavior can lead to higher mortality rates due to conflict with people (Conde et al. 2010; Ramalho 2012; Moss et al. 2016). Males and females may also show differences in the use of vegetation associations (Broomhall et al. 2003; Conde et al. 2010; Rich et al. 2017; Little et al. 2018). However, most of the conclusions related to sexual differences in habitat use of carnivores are based on studies with few individuals, low sampling effort and analyses that did not take into consideration non-independence of observations of the same individual.

The jaguar (*Panthera onca*) is the largest felid in the Neotropics and its distribution includes many biomes, different types of vegetation associations and levels of human pressure (U.S. Fish and Wildlife Service 2018; Morato et al. 2016; Morato et al. 2018). Consequently, there are large variations in the ecology and behavior of the species associated to environmental gradients (Quigley 1987; Astete et al. 2008; Morato et al. 2018). Although jaguars display different patterns of resource selection across their geographic range, they often exhibit preference for high forest cover (Vynne et al. 2011; Morato et al. 2018; Portugal et al. 2019) and areas close to watercourses (Crawshaw and Quigley 1991; Quigley and Crawshaw 1992; Hatten et al. 2005; Sunkist and Sunkist 2014), where they are able to find their main aquatic prey (Emmons 1987). Human-modified landscapes are likely to have a strong influence on resource-selection

patterns and space use by jaguars (Cavalcanti & Gese 2009; Colchero et al. 2011; Morato et al. 2016). Even though jaguars are thought to show behavioral plasticity (Rabinowitz and Nottingham 1986; Rodríguez Soto et al. 2011; Watkins et al. 2014; De La Torre et al. 2017), and have a broad geographical distribution (Sanderson et al. 2002; De La Torre et al. 2018), they are markedly less studied than other large cats (Brodie 2009; Tensen 2018).

The Amazon Forest holds the largest population of jaguars in the world (Sanderson et al. 2002; Sollmann et al. 2008; Tobler et al. 2013; De La Torre et al. 2018; Jędrzejewski et al. 2018) and it is a crucial area for the long-term conservation of the species (Sollmann et al. 2008; Tôrres et al. 2008; de Oliveira et al. 2012; Tobler et al. 2013; Jędrzejewski et al. 2018), but little is known about the ecology and behavior of the jaguar in this Biome (Astete et al. 2008), especially in seasonally flooded forests. The varzea seasonally flooded forest is inundated by sediment-laden rivers and occupy about 3% of the Amazon basin (Ayres 1993; Furch 1997). Due to the seasonal and mono-modal pulse, biological processes in varzea are highly dynamic (Junk 1989). Varzea has three main vegetation types: high varzea, low varzea and chavascal, which are broadly associated with different flood levels (Ayres 1993; Paim et al. 2018). The Mamirauá Sustainable Development Reserve (MSDR) encompasses an area of varzea forest inhabited by human communities, whose way of life is based on sustainable natural-resource exploitation systems (Queiroz 2005; Ramalho 2012). Because of the low human population density and the long-term camera-trap monitoring, MSDR is a key place to study jaguar habitat selection in varzea forests.

In this study, we investigated the space use of jaguar based on camera-trap survey data undertaken over six years in MSDR. This comprehensive dataset allowed a reevaluation of reported patterns and a more detailed assessment of sex biases in habitat selection. We took advantage of hierarchical modeling to assess sex differences in the response of occurrence probability to environmental factors while accounting for individual- and site-level autocorrelation. We investigated three environmental variables: vegetation type, distance to watercourses and distance to the nearest human settlement. In order to maximize the time their cubs have access to a dry landscape, we predicted that (1) females would show a preference for high varzea, the highest area and the last to flood, and (2) would stay at greater distances from water than males. Also, assuming that males are more tolerant to human presence, we hypothesize that (3) female probability of occurrence would be greater in areas further from human settlements, whereas males would be indifferent to human presence.

## **2. Materials e methods**

### **2.1. Study area**

This study was carried out in Mamirauá Sustainable Development Reserve (MSDR), located in Central Amazonia, Amazonas State, Brazil (1°49' to 3°09' S, 64°45' to 67°23' W). MSDR is delimited by the Amazon (Solimões), Japurá and Auati Paraná Rivers (Figure 01). The reserve area encompasses 1,124,000 ha and represents the largest Brazilian protected area dedicated to the conservation of the varzea (Queiroz 2005). The climate in the region is tropical humid with average temperature of 29.5°C and 2373 mm rainfall in the period 1993 to 2000 (Schöngart et al. 2005). The reserve is flooded annually by nutrient-rich sediment-laden rivers for up to 175 days with an average annual fluctuation of > 10m (Ramalho et al. 2009; Ferreira-Ferreira et al. 2014).

The flood season usually starts in May and runs till mid-July, usually with a peak in June. The low-water season normally occurs between September and November, with lower water levels recorded in October. The river level usually rises from the end of November to the beginning of May, and recedes from mid-July to September (Ramalho et al. 2009).

As a consequence of the difference in level and period of flooding, the MSDR has three main vegetation types within the *Várzea* landscape (Ayres 1993; Paim et al. 2018). High varzea represents the terrain of highest elevation that is flooded for approximately four months by a water column that can reach up to 2.5m. Low varzea covers most of the reserve, and occurs in intermediate terrain elevation with a generally open understory that can be flooded for up to six months by a water column of up to 5m. Chavascal covers a smaller proportion of the varzea forest. It is a swampy environment with lower vegetation and a dense understory, which can be flooded for up to eight months a year by a water column of seven meters or more (Ayres 1993).

## 2.2. Camera trapping

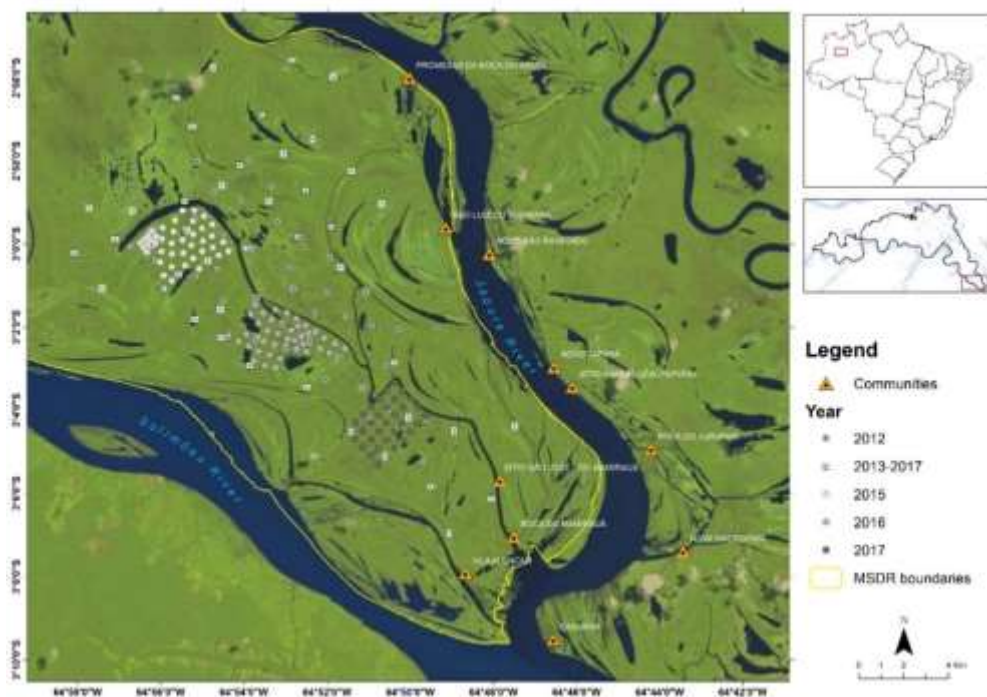
Camera trapping was carried out by the Grupo de Pesquisa em Ecologia e Conservação de Felinos na Amazônia (Ecology and Conservation Research Group for Amazonian Felines) of the Instituto de Desenvolvimento Sustentável Mamirauá (IDSM). The study was originally designed to estimate the density of jaguars in the MSDR and provided six years of camera-trap data. Sampling was carried out during the low-water season and camera-trap stations were set up on a grid covering a total area of approximately 215 km<sup>2</sup>. The data were collected from September to January between 2012 and 2017, and each site was monitored for a time that varied from 27 to 234 days, totaling 18,482 camera trap\*days sampling effort (**Table 1**).

**Table 1.** Summary of the sampling area (km<sup>2</sup>) and sampling effort per year of camera-trap monitoring in MSDR.

Year	Start date	End date	Number of stations	Camera trap/day	Sample area (Km <sup>2</sup> )
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<b>2012</b>	19.09.2012	19.12.2012	40	1718	76,5
<b>2013</b>	17.09.2013	12.12.2013	54	2225	216,3
<b>2014</b>	23.09.2014	31.12.2014	54	2294	216,3
<b>2015</b>	29.10.2015	12.01.2016	95	3498	214,6
<b>2016</b>	07.10.2016	12.01.2017	88	4092	214,6
<b>2017</b>	17.09.2017	14.01.2018	83	4655	214,6

Due to the limited number of cameras, two blocks of cameras on the grid were sampled consecutively each year. Camera traps were active for about 45 days in each block. Each camera-trap station was composed of two camera traps (model PC800 HyperFire<sup>®</sup>, ReconyxInc, Holmen, Wisconsin, USA) 4 m apart and 40 cm above ground facing each other. The distance between adjacent stations varied from 1.5 to 2 Km (**Fig. 1**).



**Fig. 1.** Map of study area showing the location of the camera traps grid from 2012 to 2017 and surrounding human settlements (communities) within the main area of the Mamirauá Sustainable Development Reserve.

Camera traps were configured to take photographs 24 h per day and to record date and time on each photograph. Each time an infrared heat-and-motion detector was triggered, a sequence of 10 pictures was taken, with one second interval between photos.

### 2.3. Predictor variables



To evaluate the influence of environmental variables on differences in habitat selection between sexes, we recorded at each camera trap station the main vegetation types (chavascal, low varzea and high varzea) in the reserve following the classification of Ayres (1993). We also estimated minimum distances (in meters) between the nearest permanent water body and each camera-trap station. The shapefile of the hydrology map of MS DR was obtained from IDSM. As a surrogate for human disturbance, we used the minimum distance between each camera trap station and the nearest human settlement. There are 11 human settlements surrounding our study area, but we only analyzed the impact of the four nearest communities to camera trap stations. All Geographic Information System (GIS) measures were taken using version 3.4 of the QGIS program (QGIS Development Team 2019). All data layers were based on 30-m spatial resolution.

#### **2.4. Individual identity and sex**

Jaguars were identified from their individual natural spot patterns and sex was attributed based on secondary sexual traits.

In order to avoid pseudo replication, only detections of the same individual at a given camera trap station at intervals greater than 24h were considered independent. When different individuals were distinguished in the same photo, they were considered separated events. Detections which did not meet those criteria or those in which sex could not be determined were excluded from analysis (n = 24).

#### **2.5. Analyses**

To test whether jaguar occurrence probability responded to environmental and anthropogenic factors and, if so, whether jaguar responses depended on sex, we used generalized linear mixed-effects models (GLMM). The dependent variable was the occurrence (presence or absence) of a given individual at a given site throughout the sampling interval (n = 38 individuals × 205 sites = 7790 observations), for which we assumed a zero-inflated binomial distribution with logit link to account for the very large proportion of zeros (97.5%). We used two environmental predictors: vegetation type (coded as a categorical variable: high varzea, low varzea, chavascal), minimum distance to nearest watercourse (m) and minimum distance to nearest human settlement (m). Sex (male or female) was included as a trait predictor, along with its pairwise interactions with each predictor to test whether any environmental and anthropogenic response depended on sex. Sampling effort (number of days) was also included as a covariate to control for its variation among sites. Lastly, the hierarchical data structure potentially created autocorrelation among observations from the same individual and/or site. Accordingly, individual and site identity were used as random factors to account for such non-independence. In doing so, we follow

recent “hierarchical models” of ecological communities or “fourth-corner analysis”, which simultaneously consider the responses of individual species to one or more environmental gradients across sites, including the effects of species traits on such responses (Pollock et al. 2012, Jamil et al. 2013, Brown et al. 2014, Warton et al. 2015). The only difference is that, in our analysis, “species” was replaced by “individual”, and the trait of interest is “sex”.

The analysis proceeded as follows. First, we built a model including all predictors, in which “site” was represented by a random intercept, and “individual” was represented by random intercept and slope. This allowed for random variation in individual responses to environmental and anthropogenic factors, beyond any sex effect (Pollock et al. 2012; Jamil et al. 2013). However, this model did not converge to stable parameter estimates; possibly due to “testing on the boundary”, (i.e. variance of random slopes was so small that they could not be discriminated from zero). Therefore, we only considered random intercepts. Next, we checked for significant ( $P < 0.05$ ) interactions between environmental and anthropogenic factors and sex. If interactions were not significant, they were excluded and the model was refit to test for independent effects. All the continuous predictors were scaled to zero mean and unit variance in order to avoid convergence problems the parameter estimation. To visualize the response of occurrence probability to each tested interaction while controlling the remaining predictors, we used conditional plots (Breheny and Burchett 2017). All models were fit using restricted maximum likelihood, as implemented in R 3.5.3 (R Core Team 2019) by the function ‘glmmTMB’ from the self-title package (Brooks et al. 2017) and package ‘Car’ (Fox et al. 2018).

### 3. Results

From the six years of camera trap surveys in MSDR we obtained 191 independent records of jaguars, 131 records of males and 60 from females. We were also able to positively identify 38 jaguar individuals, 23 males and 15 females, a sex ratio of 1.5:1 m: f.

We did not detect difference in habitat selection between males and females with respect to any environmental or anthropogenic variables (**Table 2, Fig. 2, 3, 4**). Sampling effort was the only variable with a significant effect. The longer the sampling time, the greater the chance of detecting a jaguar by a camera trap, as expected.

**Table 2.** Results of Generalized Linear Mixed Model (GLMM) of jaguar occurrence in Mamirauá Sustainable Development Reserve, testing for interactions between sex and environmental/anthropogenic variables and; for independent effects ( $n = 7790$ ). Jaguar occurrence probability was modeled assuming a logit link function and zero-inflated binomial errors, including site ( $n = 205$ ) and individual ( $n = 38$ ) as random factors.  $\chi^2 =$  chi-squared statistic; df: degrees of freedom of model term;  $P$ : probability under the null hypothesis that the true model term is zero. Bold numbers indicate significant model terms ( $P < 0.05$ ).

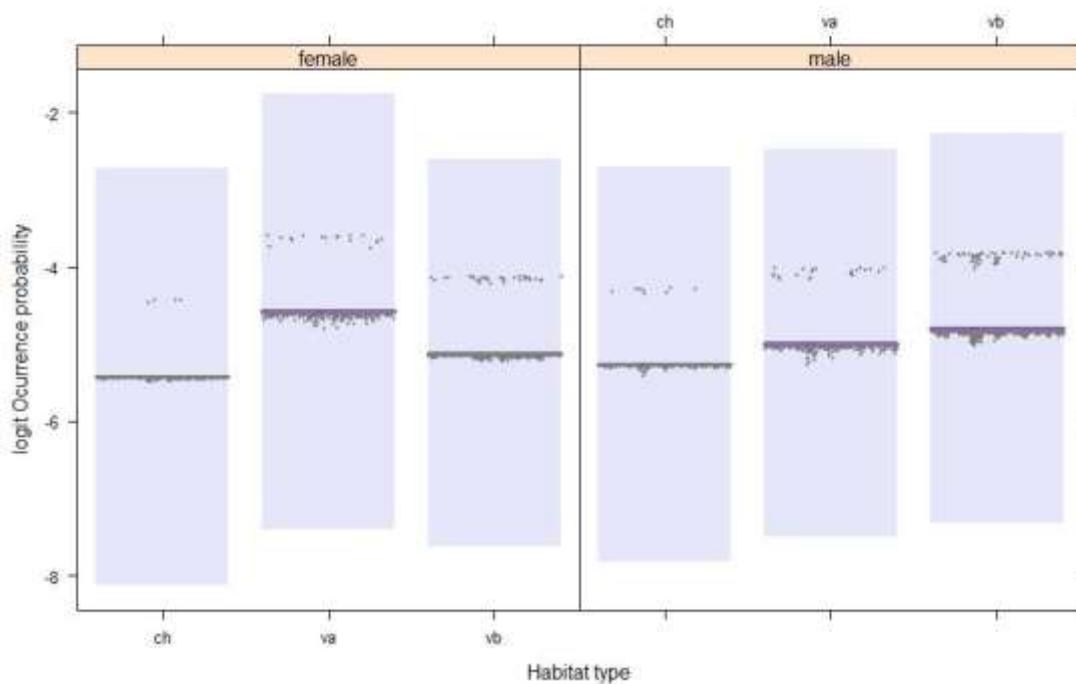
Model type

With interaction

Predictor	$x^2$	df	$\rho$
Sampling effort	15.371	1	<b>0.00008***</b>
Habitat type	1.075	2	0.584
Distance to humans settlement	1.183	1	0.276
Distance to water	0.133	1	0.715
Sex	0.170	1	0.680
Habitat type:sex	2.004	2	0.367
Distance to water:sex	0.048	1	0.826
Distance to humans settlement:sex	0.336	1	0.562

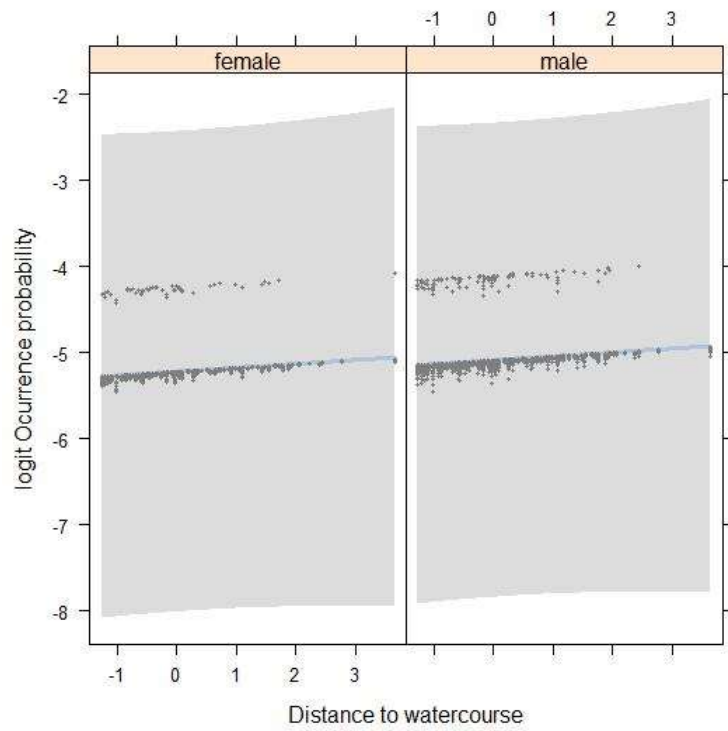
Without interaction

Sampling effort	21.142	1	<b>0.000004 ***</b>
Habitat type	1.285	2	0.525
Distance to humans settlement	1.293	1	0.255
Distance to water	0.153	1	0.695
Sex	0.185	1	0.667

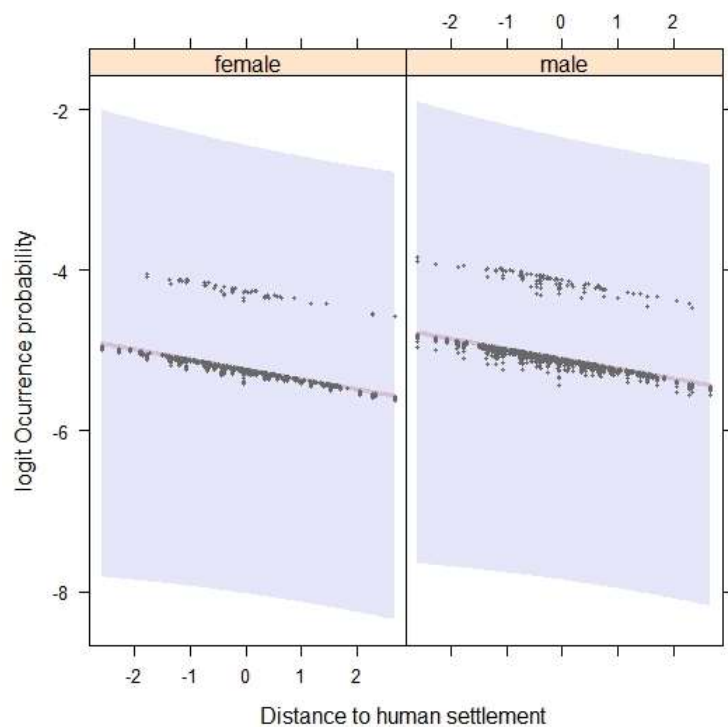


**Fig. 2.** Conditional plots of Jaguar occurrence probability in relation to habitat  $\times$  sex interaction. Occurrence probability is shown on logit scale. Each point ( $n = 7790$ ) represents a given individual

(n = 38) in a given site (n = 205). Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors. ch: chavascal; va: high varzea; vb: low varzea.



**Fig. 3.** Conditional plots of Jaguar occurrence probability in relation to distance to watercourse x sex interaction. Occurrence probability is shown on logit scale. Each point (n = 7790) represents a given individual (n = 38) in a given site (n = 205). Distance to watercourse was scaled to zero mean and unit variance. Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors.



**Fig. 4.** Conditional plots of Jaguar occurrence probability in relation to distance to human settlement  $\times$  sex interaction. Occurrence probability is shown on logit scale. Each point ( $n = 7790$ ) represents a given individual ( $n = 38$ ) in a given site ( $n = 205$ ). Distance to human settlements was scaled to zero mean and unit variance. Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors.

Even when we removed interactions between sex and other variables and tested only for independent effects, nothing other than sampling effort had detectable influence on occurrence probability (**Table 2, Supplementary data**).

#### 4. Discussion

Our long-term data set allowed us to consider individual variability induced by home-range location, which strengthens the conclusion that jaguars are generalists in the varzea of central Amazonia during the non-flooded season. However, our results do not support conclusions related to differences between sexes in habitat use, proximity to water or avoidance of humans. The difference between this and previous studies may be due to sampling and analytical features, but may also be related to the unique environmental characteristics of the varzea of central Amazonia.

Although jaguars may show preference for forested areas, strong association with watercourses, and tend to avoid human presence (Astete et al. 2008; Cullen et al. 2016; 2018; Petracca et al. 2018; Figel et al. 2019), these choices can differ between males and females (Conde et al. 2010; Colchero et al. 2011) and response may be scale dependent (Rich et al. 2017). Most of these generalizations have been based on studies with a small number of individuals and, thus, are prone to sampling bias. This makes interpretation of the results difficult, because random placement of home ranges could lead to proportion of habitat categories available different from those representing the natural variation of the landscape (Wiens 2008). Furthermore, methods of analysis of spatially correlated data, such as torus translation (Harms et al. 2001), are available, but most analyses of jaguar distributions have not taken into account potential problems due to spatial autocorrelation.

Our results indicate that, in the varzea of Central Amazonian, jaguar occurrence probability was unrelated to the type of vegetation, regardless of sex. Jaguars used high varzea, low varzea and chavascal in our study area with similar probability to their availability. Both low and high varzea have close to 100% tree cover, but chavascal is an open formation, often with flooded shrubby vegetation and few trees located in lower areas or extensive mud flats. Although preliminary studies in MS DR indicated that jaguars were most frequently found in the lowest areas in the reserve (Ramalho & Magnusson 2008; Alvarenga et al. 2018), none of the studies have discriminated jaguar habitat use between sexes. However, others studies have reported that females may select habitats with higher quality, that give them better access to shelter and prey (Oliveira et al. 2018; Gese et al. 2018), and a preference of females for primary forest, whereas

male jaguars are more likely to use open areas, such as pasture and agriculture (Conde et al. 2010). On the other hand, a recent study involving 40-telemetered individuals arising from different biomes and considering continental scale, including a few individuals from MSDR, did not find significant differences between sexes and response to environmental variables, although, they found a positive correlation between occurrence and forest cover (Morato et al. 2018). The number of individuals assessed in each site was low, and studies at a continental scale may not reveal relevant patterns occurring within local landscapes, but that study corroborates our analysis where we found that both male and female jaguars exhibited similar preferences in the same natural habitat.

Jaguar occurrence is usually higher near water bodies (Hatten et al. 2005; Zeller et al. 2011; Sollmann et al. 2012; Astete et al. 2017; Sunquist and Sunquist 2014), however, it is not clear whether this relationship varies between sexes. Although some studies have reported males selecting locations closer to water sources than females (Sollmann et al. 2011; Gese et al. 2018), in other females have higher activity associated with proximity to flowing water (Foster et al. 2010). We did not find any evidence of this association in either sex. In seasonally flooded ecosystems, a significant portions of the jaguar's diet may be comprised of aquatic and semiaquatic species (Ramalho and Magnusson 2008; Da Silveira et al. 2010; Azevedo and Verdade 2011) suggesting that there might be pressure to select areas close to water. However, in places where large and permanent water sources are available throughout the year, distance to water may have no impact on jaguar occurrence (Avila-Najera et al. 2019; Figel et al. 2019). According to a previous study in MSDR, conducted during the low-water season, the distribution of the main arboreal prey is positively correlated to jaguar occupancy (Rabelo et al. 2019). The reserve sustains high caiman densities (Da Silveira et al. 2008), one of the main prey of jaguar in this system (Ramalho 2006). Since camera traps do not detect the main prey of jaguar in MSDR, we were not able to use them to predict jaguar occurrence in this study. Because MSDR is a varzea site and an island limited by two of the widest rivers in Amazonia, it is possible that proximity to water is not a good predictor of jaguar occurrence in this environment.

Large-carnivore males can be more tolerant of human-modified areas (Conde et al. 2010; Foster et al. 2010; Gantchoff et al 2019), and are more likely to cause human-wildlife conflicts than females (Ramalho 2012). Females, on the other hand, seem to avoid human-dominated areas (Zarza et al. 2007; Conde et al. 2010), with low human densities (Colchero et al. 2011). We did not find any influence of distance to human settlement or sex on jaguar distribution, though these relationships may differ in another period of the year. Although human presence has been found to be an important factor that negatively affects the occurrence and activity of jaguars in some studies, it does not seem to influence their occurrence where undisturbed environment is surrounded by dense vegetation cover (Avila-Najera et al. 2019) and inside protected areas with low

human pressure (De Angelo et al. 2013) such as in our study site. Evidence of human activities is negatively correlated with the probability of jaguar occurrence, most likely because it is correlated with density of hunters (Jędrzejewski et al. 2017; 2018), and prey and predator abundance decline with human access (Espinosa et al. 2018). In a study conducted in MSDR, based on interviews with local people, the mortality rate for jaguars killed by hunters was almost twice as higher for males than for females, which was attributed to differences in movement patterns between sexes (Ramalho 2012). The lack of evidence for an effect of distance from human settlements on the distribution of jaguars in MSDR is probably because the density of people is low in all areas and hunting pressure on jaguar prey is relatively light.

Previous studies, suggested that jaguar populations appear to be much less vulnerable to extirpations in humid and highly productive zones than in dry and unproductive areas (Jędrzejewski et al. 2017). MSDR soils are high in plant nutrients, which results in high productivity (Furch 1997). Therefore, resources in the varzea are probably not a limiting factor for jaguars. The use of a given habitat relative to its availability strongly varies in response to environmental conditions, leading to very different habitat selection processes across contrasted environments. Thus, in productive environments, habitat selection process may not respond to habitat heterogeneity (Gaudry et al 2018). Altogether, our results indicate that, at this landscape and during the low water season, jaguars use space randomly relative to the investigated factors, a finding which is only evident when the population is reasonably sampled.

## **5. Conclusions**

Amazonia plays a key role for long-term conservation of the jaguar and holds 50% of the jaguar's current range, which is the reason why it has long been considered the species' stronghold (Sollmann et al. 2008; Lorenzana et al. 2020). The varzea, despite being the Amazonian forest type with the highest human presence, is an important stronghold for jaguars and should be protected wherever possible. While most studies have showed that jaguars are positively associated with forest cover and water source, and negatively related to human presence (De Angelo et al. 2013; Morato et al. 2018), our results suggest that in MSDR, jaguars are generalists, exploring all environments with similar probability, at least during the low water season. Human settlements apparently have little effect on space use by jaguars in the varzea, which may lead to more intense conflict with humans if the density of settlements increases.

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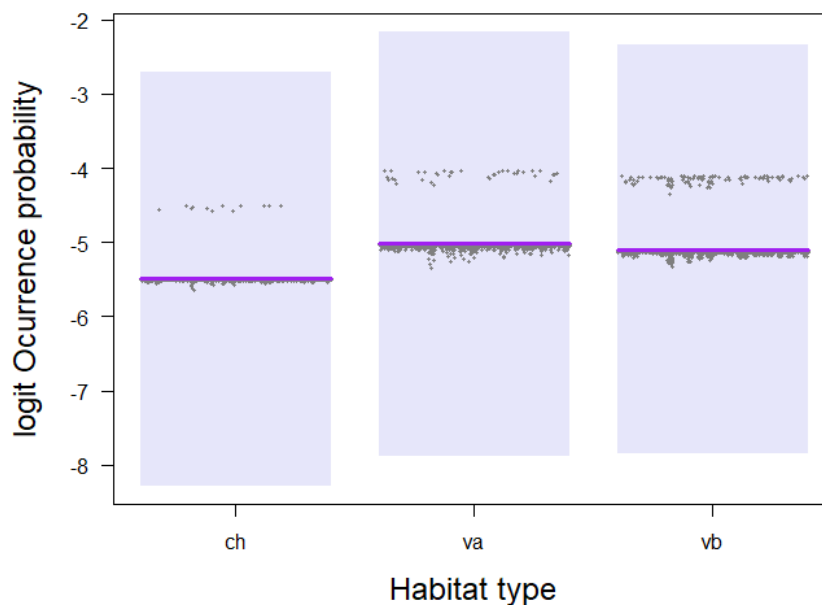


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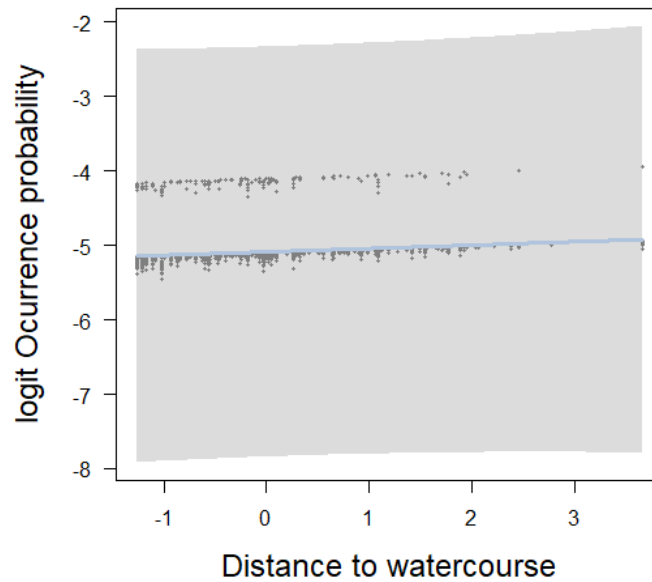
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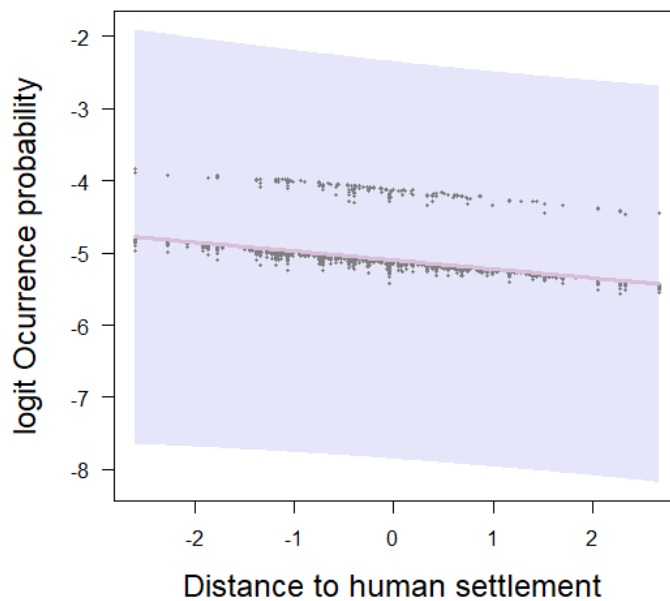
### Supplementary data



**S1 Fig.** Conditional plots of Jaguar occurrence probability in relation to habitat. Occurrence probability is shown on logit scale. Each point ( $n = 7790$ ) represents a given individual ( $n = 38$ ) in a given site ( $n = 205$ ). Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors. ch: chavascal; va: high varzea; vb: low varzea.



**S2 Fig.** Conditional plots of Jaguar occurrence probability in relation to distance to watercourse. Occurrence probability is shown on logit scale. Each point ( $n = 7790$ ) represents a given individual ( $n = 38$ ) in a given site ( $n = 205$ ). Distance to watercourse was scaled to zero mean and unit variance. Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors.



**S3 Fig.** Conditional plots of Jaguar occurrence probability in relation to distance to human settlement. Occurrence probability is shown on logit scale. Each point ( $n = 7790$ ) represents a given individual ( $n = 38$ ) in a given site ( $n = 205$ ). Distance to human settlements was scaled to

zero mean and unit variance. Grey areas indicate 95% confidence intervals. Plots show focal relationships after accounting for remaining predictors.

## **Conclusão**

Os solos da RDSM são ricos em nutrientes das plantas, o que resulta em alta produtividade (Furch 1997). Portanto, os recursos nas florestas de várzea do rio Amazonas provavelmente não são limitantes para as onças-pintadas. O uso de um determinado habitat em relação à sua disponibilidade varia em resposta às condições ambientais, e pode levar a processos na seleção de habitat muito diferentes, contudo, em ambientes altamente produtivos, a resposta seletiva à heterogeneidade de um determinado habitat pode não ocorrer (Gaudry et al 2018).

A Amazônia desempenha um papel fundamental para a conservação a longo prazo da onça-pintada, e detém 50% da área de distribuição da espécie, razão pela qual tem sido considerada refúgio da população (Sollmann et al. 2008; Lorenzana et al. 2020). A várzea, apesar de ser o tipo de floresta amazônica com maior presença humana, é um reduto para onças-pintadas e deve ser protegida sempre que possível. Embora a maioria dos estudos tenha mostrado que as onças-pintadas estão associadas positivamente à cobertura florestal e à proximidade de fontes de água e negativamente relacionadas à presença humana (De Angelo et al. 2013; Morato et al. 2018), nossos dados indicam que, na RDSM, as onças-pintadas são generalistas, explorando todos os ambientes com semelhante probabilidade, pelo menos durante a estação seca. Isso tem implicações positivas e negativas para a conservação; aparentemente, as comunidades humanas têm pouco efeito no uso do espaço por onças-pintadas na várzea, mas isso pode levar a conflitos com os seres humanos, principalmente se a densidade dessas populações humanas aumentar no futuro.

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