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Running Header: Jaguar detection and occupancy in Amazon islands

# Big cats like water: jaguar occupancy pattern in a unique Brazilian Amazon insular ecosystem

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## Abstract

Patterns of detectability and occupation of the jaguar (*Panthera onca*) vary along its distribution, being determined mainly by vegetation cover, prey availability, and anthropogenic factors. However, there is still a large gap about what determines the occupancy of jaguars, mainly in the Amazon. This knowledge is even more deficient in oceanic islands, which present unique and very sensitive ecosystems, such as in the Maracá-Jipioca islands, northeastern Brazilian Amazon. Thus, our study aims to understand the spatial ecology of jaguars in an unique insular ecosystem and provide information to allow a sustainable management of its populations. For this, we assessed how different drivers (vegetation type and prey availability) can potentially exert any influence on the detectability and occupancy patterns of jaguars in Maracá-Jipioca islands. We found that higher percentages of wetland (beach-sea and lagoon-canal) cover were the main promoters of jaguars' detectability and occupancy. In addition, the occurrence of Anseriformes, tegus, agoutis, and giant anteaters were all included in the overall best occupancy model. The present study is the first to elucidate which factors drive jaguar insular population spatial ecology and how the environmental context is currently shaping this population ecology and how it will react of the forecasted climate change scenarios. Despite imminent threats to the region, the use of the knowledge generated in this study can help the sustainable management of jaguars, and maintain the fundamental and exclusive ecosystem services provided by this top predator.

**Keywords:** Amazon rainforest, conservation plan, Maracá-Jipioca, *Panthera onca*, prey availability, wetland conservation.

## Resumo

**Comentado [LMCR1]:** Alterar de acordo com o que foi mudado na versão inglesa

Os padrões de detectabilidade e ocupação da onça-pintada (*Panthera onca*) variam ao longo de sua distribuição, sendo determinados principalmente pela cobertura vegetal, disponibilidade de presas e fatores antropogênicos. No entanto, ainda há uma grande lacuna sobre o que determina a ocupação das onças-pintadas, principalmente na Amazônia. Esse conhecimento é ainda mais deficiente em ilhas oceânicas, que apresentam ecossistemas únicos e muito sensíveis, como nas ilhas de Maracá-Jipioca, nordeste da Amazônia brasileira. Assim, nosso estudo visa compreender a ecologia espacial das onças-pintadas para um ecossistema insular único e fornecer informações para um manejo sustentável. Para isso, avaliamos como diferentes condutores (tipo de vegetação e disponibilidade de presas) podem exercer alguma influência na detectabilidade e nos padrões de ocupação de onças-pintadas nas ilhas de Maracá-Jipioca. Descobrimos que a porcentagem de cobertura praia-mar e lagoa-canal foram os principais fatores de detectabilidade e padrões de ocupação de onças-pintadas. Além disso, a ocorrência de Anseriformes, tegus, cutias e tamanduás-bandeira foram todos incluídos no melhor modelo geral de ocupação. O presente estudo é o primeiro a elucidar quais fatores impulsionam a ecologia espacial da população insular da onça-pintada e como o contexto ambiental está atualmente moldando essa ecologia populacional e como ela reagirá aos cenários de mudanças climáticas previstos. Apesar das ameaças iminentes à região, o uso do conhecimento gerado neste estudo pode auxiliar no manejo sustentável das onças-pintadas, mantendo os serviços ecossistêmicos fundamentais e exclusivos prestados por um predador de topo.

**Palavras-chave:** Floresta Amazônica, plano de conservação, Maracá-Jipioca, *Panthera onca*, disponibilidade de presas, conservação de áreas úmidas.

## INTRODUCTION

The jaguar (*Panthera onca*) is one of the most widely distributed apex predators worldwide and the biggest cat inhabiting the western hemisphere (Hunter 2020). Its extensive distribution range in the Americas have led it to explore very distinct landscapes, ranging from rainforests to savannas, dry tropical forests, and sub-tropical scrublands, some of which are seasonally flooded (Rabinowitz and Zeller 2010). Such a wide range of habitats and its threatened status (Near threatened - Quigley et al. 2017) have created the opportunity and the motivation for researchers to assess this felid 's occupancy patterns, revealing that some broader drivers (e.g., vegetation cover and food availability) shape those patterns throughout most of its distribution area (Villalva and Palomares 2022).

Although the environmental context may change drastically between areas occupied by jaguars (from Northern Mexico to Northern Argentina), three main drivers seem to determine the estimated occupancy patterns. The first two drivers, abundance of prey and the protection of its native habitats, have a positive influence, while anthropic activities have a negative effect on the jaguar's occupation: 1) prey availability, e.g., calves of domestic cattle (*Bos taurus*) and collared peccaries (*Pecari tajacu*) in the Sonora region in Northwestern Mexico (Anile et al. 2020), green turtles nesting sites in Costa Rica (Arroyo-Arce et al. 2014), and brown-throated sloths (*Bradypus variegatus*) and the red howler monkeys (*Alouatta juara*) in Amazonian floodplain river islands of Western Brazil (Rabelo et al. 2019); 2) broad native vegetation cover, e.g., subtropical vegetation cover in Sonora, Mexico (Anile et al. 2020), net primary production in central America (Calderón et al. 2022) and Cerrado cover in Central Brazil (Sollmann et al. 2012); and 3) disturbance, e.g., human settlements in central America (Calderón et al. 2022), windfarms in a Caatinga area in NE Brazil (Dias et al. 2019), and distance from Natural Park edges in the Iguazu National Park, southern Brazil (da Silva et al. 2018).

Nevertheless, jaguars seem to be tolerant to some degree of habitat disturbances, as they can move through deforested and anthropogenic areas (Balbuena-Serrano et al. 2021). But the functional role of such areas is sometimes not completely understood, i.e., migration route or a potential area to establish (de Azevedo and Murray 2007; Foster et al. 2010; Amit et al. 2013; Carral-García et al. 2021). Although occupancy studies covered most of jaguar's range and landscape contexts, no study targeted insular population of this large felid, where environmental conditions, and particularly the higher isolation, can pose extra challenges for individual survival.

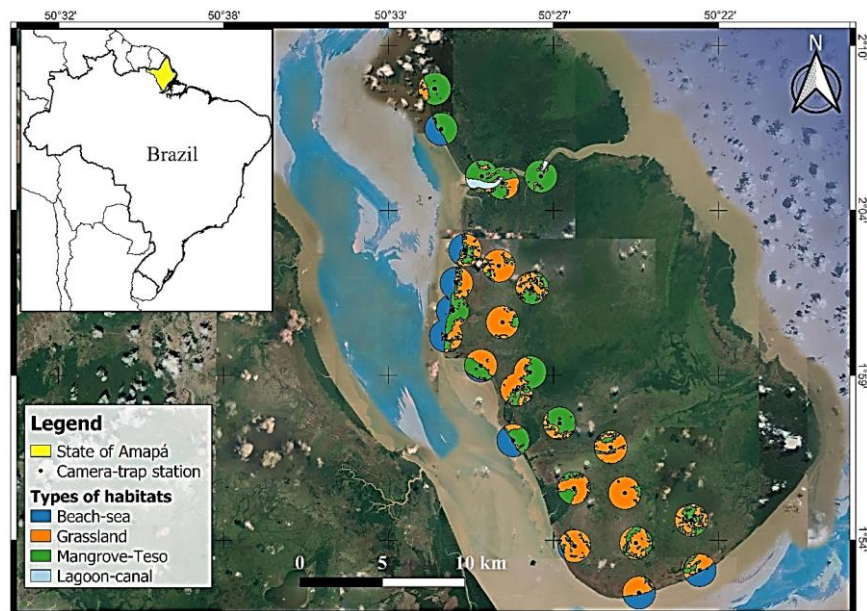
The *Estação Ecológica Maracá-Jipioca* (ESEC-MJ), located in an Amazon Sea Islands, is one of such systems. It is characterized by extensive beaches, mangroves, flooded grasslands, and wetlands, which create a Neotropical humid region with unique characteristics (Ferreira et al. 2017). Located on the northern coast of the Amazon, under the influence of the Amazon River delta, at approximately 6 km from the mainland, it is characterized by flooded areas and lagoons. A significant part of the islands experiences daily tides of 10-m amplitude, which flood extensive beach areas (Anthony et al. 2014, 2021; Santos et al. 2016; Ferreira et al. 2017). The ca. 60,000-ha islands harbor high concentrations of jaguar preys (e.g., fish, crocodilians, turtles, and wetland birds - Ferreira et al. 2017) and, consequently, hosts an abundant population of jaguars (6.67 individuals/100 km<sup>2</sup>), whose occupancy patterns are probably influenced by the hydrodynamics of the islands and its influence on water dependent preys (Duarte et al. 2022). Despite islands spatial limitation, they can still provide a wide array of food resources, both linked to aquatic and terrestrial systems, that can be exploited by a largely tolerant and opportunistic predator, such as jaguars (Jędrzejewski et al. 2018; Duarte et al. 2022; Friedeberg-Gutiérrez et al. 2022). The unique conditions of the Maracá-Jipioca islands ecosystems shape jaguar's ecology and behavior patterns, with a higher dependence of both aquatic and terrestrial resources (Sanderson et al. 2002; Morato et al. 2016; Ferreira et al. 2017; Duarte et al. 2022). These dynamic relationship to both types of ecosystems can be fundamental for the maintenance of wildlife communities and the ecosystem services this large felid provides (Arias-Alzate et al. 2017; Craighead and Yacelga 2021).

Therefore, to better understand the ecological adaptation of jaguars to this unique insular ecosystem and provide information to a sustainable management of the ESEC-MJ, it is fundamental to understand the processes that drive the use of different habitats by the jaguar, assess the occupancy pattern and the factors that determine those patterns. Our study aims to fulfill this information gap by assessing if the land/water interface habitats present near the lagoons, canals, and beaches, together with the occurrence of jaguars most consumed preys' species (e.g., fishes), can potentially exert any influence on the detectability and occupancy patterns of jaguars in Maracá-Jipioca islands. We hypothesize that jaguars will be more easily detected in habitats with reduced vegetation cover, such as beaches, and those dominated by perennial water environments (e.g., lagoons) (Duarte et al. 2022). Moreover, we predict that the jaguars' occupancy will be promoted by a higher probability of prey occurrence (Eriksson et al. 2022). We address these issues by applying a camera-trap approach supplemented by analysis of the

frequency of prey in the diet, to assess how habitat type and habitat mediated prey occurrence can influence the spatial ecology of a unique insular population of jaguars.

## METHODOLOGY

*Study area.* — Our study was conducted in Maracá-Jipioca islands (02°01'13"N, 50°30'20"W), located on the coast of the Brazilian Amazon (Fig. 1), with its origin being associated to erosion processes and deposits of tertiary sediments on consolidated mud (Allison et al. 1995; Nitttrouer et al. 1995). Maracá-Jipioca islands are a federal protected area constituted mostly of estuarine habitats in the Amazon coast (Ferreira et al. 2017). With an annual rainfall ranging from 2,300 to 2,800 mm (Am climate type according to Köppen's climate classification) and small variation in elevation, with average altitudes of three meters, the islands shelter extensive flooded areas and lagoons (Tavares 2014; Ferreira et al. 2017). The distance from the islands to the nearest continent region ranges from six kilometers to 10 km (Ferreira et al. 2017; Duarte et al. 2022). The vegetation of the islands is basically composed of mangroves, grasslands, and mixed vegetation formations (locally called *tesos*) of mangrove tree species (*Rhizophora* sp. and *Avicennia* sp.), bamboo (*Guadua* sp.), and shrubs (Ferreira et al. 2017). It harbors at least eleven vertebrate orders described and/or recorded as jaguar's prey, with e.g., Tegus, shorebirds, rodents, and ungulates. But no other species of terrestrial carnivores inhabit the islands, probably due to spatial limitation added to the hard competitive pressure that the jaguar imposes. Therefore, the jaguar functional role as a predator is irreplaceable (Duarte et al. 2022).



**Figure 1-** Maracá-Jipioca islands location and camera-trap sites used to assess jaguar detectability and occupancy patterns. The circles represent habitat composition of each camera-trap station based on four types of habitats: grassland, mangrove-Teso, beach-sea and lagoon-canal. To assess the percentage of cover of each habitat type within a buffer area of one kilometer radius around each monitoring station

**Comentado [LMCR2]:** Herbert, na resposta aos revisores diz que acrescentaste nesta figura um mapa de vegetação para o leitor ver que o que amostraste é representativo da área. Mas aqui apenas tens a vegetação nos buffers. Tens que colocar a vegetação de toda a ilha

*Field Survey.* — Camera traps are a widely used non-invasive method to survey wild felids as they provide reliable data to assess wildlife space use and occurrence patterns, allowing population-level inferences (Hebblewhite and Haydon 2010; Burton et al. 2015; Karanth et al. 2017; Carvalho et al. 2019). Our detection data was gathered from 25 camera-trap stations, installed at an average distance of  $2.4 \pm 1.1$  km from one another, that were active for a 90 days session, from November 25 2018 to February 22 2019 (Duarte et al. 2022). Each station (considered a spatial replica) contained two paired camera traps (Bushnell Trophy Cam HD), installed 30–60 cm above the ground. Due to the logistical limitations for install camera-traps across the island, we selected the major continuous region, with access, and sufficiently representative of the entire island landscape. Our camera grid minimum convex polygon covered 25% of the total area of the island (Duarte et al. 2022). The cameras were left functioning continuously and programmed to take three sequential photos and a 40s video when triggered. The total sampling effort was 2,250 station-trap days (i.e., number of stations multiplied by the number of days that they were active; Srbeek-Araujo and Chiarello 2007). We did not use baits to avoid any interference in the detection probability of jaguar and/or of your preys (Duarte et al. 2018).

*Camera-trap stations characterization.* — Each camera-trap station was characterized based on a set of environmental variables that best represent the landscape context of the islands and that, according to other studies targeting jaguars, may influence the detectability and occupancy patterns of this species (Ferreira et al. 2017; Duarte et al. 2022). Thus, we determined the habitat composition of each camera-trap station based on four types of habitats: Wetland (beach and sea, Lagoons and Canals), grassland, mangrove and *Teso* (Ferreira et al. 2017) (Table 1). We used raster information of the islands and the surrounding sea areas available in MapBiomass web platform (MAPBIOMAS 2022) to assess the percentage of cover of each habitat type (Fig. 1). These data were imported to the software QGIS, and we assessed the percentage of each habitat type within a buffer area of one kilometer radius around each monitoring station (Allen et al. 2022; McManus et al. 2022; QGIS Development Team 2022). The size of this area was determined based on the distances between camera trap stations, i.e., c.a. 50% of the average distance between each station. In addition, we also used the software Google Earth Engine, to estimate the distance from each monitoring station to the water, sea, lagoons, and canals (Gorelick et al. 2017) (Table 1).

*Prey selection.* — Data on mammals, reptiles, and birds recorded that had registrations in more than five monitoring stations and previously described or recorded as jaguar prey (see González and Miller 2002; Duarte et al. 2022), were considered as possible drivers of jaguar occupancy patterns. From all the mammals detected, we considered only four mammals' species as potential jaguar prey: agouti (*Dasyprocta leporina*), black-eared opossum (*Didelphis marsupialis*), giant anteater (*Myrmecophaga tridactyla*), and white-tailed deer (*Odocoileus virginianus* – Table 1). The lizard tegu (*Salvator merianae*) was the only species of reptile that we included in the analysis since it can be predated by the jaguar (Table 1). Finally, we included as potential jaguar prey three orders of birds: Anseriformes, Gruiformes, and Pelecaniformes (Table 1). We did not consider in species level the shorebirds, since these animals present a social behavior, and our records correspond to mixed flocks, which induce super abundance estimates (Miller 1984; Farmer and Durbian 2006; Lanctot et al. 2008). Despite the recognized consumption of crocodilians, testudines, and fishes (Supplementary Information – Table S1), we could not estimate their abundance based on the camera-trap data (camera-trap is not an adequate method to sample those species and thus no detection of all those groups were recorded). Therefore, they were not



considered as drivers in the occupancy model analysis. However, we are aware that these groups are present on the islands (personal observation) and in jaguar's diet (Supplementary Information – Table S1), and thus can also influence somehow this felid spatial ecology.

*Data Analysis.* — The detectability and occupancy patterns of jaguars and their main preys were assessed using an occupancy modelling approach, developed by MacKenzie et al. (2017). This modelling procedure estimates the probability of a site being occupied/used ( $\psi$ ) by jaguar and/or its preys when the detection is imperfect (detection probability less than 1, i.e., species is present but not detected). We structured our model considering 25 sites (stations of camera-trap) divided into six occasions of 15 days. We also scale the environmental variables (ha) and prey probability (%) for safety into maximum likelihood estimates (Arnold 2010). Prior to the modeling procedure, we tested the correlation between variables by estimating the Spearman correlation coefficient between all independent variables and considered that no important correlation existed if the correlation was lower than 0.7 and greater than -0.7 (Dormann et al. 2013).

The modeling procedure was implemented in two phases, according to the following approach. First, we tested what factors were more influential in determining the target species detectability, while maintaining the occupancy constant (i.e.,  $\psi=1$ ). We tested four environmental variables as drivers of jaguar detectability and for each of its individual prey (Table 1 – Environmental variables). We have built models corresponding to all combination of these four variables and ranked the models according to the Akaike Information Criterion (AIC) (Burnham et al. 2011). We also calculate the overdispersion factors ( $c\text{-hat}$ ) to verify the overdispersion of our best models MacKenzie et al. (2017). The model with the lowest AIC and a  $\Delta AIC=0$  (difference between the AIC of the model and the lowest AIC value; MacKenzie et al. (2017) was identified as the best models and the variables included in this best model were considered the most influential variables of the detectability component of all subsequent models (Castro et al. 2022). Secondly, we used the variables included in the best detectability model and include them in all models built subsequently to assess the drivers of occupancy. We followed the same approach described above for model building and selection (Castro et al. 2022) regarding the occupancy modeling. However, here we tested three different hypotheses: H1 - jaguar occupancy was mostly determined by environmental variables (i.e., habitat) (Table 1); H2 – Jaguar occupancy is more dependent of its potential prey occupancy pattern (Table 1) (i.e., prey); H3 – Jaguar occupancy patterns are determined by the

**Comentado [LMCR3]:** Mas atrás falas de "four environmental variables"

concurrent action of two different mechanism – habitat characteristics and prey occupancy (Table 1) (i.e., habitat + prey). Therefore, we built three sets of models. For hypothesis 2 (prey), we first built occupancy models for each of the considered prey individually and identified the best model for each species (using the same procedure as for the jaguars). We used the occupancy prediction of each of those prey models to estimate the probability of occupancy of each prey per camera-trap. Then we converted the probability obtained in percentage for consider as approximate prey availability and used these as co-variables in H2 and H3. We have identified the hypothesis with a high support as that whose best occupancy model presented the lowest AIC values (i.e., overall  $\Delta AIC=0$ ). We identified the informative variables by highlighting those whose 95% confidence interval of the coefficient did not include the 0 (Arnold 2010), i.e. we were confident that if influence on jaguar occupancy was positive or negative.

For these analyzes, we have used the software ‘R’ (R Core Team 2022) and the packages ‘camtrapR’ (Niedballa et al. 2016), ‘unmarked’ (Fiske and Chandler 2011), ‘wiqid’ (Meredith 2020), ‘AICcmodavg’ (Mazerolle and Mazerolle 2017), and ‘MuMIn’ (Barton 2009a; b).

1

2

**Table 1.—Explanatory variables used to test each formulated ecological scenarios about jaguars' detectability and occupancy patterns in Maracá-Jipioca islands**

Hypothesis	Variable	Data Type	Description
Environmental variables (H1) (Characteristics of the sites in which cameras traps were set, grouped in seven categories of environmental variables: Habitat composition [Mangrove and <i>Teso</i> ; Grasslands; Wetland (Beach and Sea; Lagoons and Canals)]; Distance to habitats (Sea, lagoons, and canals)	Grassland	Numerical continuous	proportion in hectares of Grassland within the 1 km radius
	Mangrove and <i>Teso</i>	Numerical continuous	proportion in hectares of Mangrove and <i>Teso</i> within the 1 km radius
	Wetland	Numerical continuous	proportion in hectares of Beach and sea within the 1 km radius
	Distance water	Numerical continuous	Distance of camera traps to the water (sea, canals, and lagoons) (m)
Prey variables (H2) (Occupancy probability of different jaguar prey in each camera trap station)	Probability occurrence Agouti	Numerical continuous	Probability of occurrence of Agouti (0–99%)
	Probability occurrence White-tailed deer	Numerical continuous	Probability of occurrence of White-tailed deer (0–99%)
	Probability occurrence Giant anteater	Numerical continuous	Probability of occurrence of Giant anteater (0–99%)
	Probability occurrence Back-eared opossum	Numerical continuous	Probability of occurrence of Back-eared opossum (0–99%)
	Probability occurrence Tegu	Numerical continuous	Probability of occurrence of Tegu (0–99%)
	Probability occurrence Anseriformes	Numerical continuous	Probability of occurrence of Anseriformes (0–99%)
	Probability occurrence Gruiformes	Numerical continuous	Probability of occurrence of Gruiformes (0–99%)
	Probability occurrence Pelecaniformes	Numerical continuous	Probability of occurrence of Pelecaniformes (0–99%)
Environmental and prey variables (H3)	Environmental variables + Occupancy probability of preys	Numerical continuous	Environmental variables (H1) together with the occupancy probability of each prey (H2)

3

## RESULTS

We obtained 32 independent detections of jaguars (i.e. at least 30m apart) in 16 stations and with at least one record in each of the six 15-day sessions. Mangrove and *Teso* were negatively correlated ( $r = -0.728$ ) with grassland and positively with Gruiformes occupancy ( $r = -0.857$ ). Grassland showed a negative correlation with the prey species occupancy *D. leporina*, *D. marsupialis* and *S. merianae* ( $r = -0.826$ ;  $r = -0.816$ ;  $r = -0.769$ ; respectively). *M. tridactyla* was the only species with positive correlation with the variable distance to water ( $r = 0.701$ ). The Gruiformes group was also correlated positively with *S. merianae* ( $r = 0.880$ ), and *D. leporina* with *D. marsupialis* ( $r = 0.843$ ) (Supplementary Information – Table S2). Therefore, we tested two different scenarios for the detectability models and for hypothesis H1: one with mangrove and *Teso* and the other with grassland. Four scenarios/models were considered for the hypothesis H2: *D. leporina* and *S. merianae*, *D. marsupialis* and *S. merianae*, *D. leporina* and Gruiformes, and *D. marsupialis* and *S. merianae*. Finally, for hypothesis H3 we consider the variables of the best model between the scenarios excluding those with correlation (Supplementary Information – Table S4).

Regarding the jaguar models, we identified that a greater proportion of wetlands and the distance for water were the most influential drivers promoting of detectability (i.e.,  $\Delta AIC = 0$ ; Table 2). However, for predictor of detectability on our occupancy models, we consider only the variable of wetland due its significance ( $p < 0.01$ ) and to the absence of correlation with the other variables (Supplementary Information – Table S2). Although we examined several covariates and relatively few sites, the overdispersion factors were not significant, so there was no need to consider QAIC and the presented models are the most parsimonious for the description of our data. The occupancy hypothesis that had the highest support of our data among the tested scenarios, comprising the model with the lowest AIC and significance in relation to the tested variables, was the one that considered only habitats as drivers of occupancy patterns (i.e., H1; Table 3).

**Table 2.—** Detection probability models, ranked by  $\Delta AIC$  [degrees of freedom (df), AIC and  $\Delta AIC$ ; p – detection probability;  $\Psi$  (1) – constant occupancy probability; Only the three models with the higher fit (lower AIC) and weight higher with 0.1, per scenarios, are presented] and the summary of the best overall detectability model [Estimated variables coefficients; Coef – Coefficients; SE – Standard Error; P-value; CI95% - 95%Coefficient Confidence Interval)].

Model	df	AIC	ΔAIC	Weight	
$p$ (Wetland + distance for water), $\Psi$ (1)	4	136.5	0.0	0.600	
$p$ (Wetland + distance for water + grassland), $\Psi$ (1)	5	138.5	1.95	0.226	
$p$ (Wetland), $\Psi$ (1)	3	140.1	3.57	0.101	
Best model characteristics					
Estimated variables coefficients	Coef	SE	Z value	P	CI 95%
Intercept					
Wetland	0.68	0.24	2.8	0.005	0.28 / 1.09
Distance for water	-1.02	0.55	1.8	0.06	-1.92 / -0.11

**Comentado [LMCR4]:** Herbert, faltam os valores do intercept

**Table 3. —**Top occupancy models per hypotheses and your respective scenarios; habitat, preys, and habitat + prey. The model best supported by our data (i.e., overall  $\Delta AIC = 0$ , AIC= 138.9 and weight 0.640) is the top model in habitat (Supplementary Information – Table S4). P – detection probability;  $\Psi$  – occupancy probability; df - degrees of freedom; AIC - Akaike Information Criterion;  $\Delta AIC$  – the difference in AIC between the top model within each scenario and weight.

Model	df	AIC	$\Delta AIC$	Weight
$p$ (Wetland), $\Psi$ (distance for water) (H1)	4	138.9	0.0	0.640
$p$ (Wetland), $\Psi$ (Back-eared opossum+ Gruiformes+ giant anteater) (H2)	6	137.8	0.0	0.689
$p$ (Wetland), $\Psi$ (distance for water) (H3)	4	138.9	0.0	0.412

According to the overall best model, jaguar detectability was significantly higher (i.e., the 95% confidence interval of the variables' coefficient did not include the 0) on environments with higher proportions of wetlands with access to the sea (Table 4). The occupation of the jaguar was significantly higher near environments the water; sea, lagoons, and channels (Table 4). Furthermore, some of the evaluated preys also seem to slightly influencing jaguar's occupancy pattern, as the probability of occurrence of the Gruiformes, *D. marsupialis*, and *M. tridactyla* were all included in the best prey's models (H2) (Table 4 and Information – Table S4). Although all seem to have a positive influence on jaguar occurrence, they are not present significantly relation and their effect is questionable (Table 4).

Table 4.—Estimated variables coefficients for the overall best models from H1 and H2 to explain the occupancy, produced to explain jaguars' detection and occupancy patterns (Coef – Coefficients; SE – Standard Error; Z-value; p – p-value; CI95% - 95% Coefficient Confidence Interval).

Best H1 model  <i>p</i> (Wetland), <i>ψ</i> (distance for water)	Detection	Coef	SE	Z value	P	
	Variable coefficients					CI 95%
	Intercept	-1.11	0.28			-1.58 / -0.64
	Wetland	0.75	0.23			0.35 / 1.14
	Occupancy	Coef	SE	Z value	P	
	Variable coefficients					CI 95%
	Intercept	1.49	1.25			-0.57 / 3.56
	Distance for water	-2.12	1.28			-4.24 / -0.009
	Detection					
Best H2 model  <i>p</i> (Wetland), <i>ψ</i> (Back-eared opossum+ Gruiformes+ giant anteater)	Variable coefficients					
	Intercept					
	Wetland					
	Occupancy					
	Variable coefficients					
	Intercept					
	Back-eared opossum					
	Gruiformes					
	Giant anteater					

**Comentado [LMCR5]:** Herbert esta tabela tem que ter 2 partes.

A primeira é esta que aqui tens (ou seja relativa a H1 e ao modelo: *p* (Wetland),  $\psi$  (distance for water) (H1) Mas tens também que ter uma parte relativa ao modelo a correspondente ao modelo *p* (Wetland),  $\psi$  (Back-eared opossum+ Gruiformes+ giant anteater) (H2) que tu mencionas atrás e até tem menos AICc

Nas duas partes da tabela para cada variáveis tens que ter a seguinte informação (vê Tabela 2):

Variables coefficient

Coef

SE

Z value

P

CI 95%

Our best models did no showed any significant overdispersion, since the estimated values were  $c\text{-hat}_{H1} = \text{xxx}$ , and  $c\text{-hat}_{H2} = \text{xxx}$ , and its assumed that a models shows no overdispersion or lack of fit if  $c\text{-hat}$  is approximately 1 (MacKenzie et al., 2017).

**Comentado [LMCR6]:** Herbert tens que acrescentar os valores de  $c\text{-hat}$  para os 2 modelos. Convém que sejam próximos de 1

## DISCUSSION

In Maraca-Jipiocá islands wetlands and water associated environments seem to play an important role in Jaguar's spatial ecology. The habitats on the beaches are characterized by open areas with absent and/or reduced vegetation, allowing a greater visibility and consequently a higher probability of detecting an individual which is using the area (Ferreira et al. 2017; MacKenzie et al. 2017; O'Connor et al. 2017). The features of these habitats will also facilitate the displacement of the jaguar in its foraging and territory patrolling bouts and, therefore, such behavior will surely enhance the animal's detection in places with open vegetation characteristics (O'Connell et al. 2011; Kolowski et al. 2021). The detected patterns corroborate this premise as the detection probabilities of jaguars is higher on wetlands, and specifically the beaches of Maraca-Jipiocá islands.

The detection probability of a jaguar is the capacity to detect an individual, when occurring in the monitored site, and therefore a detection indicates that an individual use the surveyed site, but the absence of detection is not indicative of avoidance (MacKenzie et al. 2002). Also, the assumption of use can be misleading as, for example, a moving animal can be detected but not necessarily be occupying that location (MacKenzie et al. 2017; O'Connor et al. 2017). However, in our study the detectability pattern is corroborated by the positive influence of the environments near the canals, lagoons, and sea on jaguar's occupancy probability. These results highlight that the detection in areas with such characteristics indicates that the use of these environments is not exclusive of animals dispersing or moving to other territories, but also of individuals with established territories that commonly use and occupancy these areas in their daily activities (e.g., catching preys). In addition to the advantages linked to an easier travelling route in open habitats, the occurrence of the jaguar in these habitats is also related to the access to prey. There are vertebrate's aggregations inside and around water dominated environments, which allow jaguars to increase their energetic intakes by preying on species linked to both terrestrial (e.g., Back-eared opossum) and aquatic (e.g., Gruiformes) ecosystems (Duarte et al. 2022; Eriksson et al. 2022; see Table 4 and S1). Furthermore, Maracá-Jipiocá islands are subject to daily tides of 10-m amplitude, which flood extensive areas of beaches (up to two kilometers) and canals, creating flooded habitats that favors' jaguar predation in both habitats (Santos et al. 2016; Ferreira et al. 2017; Duarte et al. 2022).

The best model of hypothesis H2 (preys) showed a pattern of preference in the occupancy of jaguar for areas with higher occupancy of some evaluated preys' species. However, results did not allow us to determine any preference for a specific group of prey. Inversely, the model included, a diversified

**Comentado [LMCR7]:** Troquei para corresponder ao que temos no anexo e ao que foi detectado nos modelos

set of prey - Gruiformes, Back-eared opossum (*D. marsupialis*), and giant anteater (*M. tridactyla*) - highlighting that the tested groups, except reptiles, can exert a certain relation about probability of jaguar's occupancy. Jaguars are an opportunistic predator with a varied diet and high tolerance to some degree of disturbances (de Azevedo and Murray 2007; Foster et al. 2010; Amit et al. 2013; Carral-García et al. 2021). Although our models for prey were not significant, the presence of back-eared opossum and Gruiformes corroborates the results of the jaguar feces samples (Supplementary Information – Table S1), showing that these two groups of prey can exert some real influence on the probability of jaguar's occupancy.

A diversified predation behaviors led jaguars to explore preys of both terrestrial and aquatic ecosystems, and such characteristics are highlighted by its diet, which varies between the areas of occurrence (Jędrzejewski et al. 2017; Eriksson et al. 2022; Friedeberg-Gutiérrez et al. 2022). We might have expected that as islands are spatially restricted environments with limited resources, insular populations of a large predator would face challenging survival scenarios (MacArthur and Wilson 2016). Nonetheless, the high frequency of fishes, crocodilians, and other detected prey in the jaguar feces (Supplementary Information – Table S1) show the higher diet breadth of the jaguar population that inhabits the Maracá-Jipiocá islands. Thus, the jaguar has consumed different preys that are available not only on the islands' terrestrial and lagoon environments, but also on the surrounding sea. This capacity to explore niches that are not limited by the island terrestrial boundary might be an ecological strategy that allows this insular population to overcome the adversities imposed by a terrestrial space limitation that may terrestrially prey availability.

We also believe that the inclusion in the occupancy modeling procedure of data on other important prey for this jaguar population would have increase our models' robustness. We couldn't consider fishes and crocodilians occupancy patterns in our models, since the adopted survey protocol (camera-traps) is inefficient to sample both prey groups. In other areas as in the Pantanal and Venezuelan Llanos of the jaguar range these aquatic preys play an important role in the ecology and behavior of jaguars (Jędrzejewski et al. 2017; Eriksson et al. 2022). Although it is plausible to assume that a similar pattern will occur in the Maracá-Jipiocá islands, future studies targeting this felid population in Maracá-Jipiocá islands need to investigate the relationships between aquatic preys and jaguars to assess their ecological importance and how they may influence jaguars' spatial ecology.



The present study is the first to shed light on the factors that drive jaguar insular population spatial ecology. Although we are still understanding the ecological adaptations of this uncommon sea islands population of jaguars, the environmental context currently shaping this population ecology will likely change in face of the forecasted climate change scenarios that will affect the Amazon coastal region. The introduction of exotic species (*Bubalus bubalis*), salinization of freshwater, increase poaching, reduction of land spaces due to increase in sea level, will challenge jaguar survival in the Amazon coast (Anthony et al. 2014, 2021; Dos Santos et al. 2018; Fernandez et al. 2019; Morcatty et al. 2020). Thus, is extremely urgent to understand the dynamics between jaguars and aquatic and terrestrial ecosystems (and their prey) in the area, how it affects their spatial-temporal ecology, whether there is a flux of individuals from and/or to the adjacent continent, and what is the magnitude of such flux. Despite imminent threats to the region, the use of the knowledge generated in this study can support conservation strategies and orientate definition of sustainable management plans for the region. In addition to basing the necessary tools to prevent the reduction or even local extinction of this unique population, and consequently maintain fundamental and exclusive ecosystem services provided by a top predator.

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### **Ethical Statement**

The present work did not obtain direct funding, but the data presented here were collected with the funding and operational logistics support for field research of the World Wide Fund for Nature (WWF-Brazil) and Chico Mendes Institute for Biodiversity Conservation (ICMBio). Therefore, there is no conflict of financial interests. The study is authorized by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). Our methods they are not invasive, and we do not use animal experimentation so there was no need for a specific approval by the appropriate ethics committee for research involving animals.

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## SUPPLEMENTARY INFORMATION

### Prey identification and frequency estimation

From 13 scats samples and seven evidence of consumption, we screened all undigested biological particles: bone, scales, feather, fur, nail, claw, and tooth. Using trichology and optical microscopy techniques, we compared our samples with those of collection of zoology of *Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá* (IEPA), to identify taxa consumed (Sollmann et al., 2013). Altogether we identified at least ten species of vertebrates, but it was not possible to reach the taxonomic level of species for fishes (Table 1). To each prey group  $i$ , we counted frequency of occurrence in scats ( $fs_i$ ) and in the evidence ( $fv_i$ ); when a scats sample contained remains of more than one species, these counted as fractional contributions to the frequency of the respective species (Link and Karanth, 1994). There were no calculations regarding the fractional contributions of the evidence, as they were unconsumed remains from a predation event. We calculated the relative dispersion frequency in scats ( $frs_i$ ) as:

$$frs_i = fs_i / \sum fs$$

We also calculate the global relative dispersion frequency  $frg_i$  (scats and vestiges) as:

$$frg_i = (fv_i + fs_i) / \sum f$$

Finally, we converted the frequencies of occurrences into percentages (%) and arrived at the results presented in this section.

Table S1.—Prey species identified in 13 jaguar scats and seven evidence of consumption in Estação Ecológica Maracá-Jipioça

Species (or group)	$fv_i$	$fs_i$	$frs_i$	$frg_i$
<i>Dasyprocta leporina</i>	-	23,1	6,3	3,9
<i>Didelphis marsupialis</i>	-	53,9	22,2	14,1
<i>Aramides cajaneus</i>	-	7,8	2,8	1,7
<i>Egretta thula</i>	-	7,8	2,1	1,3
<i>Eudocimus ruber</i>	14,3	-	-	5,4
<i>Caiman crocodius</i>	28,6	23,1	15,3	20,2
<i>Iguana iguana</i>	14,3	-	-	5,4
<i>Rhinoclemmys punctulata</i>	-	7,8	2,1	1,3
<i>Salvator merianae</i>	-	46,2	29,9	18,9
Fishes	42,9	30,8	19,4	28,1

**Table S2: correlation between variables by estimating the Spearman correlation coefficient between all independent variables, no important correlation existed in correlation lower than 0.7 and greater than -0.7**

<b>Correlation</b>	Beach and Sea	Mangrove and Teso	Grassland	Distance for water	Anseriformes	Gruiformes	Pelecaniformes	<i>D. leporina</i>	<i>D. marsupialis</i>	<i>M. tridactyla</i>	<i>O. virginianus</i>	<i>S. merianae</i>
Beach and Sea	<b>1</b>	-0.018	-0.438	-0.419	-0.109	-0.100	-0.537	0.624	0.446	0.224	0.121	0.102
Mangrove and Teso	-0.018	<b>1</b>	<b>-0.728</b>	-0.353	-0.557	<b>0.857</b>	-0.525	0.447	0.622	-0.437	-0.318	0.360
Grassland	-0.438	<b>-0.728</b>	<b>1</b>	0.625	0.429	-0.678	0.601	<b>-0.826</b>	<b>-0.816</b>	0.327	-0.162	<b>-0.769</b>
Distance for water	-0.419	-0.353	0.625	<b>1</b>	-0.231	-0.394	0.304	-0.533	-0.369	<b>0.701</b>	0.304	-0.416
Anseriformes	-0.109	-0.557	0.429	-0.231	<b>1</b>	-0.511	0.519	-0.376	-0.540	-0.247	-0.424	-0.550
Gruiformes	-0.100	<b>0.857</b>	-0.678	-0.394	-0.511	<b>1</b>	-0.538	0.384	0.517	-0.367	-0.012	<b>0.880</b>
Pelecaniformes	-0.537	-0.525	0.601	0.304	0.519	-0.538	<b>1</b>	-0.633	-0.576	-0.002	-0.235	-0.543
<i>D. leporina</i>	0.624	0.447	<b>-0.826</b>	-0.533	-0.376	0.384	-0.633	<b>1</b>	<b>0.843</b>	-0.147	0.361	0.493
<i>D. marsupialis</i>	0.446	0.622	<b>-0.816</b>	-0.369	-0.540	0.517	-0.576	<b>0.843</b>	<b>1</b>	-0.117	0.410	0.649
<i>M. tridactyla</i>	0.224	-0.437	0.327	<b>0.701</b>	-0.247	-0.367	-0.002	-0.147	-0.117	<b>1</b>	0.516	-0.396
<i>O. virginianus</i>	0.121	-0.318	-0.162	0.304	-0.424	-0.012	-0.235	0.361	0.410	0.516	<b>1</b>	0.109
<i>S. merianae</i>	0.102	0.360	<b>-0.769</b>	-0.416	-0.550	<b>0.880</b>	-0.543	0.493	0.649	-0.396	0.109	<b>1</b>





**Table S3:** occupancy models per hypotheses and their respective scenarios; habitat, preys, and habitat + prey. The models best supported by hypotheses are in bold in their respective scenarios. P – detection probability;  $\Psi$  – occupancy probability; df - degrees of freedom; AIC - Akaike Information Criterion; Overall  $\Delta$ AIC – the difference in AIC between the top model and other models

**Comentado [LMCR8]:** Vê as alterações que sugeri no ficheiro do material suplementar

Models H1	df	AIC	$\Delta$ AIC	Weight
Campo				
<b><i>p (beach and sea), <math>\Psi</math> (distance for water)</i></b>	<b>4</b>	<b>138.9</b>	<b>0.0</b>	<b>0.640</b>
<i>p (%beach and sea), <math>\Psi</math> (beach and sea + distance for water)</i>	5	142.0	3.06	0.139
<i>p (%beach and sea), <math>\Psi</math> (distance for water + grassland)</i>	5	142.0	3.09	0.136
<i>p (%beach and sea), <math>\Psi</math> (beach and sea + distance for water + grassland)</i>	6	143.0	4.03	0.085
Mangrove and Teso				
<i>p (beach and sea), <math>\Psi</math> (distance for water)</i>	4	138.9	0.0	0.570
<i>p (%beach and sea), <math>\Psi</math> (distance for water + mangrove and Teso)</i>	5	140.7	1.82	0.230
<i>p (%beach and sea), <math>\Psi</math> (beach and sea + distance for water)</i>	5	142.0	3.06	0.124
<i>p (%beach and sea), <math>\Psi</math> (beach and sea + distance for water + mangrove and Teso)</i>	6	143.0	4.03	0.76
Models H2	df	AIC	$\Delta$ AIC	Weight
Gruiformes and agouti				
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater)</i>	5	139.3	0.0	0.321
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater + Pelecaniformes)</i>	6	140.9	1.62	0.143
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ Pelecaniformes)</i>	5	140.9	1.66	0.140
Gruiformes and Back-eared opossum				
<b><i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater + Back-eared opossum)</i></b>	<b>6</b>	<b>137.8</b>	<b>0.0</b>	<b>0.689</b>
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater + Back-eared opossum + Anseriformes)</i>	7	141.5	3.74	0.106
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater + Back-eared opossum + Pelecaniformes)</i>	7	141.6	3.78	0.104
<i>p (%beach and sea), <math>\Psi</math> (Gruiformes+ giant anteater + Back-eared opossum + deer)</i>	7	141.6	3.85	0.101
Tegu and agouti				
<i>p (%beach and sea), <math>\Psi</math> (Tegu + giant anteater)</i>	5	139.5	0.0	0.741
<i>p (%beach and sea), <math>\Psi</math> (Tegu + giant anteater + agouti)</i>	6	143.0	3.48	0.130
<i>p (%beach and sea), <math>\Psi</math> (Tegu + giant anteater + Anseriformes)</i>	6	143.0	3.5	0.129
Tegu and Back-eared opossum				
<i>p (%beach and sea), <math>\Psi</math> (Tegu + giant anteater)</i>	5	139.5	0.0	0.466
<i>p (%beach and sea), <math>\Psi</math> (Back-eared opossum + giant anteater + Anseriformes)</i>	6	141.3	1.86	0.184
<i>p (%beach and sea), <math>\Psi</math> (Back-eared opossum + Pelecaniformes+ deer)</i>	6	142.1	2.61	0.127
Models H3	df	AIC	$\Delta$ AIC	Weight
Gruiformes, Back-eared opossum and water				
<b><i>p (beach and sea), <math>\Psi</math> (distance for water)</i></b>	<b>4</b>	<b>138.9</b>	<b>0.0</b>	<b>0.412</b>
<i>p (%beach and sea), <math>\Psi</math> (distance for water + Gruiformes)</i>	5	139.8	0.91	0.261
<i>p (%beach and sea), <math>\Psi</math> (distance for water + Back-eared opossum)</i>	5	139.8	0.91	0.261
<i>p (%beach and sea), <math>\Psi</math> (distance for water + Back-eared opossum+ Gruiformes)</i>	6	142.6	3.64	0.067

## References

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