

Título

Variação espacial e temporal no uso do habitat por jaguatirica (*Leopardus pardalis*) em florestas de terra firme da Amazônia Central, Brasil

Victor Siqueira Pimentel

Manaus, AM

Junho de 2017

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Orientador: Dr. Wilson Roberto Spironello

Coorientador: Dr. Eduardo Martins Venticinque

Dissertação apresentada à Coordenação do Programa de Pós-Graduação em Ecologia, do Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos necessários à obtenção do título de Mestre em Biologia (Ecologia).

Manaus, AM

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Banca examinadora da defesa oral pública

Dr. Bruce Nelson (INPA)

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MINISTÉRIO DA
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DISSERTAÇÃO DE MESTRADO DO
PROGRAMA DE PÓS-GRADUAÇÃO EM
ECOLOGIA DO INSTITUTO NACIONAL
DE PESQUISAS DA AMAZÔNIA.

Aos 18 dias do mês de agosto do ano de 2017, às 14h00min, no Auditório do LBA, Campus II, INPA/Aleixo. 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). **Bruce Walker Nelson**, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). **Cintia Cornelius Frische**, da Universidade Federal do Amazonas – UFAM, tendo como suplementos o(a) Prof(a). Dr(a). Adrian Ashton Barnett, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Camila Cherem Ribas, 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 VICTOR SIQUEIRA PIMENTEL**, intitulado: “**VARIAÇÃO ESPACIAL E TEMPORAL NO USO DO HABITAT POR JAGUATIRICA (*Leopardus pardalis*) EM FLORESTAS DE TERRA FIRME DA AMAZÔNIA CENTRAL**”, orientado(a) pelo(a) Prof(a). Dr(a). Wilson Roberto Spironello, do Instituto Nacional de Pesquisas da Amazônia – INPA, e coorientado(a) pelo(a) Prof(a). Dr(a). Eduardo Martins Venticinque, da Universidade Federal do Rio Grande do Norte – UFRN.

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.

Prof(a).Dr(a). MARCELO GORDO

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Cintia *h L*

Prof(a).Dr(a). BRUCE WALKER NELSON

Prof(a).Dr(a). CINTIA CORNELIUS FRISCHE

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Sinopse

O estudo analisou a variação espacial e temporal no uso do habitat por jaguatirica em relação às suas presas potenciais e algumas variáveis contidas na paisagem. A jaguatirica mostrou ser influenciada por suas presas de maneira diferente entre dois períodos do ano analisados. As variáveis de paisagem não mostraram efeito sobre a ocorrência de jaguatirica.

Palavras-chave: *Leopardus pardalis*; presas; armadilha fotográfica; Amazônia; habitat

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Resumo

A distribuição dos mamíferos nos diferentes ambientes mostra a importância de fatores bióticos e abióticos na forma como fazem o uso destes habitats. O efeito da sazonalidade tem um impacto na variação destes fatores. Entre os carnívoros, a estrutura do habitat e a disponibilidade de recursos podem ser considerados aspectos relevantes para sua persistência. Com esse foco, avaliamos o efeito de fatores ambientais na variação espacial e temporal na ocorrência de jaguatirica em ambientes de terra firme (paleo-várzea) na Amazônia Central. Assim buscamos entender os efeitos da relação das presas potenciais, da distância das comunidades tradicionais, da distância dos ecótonos com áreas alagáveis e da cobertura florestal na ocorrência de jaguatirica. Conduzimos o estudo com armadilhas fotográficas dispostas em seis blocos de amostragem em terra firme durante 132 dias, divididos em dois períodos do ano, o período das águas altas e das águas baixas. Utilizamos 50 câmeras em cada bloco, totalizando um esforço amostral de 6.600 armadilhas*dia. Nossos resultados mostraram uma variação temporal no uso das presas potenciais e nenhuma influência das variáveis de paisagem. Desta forma, concluímos que as interações bióticas foram os fatores determinantes na ocorrência de jaguatirica nestes ambientes de terra firme da Amazônia.

Abstract

Title: Spatial and temporal variation in habitat use for ocelot (*Leopardus pardalis*) in terra firme forests of Central Amazon, Brazil

The distribution of mammals in different environments shows the influence of biotic and abiotic factors on the way they use such habitats. Seasonality can have a great impact on the variation of such factors. Habitat structure and resource availability are especially relevant aspects for the persistence of carnivores in a given area.

Consequently, we evaluated the effect of environmental factors on spatial and temporal variation of ocelot occurrence in terra firme environments (paleo-várzea) in Central Amazon. Additionally, we then sought to understand the relationship between ocelot occurrence and occurrence of potential prey, distance from traditional communities, distance from ecotones with flooded areas and forest cover. We conducted the study using camera traps arranged in six blocks of terra firme for 132 days across two annual seasons, those of high and low water levels. We used 50 cameras in each block, with a total sampling effort of 6,600 traps*day. Our results showed a temporal variation in the use of potential prey species and no influence of the landscape variables. We conclude that biotic interactions were the main factors determining occurrence of ocelots in the Central Amazon terra firme forests studied.

Keywords: *Leopardus pardalis*, prey, camera trap, Amazonia, Habitat

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Introdução geral

Um dos principais objetivos da ecologia é entender os padrões de distribuição espacial e temporal das espécies e seus determinantes. Estes padrões são determinados pelas interações entre diferentes fatores, a exemplo de fatores históricos, intrínsecos e ambientais. Dentre os fatores ambientais estão os bióticos (interações ecológicas) e abióticos, ambos também considerados como recursos. A distribuição dos recursos no ambiente ocorre em função de como os habitats estão estruturados, onde a diversidade e riqueza de espécies aumentam de acordo com a complexidade e heterogeneidade ambiental. Além disso, os recursos estão sujeitos às variações sazonais. Sendo assim, é importante entender como os organismos fazem uso do habitat de acordo com a disponibilidade de recursos, visando uma melhor relação custo-benefício no espaço e no tempo.

O aumento da aptidão está diretamente relacionado à qualidade do habitat, quando o indivíduo ao usar um ambiente com mais recursos preferencialmente a outro, aumenta sua taxa de crescimento e reprodução (Fretwell 1972), refletindo na distribuição espacial e temporal diferenciada dos indivíduos. Entre os mamíferos, os estudos relacionados são baseados principalmente no uso do habitat, padrão de atividade, hábito alimentar, tamanho corpóreo e coexistência (Goulart *et al.* 2009; Oliveira *et al.* 2010; Davis *et al.* 2011). Com isso, é fundamental buscar os fatores que possuem maior influência no uso do habitat pelos organismos, como o forrageio e as características estruturais dos habitats utilizados. Entre os carnívoros, um dos aspectos determinantes é a abundância de suas principais presas, e como elas estão distribuídas no espaço e no tempo, havendo uma correlação positiva entre a densidade populacional de espécies de carnívoros com a biomassa de presas (Carbone e Gittleman 2002).

Outro fator norteador do uso do espaço é a distância para populações humanas, havendo uma tendência a uma relação negativa da abundância de carnívoros neotropicais, como *Panthera onca* (Onça-pintada), *Puma concolor* (Onça-parda) e *Leopardus pardalis* (jaguatirica) quanto mais próxima for a

distância às áreas com perturbação antrópica (Silveira 2004; Di Bitetti *et al.* 2006, 2008). Porém, os estudos avaliando pressão antrópica com carnívoros geralmente são feitos em ambientes fragmentados, diferente da área deste estudo. Em parte de nossa área, na Amazônia Central, há estudos mostrando que o foco das comunidades é na pesca, na agricultura e menos da caça (De Mattos Vieira *et al.* 2015). Isso mostra um menor impacto sobre a fauna cinegética. Por outro lado, Teles (2009) mostrou o risco de diversos carnívoros à presença humana, sendo a perseguição a grandes e pequenos felinos ocorrendo em níveis elevados, principalmente pela retaliação à morte de animais domésticos. Outro fator, é a distribuição espacial de felinos que ocorre pelo uso diferenciado do habitat em fina escala de ambientes heterogêneos (Scognamillo 2003), como em áreas de transição. Além disso, os predadores podem ser afetados de forma direta por características estruturais da vegetação, como a cobertura florestal (Murray e Gardner 1997; Pimenta 2012) ou indiretas por características do ambiente que afetam suas presas, como a disponibilidade de recursos (Silvius e Fragoso 2003). Desta forma, é possível prever a ocorrência de carnívoros neotropicais de acordo com as características mais favoráveis do habitat em determinados ambientes.

Na Amazônia existem diferentes tipos de formações vegetais, a exemplo de florestas não alagáveis (terra firme) e florestas alagáveis, como a várzea (Prance 1980). As florestas alagáveis são planícies influenciadas pelo pulso periódico de inundação, que é a dinâmica de movimentação lateral de água, nutrientes e organismos a partir do canal do rio em determinadas épocas do ano (Junk 1989). São consideradas várzeas as planícies de inundação banhadas por águas brancas advindas das Cordilheiras dos Andes, sendo habitats com alta produtividade. As florestas de terra firme não são influenciadas diretamente pelos pulsos de inundação, mas em alguns casos são influenciados de forma indireta por se localizarem adjacentes às florestas alagáveis. Na Amazônia central existe um tipo de terra firme muito abundante que é denominado paleo-várzea. As paleo-várzeas foram várzea no passado devido ao aumento do nível da água que gerou um processo de deposição rítmica de sedimentos na encosta dos rios (Irion *et al.* 2010). Os solos das paleo-várzeas possuem uma composição mineral mais parecida com a várzea,

portanto, mais ricos do que os solos de florestas de terras firmes mais antigas (Irion *et al.* 2010). Por outro lado, ambientes adjacentes de terra firme com várzea propicia um ambiente mais heterogêneo, aqui considerado áreas de transição ou ecótono.

Na Amazônia, os ambientes de ecótono são influenciados estruturalmente pela dinâmica das águas, com o período de maior nível da água (cheia) e o período de menor nível da água (seca), ambos períodos focos do estudo. A variação dos níveis da água, faz com que as áreas de transição possuam diferentes características de produtividade de acordo com a sazonalidade, isso porque as árvores da várzea e terra firme produzem frutos maduros em diferentes períodos do ano (Haugaasen e Peres, 2005). Assim é esperado que as áreas de ecótono tenham uma produtividade anual mais constante, provavelmente pelo aumento na abundância de presas no período de cheia dos rios, que ocorre logo após o período de maior produtividade de frutos nas florestas de terra firme. Com isso, essas áreas tenderiam a suportar uma maior abundância de carnívoros, a exemplo do ecótono savana-floresta na Venezuela (Polisar 2000). Além desses, classifica-se outros dois períodos relacionados ao regime de pluviosidade, o período das chuvas e o período em que as chuvas cessam e começa a diminuir o nível da água (vazante). No entanto, na Amazônia Central não há estudos da resposta de carnívoros à sazonalidade de presas, de quais são consumidas e da influência de diferentes fatores ambientais.

Na região deste estudo, há uma variação na produtividade de frutos e consequente variação na população de frugívoros (Haugaasen e Peres 2007), parte destes frugívoros são presas de jaguatirica, espécie foco deste estudo. A disponibilidade de recursos é um fator chave na distribuição dos predadores. Além do fator presas, alguns outros fatores também afetam a ocorrência de predadores como a pressão antrópica (Teles 2009), heterogeneidade ambiental (Maffei *et al.* 2005; Di Bitetti *et al.* 2006) e estruturas da vegetação (Murray e Gardner 1997). Desta forma, torna-se necessário a melhor compreensão sobre como um mesopredador pouco estudado na Amazônia, como a jaguatirica, seleciona e utiliza diferentes ambientes e áreas de transição, relacionado a fatores ambientais, antrópicos e da disponibilidade de recursos. Sendo assim, o

objetivo do estudo é avaliar o efeito de fatores ambientais na variação espacial e temporal na ocorrência de jaguatirica em ambientes de terra firme (paleo-várzea) na Amazônia Central, testando quatro hipóteses: 1) a presença de presas potenciais afeta positivamente a ocorrência de jaguatirica em ambos os períodos do ano; 2) haverá um efeito positivo na ocorrência de jaguatirica com a proximidade dos ecótonos; 3) haverá um efeito positivo da cobertura florestal na ocorrência de jaguatirica; e 4) não haverá efeito das comunidades tradicionais na ocorrência de jaguatirica, por ser uma área com baixo impacto de caça.

Objetivos

Objetivo Geral

Avaliar o efeito de fatores ambientais na variação espacial e temporal na ocorrência de jaguatirica em ambientes de terra firme (paleo-várzea) em uma paisagem na Amazônia Central

Objetivo Específicos

- Avaliar o efeito das presas potenciais na ocorrência de jaguatirica.
- Avaliar o efeito da proximidade com comunidades tradicionais na ocorrência de jaguatirica.
- Avaliar o efeito da proximidade dos ecótonos com áreas alagáveis na ocorrência de jaguatirica.
- Avaliar o efeito da cobertura florestal na ocorrência de jaguatirica.

Capítulo I

Pimentel, S. P.; Gonçalves, A. L. S.; Muhlen, E. M.; Venticinque, E. M. & Wilson R. Spironello. Spatial and temporal variation in habitat use for ocelot (*Leopardus pardalis*) in terra firme forests of Central Amazon, Brazil. Manuscrito formatado para *Biological Conservation*

Spatial and temporal variation in habitat use of ocelot (*Leopardus pardalis*) in terra firme forests of Central Amazon, Brazil

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Introduction

One of the main objectives in ecology is to understand patterns and determinants of species spatial and temporal distributions. These patterns are determined by the interactions between a variety of factors, including historical, intrinsic and environmental. Environmental factors include biotic (ecological interactions) and abiotic, both of which can also be considered as resources. Resource distribution in the environment occurs as a function of habitat structure, where species diversity and richness increase according to environmental complexity and heterogeneity. In addition, resources are subject to seasonal variations. It is therefore important to understand how an organism's use of a habitat reflects the availability of resources, especially in terms of cost-benefit of spatial and temporal use patterns.

When an individual, using one environment with more resources in preference to another, increases growth rate and reproduction, any resulting increase in fitness is likely to be directly related to habitat quality, reflecting the spatial and temporal distribution of individuals (Fretwell 1972). For mammals, studies of this kind consider mostly habitat use, activity pattern, feeding habits, body size and coexistence (Davis et al., 2011; Oliveira et al., 2010). From such studies it became apparent that certain key factors determine habitat use by organisms, including probability of foraging opportunities and the structural characteristics of the habitat. Among carnivores particularly, a fundamental determining factor is the abundance of their main prey species and how these are distributed in space and time; globally, there is a positive correlation between carnivore population density and prey biomass (Carbone and Gittleman 2002).

Another factor influencing the use of space is the distance to human populations. In general, human proximity tends to have a negative relation with abundance of neotropical carnivores, including *Panthera onca* (jaguar), *Puma concolor* (puma) and *Leopardus pardalis* (ocelot) (Di Bitetti et al., 2006, Silveira 2004). Studies evaluating the influence of anthropogenic pressure on carnivores

are usually undertaken in fragmented environments. However, areas retaining extensive continuous forest cover are not nearly as well studied.

Within human communities of the Central Amazon, fishing and agriculture are emphasized over hunting (De Mattos Vieira et al., 2015). Therefore, human impact on wild felids resulting from overhunting of prey species (peccary, paca, agouti) is likely lower than in areas where humans hunt these species more intensely. However, wild carnivores are still at risk when in proximity to agricultural/fishing communities, especially from punitive hunting, often related to the death of domestic animals. This may lead to strong persecution of large and small felines (Teles 2009). In addition to human communities, another factor influencing the spatial distribution of wild felids is the differential use of heterogeneous environments, due to fine-scale habitat preferences, especially in transition areas between vegetation types (Scognamillo 2003). In addition, predators may be directly affected by structural characteristics of vegetation, such as density of canopy, understory and/or woody stems (Murray and Gardner 1997; Pimenta 2012). Environmental characteristics that affect prey species, such as the availability of resources such as food and forest cover, also influence the distribution of wild felids (Silvius and Fragoso 2003). Analysis of such features in continuous forest habitats should make it possible to predict the occurrence of neotropical carnivores with regard to more favorable habitat characteristics.

The Amazonian region contains a variety of habitats, such as non-flooded forests (*terra firme*) and floodplain forests, such as *várzea* and *igapó*, which border sediment-rich and sediment-poor rivers, respectively. Floodplain forests grow in areas influenced by periodic flood pulses, which are characterized by protracted lateral movement of water, accompanied by nutrients and organisms from the river channel at certain times of the year (Junk 1989). *Várzea* floodplains receive white (sediment-rich) waters from the Andes Mountains, and are characterized by high productivity (Long et al., 1989). *Terra firme* forests are not directly influenced by flood pulses, but in some cases they are indirectly influenced by proximity to floodplains, and by historical factors. In the central Amazon one very common type of *terra firme* forest is known as paleo-*várzea*, which is *terra firme* forest growing on old floodplains that became

elevated due to sequential sediment deposition on white-water river margins (Irion et al., 2010). In consequence, paleo-várzea soils have a mineral composition similar to that of current várzea, and are therefore richer in nutrients than terra firme soils, which are derived from much older, non-replenished, sources (Irion et al., 2010). In addition, the junction of terra firme and várzea produces a heterogeneous transitional environment, with the characteristics of an ecotone.

In the Amazon, the structure of ecotone environments are influenced by flood dynamics, with the period of high water level (flood) and the period of low water level (dry). Water level variation means that productivity characteristics of transitional areas vary greatly according to the season, as várzea and terra firme trees produce mature fruits at different periods of the year (Haugaasen and Peres, 2005). Consequently, it is expected that ecotone areas will have more constant annual fruit productivity and, as a result, are likely to show an increase in the abundance of felid prey species during the river flood period, which occurs soon after the period of highest fruit yield in terra firme forests. As a result, these areas would be expected to support a greater abundance of carnivores. A similar effect was reported in the savanna-forest ecotone in Venezuela (Polisar 2000). However, in the Central Amazon there is a lack of studies on the response of carnivores to seasonal changes in prey availability, type of prey consumed, and the influence of different environmental factors on the occurrence of carnivores.

In the Central Amazon, there is seasonal variation in fruit productivity and, correspondingly, variation in the abundance of frugivore populations (Haugaasen and Peres 2007). Additionally, some of the frugivore species involved form part of the prey base of the focal species of this study, the ocelot. The availability of resources is a key factor in determining the distribution of predators. In addition to availability of prey, other factors also influence predator occurrence, including anthropogenic pressure (Teles 2009), environmental heterogeneity (Di Bitetti et al., 2006) and vegetation structure (Murray and Gardner 1997). With these considerations in mind, the objective of this study was to evaluate the effect of environmental factors on the spatial and temporal variation in ocelot occurrence in paleo-várzea terra firme environments in the

Central Amazon. The study had four hypotheses, that: (I) the presence of potential prey positively affects ocelot occurrence in both seasons (high and low water level) of the year, (II) there will be a positive affect on ocelot occurrence with proximity to ecotones, (III) there will be a positive relationship between increased forest cover and ocelot occurrence, and (IV) there will be no relationship between distance to traditional communities and ocelot occurrence.

Materials and Methods

Study area

We conducted this field study in the Piagaçu-Purus Sustainable Development Reserve - RDS-PP ($4^{\circ}05'$ - $5^{\circ}35'$ S and $61^{\circ}73'$ - $63^{\circ}35'$ W) and the Abufari Biological Reserve - Rebio Abufari ($4^{\circ}50'$ - $5^{\circ}30'$ S and $62^{\circ}35'$ - $63^{\circ}15'$ W), both located on the lower Purus River, Amazonas State, Brazil (Fig. 1). RDS-PP has an area of 834,245 ha and Rebio Abufari an area of 233,865 ha. The two reserves are part of a mosaic of conservation units, covering parts of Anori, Beruri and Tapauá municipalities and located on the banks of the Purus River, and part of the municipality of Coari, located on the banks of the Solimões River.

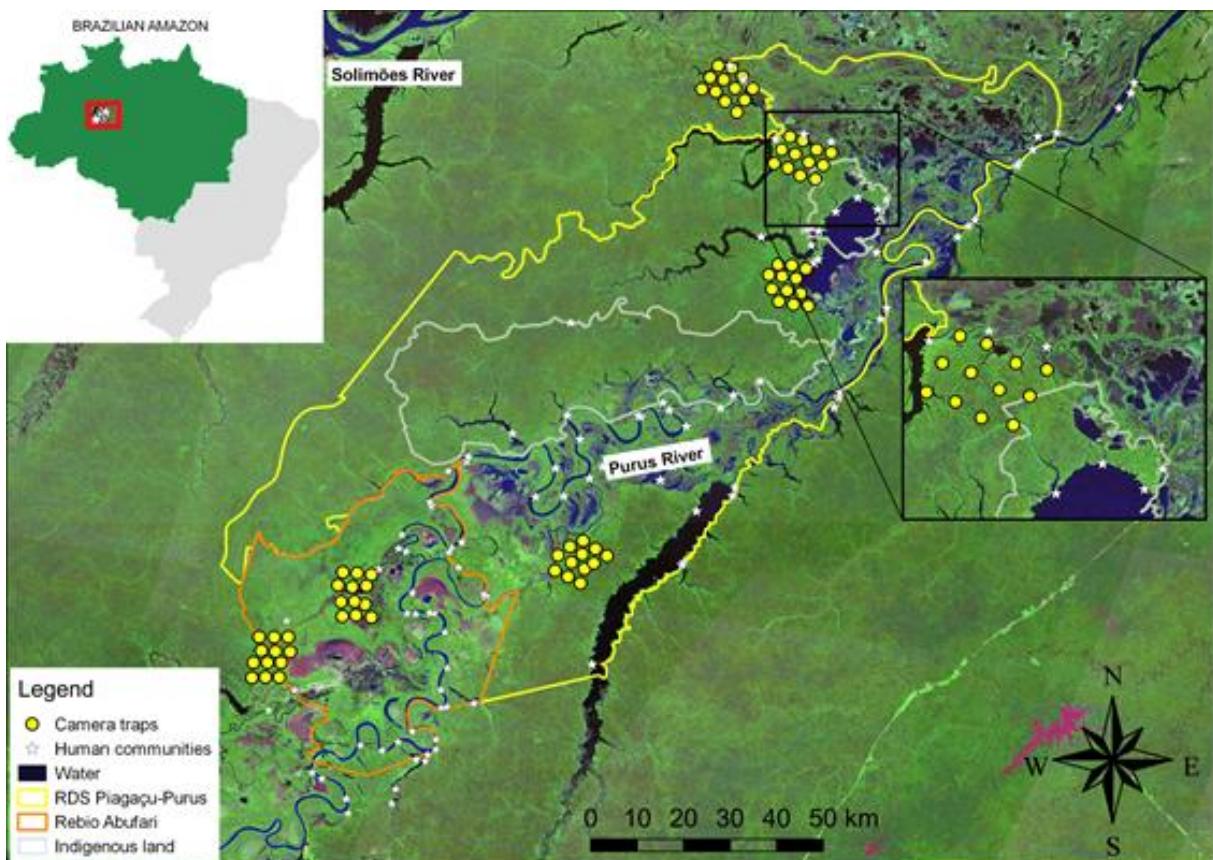


Figure 1. Location of the study area, the Piagaçu-Purus Sustainable Development Reserve (RDS) and Abufari Biological Reserve (Rebio), Amazonas State, Brazil. The yellow dots represent blocks of camera traps located in terra firme forest areas.

Data Collection

Sampling Methods

We recorded animals using camera traps, a non-invasive method for studying wildlife; the waterproof equipment consisted of an infrared sensor coupled to a camera, so that a photograph is taken when the presence of an animal is detected. This method has been widely used in studies of medium- and large-sized terrestrial mammals (Ahumada et al., 2011, Clare et al., 2015, Karanth and Nichols 1998, O'Connell et al., 2011) and small mammals (Murphy et al., 2011; Sarmento et al., 2011). We placed 72 unpaired traps (either Bushnell

Trophy Cam HD or Reconyx HC500 HyperFire) models in the field for 66 days during the flood period (late May to late July) and 66 days during the dry season (early October to early December) during 2016, totalizing 132 days of sampling. We did not use bait to attract animals, so as to avoid interfering with natural movement and habitat use. To maintain independence between records from the same camera trap, we used only one record of the same species each hour (O'Brien et al., 2003).

This study was performed in areas of paleo-várzea terra firme forest, during periods when the forest was flooded and non-flooded. We established six blocks of 12 traps distributed in three lines, on both sides of the Purus River (total 72 traps) (Figure 1). We placed the first line of traps in the area of the flood boundary in 2016, and so represented the terra firme / várzea ecotone. The other two lines were positioned toward the interior of the terra firme forest. To maximize sampling independence we maintained a 3-km spacing between the traps in each block, this minimum spacing being based on known patterns of movement for ocelot (Dillon and Kelly 2007) and other, larger species, such as jaguar. The distance between the farthest traps in the sampling area was 170 km. For ocelot photographic records we calculated the Relative Abundance Index (RAI), using the formula $RAI = \text{number of records}/(\text{number of traps} \times \text{day})$ (Carbone et al., 2001).

Explanatory Variables

To evaluate differences in ocelot habitat use, we tested variables selected a priori, based on knowledge of ocelot ecology. Predictor variables were: relative abundance of potential prey, distance from ecotone boundary, distance to the nearest traditional community, and forest cover ratio. For relative abundance of potential prey, we considered all regional non-aquatic bird and mammal species recorded in the literature as having a maximum weight of 10 kg (Abreu et al., 2008; Emmons 1987, 1988; Villa Meza et al., 2002; Wang 2002), because there are no studies on ocelot diet for the central Amazon. In subsequent analyses

we selected prey species with at least 10 records and used this to calculate the RAI for each potential prey species.

For distance from the ecotone boundary between terra firme and várzea, we used the straight-line distance from the point location of each trap to the nearest floodable area. In defining the ecotone boundary, we used the classification of flooded areas of the Amazon given by Hess et al. (2015). Because human movement in the RDS Piagaçu-Purus and Rebio Abufari occurs almost exclusively on the river, we calculated distance from the communities to the photographic traps, using river length, rather than straight-line distances. Calculations were performed using SDM tools software with the "Least Cost Path" function. For this variable we used the Amazon basin waterways database of Venticinque et al. (2016). For forest cover ratio, we calculated the average percentage of canopy cover in a 1.5-km buffer around the trap, using a database of satellite images of forest cover (Hansen et al., 2013).

Statistical Analyses

To test whether environmental variables were correlated, we used a Spearman correlation test for non-parametric data. We used the correlation cut-off limit ($r > 50$) to define which sets of variables would not be inserted simultaneously into the model. However, analysis revealed that no variables were correlated.

We used the generalized linear model (GLM) with multiple distributions (Poisson, Quasi-poisson, Negative Binomial and Zero-Inflated models) for the analysis. Dispersion tests of all models generated in Poisson distribution had low dispersion estimates (<1.2), allowing data analysis based on this distribution (Zuur et al., 2009). Thus, within the selected models, we progressively excluded variables with low explanatory power until we reached the most parsimonious model according to the Akaike Information Criteria (AIC) (Burnham and Anderson 2002). All statistical analyses were performed using the R environment (R Development Core Team 2017), using the packages lme4

(Bates et al., 2015), vegan (Oksanen et al., 2017), AER (Kleiber and Zeileis 2008) and visreg (Breheny and Burchett 2017).

Results

Due to camera trap malfunctions ($N = 22$ of the 72 used), we used data from a total of 50 traps. Across the two sample periods combined, the sample effort for the study was 6,600 trap*days. We had a total of 90 ocelot records.

In the flood and dry seasons the best models included the following potential ocelot prey species: *Nasua nasua* (coati), *Didelphis marsupialis* (common opossum), *Tinamus major* (great tinamou), *Proechimys* sp. (spiny rat), *Dasyprocta fuliginosa* (agouti), *Tamandua tetradactyla* (tamandua), *Leptotila rufaxilla* (gray-fronted dove) and a Caprimulgid (nightjar). In the flood season, the best model (explanatory deviation = 22.7%) indicated that ocelots were influenced by species richness and RAI of coati (Table 1). Ocelots occurred in places with greater species richness, and there was a negative relationship with coati occurrence (Figure 2a, b). In the dry season, the selected model (explanatory deviation = 24.9%) showed a relationship between ocelots and RAI of coati, common opossum, great tinamou and spiny rat (Table 2). There was a positive relationship with occurrence of great tinamou and spiny rat (Figure 3a, b), and a negative relationship with occurrence of common opossum and coati (Figure 3c, d). In the graph for coati in the dry period, an outlier was removed to evaluate the affect it had on the analysis (Figure 3d). However, this treatment resulted in no significant change.

There was no relationship between distance from the ecotone, distance from the community and forest cover ratio and ocelot occurrence. This was true for both the flood (Table 3) and dry seasons (Table 4).

Table 1. Selection of potential prey by *Leopardus pardalis* (ocelot) analyzed by generalized linear models (GLM) in the 2016 flooding season in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil. SE: Standard error; AIC: Akaike Information Criteria.

Models	AIC	Intercept	Richness	Coati	Common opossum	Great tinamou	Spiny Rat	Agouti	Tamandua	Dove	Nightjar
		Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SEe)	Estimativa (±EP)	Estimativa (±EP)
Null model	145.6	0.05 (0.13)	-	-	-	-	-	-	-	-	-
Model 1	141.3	-1.22 (0.44)**	0.39 (0.14)**	-1.06 (0.43)*	0.14 (0.17)	-0.06 (0.16)	-0.20 (0.72)	0.02 (0.01)	-0.42 (0.42)	0.29 (0.68)	-23.87 (14.76)
Model 2	137.6	-1.21 (0.43)**	0.39 (0.13)**	-1.06 (0.42)*	0.13 (0.16)	-0.06 (0.15)	-	0.01 (0.01)	-0.41 (0.41)	-	-20.43 (12.81)
Model 3	134.3	-1.18 (0.42)**	0.39 (0.11)***	-1.06 (0.43)*	-	-	-	0.02 (0.01)	-0.39 (0.40)	-	-22.31(12.72)
Model 4	133.4	-0.86 (0.37)*	0.30 (0.09)***	-1.02 (0.42)*	-	-	-	-	-	-	-

Significance values: P < 0.05*; P < 0.01**, P < 0.0001 ***

Data below for final model:

Null departure: 71.34 [degrees of freedom (GL) = 49];

Residual departure: 55.15 (GL = 47)

Table 2. Selection of potential prey of *Leopardus pardalis* (ocelot) analyzed by generalized linear models (GLM) in the dry season of 2016 in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil. SE: Standard error; AIC: Akaike Information Criteria.

Models	AIC	Intercept	Richness	Coati	Common opossum	Great tinamou	Spiny Rat	Agouti	Tamandua	Dove	Nightjar
		Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)	Estimate (±SEe)	Estimativa (±EP)	Estimativa (±EP)
Null model	122.3	-0.30 (0.16)	-	-	-	-	-	-	-	-	-
Model 1	121.3	-0.76 (0.51)	0.10 (0.21)	-2.59 (0.88)**	-0.77 (0.34)*	1.07 (0.52)*	1.93 (1.08)	0.02 (0.03)	-1.24 (1.47)	-0.89 (4.36)	-29.05 (53.49)
Model 2	117.7	-0.76 (0.51)	0.09 (0.21)	-2.55 (0.88)**	-0.73 (0.33)*	0.97 (0.45)*	1.90 (1.08)	0.03 (0.03)	-1.05 (1.37)	-	-
Model 3	114.6	-0.59 (0.26)*	-	-2.39 (0.86)**	-0.71 (0.33)*	0.95 (0.36)**	2.14 (0.98)*	0.03 (0.03)	-	-	-
Model 4	113.7	-0.47 (0.22)*	-	-2.17 (0.85)*	-0.73 (0.33)*	1.03 (0.35)**	2.67 (0.89)**	-	-	-	-

Significance values: P < 0.05*; P < 0.01**, P < 0.0001 ***

Data below for final model:

Null departure: 67.01 [graus de liberdade (GL) = 49];

Residual departure: 50.35 (GL = 45)

Table 3. Selection of *Leopardus pardalis* (ocelot) models with landscape variables analyzed by generalized linear models (GLM) in the 2016 flooding season in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil. SE: Standard error; AIC: Akaike Information Criteria.

Models	AIC	Intercept	Distance to ecotone	Forest cover rate	Distance to community
		Estimate (\pmSE)	Estimate (\pmSE)	Estimate (\pmSE)	Estimate (\pmSE)
Null model	145.68	0.06 (0.14)	-	-	-
Model 1	151.08	-1.14 (1.96)	-4.44x10 ⁻⁶ (2.17x10 ⁻⁴)	1.37x10 ⁻² (2.07x10 ⁻²)	-9.25x10 ⁻⁶ (2.18x10 ⁻⁵)
Model 2	149.08	-1.13 (1.91)	-9.40x10 ⁻⁶ (2.05x10 ⁻⁵)	1.37x10 ⁻² (2.02x10 ⁻²)	-
Model 3	147.29	-1.09 (1.90)	-	0.01 (0.02)	-

Table 4. Selection of *Leopardus pardalis* (ocelot) models with landscape variables analyzed by generalized linear models (GLM) during the dry season of 2016 in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil. SE: Standard error; AIC: Akaike Information Criteria.

Models	AIC	Interception	Distance to ecotone	Forest cover rate	Distance to community
		Estimate (\pmSE)	Estimate (\pmSE)	Estimate (\pmSE)	Estimate (\pmSE)
Null model	122.32	-0.30 (0.16)	-	-	-
Model 1	124.35	-3.13 (2.77)	2.97x10 ⁻⁴ (2.14x10 ⁻⁴)	2.97x10 ⁻² (2.89x10 ⁻²)	-1.28x10 ⁻⁵ (2.68x10 ⁻⁵)
Model 2	122.58	-3.18 (2.76)	0.00 (0.00)	0.02 (0.02)	-
Model 3	121.72	-0.45 (0.20)	0.00 (0.00)	-	-

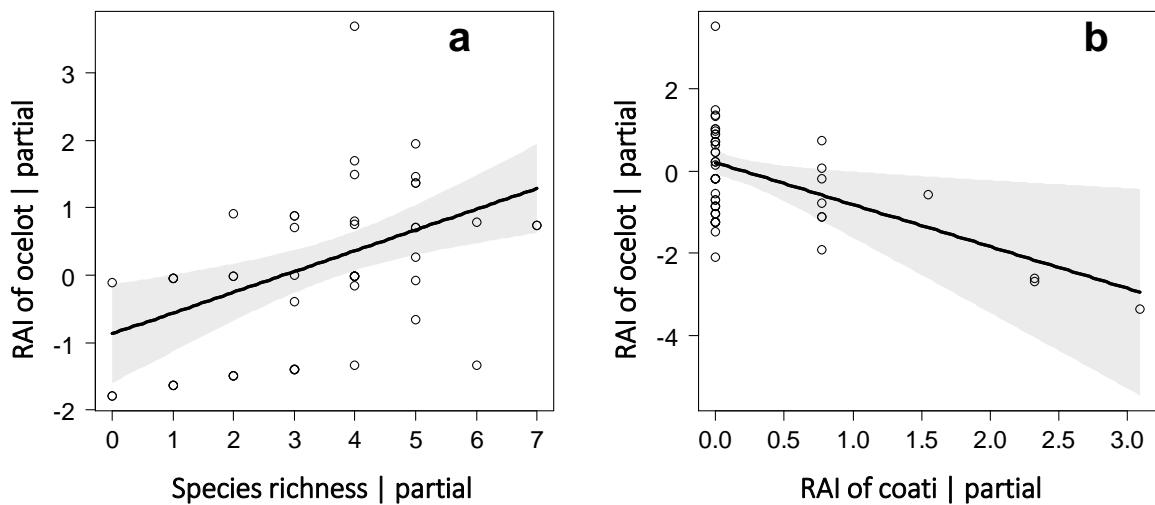


Figure 2. Relationship between the Relative Abundance Index for *Leopardus pardalis* (ocelot) and its potential prey species in the flooding season of 2016 in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil.

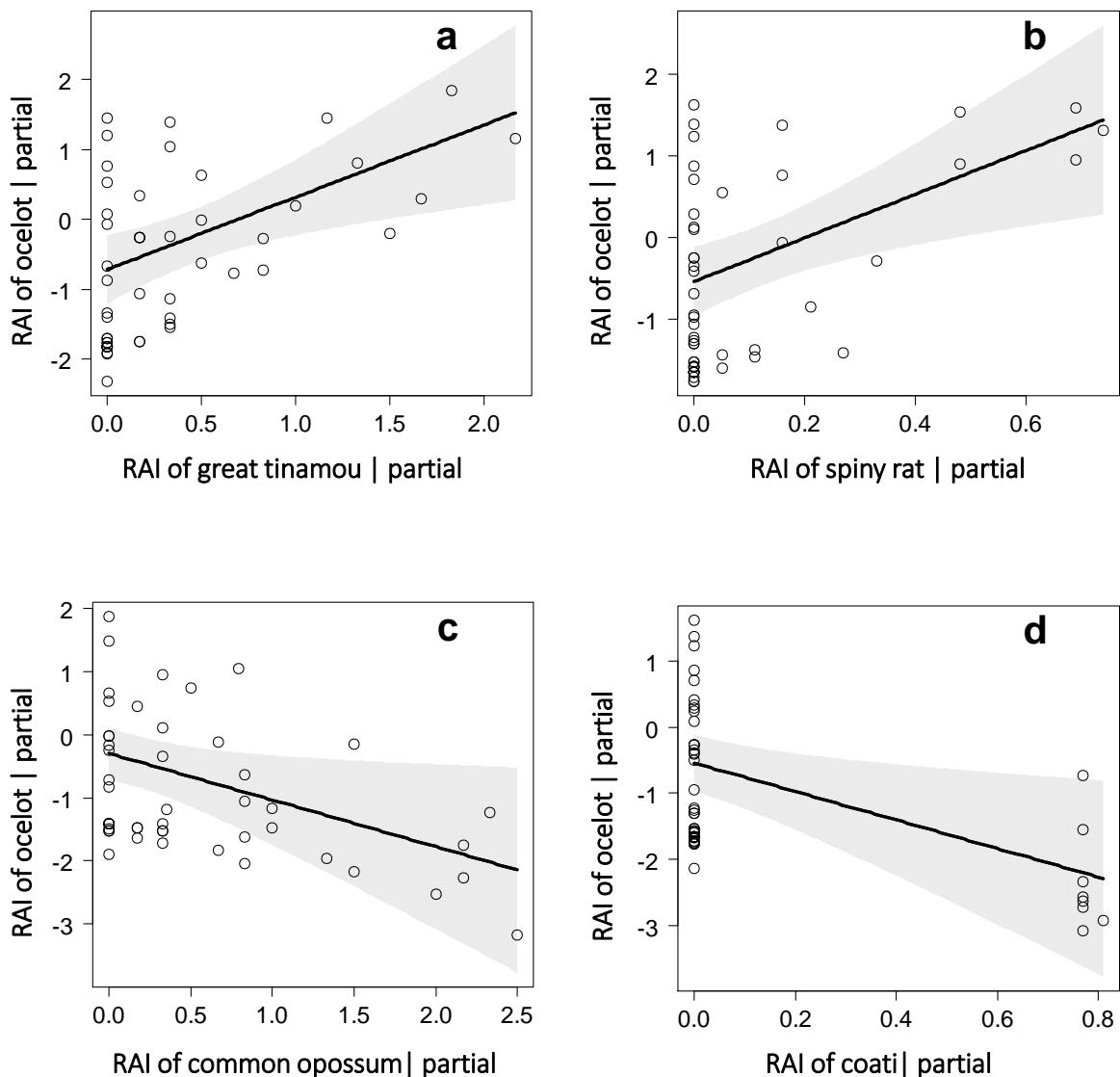


Figure 3. Relationship between the Relative Abundance Index of *Leopardus pardalis* (ocelot) and its potential prey species in the dry season of 2016 in the Piagaçu-Purus Sustainable Development Reserve and the Abufari Biological Reserve, Amazonas, Brazil.

Discussion

The hypothesis that ocelots respond to seasonal changes in prey abundance was partially supported, with ocelots being more numerous during times when prey abundance was higher. However, abundance of ocelots was not correlated with ecological variables, i.e., proximity to the ecotone, proximity to human communities, or to forest cover, in either of the two annual periods analyzed. During the flood period, ocelot abundance was higher at sites with a greater species richness of potential prey. However, during both the flood and dry periods, coati abundance was reduced at locations where ocelot abundance was highest. This suggests that coatis avoid environments where ocelots are most abundant. During the dry season, a similar trend was also observed in opossums. In the dry season, a positive relationship with ocelot occurrence was observed with only two prey species, great tinamou and spiny rat. There was no difference between the variables proximity of ecotone, proximity of human communities and forest cover and of ocelot occurrence. Accordingly, the spatial and temporal variation in ocelot habitat preference that we recorded in the different periods of the year appears to be related only to the occurrence of potential prey.

Spatial and temporal variation in resource productivity can influence consumers in a synergistic fashion, such as an increase in fruit abundance leading to an increase in frugivorous community abundance (Flowerdew et al., 2017; Moegenburg and Levey 2003). In consequence, the increase of prey biomass results in a concomitant increase in predator density (Carbone and Gittleman 2002). In Amazonian terra firme environments, productivity is higher during the rainy season, when most trees produce fruits (Haugaasen and Peres 2007, Michalski et al., 2015). This period of high fruit production is generally followed by an increase in the abundance of frugivores (Moegenburg and Levey 2003), a phenomenon which is also influenced by an increase in number and volume of water bodies inside the forest, such as streams and small ponds. This is key since potential prey species, such as rodents and birds, tend to be more abundant in proximity to water bodies (Michalski et al., 2015). Thus, the higher species richness that is seen in the ocelot's diet during the flood season is likely due to the higher abundance of prey species

during this time. This is amplified by the fact that the ocelot has a known prey base of more than 50 species (Oliveira et al., 2010, Sunquist and Sunquist 2017).

If the relationship between coati and ocelot is one of predator and prey, rather than of two generalist competitors, then predation events must be very rare, as coatis are both communal and large in comparison to the ocelot and other prey items (Emmons 1987). The ocelot typically feeds on smaller prey items or on the young of larger species (Emmons 1987). In addition, the coati is a scansorial species, has a well-developed ability to climb trees and traverse the canopy, and usually moves in bands (2 to 27 individuals: Desbiez and Borges 2010). Such communal behavior could well assist in detection of predators, such as ocelot, and in the protection of more vulnerable individuals, such as young animals. Another factor is a possible spatial and temporal segregation between coatis and ocelots, with coatis having a different activity pattern and utilizing more open environments (Bianchi et al., 2016). Consequently, it is likely that coatis will frequently avoid ocelots, explaining the negative correlation in abundance between these two species, during both the dry and flood seasons.

However, during the dry season, the terra firme has a low fruit yield (Haugaasen and Peres 2007) and so food resources for ocelot prey species are reduced, potentially leading to behavioral changes in this predator. Predators can hunt either opportunistically or by active foraging, according to prey availability (Emmons 1987, Weckel and Silver 2006). Ocelots in Venezuela, for example, show seasonal changes in the species of prey selected (Ludlow and Sunquist 1987). In the study area, the relative abundance of all potential prey species was lower in the dry season than in the flood season. Therefore, to optimize their foraging strategy during the dry season, ocelots likely focus hunting activities in locations where two potential prey species, great tinamou and spiny rat, occur. Both great tinamou and spiny rat were highly abundant ($N = 176$ and $N = 123$, respectively), and are solitary, strictly terrestrial, and small (1 kg and 350 g, respectively (Cabot et al., 2017, Paglia et al., 2012)). In general, ocelots catch small species (≤ 1 kg) more frequently, as these species have higher availability (Emmons 1987, Ludlow and Sunquist 1987, Villa Meza et al., 2002), which could make these two species principal prey items. Importantly, the great tinamou is a diurnal / crepuscular species (Cabot et al., 2017, Pratas-Santiago et al., 2016), whereas the spiny rat is a nocturnal / crepuscular

species (Pratas-Santiago et al., 2016, Reis et al., 2011). The ocelot may be active throughout the circadian cycle (Emmons 1988, Crawshaw and Quigley 1989, Pratas-Santiago et al., 2016) and is known to feed mainly on small mammals (Emmons 1987; Sunquist and Sunquist 2017). Indeed, the spiny rat may comprise 32% of the ocelot's diet (Emmons 1988). However, as these small mammals are mostly nocturnal (Reis et al., 2011), the ocelot would additionally require a diurnal prey item, which may well be the great tinamou.

As with the coati, abundance of opossums and ocelots was negatively correlated, indicating that, like the coati, opossums appear to avoid environments with high ocelot abundance. These two potential prey are scansorial, with a pronounced ability to use the tree canopy for escape. However, opossums are a frequent diet item throughout the ocelot's range (Crawshaw 1995; Konecny 1989; Wang 2002), including in the flooded forests of the Amazonia (W. Spironello, unpublished data). Thus, it is probable that the ocelot is focusing hunting activities on predominantly terrestrial animals (Emmons 1988, Sunquist and Sunquist 2017), which demonstrates the different strategies deployed by this carnivore in the various habitats studied, focusing less on species like opossums, which appear to avoid this predator.

In addition to the effects of prey availability, a number of studies have shown that the intensity of human activities can negatively impact the occurrence of carnivores. Typically, the presence of ocelots is negatively related to anthropic disturbance levels in regions where human occupation is high (Di Bitetti et al., 2008, 2006; Jackson et al., 2005). However, as expected, when human disturbance is low, the impact on occurrence of carnivores is minimal or nonexistent. This corroborates with Pimenta (2012), but not Teles (2009), both of which took place in the RDS – PP. However, while the former study used only camera traps, the latter used camera traps, censuses and interviews. In addition, low impact on medium-sized birds and rodents by traditional communities in eastern Amazonia has been demonstrated (Michalski et al., 2015).

Ecotone environments, considered in this study to be the interface between terra firme forests and floodplain forests, provide levels of environmental heterogeneity that are important for the maintenance of frugivores. This is because

fruits are available for a greater period of the year, due to the close spatial proximity of two asynchronously fruiting habitat types, terra firme and várzea (Haugaasen and Peres 2005, 2007). Therefore, higher ocelot occurrence would be expected in this environment due to the higher incidence of prey, however, this effect was not observed in this study. A probable explanation is that both the terra firme bordering the ecotone and the more distant terra firme are considered paleo-várzea (Irion et al., 2010). Paleo-várzeas display little variation in elevation and are always close to flooded forests. Therefore, these distances were not great enough to affect ocelot occurrence.

Although we did not detect a relationship between ocelot occurrence and forest cover, the effect of this ecological variable is well documented throughout the geographical range of the ocelot, and indicates that while this species can utilize habitats with different levels of forest cover, denser habitats are preferred (Goulart et al., 2009, Handley 1978, Murray and Gardner 1997). However, these results come from studies which occurred in landscapes with variable forest cover, including open areas, such as pastures and agricultural land, as well as areas with denser cover. In the current study, the landscape analyzed was more uniform, consisting of forest with low anthropogenic disturbance, with the lowest percentage of forest cover being around 70%. It is likely that in more intact forests, factors positively affecting ocelot occurrence are on a finer scale, such as understory density (Pimenta 2012).

The spatial distribution of organisms occurs through the differential use of habitat patches cued by a variety of environmental factors (Cavallini and Lovari 1991, Scognamillo et al., 2003). In addition, resources are distributed heterogeneously in time and space, and seasonally variable productivity must be taken into consideration. Variation in distribution and abundance of resources may determine the type of foraging behavior exhibited by consumers (Fretwell 1972), and commonly results in changes in prey selection of foraging predators (Foster et al., 2013; Harmsen et al., 2011), as was found in this study. We conclude that in well-protected areas, the determinants of spatial and temporal variation in ocelot occurrence seem to come not from the association of these mesopredators with large-scale environmental factors, but rather from the interaction of their potential prey with biotic factors, and other fine-scale environmental factors.

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Conclusões

Nosso estudo mostrou que as jaguatiricas em relação às presas mostraram um comportamento diferente no período da seca em relação ao período da cheia, tendo a sobreposição mais voltada pra determinadas espécies. Além disso, variáveis em maior escala medidas por nós não afetaram a ocorrência de jaguatirica, mas houve um estudo em áreas adjacentes que mostrou uma relação deste mesopredador com variável em fina escala (Pimenta 2012). Isso mostra que as interações bióticas entre espécies, a disponibilidade de recursos e estruturas do habitat em fina escala parecem ser os fatores determinantes para jaguatirica em ambientes de terra firme na Amazônia Central. Sendo assim, sugerimos que sejam feitas pesquisas conjuntas, analisando dieta e utilizando radiocolares, para saber como as jaguatiricas estão sendo determinadas por suas presas e como cada uma está contribuindo para sua persistência. Assim como, a avaliação populacional da jaguatirica e de suas presas potenciais para entender como as mudanças na estrutura do ambiente afetam esses animais.