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

SOBREPOSIÇÃO DE ATIVIDADE ENTRE DOIS MESOPREDADORES SIMPÁTRICOS, JAGUATIRICA (*LEOPARDUS PARDALIS)* E IRARA (*EIRA BARBARA)*, NA RESERVA ECOLÓGICA DE MARACÁ

NATUSHA CACAU PINHEIRO COSTA

Manaus, AM

Setembro de 2022

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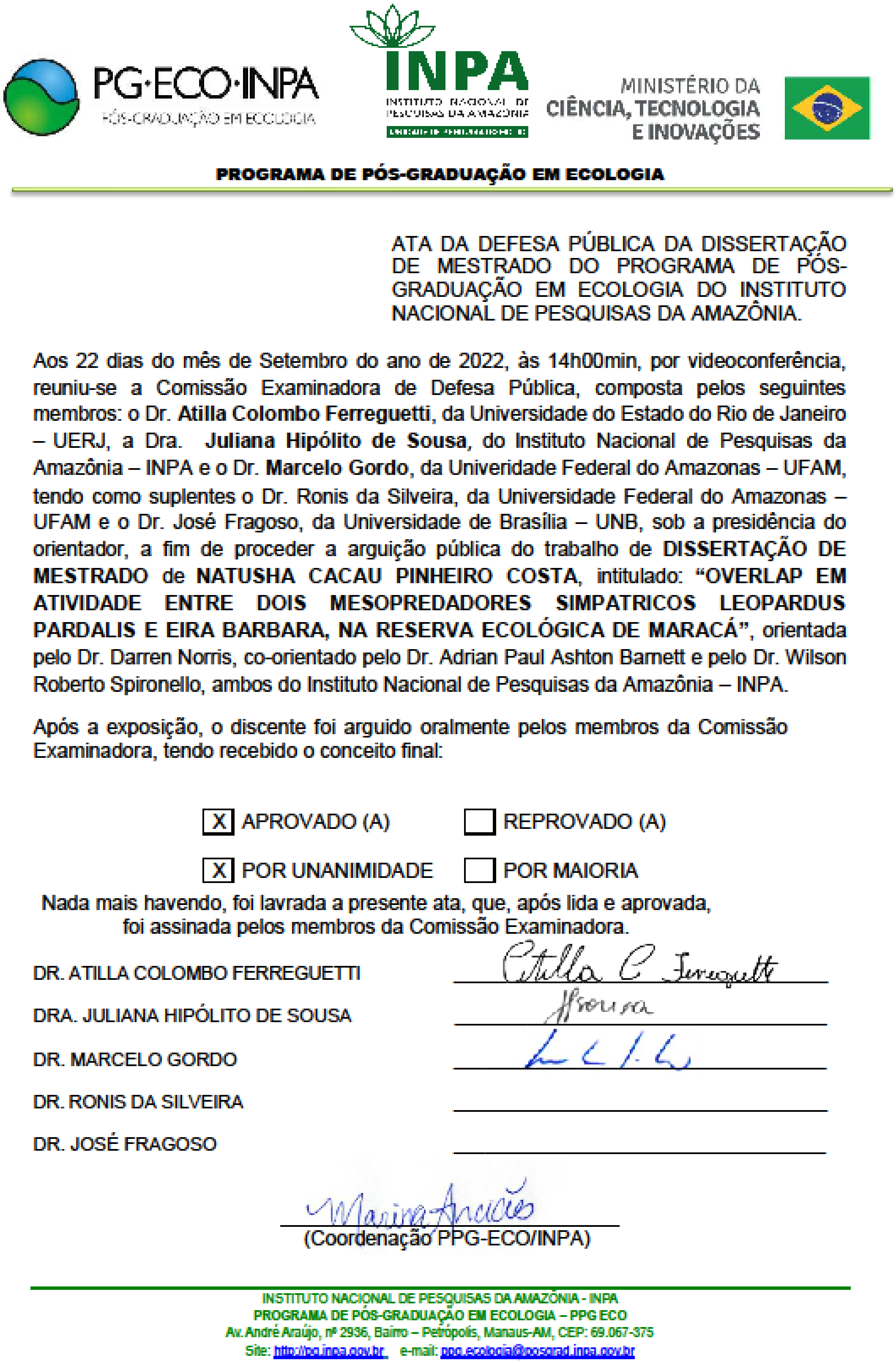
Dissertação apresentada ao Instituto Nacional de Pesquisas da Amazônia, Programa de Pós-Graduação em Ecologia, como parte dos requisitos necessários à obtenção do título de Mestre em Biologia com ênfase em Ecologia.

Manaus, AM
Setembro de 2022

BANCA EXAMINADORA DA DEFESA ORAL PÚBLICA



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

Aos 22 dias do mês de Setembro do ano de 2022, às 14h00min, por videoconferência, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o Dr. **Atilla Colombo Ferreguetti**, da Universidade do Estado do Rio de Janeiro – UERJ, a Dra. **Juliana Hipólito de Sousa**, do Instituto Nacional de Pesquisas da Amazônia – INPA e o Dr. **Marcelo Gordo**, da Univeridade Federal do Amazonas – UFAM, tendo como suplentes o Dr. Ronis da Silveira, da Universidade Federal do Amazonas – UFAM e o Dr. José Fragoso, da Universidade de Brasília – UNB, sob a presidência do orientador, a fim de proceder a arguição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **NATUSHA CACAU PINHEIRO COSTA**, intitulado: **“OVERLAP EM ATIVIDADE ENTRE DOIS MESOPREDADORES SIMPATRICOS LEOPARDUS PARDALIS E EIRA BARBARA, NA RESERVA ECOLÓGICA DE MARACÁ”**, orientada pelo Dr. Darren Norris, co-orientado pelo Dr. Adrian Paul Ashton Barnett e pelo Dr. Wilson Roberto Spironello, ambos do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o discente foi arguido 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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DRA. JULIANA HIPÓLITO DE SOUSA JSousa
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Sinopse:

Estudamos os padrões de sobreposição temporal e espacial entre jaguatirica (*Leopardus pardalis*), irara (*Eira barbara*) e suas presas em um ambiente protegido da Amazônia, utilizando dados de campo de armadilhas fotográficas de dois anos na Estação Ecológica da Ilha de Maracá.

Palavras-chave: Padrões de atividade, Amazonia, armadilha fotográfica, carnívoros, competição, felídeo, mustelídeo, mamífero, vertebrado, segregação de nicho, interações predador-presa.

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“We are gonna leave you with this one, this song goes out to anybody here that believes that maybe, just maybe, we were all born with the moral obligation to leave this world a better place than the world that we’ve found”

“Rise Against”

RESUMO

As interações predador-presa são um foco em ecologia e conservação devido à sua importância como mecanismo estrutural para comunidades bióticas. Para fornecer referências para planejamento e conservação, é importante entender como os carnívoros interagem com suas presas e com competidores em áreas que não sofrem impactos antropogênicos diretos. Neste estudo, investigamos os padrões de atividade temporal de jaguatirica (*Leopardus pardalis*), irara (*Eira barbara*) e suas presas, em uma grande ilha protegida na Amazônia brasileira. Usando registros obtidos por armadilhas fotográficas ao longo de dois anos e meio (2018-2020), avaliamos os padrões de sobreposição e separação temporal entre ambas as espécies de carnívoros e de várias espécies de presas, mamíferos e aves. Estimamos padrões de atividade usando densidade de kernel e medimos a sobreposição entre distribuições pareadas estimadas usando um coeficiente de sobreposição. Usando diferenças de tempo entre as coocorrências, testamos as previsões de que irara e jaguatirica apareceriam com menos frequência em locais anteriormente visitados pela outra espécie e com mais frequência em locais anteriormente visitados por suas respectivas presas. A sobreposição temporal entre os predadores ($\Delta = 0{,}35$) foi menor do que com suas presas ($\Delta = 0{,}58 – 0{,}84$ e $\Delta = 0{,}66 – 0{,}73$ para irara e jaguatirica, respectivamente). Não houve evidência de distinção na atividade entre câmeras com ou sem ambos os carnívoros. Na verdade, encontramos mais que o dobro do número de fotos de irara em armadilhas fotográficas que também tinham jaguatiricas. Irara pareceu evitar locais anteriormente visitados por jaguatiricas por pelo menos 24 horas, não houve, no entanto, diferença aparente na frequência de fotos de jaguatirica antes ou depois do aparecimento de iraras. Os resultados fornecem a primeira visão sobre interações temporais envolvendo carnívoros simpátricos e suas presas em potencial em uma ilha amazônica. Em geral, nossos resultados sugerem que irara pode adaptar sua atividade diariamente para manter a separação temporal das jaguatiricas. Estudos futuros devem levar em consideração a pouca documentação dos padrões em estratos florestais verticais para carnívoros parcialmente arbóreos.

ABSTRACT

Title: Overlap in activity between two sympatric mesopredators *Leopardus pardalis* and *Eira barbara*, in the Ecological Reserve of Maracá

Predator-prey interactions are a focus in ecology and conservation due to their importance as a key structuring mechanism in biotic communities. To provide a baseline reference for conservation planning, it is important to understand how carnivores interact with their prey and competitors in areas that do not experience direct anthropogenic impacts. In this study, we investigated the temporal activity patterns of the Ocelot (*Leopardus pardalis*) and Tayra (*Eira barbara*) and their prey on a large, protected island in Brazilian Amazonia. Using photographs taken by camera-traps over two and a half years (2018-2020), we assessed the patterns of temporal overlap and separation between both carnivore species and multiple mammal and bird prey species. We estimated activity patterns using kernel density and measured the overlap between estimated paired distributions using an overlap coefficient. Using time differences between co-occurrences, we tested predictions that Tayra and Ocelot would appear less frequently at locations previously visited by the other species, and more frequently at locations previously visited by their prey. The temporal overlap between predators was lower ($\Delta = 0.35$) than with their prey ($\Delta = 0.58 – 0.84$ and $\Delta = 0.66 – 0.73$ for Tayra and Ocelot respectively). There was no evidence of changes in activity between cameras with or without both carnivores. Indeed, we found more than double the number of images of Tayra at camera-traps that also had Ocelots. The subordinate Tayra appeared to avoid locations with Ocelot by at least 24 hours, whereas there were no apparent differences in the frequency of Ocelot images before or after Tayra. The results provide the first insight into temporal interactions involving sympatric carnivores and their potential prey on an Amazonian island. In general, our results suggest that Tayra may tailor their activity daily to maintain temporal separation from Ocelots. Future studies should address the poorly documented patterns across vertical forest strata for these partially arboreal carnivores.

SUMÁRIO

INTRODUÇÃO

Nicho é a soma de diversas variáveis, incluindo dieta, padrões de atividade, sazonalidade, uso de habitat e interações interespecíficas. Foi definido por Wiens como a combinação de condições bióticas e abióticas onde uma espécie pode persistir. (WIENS, 2011) Mamíferos da ordem carnívora são considerados um grupo paradigmático, com espécies modelo que facilitam o entendimento de interações intraguilda que estruturam comunidades ecológicas (CREEL; SPONG; CREEL, 2001; RITCHIE; JOHNSON, 2009). Muitos estudos se concentraram em carnívoros grandes e carismáticos, como felinos e ursos, para monitorar mudanças globais e indicar o nível de conservação de habitats (TROUWBORST; BLACKMORE, 2020; WEBER; RABINOWITZ, 1996), mas estudos recentes sugerem que carnívoros menores podem ser mais adequados para monitorar mudanças antropogênicas em habitats e comunidades ecológicas devido a fatores como, respostas relativamente rápidas, infinidade de fatores ambientais e à diversidade de espécies de presas (LOZANO; OLSZAŃSKA; MORALES-REYES; CASTRO *et al*., 2019; MARNEWECK; BUTLER; GIGLIOTTI; HARRIS *et al*., 2021; MARNEWECK; ALLEN; BUTLER; SAN *et al*., 2022).

Interações competitivas entre espécies com requisitos de nicho semelhantes, incluindo dieta, devem ser consideradas ao estudar a estrutura da comunidade carnívora (ST-PIERRE; OUELLET; CRETE, 2006). A coexistência entre carnívoros simpátricos com tamanhos corporais/dietas semelhantes pode ser facilitada pela segregação temporal e espacial (CAROTHERS; JAKSIC, 1984; DONADIO; BUSKIRK, 2006; RAUSET; MATTISSON; ANDREN; CHAPRON *et al*., 2013; RITCHIE; JOHNSON, 2009; VANAK; FORTIN; THAKER; OGDEN *et al*., 2013). A segregação temporal pode facilitar a coexistência de carnívoros simpátricos quando compartilham habitats e presas. Mas mesmo quando não há evidência de segregação temporal ou espacial, carnívoros simpátricos com dietas sobrepostas podem ativamente se evitar para reduzir o risco de encontros e interações potencialmente agonísticas (MATTISSON; PERSSON; ANDREN; SEGERSTROM, 2011; VIOTA; RODRÍGUEZ; LÓPEZ-BAO; PALOMARES, 2012). Compreender as estratégias usadas pelas espécies para minimizar essa pressão agonística é um desafio, mas o particionamento de atividade temporal e de habitat têm sido propostos como os principais mecanismos para reduzir a probabilidade de encontros do tipo entre espécies carnívoras concorrentes

(CAROTHERS; JAKSIC, 1984; DURANT, 1998; HAYWARD; SLOTOW, 2009). As interações negativas também terão uma forte influência no tamanho da população, padrões de atividade e coexistência entre espécies, mas podem diminuir por segregação espacial ou temporal (COZZI; BROEKHUIS; MCNUTT; TURNBULL *et al*., 2012; DONADIO; BUSKIRK, 2006; MATTISSON; PERSSON; ANDREN; SEGERSTROM, 2011; RAUSET; MATTISSON; ANDREN; CHAPRON *et al*., 2013; RITCHIE; JOHNSON, 2009; VANAK; FORTIN; THAKER; OGDEN *et al*., 2013; VIOTA; RODRÍGUEZ; LÓPEZ-BAO; PALOMARES, 2012). Os carnívoros neotropicais são conhecidos por evitar a competição utilizando-se de uma variedade de mecanismos, alguns utilizam diferentes itens alimentares, ou, quando há alta sobreposição alimentar, utilizam recursos de forma diferente nas dimensões espaciais e/ou temporais (DE OLIVEIRA; TORTATO; SILVEIRA; KASPER *et al*., 2010; DIAS; DE CAMPOS; RODRIGUES, 2018; KONECNY, 1989; SUNQUIST, 1989; ZUERCHER; OWEN; TORRES; GIPSON, 2022).

A jaguatirica (*Leopardus pardalis*) é um felino malhado neotropical amplamente distribuído, com adultos tipicamente pesando de 8 kg a 16,5 kg para machos de 7,2 kg a 9 kg para fêmeas (EMMONS; FEER, 1997), utiliza-se tanto da visão quanto da audição como mecanismo de caça (TEWES; SCHMIDLY, 1987). Tem sido sugerido que esta espécie impacte negativamente os padrões de abundância e atividade de outras espécies por interações intraguilda agressivas e/ou limitando de recursos (CUELLAR; MAFFEI; ARISPE; NOSS, 2006; DE OLIVEIRA; TORTATO; SILVEIRA; KASPER *et al*., 2010). Resultados anteriores sugerem que as jaguatiricas exercem uma força supressora sobre outros carnívoros através da competição por interferência, de OLIVEIRA *et al*. (2010) descreveu o que chamamos de “efeito jaguatirica”, onde as densidades crescentes dessa espécie impactaram negativamente carnívoros menores em muitas partes de sua área de distribuição e, em alguns casos, impõem uma ameaça maior do que a dos grandes carnívoros (DE OLIVEIRA; PEREIRA, 2014; DE OLIVEIRA; TORTATO; SILVEIRA; KASPER *et al*., 2010). A maior densidade populacional de jaguatiricas relatada vem da Ilha Barro Colorado (RODGERS; GIACALONE; HESKE; JANEČKA *et al*., 2014), que representa talvez a população de jaguatiricas mais intensamente estudada em toda a gama de espécies. A área de vida média nesta ilha foi de 3,48 km^2 para machos e 1,48 km^2 para fêmeas, enquanto a distância média percorrida foi de 1,15 km por noite (MORENO; KAYS; GIACALONE-WILLIS; ALIAGA-ROSSEL *et al*., 2012). Embora estudos anteriores não tenham encontrado evidências de interações agressivas com membros de outras ordens carnívoras, por exemplo, mustelídeos (KONECNY, 1989) em florestas terrestres, poderiam esses padrões mudar como resultado da densidade elevada e, portanto, elevada competição inter e intraguilda de populações insulares?

A irara (*Eira barbara*) é um mustelídeo neotropical com ampla distribuição geográfica (EWER, 1973; PRESLEY, 2000). São caçadores ativos que perseguem presas utilizando o olfato como principal método de detecção de presas (GALEF JR; MITTERMEIER; BAILEY, 1976; PRESLEY, 2000). Pesando de 3,7 kg a 11,1 kg, as iraras são caçadoras igualmente hábeis em estratos arbóreos e terrestres (GALEF JR; MITTERMEIER; BAILEY, 1976; PRESLEY, 2000). Possuem dieta onívora generalista (GALEF JR; MITTERMEIER; BAILEY, 1976; KONECNY, 1989; PRESLEY, 2000), incluindo uma variedade de frutas, mel, carniça, vertebrados e insetos (CABRERA; YEPES, 1960; EMMONS; FREER, 1990; GALEF JR; MITTERMEIER; BAILEY, 1976; HALL; DALQUEST, 1963). Embora a irara tenha uma dieta muito mais ampla (por exemplo, incluindo frutas), há uma alta sobreposição alimentar com jaguatirica em locais onde ocorrem em simpatria (KONECNY, 1989; ZUERCHER; OWEN; TORRES; GIPSON, 2022). A partição de habitat para evitar a competição por recursos alimentares é possível para carnívoros quando há espaço adequado e qualidade de habitat (RAUSET; MATTISSON; ANDREN; CHAPRON *et al.*, 2013; SUNQUIST; SUNQUIST; DANEKE, 1989; VANAK; FORTIN; THAKER; OGDEN *et al.*, 2013). Estudos anteriores constataram que jaguatirica e irara em simpatria têm padrões semelhantes de uso de habitat (KONECNY, 1989), o que sugere que a segregação espacial não é utilizada para evitar a competição.

Apesar da cobertura vegetal se mostrar uma variável positiva para a ocupância da jaguatirica (WOLFF *et al*,. 2019), as variáveis ambientais não explicam fortemente a distribuição espacial de espécies generalistas (DE OLIVEIRA; TORTATO; SILVEIRA; KASPER *et al.*, 2010; KONECNY, 1989; MICHALSKI; NORRIS; DE OLIVEIRA; MICHALSKI, 2015; PRESLEY, 2000; ZUERCHER; OWEN; TORRES; GIPSON, 2022). A distribuição espacial de ambas as espécies, entretanto, tem sido associada a elementos estruturais de habitat e de disponibilidade de presas (KONECNY, 1989; MICHALSKI; CRAWSHAW; DE OLIVEIRA; FABIAN, 2006; MORENO-SOSA; YACELGA; CRAIGHEAD; KRAMER-SCHADT *et al.*, 2022). Um estudo de telemetria em florestas tropicais úmidas de Belize mostrou que ambas as espécies tinham associações com habitats generalistas, sem evidência de evasão espacial, pois as áreas de vida de ambas as espécies se sobrepunham consideravelmente (KONECNY, 1989). O mesmo estudo mostrou que as jaguatiricas percorreram 6,4 km em 24h, e tinham áreas de vida de 14 e 31 km^2 (fêmea adulta e macho subadulto, respectivamente). Irara percorreu 6,9 km em 24h e habitava áreas de 16 e 24 km^2 (adultos, fêmea e macho, respectivamente) (KONECNY, 1989). Ambas as espécies têm áreas de vida flexíveis e o uso do espaço e os padrões variam com o habitat. Por exemplo, jaguatiricas tinham áreas de vida de 1,5 – 3,5 km^2 em 15 km^2 da Ilha Barro Colorado (MORENO; KAYS; GIACALONE-WILLIS; ALIAGA-ROSSEL *et al.*, 2012), e iraras áreas de 5 km^2 em Mata Atlântica fragmentada (MICHALSKI; CRAWSHAW; DE OLIVEIRA; FABIAN, 2006). Sabendo que ambas as espécies utilizam o mesmo habitat, e com isso, era provável que não houvesse uma segregação espacial no sentido amplo, procuramos uma alternativa pouco abordada e presumimos a possibilidade de haver segregação espacial em momentos pontuais, em que uma espécie evitaria locais em que a outra estivesse utilizando.

Décadas de estudos mostram que a segregação temporal é provavelmente o principal mecanismo para a coexistência de jaguatirica e irara (FINNEGAN; GANTCHOFF; HILL; SILVEIRA *et al.*, 2021; KONECNY, 1989; SUNQUIST; SUNQUIST; DANEKE, 1989). Sendo assim, presumimos que esse mecanismo será utilizado ao máximo, tanto para evitar o contato com o outro predador quanto para aumentar o contato com suas respectivas presas.

Estudos mostram que a presença humana (trilhas, estradas de terra, cães) e distúrbios no habitat (extração de madeira) podem afetar a presença de ambas as espécies (BAILEY; DOHERTY *et al.*, 2018; MICHALSKI; CRAWSHAW; DE OLIVEIRA; FABIAN, 2006). No entanto, há uma falta de evidências plurianuais de grandes áreas não perturbadas/protegidas para fornecer referências para monitorar a força e a direção das mudanças antrópicas nas florestas perturbadas da Amazônia. Aqui usamos dados de campo de 2018 até 2020, com duas estações secas e uma chuvosa, para examinar padrões temporais na atividade de jaguatirica e irara em uma grande ilha protegida da Amazônia. Testamos a hipótese de que, dadas as semelhanças na dieta, tamanho do corpo e uso do habitat, jaguatirica (*Leopardus pardalis*) e irara (*Eira barbara*), usariam particionamento temporal para reduzir a probabilidade de encontros agonísticos.

Prevemos que:

i) Irara e jaguatirica terão baixa sobreposição temporal, mas maiores sobreposições com espécies de presas.
ii) Irara e jaguatirica aparecerão com menos frequência em locais previamente visitados pela outra espécie, e mais frequentemente em locais previamente visitados por suas presas.

OBJETIVO GERAL

Avaliar as interações interespecíficas por meio da variação na sobreposição temporal e espacial de mesocarnívoros na ESEC de Maracá e de suas presas durante o ciclo circadiano e comparando o lapso de tempo entre os registros de dada espécie e o próximo e último predador registrado no mesmo local.

OBJETIVOS ESPECÍFICOS

1 – Definir as taxas de sobreposição temporal para as espécies irara, jaguatirica e suas presas na ESEC de Maracá.

2 – Estimar a variação no número de registros de irara e jaguatirica em um período de 48h antes e após o registro da outra espécie no mesmo local.

3 – Comparar o comportamento da variação no número de registros de irara e jaguatirica em um período de 48h antes e após o registro da outra espécie no mesmo local

Capítulo 1

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Temporal partitioning among two sympatric mesopredators and their prey on a large protected Amazonian island

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Abstract

Predator-prey interactions are a focus in ecology and conservation due to their importance as a key structuring mechanism in biotic communities. To provide a baseline reference for conservation planning, it is important to understand how carnivores interact with their prey and competitors in areas that do not experience direct anthropogenic impacts. In this study, we investigated the temporal activity patterns of the Ocelot (Leopardus pardalis) and Tayra (Eira barbara) and their prey on a large, protected island in Brazilian Amazonia. Using records obtained by camera-traps over two and a half years (2018-2020), we assessed the patterns of temporal overlap and separation between both carnivore species and multiple mammal and bird prey species. We estimated activity patterns using kernel density and measured the overlap between estimated paired distributions using an overlap coefficient. Using time differences between co-occurrences, we tested predictions that Tayra and Ocelot would appear less frequently at locations previously visited by the other species, and more frequently at locations previously visited by their prey. The temporal overlap between predators was lower ($\Delta = 0.35$) than with their prey ($\Delta = 0.58 – 0.84$ and $\Delta = 0.66 – 0.73$ for Tayra and Ocelot respectively). There was no evidence of changes in activity between cameras with or without both carnivores. Indeed, we found more than double the number of images of Tayra at camera-traps that also had Ocelots. The subordinate Tayra appeared to avoid locations with Ocelot by at least 24 hours, whereas there were no apparent differences in the frequency of Ocelot images before or after Tayra. The results provide the first insight into temporal interactions involving sympatric carnivores and their potential prey on an Amazonian island. In general, our results suggest that Tayra may tailor their activity daily to maintain temporal separation from Ocelots. Future studies should address the poorly documented patterns across vertical forest strata for these partially arboreal carnivores.

Keywords: activity patterns; Amazonia; camera trapping; carnivore; competition; Felid; Mustelid; mammal; vertebrate; niche segregation; predator-prey interactions.

Introduction

Mammalian carnivores have been considered a paradigmatic group, with model species that make it easier to understand intraguild interactions that structure ecological communities[1,2]. Many studies focused on charismatic large carnivores including cats and bears to monitor global changes and inform habitat conservation[3,4], but recent studies suggest that smaller carnivores can be better suited for monitoring anthropogenic changes to habitats and ecological communities due to the relatively quick responses to a multitude of environmental factors and diversity of prey species [5-7].

Coexistence among sympatric carnivores with similar body sizes/diets can be facilitated by temporal and spatial segregation[2,8-11]. Temporal segregation can facilitate the coexistence of sympatric carnivores when they share habitats and prey. But even when there is no evidence of temporal or spatial segregation, sympatric carnivores with overlapping diets can display active avoidance to reduce the risk of encounters and potentially agonistic interactions[12,13]. Understanding the methods used by species to minimize that pressure is a challenge, but mechanisms including partitioning of temporal activity and habitat have been proposed as the main mechanisms to reduce the probability of risky encounters between competing carnivore species[10,14,15]. Negative interactions will also have a strong influence on population size, activity patterns, and coexistence between species, but may decrease by spatial or temporal segregation[2,8,9,11-13,16]. Neotropical carnivores are known to avoid competition by a variety of mechanisms, some utilizing different food items, or, in the case of high dietary overlap, utilizing resources differently across spatial and/or temporal dimensions [17-21].

The Ocelot (*Leopardus pardalis*) is a widespread Neotropical spotted cat, with adults typically weighing between 8 kg and 16.5kg for males and 7.2 kg and 9 kg for females[22]. Using sight and hearing to hunt[23], they have been suggested to negatively impact the abundance and activity patterns of other species by aggressive intraguild interactions and/or resource limitation[19,24]. Previous results suggest Ocelots exert a suppressive force on other carnivores through interference competition [19]. Specifically, de Oliveira, et al. [19] described what they called the “ocelot effect”, where increasing densities of this species negatively impacted smaller carnivores in many parts of their range, and in some cases may impinge more strongly than large carnivores [19,25]. The highest reported Ocelot population density is from Barro Colorado Island (BCI) [26], which represents perhaps the most intensely studied population across the species´ range. The average home range on BCI was 3.48 km^2 for males, and 1.48 km^2 for females, while the average distance travelled was 1.15 km per night[27]. Although previous studies found no evidence of aggressive interactions with members of other carnivore orders (e.g. mustelids) [18] in mainland forests, it is possible that such patterns change as a result of elevated density and therefore elevated inter- and intra-guild competition in island populations.

The Tayra (*Eira barbara*) is a Neotropical mustelid with a broad geographic distribution [28,29]. They are active hunters that chase and follow prey using olfaction as the primary method of prey detection [29,30]. Weighing from 3.7 kg to 11.1 kg, Tayra are equally adept hunters in arboreal and terrestrial strata[29,30]. They have a generalist omnivorous diet [18,29,30], including a variety of fruits, honey, carrion, vertebrates, and insects [30-33]. Although Tayra have a much broader diet (e.g. including fruits), high dietary overlap occurs between Ocelot and Tayra where they exist in sympatry[17,18]. Habitat partitioning to avoid competition over food resources is possible for carnivores when there is adequate space and habitat quality [8,9,34]. Previous studies found that sympatric Ocelot and Tayra have similar patterns of habitat use[18], which suggests that spatial segregation is not used to avoid competition.

Environmental variables do not strongly explain the spatial distribution of either of these widespread and generalist species[17-19,29,35]. The spatial distribution of both species has however been associated with structural elements of the habitat and prey availability [18,36,37]. A telemetry study in the moist tropical forests of Belize showed both species had generalist habitat associations with no evidence of spatial avoidance as home ranges of both species overlapped considerably [18]. Both species used all available habitat types, but used early secondary growth more than late secondary growth/mature forest in the protected area studied[18]. The same study showed Ocelots moved 6.4 km in 24h, with home ranges of 14 and 31 km^2 (adult female and subadult male, respectively). Tayra moved 6.9 km in 24h and ranged across areas of 16 and 24 km^2 (adult female and male, respectively)[18]. Both species have flexible ranges, and the use of space and ranging patterns vary with habit. For example, Ocelots on on 15 km^2 BCI had home ranges of 1.5 – 3.5 km [27], while in fragmented Atlantic Forest and Tayra ranges were 5 km^2 [37].

Decades of studies across the species ranges show temporal segregation is most likely to be the principal mechanism for Ocelot and Tayra coexistence [18,34,38]. Studies have documented that human presence (e.g., trails, dirt roads, dogs) and habitat disturbances (e.g., logging) can affect the presence of both species [6,37,39]. Yet, there is a lack of multiyear evidence from large undisturbed/protected areas to provide a baseline reference for monitoring the strength and direction of anthropogenic changes in disturbed Amazonian forests. Here we used field data from 2018 to 2020, two dry and one wet season, to examine temporal patterns in the activity of Ocelot and Tayra on a large, protected Amazonian island. We tested the hypothesis that given the similarities in diet, body size, and habitat use, Ocelot (*Leopardus pardalis)* and Tayra (*Eira Barbara)*, would use temporal partitioning to reduce the probability of agonistic encounters.

We predict that:

i) Tayra and Ocelot will have low temporal overlap, but higher overlaps with prey species.

ii) Tayra and Ocelot will appear less frequently at locations previously visited by the other species, and more frequently at locations previously visited by their prey.

Results

We obtained a total of 172 independent registers of Ocelot and 168 of Tayra from 11,538 camera-trap days (3540 from 15 December 2018 to 20 February 2019 and 7998 from 7 February to 18 July 2020). Independent photos of prey species were dominated by Agoutis (*Dasyprocta* sp.), which accounted for nearly half (48.2%, 5074) of the 10,529 photos of prey species (Table 1). Indeed, more than three-quarters of prey photos were from only two widespread and relatively abundant diurnal species groups (i.e. Agoutis and Trumpeters 77.7%, n = 8183 photos, Table 1).

Table 1 - Focal prey species found on the Maracá Island Ecological Reserve. Summary of photos and species traits (activity, weight) and predator for the selected prey species groups. The taxa included within more general groups are listed.

Species group	Family	Taxa included	Photos (cameras) [a]	Activity (documented / present study) [b]	Weight (kg) [c]	Predated by	
						Ocelot	Tayra
Mammal							
Rodentia							
Agoutis	Dasyproctidae	Dasyprocta agouti	5076 (60)	Diurnal / Diurnal	4	+ [36,40]	+ [17,41,42]
Pacas	Cuniculidae	Cuniculus paca	83 (18)	Nocturnal / Nocturnal		+ [17]	
Spiny rats	Echymyidae	Dactylomys / Proechimys	259 (28)	Nocturnal / Nocturnal	<1	+++ [40]	+++ [21,41,43,44 18,21,29]
Squirrels	Sciuridae	Sciurus / Microsciurus	185 (37)	Diurnal / Diurnal	<1	+++ [17,40]	+++ [21,41,43,44 18,21,29]
Didelphimorphia							
Opossums	Didelphidae	Didelphis / Philander	268 (36)	Nocturnal / Nocturnal	1.5	+++ [18,36,40]	+ [17,29,41]
Cingulata							
Armadillos	Dasypodidae	Dasypus novemcinctus / septemcinctus	107 (28)	Cathemeral and Nocturnal / Nocturnal	4	++ [18,36,40]	+ [45]
Birds							
Tinamiformes							
Tinamous	Tinamidae	Tinamus spp / Crypturellus spp	608 (55)	Diurnal / Diurnal	<1	+ [17,36,40]	+ [17,46]
Gruiformes							
Trumpeters	Psophiidae	Psophia crepitans	3120 (58)	Diurnal / Diurnal	2	+ [17]	+ [17]
Galliformes							
Curassows	Cracidae	Crax alector	834 (60)	Diurnal / Diurnal	3	+ [17,36]	+ [17]

[a] Number of independent photos and cameras in which the species appeared.
[b] Activity documented in the literature and the present study.
[c] Mean adult body weight (kg).
[d] Documented predator, with sources. Including a qualitative indication of the relative frequency of predation /occurrence in the diet obtained from the source literature.

Temporal overlap

There was strong temporal segregation between the two carnivores (Fig. 1). Indeed, the peak of Tayra activity corresponded to the hours when Ocelots were least active (Fig. 1). Tayras were "strictly diurnal" and Ocelot "predominantly nocturnal" and these differences were reflected in low and insignificant overlap in temporal activity (35%, Fig. 1). There was a clear peak in Tayra activity around midday (Fig. 1) and Tayra were recorded during the night on only three occasions (22h, 1h, 3h). In contrast, 59% of Ocelot photos were nocturnal (between one hour after sunset and one hour before sunrise), with Ocelot activity peaking at 21h and 2h and declining throughout the day to the lowest levels in the afternoon/early evening (Fig. 1). Although there was no significant difference in activity between seasons, peaks in activity were more pronounced during the wet season for both Ocelot and Tayra (Fig. 1).

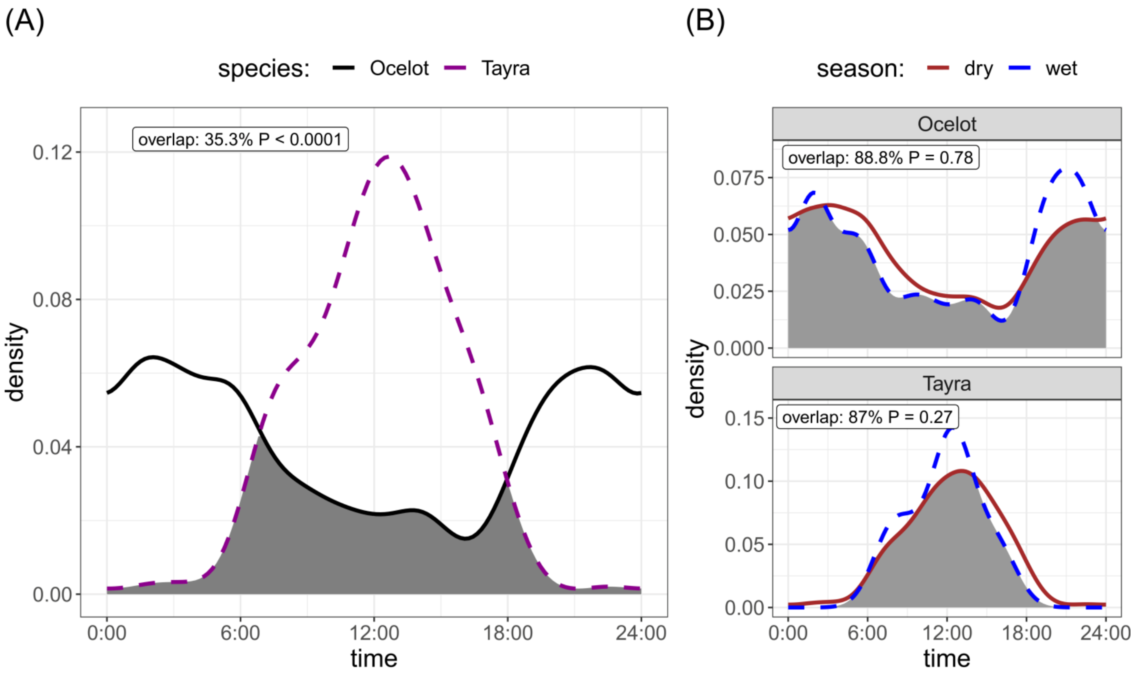
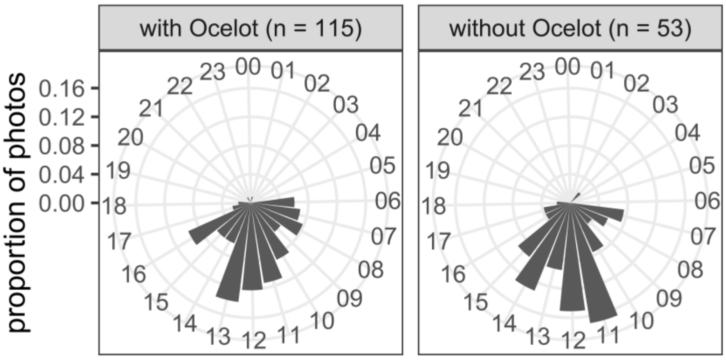


Figure 1. Temporal distribution and overlap of Ocelot and Tayra activity. Kernel density estimates for the distribution of photos per hour of Tayra (*Eira barbara*) and Ocelot (*Leopardus pardalis*) at Maracá Island Ecological Reserve, Roraima, Brazil. Camera-trap samples occurred during two consecutive dry seasons (14 December 2018 to 20 February 2019 and 7 February to 30 April 2020) and three months of heavy rainfall (1 May to 18 July 2020). Graphs show (A) overall distribution for each species (n = 172 and 168 photos for Ocelot and Tayra respectively) and (B) comparison between dry and wet season activity. Activity pattern overlap values are calculated from the area under the lower of the two density curves, with P values obtained from a bootstrap Randomization test of similarities in the distributions.

Ocelots can be classified as cathemeral at Maracá as they were active >30% during the nonpeak (diurnal) time of the 24-hr cycle (Fig. 2). There was no clear change in temporal activity between camera-traps with and without the other species. The peak timing of Tayra activity changed from 13H to 11H at cameras with and without Ocelot photos. However, such small differences did not represent a substantial change considering the variation in the timing of activity and there was no significant difference in the mean timing of activity between cameras with and without the other species (Circular Analysis of Variance, *P* >0.4 for both Ocelot and Tayra). There was also more than double the number of photos of Tayra at camera-traps that also had Ocelots (Fig. 2). This increase came from the presence of both species at nearly two thirds of the camera-traps with Tayra photos (64%, 64%, and 65% of camera-traps with Tayra photos also had Ocelot photos during the three sampling events).

(A) Tayra



(B) Ocelot

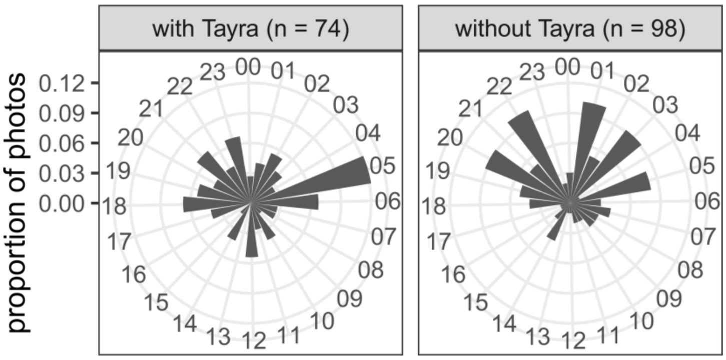


Figure 2. Activity patterns of Tayra and Ocelot. Comparison of activity (proportion of photos per hour) of Tayra (*Eira barbara*) and Ocelot (*Leopardus pardalis*) at Maracá Island Ecological Reserve, Roraima, Brazil. Temporal activity compared between camera-traps with and without the presence of the other species.

The temporal activity overlap between Tayra and most diurnal prey was high (Figure 3), yet all patterns of activity differed significantly. The greatest overlaps were: Trumpeter [$\Delta_4 = 0.84$ (0.77 - 0.88) $p<0.0001$], Curassow [$\Delta_4 = 0.78$ (0.69 - 0.82) $p<0.0001$], Agouti [$\Delta_4 = 0.76$ (0.69 - 0.81) $p<0.0001$], Tinamous [$\Delta_4 = 0.69$ (0.60 - 0.73) $p<0.0001$] and Squirrel [$\Delta_4 = 0.58$ (0.47 - 0.64) $p<0.0001$]. Tayra showed little overlap with the nocturnal prey ($\Delta_4 \leq 0.15$), and only overlapped minimally around sunrise and sunset with Armadillo [$\Delta_4 = 0.15$ (0.03 - 0.14) $p<0.0001$], Paca [$\Delta_1 = 0.14$ (0.03 - 0.13) $p<0.0001$], Spiny rat [$\Delta_4 = 0.12$ (0.02 - 0.10) $p<0.0001$] and Opossum [$\Delta_4 = 0.11$ (0.02 - 0.10) $p<0.0001$].

Considering the overlap between Ocelots and their potential prey, this felid had little ($\Delta_4 < 0.45$) coincidence of activity times with the diurnal species: Tinamous [$\Delta_4 = 0.44$ (0.33 - 0.45) $p<0.0001$], Agouti [$\Delta_4 = 0.40$ (0.32 - 0.44) $p<0.0001$], Curassow [$\Delta_4 = 0.39$ (0.29 - 0.42) $p<0.0001$], Trumpeter [$\Delta_4 = 0.38$ (0.29 - 0.41) $p<0.0001$] and Squirrel [$\Delta_4 = 0.35$ (0.26 - 0.39) $p<0.0001$], with patterns of activity differing significantly. Ocelots had greater overlap with nocturnal prey, with significant differences in activity patterns, Armadillo [$\Delta_4 = 0.73$ (0.64 - 0.80) $p=0.0001$], Spiny rat [$\Delta_4 = 0.71$ (0.63 - 0.76) $p<0.0001$], Opossum [$\Delta_4 = 0.69$ (0.62 - 0.75) $p<0.0001$] and Paca [$\Delta_1 = 0.66$ (0.57 - 0.72) $p<0.0001$].

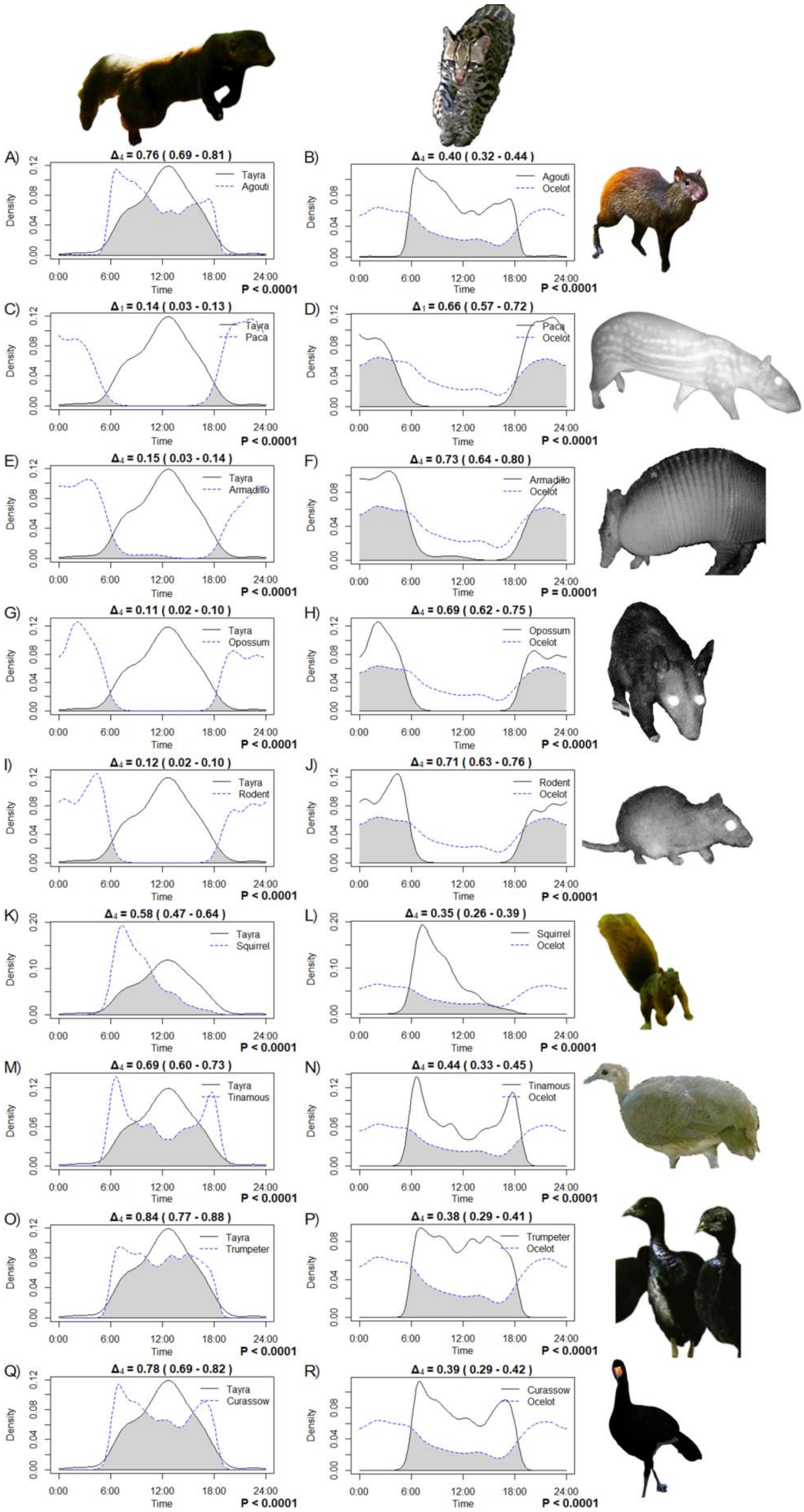


Figure 3. Temporal overlap between carnivores and potential prey species on the Maracá Island Ecological Reserve. A) Tayra and Agouti; B) Ocelot and Agouti; C) Tayra and Paca; D) Ocelot and Paca; E) Tayra and Armadillo; F) Ocelot and Armadillo; G) Tayra and Opossum; H) Ocelot and Opossum; I) Tayra and Spiny rat; J) Ocelot and Spiny rat; K) Tayra and Squirrel; L) Ocelot and Squirrel M) Tayra and Tinamous; N) Ocelot and Tinamous; O) Tayra and Trumpeter; P) Ocelot and Trumpeter; Q) Tayra and Curassows; R) Ocelot and Curassows.

Agouti was the only prey species with statistically significant differences in activity between the rainy and dry seasons. During the dry season, agoutis had more prominent crepuscular peaks and reduced activity around midday [$\Delta_4 = 0.91$ (0.89 - 0.93) $p<0.0001$]. We did not find significant differences in activity patterns between the rainy and dry seasons for any other prey species. It was not possible to compare seasonal activity for Paca due to the low number of wet season photos (n = 6), as 93% of the records were in the dry seasons (n = 77). However, this species was strictly nocturnal in both seasons.

Temporal separation

A comparison of temporal differences between Ocelot and Tayra images at the same camera showed that Tayra appeared only after a noticeable delay following an Ocelot photograph. The frequency of Tayra images started to increase 24 hours after that of an Ocelot, with a maximum frequency 5 days after. In contrast, there were no apparent differences in the frequency of Ocelot images either before or after Tayra (Figure 4). The frequency distribution of images also suggested differences in species movement patterns, as if a camera had an image of the species, there was likely to be another image of the same species within three days for Tayra and up to 10 days for Ocelot, with peaks at one or two days for Tayra and Ocelot respectively (Figure 4).

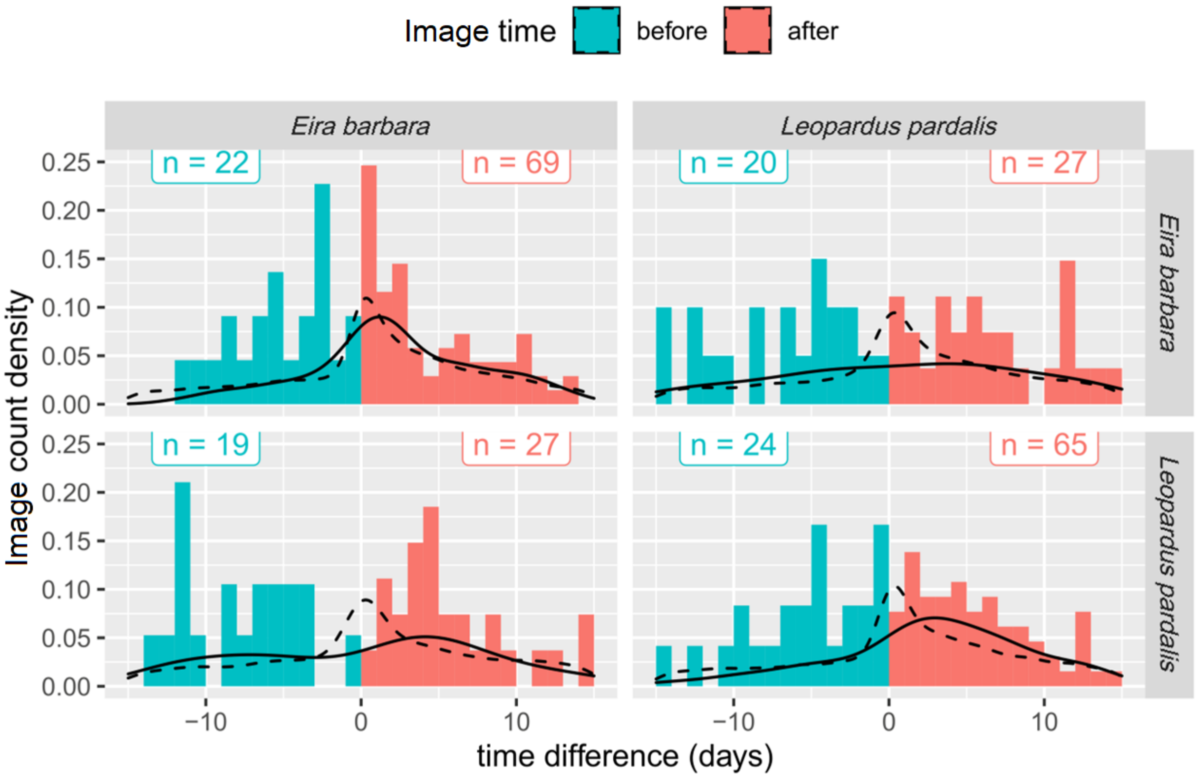


Figure 4. Time differences between Ocelot and Tayra. Comparison of time differences from camera-traps where both species were imaged at Maracá Island Ecological Reserve, Roraima, Brazil. Density distribution of images of the focal species in columns before (blue bars) and after (red bars) the potentially subordinate species (rows). Solid line is the kernel density estimate of the histogram and dashed line represents the kernel density expected from a random distribution of differences obtained via bootstrap randomization.

The strongest evidence for a temporal association with prey species came from Tayra and diurnal prey (Figure 5). The frequency of Tayra images peaked within one to two hours of the diurnal prey, then declined steadily across 48 hours. In contrast, Ocelot images were most frequent six hours before those of diurnal prey (Figure 5). There was little evidence to indicate a direct association between ocelots and the nocturnal prey, as the peak frequency of Ocelot images occurred from 21 to 31 hours before the nocturnal prey (Figure 5).

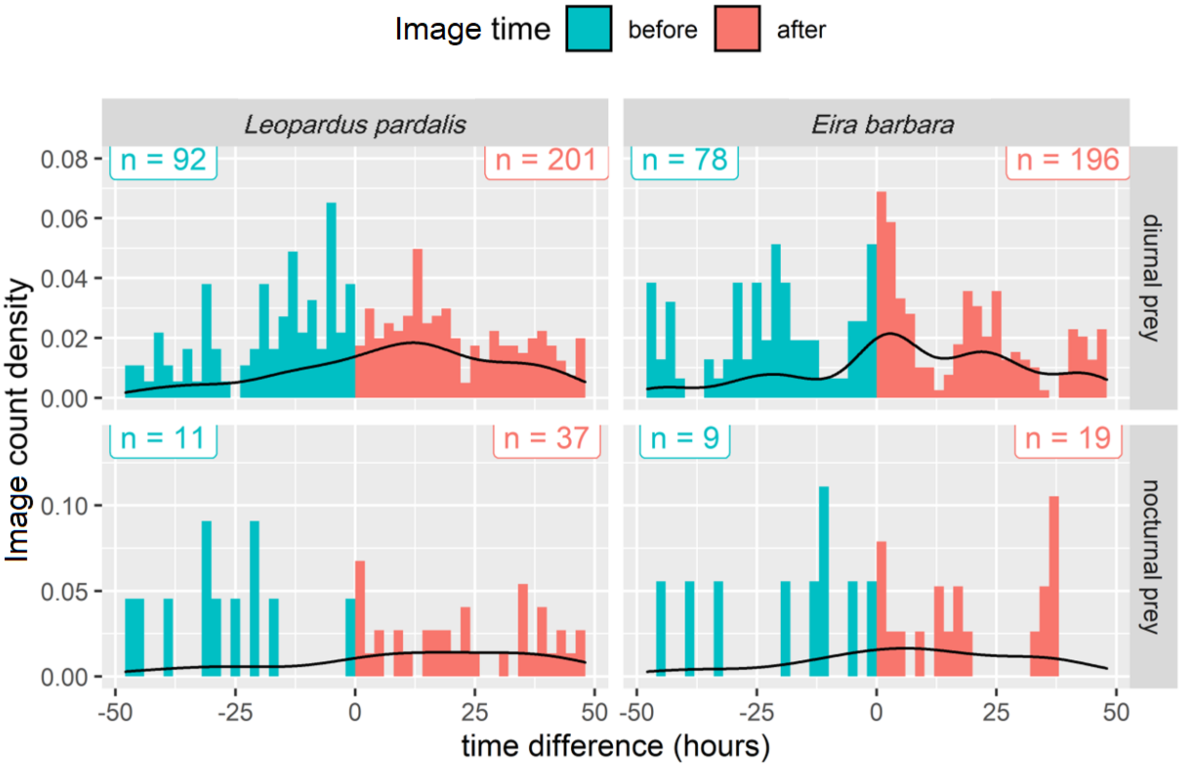


Figure 5. Time differences between carnivores and prey. Comparison of the time differences between species from the same camera-trap at Maracá Island Ecological Reserve, Roraima, Brazil. Density distribution of images of the carnivores in columns before (blue bars) and after (red bars) the potential prey species, grouped by activity (rows). Solid line is the kernel density estimate of the histogram.

The temporal differences patterns between predators and diurnal prey strongly reflected those of the two most common species types - Agoutis and Trumpeters (Table 2, Fig. 6). There were far fewer images of Tayra before Agouti (n=30) compared with after (n = 97), with a clear peak within 1 to 2 hours after the prey was captured on camera. In the hours that followed, the records remained high, with an accentuated drop that coincided with the night, and then, in the first hours of the next day, there was a secondary peak of Tayra appearance. This pattern indicates that the predator is more active at locations that have been visited recently by Agoutis. Trumpeters elicited a similar response, with numbers of Tayra images being before low numbers (n=22), and higher numbers 1 to 4 hours after (n=59) passage of the birds. This was followed by low frequencies corresponding to the night, followed by an increase in photos during the diurnal hours of the second day. In contrast, nocturnal prey did not have enough encounters across 48 hours to identify any strong patterns.

For the Ocelot, the prey with the clearest pattern was also the Agouti (Fig. 6). With few Ocelot images before (n=31) and 97 after. Similarly, the Trumpeter also showed relatively few (n=33) photos before, but the same strong (n=80) bell curse response after, followed by a drop in number of images during the day and a second curve the following night. There were also too few images of ocelots and the other diurnal and nocturnal species during 48 hours to establish any pattern.

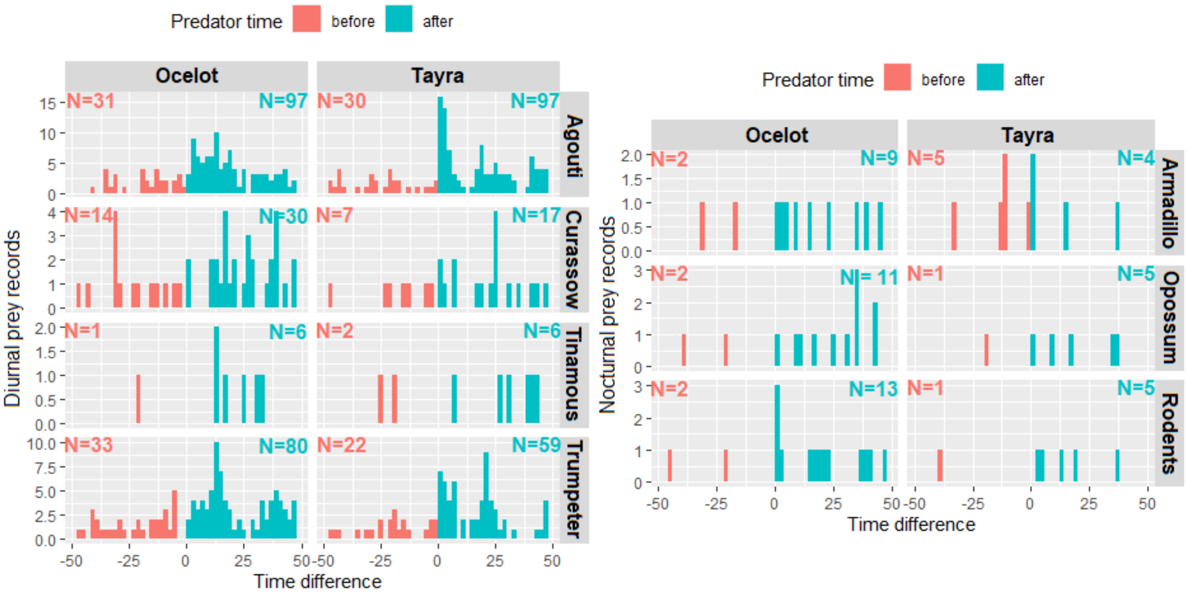


Figure 6. Rate of appearance of Tayra and Ocelot 48h before and after prey species were recorded at the same location. The difference in the number of predator records of 48h after prey was recorded is about three times higher than the 48h before the prey's appearance, the rate variating between species.

Table 2 – Common prey species of Tayra and Ocelot. Showing the percentage of registers at different times of the circadian cycle.

Common Name	Diurnal	Nocturnal	Crepuscular	Prey and Tayra Within 48h Same camera before/after	Prey and Ocelot Within 48h Same camera before/after
Mammals					
Agouti	73%	1%	26%	30/97	31/97
Opossum	0%	93%	7%	1/5	2/11
Armadillo	3%	92%	5%	5/4	2/9
Rodent	0%	90%	10%	1/5	2/13
Birds					
Tinamou	60%	0%	40%	2/6	1/6
Trumpeter	81%	0%	19%	22/59	33/80
Curassow	77%	0%	23%	7/17	14/30

Discussion

Our survey across multiple years showed temporal segregation between Tayra and Ocelot on Maraca Island. Although there was substantial overlap in space, Tayra appeared to reduce the chances of agnostic interactions with Ocelot by avoiding camera-traps at times when Ocelot had recently passed. There was temporal overlap with prey species at this well-preserved island environment on the Brazilian Amazon forest. We first addressed the temporal overlap between the carnivores and prey, then the contrasts in temporal separation, comparing the apparent temporal avoidance of Ocelots by Tayra and the temporal proximity of these predators to the potential prey species.

There was no evidence of seasonal differences in activity for either species. This supports results from the Brazilian Pantanal, which also found no differences in Ocelot activity between dry and wet seasons [47]. We predicted that Ocelot and Tayra would show low temporal overlap; and, indeed, the value was only 35.3%. Additionally, there was a clear difference in peak timing of activities and use of the circadian cycle between the species. This clear segregation confirmed our first prediction that the two carnivores would display low temporal overlap. The distinct unimodal activity patterns of the Tayra observed in this study (Fig. 1) support the avoidance hypothesis. Although Tayra's eyes possess a tapetum lucidum, their relatively smaller eye size and fewer cell layers of this intraocular "retroreflector" structure suggest reduced visual acuity at night compared to the Ocelot [48]. It seems likely that such reduced visual nocturnal acuity also explains why Tayra are active during the day. In addition to the temporal segregation, there is also likely to be vertical segregation between forest strata. Such vertical separation could change our understanding of the observed temporal patterns, but this remains unknown. The possibility of vertical segregation requires further investigation, perhaps via the use of arboreal camera-traps in future studies.

The second part of the prediction stated that both carnivore species would have higher temporal overlap with the prey species, which was also confirmed between Tayra and all the diurnal selected species. Agouti, Trumpeter, and Curassow have a high overlap (>75%), and Tinamous exhibits a moderately high overlap (69%). For Ocelot and the nocturnal prey species (e.g. Armadillo, Opossum, and Rodent) exhibited a moderately high overlap, ranging from73% to 69%. However, this prediction did not hold for Ocelot and any of its diurnal prey, where the overlap value was low (>45%). Although there was little temporal overlap, the elevated frequency of Agouti images strongly suggests that Agoutis are an accessible target, even if for only a proportionally short period of time. In the wild, adult Ocelots are estimated to consume some 0.56-0.84 kg of meat per day [19]. An agouti would therefore provide sufficient meat for one to two days. The presence of this species in the diet, therefore, follows optimal foraging theory[49], as Agoutis are an abundant and highly-available potential prey for this generalist predator within the Maraca Island Reserve.

Our second prediction was that each of the carnivores would appear less frequently at locations previously visited by the other species, which was demonstrated by the absence of the slight peak in Ocelot and Tayra appearance on the first days after the other species. Tayra showed a strong response, with frequent occurrences only reappearing five days after the presence of Ocelot. The gap in time between images of the same predator suggested differences in movement patterns, with Tayra using the same location more intensively for up to three days, in comparison to Ocelot which had images distributed across 10 days.

Based on previous studies, it was expected that both predators would appear more frequently at locations previously visited by their prey. This expectation was observed for the Agouti, the strictly diurnal specie that elicited a clear reaction from both predators, Tayra having a more immediate response, with a very prominent peak within the first hours after the prey appeared, and with Ocelot having a delayed reaction by a few hours, what could be explained by its peak in activity being a few hour past the peak of appearance of the prey. Additional evidence, that strengthens our claim, was that the number of records of the predators tripled after the appearance of prey. We found the same pattern with Trumpeter, where number of records following prey appearance was between double and triple that before the appearance. Curassow elicited some reaction, but not as clearly as the other two.

The high overlap in activity and increase in the appearance of Tayra for the presented bird groups complements the literature, as in, while it seldom points down to those specific species as Tayra prey, most studies of Tayra show that they feed on "birds" or mention unidentifiable remains of feathers in their diet. Tayra is known for using scent to hunt[29]. It is, therefore, possible that individuals use this sense to locate sites previously visited by prey, thus explaining why the response was so immediate compared to that of Ocelots, which are more visual hunters. Both Tinamous and Curassows only began their daily activities at the time when Ocelot activity started to decrease and ended their daily activity at the time Ocelot activity started to increase. Similarly, they also showed a decrease in activity at midday, when Tayra was most frequently imaged being active on the ground.

We predicted that Ocelots would show high levels of overlap with the activity cycles of their nocturnal prey. This expectation was from the documented preference of this wild cat for small mammals, a group that is predominantly nocturnal[36]. While there was a strong overlap between Ocelot and nocturnal prey, there were few images of ocelots within 48 hours of the nocturnal prey. This may be explained by the movement patterns of ocelots. Data from the camera traps (N. C. Pinheiro-Costa, unpublished data) indicates that Ocelots may be ranging through the area covered by an individual camera for up to 10 days following the presence of a prey species individual (as indicted by the presence of an image). This suggests a far more dispersed ranging pattern than with the Tayra. In contrast, Tayra appeared for up to 3 days at the same camera, suggesting a more concentrated ranging behavior. This matches findings from a telemetry study that showed Tayra remained from one to three days in the same area before moving to another[18]. Additional surveys are required to achieve a larger sample size that could enable individual identifications and a more detailed understanding of these temporal patterns.

It is extremely difficult to determine whether the temporal overlap between carnivores and a specific prey species is direct evidence of dietary preferences and active effort to match their time of activity. Hunting and avoidance behaviors are rarely captured by camera-traps and can only be inferred from the responses elicited from other species. It is extremely difficult to determine whether a lack of temporal overlap and/or increased temporal separation is direct evidence of avoidance or indirect consequence of surrounding factors. However, combined evidence from the two complementary measurements provide key insights into the nature of the interactions between the species. Considering the low temporal overlap between Tayra and Ocelot, we conclude that our hypotheses concerning interspecific interactions are supported by our results. Our hypotheses concerning prey were only supported in a few groups, taking into consideration daily overlap and the response elicited by the carnivores before and after the prey appearance. We can suggest that at least Agouti and Trumpeter supported our hypotheses for both Tayra and Ocelot, and Tinamous for Ocelot. Additional investigation is required to establish the robustness of the approach we adopted, particularly the influence of sample sizes. It remains plausible that patterns for these generalist species observed in the present study and elsewhere[50] reflect species abundances and not necessarily interspecific interactions.

While previous studies reported forests extending thousands of kilometers to the north, south, and west of Maracá, vast swathes of forest have been cleared to the south and north of Maracá from 1985 to 2020 (Google Earth Timelapse, accessed 19 September 2022: https://earthengine.google.com/timelapse#v=3.32936,-62.08477,8.021,latLng&t=3.63&ps=50&bt=19840101&et=20201231&startDwell=0&endDwell=0). Continued monitoring of the biodiversity of this island is therefore vital to help inform the conservation and restoration of forests impacted by continued anthropogenic land cover changes in the surrounding areas in the 21st century.

Methods

Study Site

We conducted this field study at Maracá Island Ecological Reserve, a large island of mainly old-growth Amazonian rainforest[51] (Fig. 7).

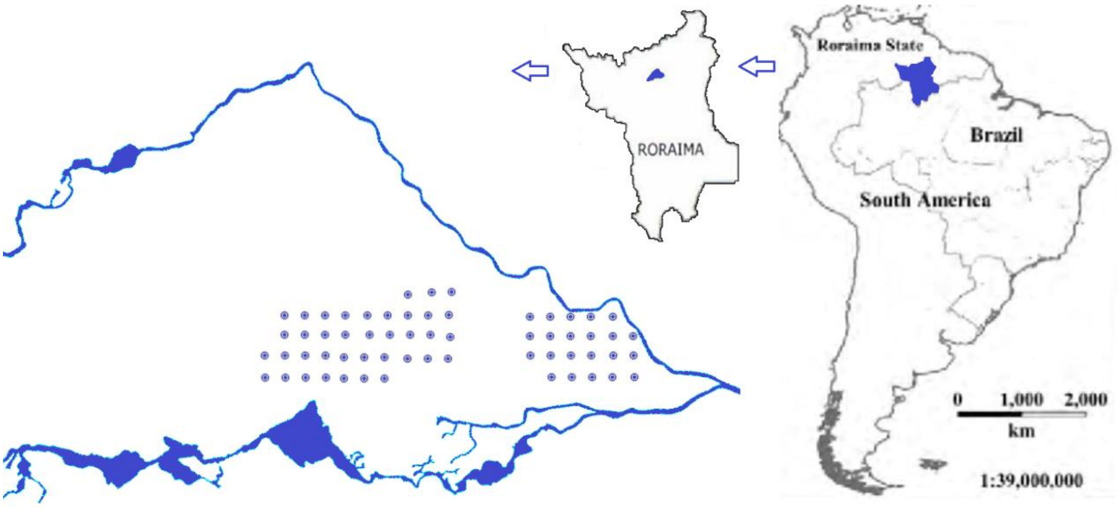


Figure 7. Maracá Island Ecological Reserve. Map of the study site showing camera-trap locations (white circles).

Maracá Island Ecological Reserve covers approximately 1035 km^2 in the Brazilian state of Roraima, in the middle of the Uraricuera River, in between the administrative districts (“municipalities”) of Alto Alegre and Amajarí (3º24’26” N, 61º29’13” W, Fig. 7). Maracá Island Ecological Reserve was created in 1981 and is categorized by the International Union for Conservation of Nature (IUCN) as a Strict Nature Reserve, and as a fully protected area by the Brazilian National System of Conservation Units (SNUC). The vegetation of Maracá is composed of forest mosaics transitioning between savanna and tropical forest, with most of the area unflooded *terra-firme* forest formations [51,52]. The climate is humid tropical, with an average annual temperature between 26ºC and 32ºC, and annual precipitation ranges between 1700 mm and 2400 mm[53]. Heavy precipitation occurs during the rainy season, which starts in May and lasts until July (Fig. 8).

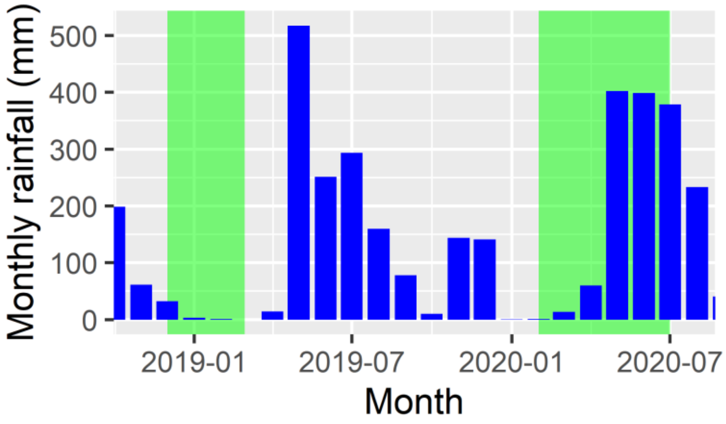


Figure 8. Rainfall and camera-trap surveys. Monthly rainfall (blue bars) and camera-trap sample months (green shading) at Maracá Island Ecological Reserve, Roraima, Brazil.

Sampling design

Camera-trap sampling is an effective technique for monitoring medium- and large-bodied terrestrial mammals. With advances in statistical analysis, camera-trap surveys are increasingly used to understand behavioral patterns, including temporal activity [54,55]. Camera-traps help minimize disturbance to the study species as they capture the animal's image remotely, so interference minimally with natural behavior. They are widely used in remote environments, such as in ecological reserves, as it is possible to independently maintain continuous monitoring for months, accumulating all images on a removable memory card. Camera-traps are remotely activated and capture the moment when an animal passes in front of the heat/motion sensor. Sensor activation generates an image with additional information on the date, time, and camera location.

We conducted camera-trap surveys across two years (Fig. 8). A total of 60 Bushnell Trophy cam HD were installed during two consecutive dry seasons (15 December 2018 to 20 February 2019 and 7 February to 30 April 2020) and three months of heavy rainfall (1 May to 18 July 2020). Cameras were installed following the Tropical Ecology Assessment and Monitoring (TEAM) protocol for Vertebrates[56]. The 2020 survey was extended due to the Covid-19 pandemic when, following lockdown guidelines, Maracá was closed to outside researchers and the removal of cameras was consequently delayed. During both years, a total of 60 cameras were installed in a grid arrangement extending across approximately 12% (129 km^2) of the reserve, with a spacing of approximately 1.4 kilometers between nearest neighboring traps (range 1.2 to 1.4 km, Fig. 7). The areas chosen for the camera-traps were representative of habit type and distribution and accessible enough for the cameras to be installed and retrieved with minimal disturbance. We chose the most suitable location to detect mammals within a radius of up to 100 meters from each predetermined GPS point. To maximize the chances of obtaining images attention was given to the presence of trails, fruiting or flowering trees, tracks, and other signs. The cameras were securely fixed to trees at a height of approximately 50 centimeters above the ground. Excess foliage and undergrowth were removed from in front of the cameras to reduce false triggers. Cameras were installed so that there was enough battery and memory autonomy throughout the study, without direct sunlight over the motion sensor, which also helps to avoid any false triggers from sun flecks and shadows. The camera-traps were unbaited, programed to trigger at any movement with no time interval between photos, remained undisturbed by researchers and continuously active 24 hours a day .

Data Analyses

We excluded from the analysis cameras where the date and time were not reliably recorded due to malfunction or memory card failure, retaining data from 54, 57, and 45 cameras from the three sampling events (an overall success rate of 87%). We identified the genus and, when possible, the species in the image, the date, time, and camera station where it was recorded with the help of the program Wild ID. The presence of multiple individuals in the same photo was considered a single record for the species. We only considered independent the photos that respected a threshold of >30 min between consecutive photos of the same species at the same camera-trap [57,58].

We selected prey species by searching the published literature documenting Tayra and Ocelot's diet and hunting. Despite most of the literature using the term “generalist” when referring to the diet of both species, we focused on nine terrestrial prey species groups that were both well established in the literature and imaged frequently in both study years. Following previous studies, prey species that were functionally similar in terms of size, activity, and habits and that were challenging to identify unambiguously were grouped together [17,55].

To classify the temporal activity, the temporal partitioning of the species was analyzed according to the circadian cycle of the species[57]. Strictly diurnal or nocturnal animals were those recorded 90% in one of these periods[59-20]. Species that had > 30% of records during the nonpeak time of the 24-hr cycle were considered cathemeral. Animals were considered as predominantly nocturnal when more than 60% of photos were taken between one hour after sunset and one hour before sunrise. We classified a species as predominantly diurnal was used when individuals appeared at least 60% between one hour after sunrise and one hour before sunset. We considered as crepuscular those species where at least 50% of the images lay within the period one hour before and one after sunrise and one hour before and one after sunset [39]. These classifications were made using the average sunrise (06:13) and sunset (18:16) times for the study area. As both times varied little throughout the year (with a maximum difference of 20 minutes), we did not consider it useful to further standardize the times [60], particularly as a study on daily activity patterns across latitudes and seasons concluded that transformation of time might not be necessary at latitudes below 20° [61].

The interactions between species were examined by comparing the overlap and separation between images. We used the method developed by Ridout and Linkie [54] to determine the daily activity pattern of each species and measure the overlap between Tayra, Ocelot, and prey. First, a non-parametric circular kernel-density function was employed to assess daily activity patterns. As a smoothing parameter, we used $h = 1$ when ≤ 50 records and $h = 4$ when > 50 records [54]. Second, a coefficient of overlap (D), was used to measure the extent of overlap between kernel-density estimates. Overlap was calculated from the area lying under both density curves. The coefficient of overlap ranged from 0 (no overlap) to 1 (complete overlap) [54,57]. Kernel density estimation curves were produced using the R-package ‘Overlap’ v.0.3.4 [54]. We used the function ‘compareCkern()’ in the package ‘Activity’ v.1.1 [55], which provided a test of the probability that two sets of circular observations came from the same distribution. We set the number of bootstrap iterations to 10 000. Although not a primary objective, we also took advantage of the extended 2020 sample to compare species activity between dry and wet seasons using overlap and circular statistics to compare mean timing [62].

We calculated the differences in time between species at the same camera-trap to establish patterns of separation. The results were compiled to examine a possible hunting effort and distinguish two separate behaviors, waiting for prey, as is common for ambush predators such as Ocelot, and following prey, as is expected for Tayra [29]. Previous studies have examined predator-prey co-occurrence networks by comparing daily records across extended periods (e.g. 20 days[50]). To focus more closely on possible predator-prey interactions, we limited the time to 48 hours before or after a prey species. We also adopted an alternative approach based on the observed frequency of predator photos before and after the prey species. All statistical analyses were performed in R-software v. 4.1.3 [63].

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CONCLUSÃO

Apesar de não haver segregação substancial no espaço, percebemos que a irara pareceu reduzir as chances de interações agnósticas com jaguatirica, evitando armadilhas fotográficas nas quais a jaguatirica houvesse passado recentemente. Primeiro abordamos a sobreposição temporal entre os carnívoros e as presas e depois os contrastes na separação temporal, comparando a aparente evitação das jaguatiricas pela irara e a proximidade temporal dos predadores com as prováveis espécies de presas.

Não houve evidência de diferenças sazonais na atividade para ambas as espécies. Isso corrobora os resultados do Pantanal brasileiro, que também não encontrou diferenças na atividade da jaguatirica entre as estações seca e chuvosa (PORFIRIO *et al*., 2016). Previmos que jaguatirica e irara teriam uma sobreposição temporal baixa; o que se confirmou, sendo de apenas 35,3%. Além disso, houve uma clara diferença no horário de pico das atividades e no uso do ciclo circadiano. Essa segregação confirma nossa primeira previsão, de que os carnívoros teriam uma baixa sobreposição temporal. Os distintos padrões de atividade unimodal de irara observados neste estudo (Fig. 1) suportam a hipótese de evitação.

Além da segregação temporal, também é provável que haja segregação vertical entre os estratos florestais. Essa separação vertical pode mudar nossa compreensão dos padrões temporais observados, mas esse aspecto permanece desconhecido. A possibilidade de segregação vertical requer mais investigações, talvez através da adição de armadilhas fotográficas arbóreas em estudos futuros.

A segunda parte da previsão afirmou que as espécies carnívoras teriam maior sobreposição temporal com as respectivas espécies de presa, o que também foi confirmado entre irara e todas as espécies diurnas selecionadas. cutia, jacamim e mutum tiveram uma sobreposição alta (> 75%), tinamus e esquilos exibiram uma sobreposição moderadamente alta (69% e 58%, respectivamente). Para a jaguatirica e as presas noturnas, tatu, gambá, rato e paca exibiram uma sobreposição moderadamente alta, variando de 73% a 66%. No entanto, essa previsão não se mostrou verdadeira para jaguatirica e nenhuma de suas presas diurnas, apresentando uma baixa sobreposição (<45%). Embora tenha havido pouca sobreposição temporal, a frequência elevada de fotos de cutias sugere fortemente que as cutias são um alvo acessível, mesmo que por um período de tempo proporcionalmente curto. Estima-se que jaguatiricas adultas consumam entre 0,56-0,84 kg ou mais de carne por dia, na natureza (DE OLIVEIRA *et al*., 2010), a cutia forneceria carne suficiente para um a dois dias. A presença na dieta, portanto, segue a teoria do forrageamento ótimo (KŘIVAN; EISNER, 2003), pois as cutias são uma presa em potencial abundante e disponíveis para esse predador generalista na Reserva da Ilha de Maraca.

Nossa segunda previsão foi que jaguatirica e irara apareceriam com menos frequência em locais previamente visitados pela outra espécie carnívora, o que foi demonstrado pela ausência do leve pico no aparecimento de jaguatirica e irara nos primeiros dias após a outra espécie, fato que era esperado de encontros aleatórios. Uma resposta mais forte pode ser a observada em irara, onde o pico de aparecimento ocorre apenas cinco dias após a presença de jaguatirica. As diferenças de tempo entre fotos da mesma espécie sugeriram diferenças nos padrões de movimento, com irara usando o mesmo local de forma mais intensa por até três dias, em comparação com jaguatirica com fotos distribuídas mais amplamente em 10 dias.

Com base em estudos anteriores, esperava-se que ambos os predadores aparecessem com mais frequência em locais previamente visitados por suas presas. Essa expectativa foi observada em cutia, a presa, estritamente diurna, provocou a reação mais clara de ambos os predadores, irara tendo uma resposta mais imediata, com um pico muito proeminente durante as primeiras horas, e jaguatirica observando o atraso de algumas horas, condizente com o uso temporal da mesma. Evidência adicional, que fortalece nossa afirmação, foi que o número de registros dos predadores triplicou após o aparecimento da presa. Encontramos o mesmo padrão com o jacamim, exceto que o número de registros após foi entre o dobro e o triplo que antes do aparecimento da presa. Mutum provocou alguma reação, mas não tão clara quanto das duas anteriores.

A alta sobreposição de atividade e aumento na aparição de irara para os grupos de aves apresentados complementa a literatura, pois, embora raramente apontem para essas espécies específicas como presas de irara, a maioria de seus estudos mostra que elas se alimentam de “pássaros” ou mencionam restos não identificáveis de penas em sua dieta. Irara é conhecida por usar o cheiro para caçar, portanto, é possível que estivesse usando esse sentido para encontrar locais anteriormente visitados por presas, explicando por que a resposta foi tão imediata em comparação com a de jaguatiricas. Tanto o tinamus quanto o mutum só iniciam suas atividades diárias no horário em que a atividade da jaguatirica começou a diminuir, e encerraram sua atividade diária no momento em que a atividade da jaguatirica começou a aumentar, da mesma forma, também mostraram uma diminuição na atividade ao meio-dia, quando irara era mais frequentemente fotografada no chão.

Esperávamos que as jaguatiricas sobrepujassem sua atividade em maior grau com as presas noturnas. Essa expectativa vem da preferência documentada por pequenos mamíferos que são predominantemente noturnos (MORENO-SOSA *et al.*, 2022). Embora houvesse uma forte sobreposição entre jaguatirica e as presas noturnas, houveram poucas fotos de jaguatirica dentro de 48 horas em relação às presas. Os padrões de movimento da jaguatirica também podem ajudar a explicar o número relativamente menor de fotos antes e depois das presas noturnas. Descobrimos que jaguatiricas podem estar rondando a mesma câmera até 10 dias após a foto anterior, o que sugere um padrão de alcance muito mais disperso em comparação com irara. Em contraste, a irara apareceu por até três dias na mesma câmera, sugerindo uma rota mais pontual. Isso corrobora com os achados de um estudo de telemetria anterior que mostrou que irara permaneceu de um a três dias na mesma área antes de se mudar para outra (KONECNY, 1989). Pesquisas adicionais são necessárias para alcançar um tamanho amostral mais extenso, que possa permitir identificações individuais e uma compreensão mais detalhada desses padrões temporais, pelo menos para jaguatiricas.

É extremamente difícil determinar se a sobreposição temporal entre carnívoros e uma espécie de presa específica é evidência direta de segmentação. Comportamentos de caça e evitação raramente são capturados por armadilhas fotográficas, e só podem ser sugeridos pela resposta elicitada de outras espécies. De semelhante forma é extremamente difícil determinar se a falta de sobreposição temporal e/ou aumento da separação temporal é evidência direta de evitação ou mera coincidência, mas juntando as duas medidas, temos uma visão mais fiel das interações entre as espécies. Considerando a baixa sobreposição temporal entre irara e jaguatirica, concluímos que nossas hipóteses sobre as interações interespecíficas foram corroboradas por nossos resultados. As hipóteses sobre as presas foram apenas parcialmente suportadas para algumas espécies, levando em consideração a sobreposição diária e a resposta eliciada pelos carnívoros antes e depois do aparecimento da presa. Podemos sugerir que pelo menos cutia e jacamim apoiaram nossas hipóteses para irara e jaguatirica, e tinamus somente para jaguatirica. Investigações adicionais são necessárias para estabelecer a robustez da abordagem que adotamos, particularmente a influência dos tamanhos das amostras. Permanece plausível que os padrões para essas espécies generalistas observados no presente estudo e em outros lugares (FLORES-MARTÍNEZ *et al.*, 1998) reflitam abundâncias de espécies e não necessariamente interações interespecíficas.

Embora estudos anteriores tenham relatado florestas que se estendem por milhares de quilômetros ao norte, sul e oeste de Maracá, vastas áreas de floresta foram desmatadas ao sul e ao norte de Maracá de 1985 a 2020. O monitoramento contínuo da biodiversidade desta ilha é, portanto, vital para ajudar a informar a conservação e restauração das florestas impactadas pelas contínuas mudanças antropogênicas da cobertura da terra nas áreas circundantes no século XXI.

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