Universidade de São Paulo
Escola Superior de Agricultura "Luiz de Queiroz"
Centro de Energia Nuclear na Agricultura

Fatores determinantes da variação espacial na densidade populacional da jaguatirica *Leopardus pardalis* (Carnivora: Felidae) - da escala continental para a local

Henrique Villas Bôas Concone

Tese apresentada para a obtenção do título de Doutor em Ciências. Área de concentração: Ecologia Aplicada

Piracicaba
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versão revisada de acordo com a Resolução CoPGr 6018 de 2011

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DEDICATÓRIA

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meu grande incentivador, que sempre me estimulou e motivou, saudade eterna

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EPÍGRAFE

“Num tempo
Página infeliz da nossa
História
Passagem desbotada na
Memória
Das nossas novas
Gerações
Dormia
A nossa pátria mãe tão
Distraída
Sem perceber que era
Subtraída
Em tenebrosas
Transações
*(**Chico Buarque**)*

“Mas sei que uma dor assim pungente
Não há de ser inutilmente
A esperança dança
Na corda bamba de sombrinha
E em cada passo dessa linha
Pode se machucar
Azar, a esperança equilibrista
Sabe que o show de todo artista
Tem que continuar”
*(**Aldir Blanc e João Bosco**)*

SUMÁRIO

RESUMO

Fatores determinantes da variação espacial na densidade populacional da jaguatirica *Leopardus pardalis* (Carnivora: Felidae) - da escala continental para a local

Dentre as diversas atividades humanas com impacto em larga escala, uma das principais causadoras de mudanças na paisagem e perda de biodiversidade é a agricultura. No Brasil, isso é evidente pela quantidade de áreas atualmente usadas na produção agrícola, sendo que a área destinada a lavouras temporárias triplicou nos últimos 40 anos. O Cerrado é o bioma brasileiro mais ameaçado pela expansão agrícola e diversas espécies da fauna encontram-se ameaçadas pela antropização. Por outro lado, apesar da pecuária extensiva estar presente há 300 anos, o Pantanal é o segundo bioma mais bem conservado do Brasil, considerado importante refúgio de vida silvestre. Entretanto, no ecótono Pantanal-Cerrado, os planaltos que circundam o Pantanal respondem por 83% das áreas antropizadas da Bacia do Alto Paraguai. Nossa área de estudo encontra-se nessa região, sendo exemplo característico de um agroecossistema, com áreas de lavouras de arroz, milho, soja e pastagens para pecuária contíguas a extensas áreas de vegetação nativa. A jaguatirica é uma das espécies mais comuns nesse agroecossistema, e pela ampla distribuição geográfica ao longo da região neotropical, apresenta-se como excelente modelo para avaliar os fatores que determinam o tamanho de suas populações. Esta tese buscou investigar a ecologia populacional da jaguatirica em duas escalas espaciais distintas, uma escala ampla, abrangendo a distribuição geográfica da espécie, e uma escala local, avaliando a densidade da espécie em um agroecossistema no ecótono Pantanal-Cerrado. Através de extensa e sistemática revisão bibliográfica, compilamos dados de densidade para área total de distribuição da jaguatirica e utilizamos modelos meta-analíticos para estimar a densidade média. Testamos o efeito da cobertura florestal, sazonalidade da produtividade primária e massa corporal sobre essas estimativas. Aplicamos modelos espacialmente explícitos de captura-recaptura associados a dados de armadilhas fotográficas para estimar a densidade da jaguatirica no agroecossistema, testando hipóteses relacionadas à detecção e à variação espacial em função do uso e cobertura do solo. Na escala continental a densidade média de jaguatiricas foi de 20,3 indivíduos/100 km², havendo diferenças significativas entre os métodos usados nos estudos originais. Encontramos efeitos significativos da cobertura florestal e massa corporal, e um efeito marginalmente significativo da sazonalidade na densidade de jaguatirica ao longo da sua distribuição. Na escala local do agroecossistema, a densidade de jaguatirica foi de 46,7 indivíduos/100 km². Embora o modelo para variação espacial tenha tido menos suporte, ele mostrou estimativas mais altas para os habitats de floresta nativa e agricultura, do que nas pastagens e campos nativos. Nossos resultados mostraram que na escala continental, as densidades populacionais são mais altas em habitats mais florestais, com copas mais altas. Além disso, populações com massas corporais médias menores atingem densidades mais altas do que populações com pesos médios maiores em condições ecológicas semelhantes. Na escala local, os resultados revelaram padrões de uso do espaço variando entre os sexos, resultando em diferenças significativas nas densidades entre machos (8,8 indivíduos/100 km²) e fêmeas (37,9 indivíduos/100 km²). Verificamos uma população residente no agroecossistema, com densidade similar entre áreas nativas e lavouras temporárias, embora esses resultados mereçam mais investigação. Sugerimos que a alta densidade encontrada pode ser resultado de populações grandes de pequenos roedores nas lavouras. Entretanto, chamamos a atenção também para o fato de que esse ambiente tem uso constante de pesticidas que podem causar danos à saúde dos animais e, portanto, o tamanho da população não deve ser o único parâmetro a ser monitorado em agroecossistemas.

Palavras-chave: Agroecossistema, Armadilhas fotográficas, Captura-recaptura, Cerrado, Cobertura florestal, Massa corporal, Meta-análise, Neotrópico, Pantanal, Sazonalidade, SECR

ABSTRACT

Determining factors of spatial variation in population density of the ocelot *Leopardus pardalis* (Carnivora: Felidae) - from continental to local scale

Among several human activities with large-scale impact, one of the main causes of changes in landscape and biodiversity loss is agriculture. In Brazil, this is evidenced by the amount of land currently used in agricultural production, with the area destined for temporary crops having tripled in the past 40 years. The Cerrado is the Brazilian biome most threatened by agriculture expansion and many wildlife species are imperiled by anthropization. On the other hand, despite livestock ranching taking place for 300 years, the Pantanal is the second most conserved biome of Brazil, considered an important wildlife refuge. However, in the Pantanal-Cerrado ecotone, the highlands surrounding the Pantanal account for 83% of the anthropized areas in the Upper Paraguay Basin. Our study area is in this region, being a typical example of an agroecosystem, with pastures, corn, soybean, and rice crops adjacent to extensive areas of native vegetation. The ocelot is one of the most common species in this agroecosystem, and due to its wide geographic distribution throughout the Neotropics, it presents itself as an excellent model to evaluate the factors determining its population size. This thesis sought to investigate the population ecology of the ocelot at two distinct spatial scales, a broad scale, covering the geographic distribution of the species, and a local scale, evaluating ocelot density in an agroecosystem in the Pantanal-Cerrado biome. Through an extensive and systematic bibliographic review, we compiled density data for the entire ocelot distribution and used meta-analytic models to estimate mean density. We tested the effect of forest cover, primary productivity seasonality and body mass on these estimates. We used spatially explicit capture-recapture models associated with camera-trapping data to estimate ocelot density in the agroecosystem, testing hypothesis related to detection and spatial variation as a function of land use and cover. On the continental scale, the mean ocelot density was 20.3 individuals/100 km^2, with significant differences between the methods used in the original studies. We detected significant effects of forest cover and body mass, and a marginally significant effect of seasonality on ocelot density throughout the Neotropics. At the local scale of the agroecosystem, ocelot density was 46.7 individuals/100 km^2. Although the model for spatial variation had less support, it showed higher estimates for native forest and agricultural habitats than for pastures and native open vegetation types. Our results showed that at the continental scale, population densities are higher in more forested habitats, with higher canopies. Furthermore, populations with lower mean body masses reach higher densities than populations with higher mean body masses under similar ecological conditions. At the local scale, the results revealed space use patterns varying between sexes, resulting in significant differences of male (8.8 individuals/100 km^2) and female (37.9 individuals/100 km^2) densities. We found a resident ocelot population in the agroecosystem, with similar density between native areas and temporary crops, although these results deserve further investigation. We suggest that the high density found may be the result of large populations of small rodents in crops. However, we also draw attention to the fact that this area is subject to constant use of pesticides that can harm the health of animals and, hence, population size should not be the only parameter to be monitored in agroecosystems.

Keywords: Agroecosystem, Body-mass, Camera-trap, Capture-recapture, Cerrado, Forest cover, Meta-analysis, Neotropic, Pantanal, Seasonality, SECR

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1. INTRODUÇÃO GERAL

1.1. Contexto e área de estudo

1.1.1. A antropização da natureza

Para sua sobrevivência, todas as espécies do planeta interagem com o meio biótico e abiótico promovendo, propositada ou inadvertidamente, mudanças em diferentes escalas no seu entorno imediato (Buchman et al. 2007; Lavelle et al. 2016). De bactérias (Ratzke & Gore 2018) a baleias (Roman et al. 2014), passando por uma diversidade de organismos (e.g., Desbiez & Kluyber 2013; Fritz 2017), as mudanças provocadas têm efeitos importantes no ambiente possibilitando que diversas outras espécies se beneficiem, num processo conhecido como engenharia de ecossistemas (Cuddington 2007).

Nenhuma outra espécie, entretanto, causou alterações tão extensas, seja na escala espacial, seja na escala temporal, quanto a espécie humana. As mudanças são, de fato, tão profundas, afetando toda a vida no planeta, que temos um processo de extinção em massa em curso, e por isso o período em que vivemos passou a ser chamado de Antropoceno (Crutzen 2002). Acredita-se que o processo de antropização venha ocorrendo há aproximadamente 300 anos, mas tenha se intensificado a partir da revolução industrial no final do século XVIII, com o advento do motor a vapor, quando o Antropoceno teve sua marcação geológica (Crutzen 2002). Já no final do século XIX, o geólogo italiano Antonio Stoppani chamava a atenção para o fato de que a espécie humana era uma nova força instalada no planeta com capacidades equiparáveis às outras forças da natureza:

> *"It is in this sense, precisely, that I do not hesitate in proclaiming the Anthropozoic era. The creation of man constitutes the introduction into nature of a new element with a strength by no means known to ancient worlds. And, mind this, that I am talking about physical worlds, since geology is the history of the planet and not, indeed, of intellect and morality. But the new being installed on the old planet, the new being that not only, like the ancient inhabitants of the globe, unites the inorganic and the organic world, but with a new and quite mysterious marriage unites physical nature to intellectual principle; this creature, absolutely new in itself, is, to the physical world, a new element, a new telluric force that for its strength*

and universality does not pale in the face of the greatest forces of the globe." (Antonio Stoppani, 1873)[1]

1.1.2. O agronegócio, o Cerrado e o Pantanal

Dentre as diversas atividades humanas com impacto em larga escala, temporal e espacial, uma das principais causadoras de mudanças na paisagem e perda de biodiversidade é a agricultura (Laurance et al. 2014). A escala espacial e temporal dessas mudanças e o potencial de impacto fica bastante evidente quando vemos as projeções do agronegócio brasileiro, onde a quantidade de áreas destinadas para a produção agropecuária deve crescer aproximadamente 14% em 10 anos, passando dos atuais 82 milhões de hectares para 93,3 milhões de hectares até 2030/31 (MAPA 2021). Em relação apenas às lavouras temporárias, como soja e arroz, a área no Brasil mais que triplicou nos últimos quase 40 anos, chegando atualmente próximo dos 60 milhões de hectares (Souza et al. 2020).

O Cerrado é considerado a savana mais biodiversa do mundo e é o bioma brasileiro mais ameaçado pela expansão agrícola (Strassburg et al. 2017, da Silva & Lacher 2020). Atualmente, dos 46% do bioma Cerrado antropizados, as lavouras temporárias respondem por aproximadamente 30% (Souza et al. 2020), e apenas cerca de 8,5% dos seus quase 2 milhões de km² estão protegidos (da Silva & Lacher 2020). Além disso, há a preocupação de que a expansão agrícola sobre o Cerrado não se dá apenas pela transição de áreas improdutivas de pecuária, mas há também grandes áreas de vegetação nativa sendo convertidas (Souza et al. 2020). Com isso, diversas espécies da fauna do Cerrado encontram-se sob pressão pela perda e fragmentação de habitats naturais e demais efeitos da expansão agrícola (Medici et al. 2021, Ferraz et al. 2021, Versiani et al. 2021).

Por outro lado, com 83% de sua área em estado natural, o Pantanal é o segundo bioma mais bem conservado do Brasil, atrás apenas da Amazônia (Souza et al. 2020),

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[1] Tradução livre: "É nesse sentido, precisamente, que eu não hesito em proclamar a era Antropozoica. A criação do homem constitui a introdução na natureza de um novo elemento com uma força desconhecida dos mundos antigos. E, preste atenção, que estou falando de mundos físicos, uma vez que a geologia é a história do planeta, e não, de fato, de intelecto e moralidade. Mas o novo ser instalado no velho planeta, o novo ser que não apenas, como os antigos habitantes do globo, une os mundos orgânico e inorgânico, mas também com um novo e misterioso casamento une a natureza física ao princípio intelectual; esta criatura, absolutamente nova em si mesma, é, para o mundo físico, um novo elemento, uma nova força telúrica que por sua força e universalidade não se diminui diante das maiores forças do globo." Texto extraído de Federighi (2013)

embora, ao contrário desta, somente pouco mais de 7% de sua área esteja formalmente protegida sob a forma de Unidades de Conservação, públicas ou privadas (Tomas et al. 2019). A atividade econômica predominante há mais de 300 anos é a pecuária, com um rebanho aproximado de 3,8 milhões de cabeças de gado mantido em densidades relativamente baixas pelas cerca de 3000 propriedades privadas que detêm quase 95% das terras (Zimmermann et al. 2005, Oliveira et al. 2016, Tomas et al. 2019). Ainda assim, o bom estado de conservação da planície pantaneira com sua paisagem formando um mosaico natural de campos nativos, brejos, vazantes, savanas e florestas, abriga grande diversidade de fauna e flora, sendo considerado um dos mais importantes refúgios naturais de vida silvestre do mundo (Harris et al. 2005).

No estado do Mato Grosso do Sul, onde a maior parte do bioma Pantanal se encontra, o uso da terra para produção agropecuária corresponde a 59% do território, com as áreas de plantações temporárias concentradas basicamente no Cerrado (Souza et al. 2020). Entretanto, a interface entre Pantanal e Cerrado na Bacia do Alto Paraguai (BAP), mostra claramente os riscos da expansão agrícola no Cerrado sobre a planície pantaneira. A situação de conservação da BAP é preocupante, uma vez que os planaltos do entorno do Pantanal respondem por 83% das áreas antropizadas da bacia (Souza et al. 2020). É justamente nos planaltos da BAP onde nascem todos os rios que cortam a planície pantaneira e o avanço do agronegócio nos últimos 50 anos tem causado uma série de problemas ambientais na planície (Da Silva et al. 1998, Silva et al. 2010).

1.1.3. A Fazenda San Francisco

A área de estudo investigada nesta tese encontra-se exatamente no ecótono Pantanal-Cerrado, ao sul da BAP, e fornece um exemplo bem característico do uso da terra na região. A Fazenda San Francisco (FSF) iniciou as atividades agropecuárias em 1975, quando aproximadamente 2100 hectares de florestas semidecíduas e cerradões foram suprimidos para o plantio de pastagens para a pecuária bovina, restando apenas pequenos fragmentos de 1 a 2 hectares. A partir de 1984, foi implementado um projeto de plantio de arroz irrigado, que contou com a construção de uma infraestrutura de estradas e canais de irrigação e drenagem, bem como de estações de captação e bombeamento de água do rio Miranda. Naquele período, foram construídos também cerca de 40 km de diques de contenção, para que as águas das inundações periódicas do Pantanal não interferissem na lavoura. A partir do ano de 2013, parte das áreas anteriormente destinadas ao plantio de arroz irrigado ou a pastagens para pecuária passou a ser utilizada para produção de soja em rotação com milho ou pasto. Aproximadamente 40% da FSF permanece coberta de vegetação nativa composta de florestas estacionais semideciduais, matas ciliares, brejos, campos e savanas sazonalmente alagáveis. Este mosaico de áreas de produção agropecuária e vegetação nativa caracterizam um agroecossistema, onde a alteração e manipulação de um ecossistema pelo homem é feita com o propósito de estabelecer produção agropecuária (Gliessman 2004).

Desde 1996, a área começou a explorar atividades relacionadas ao turismo rural e à observação de espécies da fauna silvestre. Deste período em diante, A FSF foi objeto de diversos estudos de mestrado e doutorado relacionados à fauna, contribuindo com o acúmulo de conhecimento acerca desse agroecossistema (Concone 2004; Azevedo 2006; Teribele 2007; Landgref Filho 2009; Piatti 2009; Martins 2010; Braga 2019; Fraga 2020; Silva 2020). Nesta fazenda, foram registradas 33 espécies de mamíferos de médio e grande porte (Fraga 2020), incluindo espécies ameaçadas típicas dos dois biomas, como onça-pintada (*Panthera onca*), cervo-do-pantanal (*Blastocerus dichotomus*), tamanduá-bandeira (*Myrmecophaga tridactyla*), lobo-guará (*Chrysocyon brachyurus*), gato-palheiro (*Leopardus braccatus*) e ariranha (*Pteronura brasiliensis*). A jaguatirica (*Leopardus pardalis*) foi a espécie mais registrada por armadilhas fotográficas, com mais da metade dos registros em áreas de lavoura (Fraga 2020) e teve altas taxas de observação direta em saídas noturnas para observação de fauna (Concone 2004; Teribele 2007). Uma vez que a espécie é normalmente associada a habitats com cobertura vegetal densa (Sunquist e Sunquist 2002; Horne et al. 2009; Oliveira et al. 2010), a grande quantidade de observações e registros da espécie nas lavouras da FSF despertou o interesse em investigar questões relacionadas aos efeitos desse agroecossistema sobre a ecologia da jaguatirica.

1.1.4. O Projeto Jaguatiricas

O Projeto Jaguatiricas é um projeto vinculado ao Instituto Pró-Carnívoros, em parceria com o Laboratório de Mamíferos da Universidade Federal da Paraíba (UFPB) e com o Laboratório de Ecologia, Manejo e Conservação da Fauna Silvestre (LEMaC) do

Departamento de Ciências Florestais da ESALQ (USP), e apoio da Fazenda San Francisco Agro-Ecoturismo Ltda. O projeto tem por objetivos investigar a ecologia da jaguatirica e outros carnívoros de porte médio, além de suas presas potenciais, em um agroecossistema no ecótono Pantanal-Cerrado. O trabalho começou formalmente em meados de 2013, com o início da sistematização de coletas de dados com armadilhas fotográficas. Entretanto, o projeto conta com uma base de dados de registros fotográficos de jaguatiricas desde o ano de 2005, o qual é atualizado anualmente com novos registros obtidos por armadilhas fotográficas e colaboradores. Esse banco de dados serviu de base para a criação das pranchas de identificação de indivíduos da espécie na área da FSF usados para estimar a densidade populacional da espécie.

Em 2015, foram iniciados contatos com os pesquisadores Dr. Pedro Cordeiro Estrela (UFPB) e Dra. Fabiana Lopes Rocha (UFPB, IUCN), para estabelecermos uma parceria de trabalho e colaboração em estudos envolvendo carnívoros e pequenos mamíferos na área de estudo. Em 2017, fui aceito como orientado da Prof. Dra. Katia M.P.M.B. Ferraz (LEMaC/LCF/ESALQ/USP), e ingressei no Programa de Pós-Graduação Interunidades em Ecologia Aplicada para iniciar meu doutoramento, analisando parte dos dados coletados no Projeto Jaguatiricas. No ano de 2018, iniciamos colaboração com os pesquisadores Dr. Anthony Giordano (S.P.E.C.I.E.S., EUA) e Dr. Clay Nielsen (Southern Illinois University, EUA), os quais disponibilizaram 50 armadilhas fotográficas para uso no projeto. No mesmo ano, o Prof. Dr. Luiz Gustavo Oliveira-Santos aceitou convite para coorientação e disponibilizou mais 16 armadilhas fotográficas para as atividades de pesquisa.

Desde o início dessas colaborações, o Projeto Jaguatiricas vem contribuindo com pesquisas que se desenvolveram em três dissertações de mestrado (Braga 2019; Fraga 2020; Silva 2020) e duas teses de doutorado, uma finalizando agora e outra em andamento. As dissertações de mestrado investigaram a saúde de jaguatiricas e lobinhos (*Cerdocyon thous*; Braga 2019), a riqueza e diversidade de mamíferos de médio e grande porte (Fraga 2020), e a comunidade de pequenos mamíferos (Silva 2020) na FSF. Uma tese de doutorado está sendo desenvolvida com objetivo de estudar a diversidade funcional e filogenética dos pequenos mamíferos, bem como avaliar o impacto do agroecossistema sobre esse grupo de mamíferos através da análise da presença de metais pesados e pesticidas e seu efeito na saúde (E. Gomes, com. pess.). Essas pesquisas estão ajudando a construir um melhor entendimento das relações ecológicas entre carnívoros de porte médio, presas potenciais, e parasitos, e como essas relações são afetadas pelo uso humano intenso da área. Os resultados desse acúmulo de conhecimento podem contribuir bastante para o planejamento e direcionamento de ações futuras de manejo de áreas privadas e conservação de espécies e serviços ecossistêmicos em paisagens antropizadas.

1.2. Jaguatirica como modelo de estudos ecológicos populacionais

Entender processos demográficos que influenciam dinâmicas populacionais é fundamental para o direcionamento de ações voltadas ao monitoramento, manejo e conservação de espécies e populações. Informações sobre tamanho e densidade populacional, taxas de natalidade, mortalidade e sobrevivência, uso e ocupação de habitats, recrutamento e migração, são todos parâmetros necessários para o conhecimento aprofundado de uma população de organismos sem os quais gestores, pesquisadores e conservacionistas não conseguem avaliar a efetividade de medidas de manejo ou o impacto de ações antrópicas. Alguns desses parâmetros, como taxas de sobrevivência ou mortalidade, necessitam de acompanhamento por períodos relativamente longos para serem estimados (Pollock et al. 2012; Murray & Bastille-Rousseau 2020), enquanto outros, como ocupação, abundância e densidade, podem ser obtidos em períodos comparativamente mais curtos (Otis et al. 1978, Efford 2004, MacKenzie et al. 2006). Assim, estudos interessados em compreender os processos demográficos que influenciam a dinâmica de uma população, deveriam, idealmente, iniciar estimando parâmetros de curto-prazo para estabelecer a base para um monitoramento de longo-prazo.

Ao mesmo tempo, avaliar como esses parâmetros variam ao longo da distribuição inteira das espécies, é vital para compreender padrões globais, entender a história evolutiva, planejar a conservação em amplas escalas e direcionar esforços em escalas locais. Entretanto, avaliar as diferentes estimativas de densidade de uma mesma espécie não é, ou pelo menos não deveria ser, um simples processo de comparação de números, uma vez que uma série de fatores influenciam o resultado dessas estimativas. Por exemplo, métodos distintos de calcular as áreas efetivamente amostradas geram estimativas bastante distintas para um mesmo conjunto de dados de uma mesma população (e.g., Dillon & Kelly 2007; 2008). Da mesma forma, a escolha entre modelos diferentes para calcular as estimativas geram diferenças que também precisam ser levadas em conta (Tobler & Powell 2013).

Devido a sua ampla distribuição geográfica pela região neotropical (Paviolo et al. 2015) e pela grande quantidade de estudos relacionados a densidades populacionais (apêndice 1 em Di Bitetti et al. 2008; tabela 2 em Rocha et al. 2016), a jaguatirica se apresenta como uma espécie modelo para avaliar os fatores ecológicos que influenciam os parâmetros demográficos que fundamentalmente determinam o tamanho de suas populações ajudando a compreender a variação encontrada ao longo de toda sua distribuição.

Meta-análise é um procedimento estatístico para analisar um conjunto de dados de diferentes estudos, e pode ser uma fonte importante de informações atualizadas e concisas (Nakagawa et al. 2017). O uso dessa abordagem é considerado relativamente recente na ecologia e evolução quando comparado às ciências humanas, mas seu uso vem superando as revisões bibliográficas qualitativas e descritivas por ser uma forma mais objetiva e informativa de resumir tópicos de interesse (Koricheva et al. 2013; Nakagawa et al. 2017). Por estes motivos, escolhemos a abordagem meta-analítica como forma de sumarizar, de forma objetiva e clara, os dados de densidade populacional de jaguatiricas após levantamento bibliográfico sistemático. A partir disso, pudemos identificar lacunas de conhecimento e direcionar nossos esforços para testar hipóteses (Nakagawa et al. 2017; Koricheva et al. 2013) que ajudem a entender padrões ecológicos e evolutivos em duas escalas espaciais, a distribuição toda da espécie e um agroecossistema local.

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2. ESTRUTURA E OBJETIVOS DA TESE

Esta tese está estruturada em dois capítulos que analisam a densidade populacional da jaguatirica em duas escalas espaciais distintas: uma escala ampla, avaliando os fatores ecológicos que determinam a variação na densidade ao longo de toda sua distribuição geográfica (Capítulo 1); e uma escala local, avaliando como a densidade da espécie varia em função do uso e cobertura do solo em um agroecossistema no ecótono Pantanal-Cerrado (Capítulo 2). Redigi os dois capítulos em inglês, e todas as referências bibliográficas da tese seguem o padrão do periódico científico *Mammal Review* (The Mammal Society, Reino Unido), para onde submeterei o capítulo um para publicação.

No Capítulo 1, realizei uma revisão sistemática da literatura para compilar um extenso conjunto de dados sobre densidades de jaguatiricas e apresentei resumos dos principais resultados reportados e desenhos amostrais utilizados. A partir de uma abordagem meta-analítica, ajustei modelos aleatórios e de efeitos mistos multiníveis para derivar estimativas de densidade média de jaguatiricas para a distribuição da espécie e para os três principais métodos usados na literatura. Também ajustei um modelo de meta-regressão multivariado para testar o efeito de covariáveis ambientais e ecológicas sobre as densidades populacionais da espécie ao longo da região neotropical.

No Capítulo 2, apliquei modelos espacialmente explícitos de captura-recaptura associados a dados de armadilhas fotográficas para estimar a densidade populacional da jaguatirica em um agroecossistema localizado em área de ecótono do Pantanal-Cerrado no MS (FSF). Incluí nos modelos a informação do sexo dos indivíduos e o local das estações para avaliar variações na detecção e estimar a densidade em função do sexo e a razão-sexual da população. Por último, avaliei a variação espacial na densidade populacional da jaguatirica em relação a covariáveis de uso e cobertura da terra, testando a hipótese que campos abertos de agricultura na área de estudo podem ajudar a suportar a população de jaguatiricas.

2.1. Objetivos do capítulo 1

Os objetivos do capítulo 1 foram (1) compilar todos os dados disponíveis sobre estimativas de densidade de jaguatiricas, (2) estabelecer parâmetros para comparação entre estudos e áreas, considerando diferenças entre desenhos amostrais e métodos analíticos, (3) avaliar como cobertura florestal densa, sazonalidade na produtividade primária e massa corporal média da jaguatirica influenciam as estimativas ao longo da distribuição da espécie e (4) fornecer diretrizes para a publicação de resultados de estimativas e respectivos desenhos amostrais.

2.2. Objetivos do capítulo 2

Os objetivos do capítulo 2 foram (1) estimar a densidade populacional da jaguatirica em um agroecossistema, (2) detectar possíveis diferenças nos parâmetros da função de detecção relacionados ao sexo dos indivíduos que pudesse afetar as estimativas de densidade, (3) avaliar como a densidade populacional da jaguatirica varia em relação ao uso e cobertura da terra e (4) fornecer informações sobre história de vida de jaguatiricas necessárias para o monitoramento populacional de longo prazo.

3. SPOTS AND STRIPES: ARE WE COUNTING THEM PROPERLY? LIMITATIONS, PERSPECTIVES, AND CHALLENGES ON ESTIMATING POPULATION DENSITY OF A NEOTROPICAL CAT

Resumo

Pintas e listras: estamos contando corretamente? Limitações, perspectivas e desafios em estimar densidade populacional de um felino neotropical

Densidades populacionais de mamíferos carnívoros, tal como a jaguatirica (*Leopardus pardalis*), podem variar amplamente ao longo de sua distribuição geográfica e, enquanto diferenças metodológicas ou desenhos amostrais inapropriados podem muitas vezes explicar parte desta variação, as razões biológicas que sustentam essa ampla variabilidade não são bem determinadas. O método mais utilizado para estimar a densidade de jaguatiricas é o armadilhamento fotográfico associado a modelos de captura-marcação-recaptura, contando com duas estruturas principais de modelagem, captura-recaptura espacialmente explícita e captura-recaptura não-espacial, que por sua vez pode ser separada em duas abordagens em relação à forma de calcular a área efetivamente amostrada. Neste capítulo, procuramos abordar questões relacionadas à variação das estimativas de densidade de jaguatiricas ao longo de sua distribuição, usando uma abordagem meta-analítica para considerar fontes distintas de variabilidade. Realizamos uma revisão sistemática da literatura para compilar um extenso conjunto de dados sobre densidades de jaguatiricas e apresentamos resumos dos principais resultados e desenhos amostrais relatados, apontando limitações, perspectivas e direções para estudos futuros. Usando uma estrutura meta-analítica para considerar fontes distintas de variabilidade, ajustamos modelos aleatórios e de efeitos mistos multiníveis para derivar estimativas de densidade média de jaguatiricas para toda a distribuição da espécie e para as três principais abordagens analíticas usadas na literatura. Depois de controlar os efeitos das abordagens analíticas utilizadas, a correlação espacial e a não-independência das estimativas provenientes da mesma referência, ajustamos um modelo de meta-regressão multivariado para testar como a sazonalidade da produtividade primária bruta ('variação' GPP), altura global do dossel florestal (GFCH) e a massa corporal da jaguatirica (BM) modulam as densidades populacionais da espécie ao longo da região neotropical. A densidade média de jaguatiricas estimada foi de 20,3 ± 2.2 indivíduos/100 km², havendo diferenças significativas entre as abordagens analíticas. Encontramos efeitos significativos de GFCH e BM, e um efeito marginalmente significativo de 'variação' GPP na densidade de jaguatirica. As populações de jaguatiricas prosperam em habitats mais florestais, com copas mais altas, embora essa relação pareça ser limitada pela sazonalidade do ambiente. Não é a produtividade primária em si que permite maior densidade, mas sim sua estabilidade. A variação adicional nas densidades de jaguatirica é definida pela variação na morfologia, com populações com massas corporais médias menores atingindo densidades mais altas do que populações com pesos médios maiores em condições ecológicas semelhantes. Por fim, sugerimos fortemente que estudos futuros forneçam informações mais precisas e detalhadas sobre desenhos amostrais, métodos e parâmetros adicionais relacionados aos resultados gerais.

Palavras-chave: altura global do dossel; densidade; jaguatirica; *Leopardus pardalis*; massa corporal; sazonalidade; variação.

Abstract

Population densities of carnivore mammals, such as the ocelot (*Leopardus pardalis*), may vary broadly along its distribution range and, while methodological differences or inappropriate sampling designs can often explain part of this variation, the biological reasons underpinning this wide variability are not well determined. The most used method for estimating ocelot density is camera-trapping associated to capture-mark-recapture models, relying on two main modelling frameworks, spatially explicit capture-recapture (SECR) and non-spatial capture-recapture, which in turn can be further split in two approaches for calculating the effective sampled area. In this chapter we seek to address questions related to the variation of ocelot density estimates across its distribution range, using a meta-analytical framework to account for distinct sources of variability. We carried out a systematic literature review to compile an extensive dataset on ocelot densities, and present summaries of main results and study designs reported, pointing out limitations, perspectives, and directions for future studies. Using a meta-analytical framework to account for distinct sources of variability, we fitted multilevel random and mixed-effects models to derive mean ocelot density estimates for the whole species distribution and for the three main analytical approaches used in the literature. After controlling the effects of the analytical approaches used, spatial correlation, and non-independence of estimates coming from the same reference, we fitted a multivariate meta-regression model to test how gross primary productivity seasonality ('variation' GPP), global forest canopy height (GFCH) and ocelot body mass (BM) modulate population densities of the species throughout the neotropics. Mean ocelot density estimated was 20.3 ± 2.2 individuals/100 km², and there were significative differences among analytical approaches. We found significative effects of GFCH and BM, and a marginally significant effect of 'variation' GPP on ocelot density. Ocelot populations thrive in more forested habitats, with higher canopies, but this relationship seems to be restrained by the seasonality of the environment. It is not the primary productivity per se that allows higher density, but rather its stability. Further variation in ocelot densities is defined by variation in morphology, with populations with smaller average body masses attaining higher densities than large-bodied populations in similar ecological conditions. Finally, we strongly suggest that future studies provide more precise and detailed information regarding study designs, methods and additional parameters related to general results.

Keywords: body mass; density; global forest canopy height; *Leopardus pardalis*; ocelot; seasonality; variation.

3.1. Introduction

A solid understanding of demographic processes is essential for actions directed to management, monitoring and conservation of species and populations. Information on population size and density, natality, mortality, survival, recruitment, occupancy, and migration, are necessary for a sound knowledge of a population of organisms, without which we are "blind" in face of management measures taken or when impacts fall upon them. Depending on the species, some populational parameters require continuous surveillance for relatively extensive periods to be estimated, like survival and mortality rates, migration, and reproduction (Pollock et al. 2012; Murray & Bastille-Rousseau 2020). Others, like occupancy, abundance, and density, might be estimated in comparatively shorter periods (Otis et al. 1978; Efford 2004; MacKenzie et al. 2006). Ideally, studies interested in understanding demographic processes should initiate by estimating short-term parameters and setting the baseline for long-term monitoring.

The interest in estimating natural population sizes and providing methods and models to deal with this challenge has been built up for the past 100 years or so (Lincoln 1930, Gause 1932; DeLury 1947; Bailey 1951; Chapman 1954; Seber 1965; Jolly 1965; Otis et al. 1978; Buckland et al. 1993; 2004; Royle et al. 2014; Cooch & White 2019; McClintock &

Thomas 2020). Methods for estimating population parameters involves either unmarked or marked populations (McClintock & Thomas 2020; Royle & Converse 2020), and the choice of methodology will depend on a number of factors like cost, logistics, time and the taxonomic group of interest (Kelly et al. 2012). Most carnivore species occur at low densities, are elusive, move through great distances, have large home ranges, and many are active at night, making it difficult to use techniques like visually counting for distance sampling models (Buckland et al. 2004; Pollock et al. 2012). Moreover, capturing and handling carnivores is expensive, stressful, and potentially dangerous for researchers and subjects, and should not be the main option for estimating population parameters such as abundance or density, as there are many non-invasive techniques to collect reliable data and make meaningful inferences about animal populations (Kelly et al. 2012; McClintock & Thomas 2020).

Among the many non-invasive techniques for studying animal population parameters, one of the most used for estimating carnivore densities is camera-trapping associated to capture-mark-recapture models (Karanth & Nichols 1998; O’Connell et al. 2011; Kelly et al. 2012). The basic framework involves setting an array of capture devices (e.g., camera-traps) over an area of interest to collect data on consecutive captures and recaptures of marked individuals (Otis et al. 1978). The marking phase is not needed in case of animals with natural markings and researchers will identify individuals through their unique spot or stripe patterns (O’Connell et al. 2011). The data collected during capture-recapture occasions are used to build “capture-histories” for individuals that will be used in mathematical models to estimate the abundance of the population exposed to the capturing devices (Otis et al. 1978). There is a large set of models that can be used, with variations in assumptions needed and parameters that can be estimated and we do not intend to provide a thorough review on the subject (Otis et al. 1978; O’Connell et al. 2011; Royle et al. 2014; Royle & Converse 2020).

Most studies using camera-trapping of naturally marked species to estimate abundance and density rely on two main modelling frameworks, non-spatial capture-recapture, and spatially explicit capture-recapture (Di Bitetti et al. 2008; Karanth et al. 2011; Tobler & Powell 2013; Thornton & Pekins 2015; Rocha et al. 2016). The main distinction between these frameworks regards how density is estimated, or rather, how the inference area is calculated (Karanth & Nichols 1998; Efford 2004; Royle et al. 2014). While spatially explicit capture-recapture (SECR) modelling includes in the individual capture-histories the location of sampling devices to directly infer on the estimate space (Efford 2004), non-spatial models use an *ad-hoc* approach, where a buffer area will be added either to the spatial polygon formed by the outermost camera-traps or to each camera-trap station (Karanth & Nichols 1998; Foster & Harmsen 2012). This buffer area is usually calculated by averaging the maximum distances moved by distinct individuals between trap stations as a surrogate for the species home range diameter, although some studies have also used actual home range values to establish the buffer (Maffei & Noss 2008). Researchers then, decide whether they will use the full mean maximum distance moved (MMDM) or half this value (henceforth hMMDM) as the buffer to establish the effective sampled area (ESA). Then, the abundance estimated using the non-spatial capture-recapture model is divided by the ESA created using MMDM (CR-MMDM) or hMMDM (CR-hMMDM) to calculate density. The great variation in resulting estimates using these three analytical approaches (SECR, CR-hMMDM, CR-MMDM) have raised important discussions about the most appropriate methodology (Foster & Harmsen 2012; Tobler & Powell 2013).

Ecological and environmental sources of variation in population density

Population densities of carnivore mammals may vary from one to three orders of magnitude for the same species along its distribution range. While methodological differences or inappropriate sampling designs can often explain part of this variation, the biological reasons underpinning this wide variability are not well determined in many cases (Smallwood & Schonewald 1996; Fuller & Sievert 2001; Santini et al. 2018). Potential population densities that species might reach are usually understood from the perspective of food resource abundance, which for carnivore mammals are their prey populations (Fuller & Sievert 2001; Stephens et al. 2019). For many species in this Order, variation in abundance and availability of prey throughout time and space are the main determinants of size and viability of their populations (Fuller & Sievert 2001; Stoskopf 2012).

Although there is an inverse relationship between carnivore's body size and population density, this correlation is much stronger when using population density as a function of prey biomass (Carbone & Gittleman 2002). Thus, understanding the relationship between the density of carnivores and their prey is important to predict the size that a population would or could be (Fuller & Sievert 2001; Carbone & Gittleman 2002; Sinclair et al. 2006).

Ocelot as model species

Among the many neotropical carnivore mammals, the ocelot (*Leopardus pardalis*) is one of the most studied species, with a large bibliography on its ecology (e.g., Emmons 1988; Nagy-Reis et al. 2019), health (e.g., Lozano et al. 2015; Sousa et al. 2017) and conservation (e.g., Massara et al. 2015; Paolino et al. 2018). One of the most evaluated questions about the species is related to population density estimates, with several studies carried out along its distribution (e.g., Dillon & Kelly 2008; Kolowski & Alonso 2010; Noss et al. 2012). However, the variation in estimates is quite marked (e.g., Maffei et al. 2005;, Moreno & Bustamante 2009; Garrote et al. 2019) and despite attempts to understand the factors causing this variation (Di Bitetti et al. 2008), more recent estimates did not meet the expected patterns, indicating that more factors may be influencing this variation (Penido et al. 2016; Rocha et al. 2016; Monterrubio-Rico et al. 2018).

It has been shown that ocelot density estimates are positively correlated to pluviosity and negatively correlated to latitude, supporting the hypothesis that, on a continental scale, more productive areas contain larger ocelot populations (Di Bitetti et al. 2008). Di Bitetti et al. (2008) used rainfall and latitude as proxies for primary productivity which, in turn, was used as an indicator of carrying capacity for prey and predators. However, estimates published afterwards (e.g., Penido et al. 2016; Rocha et al. 2016) do not fit the linear models presented by Di Bitetti et al. (2008), suggesting that more factors may be playing an important part in determining ocelot density variation.

In this chapter we seek to address questions related to the variation of ocelot density estimates across its distribution range, and further the hypothesis relating ocelot density to direct measures of gross primary productivity as surrogates for prey abundance. Through a systematic literature review of papers, thesis and research reports we have compiled an extensive dataset and present summaries of main results and study designs reported, pointing out limitations, perspectives, and directions for future studies. Using a meta-analytical framework to account for distinct sources of variability, we used multilevel random and mixed-effects models to derive mean ocelot density estimates for the whole species distribution and for the three main methods used in the literature. Furthermore, we fitted multivariate meta-regression models to test how gross primary productivity seasonality (Radeloff et al. 2019), extent of forested habitats (Potapov et al. 2021) and ocelot body mass (Carbone & Gittleman 2002) modulate population densities of the species throughout the neotropics. We predicted that ocelot densities would be greater in areas of denser forest cover and higher primary productivity (indicating higher prey availability) and where ocelots attain smaller body sizes.

3.2. Methods

3.2.1. Literature search

After an initial scoping of the literature to assess the feasibility of the proposed study and to identify proper keywords (Côté et al. 2013), we performed a thorough systematic search for relevant studies regarding ocelot density estimates using the following search engines: Web of Science (WoS), Scopus and SciELO. We also searched the Brazilian databases of thesis and dissertations as well as Google Scholar using terms in Portuguese, Spanish, and English, to increase the chances of finding original studies not published in peer-reviewed journals to enhance sample size and minimize publication bias (Murtaugh 2002; Jennions et al. 2013). We used the freely available software 'Publish or Perish' (Harzing 2007) to export search results from Google Scholar and organize the database. We cross-referenced a set of keywords related to the species identity (common and Latin names) with a set of keywords relating to population parameters (e.g., 'density', 'abundance') or estimation methods (e.g., 'camera-trapping', 'capture-recapture'). The systematic search for references was done until no new record was found, with the last search on 25th December 2019.

In addition to database searching, we used other methods to look for new references. We set the monthly alert system of Scopus and WoS with the same searching terms to receive any newly published estimates until December 2021 to finalize data screening and coding and start analysis protocols. Also, some studies identified in the literature search presented information from other studies (e.g., Di Bitetti et al. 2008, Rocha et al. 2016), so we performed a forward search in the literature cited to recover the largest number of studies related to the theme. We found some studies in Research Gate platform when trying to get access to references recovered through the systematic search. Lastly, we included five references that were not recovered through any other method. In brief, for including retrieved studies in the final dataset, we have first screened titles and abstracts looking for the mention of the focal species and population parameters or estimation methods. We looked for studies that presented data on ocelot numbers (i.e., number of individuals recorded, number of individuals estimated), methodology (i.e., use or not of camera-traps), sampling effort (e.g., number of cameras and surveyed-area size), and study area location and size. For details regarding databases covered, inclusion criteria, search terms and period see Appendix A (Table A1).

3.2.2. Data extraction and coding

Each reference received a unique code for distinction and the data extracted from original studies and respective supplemental materials were: authors, publishing year, title, source (journal name, thesis, etc.), study location, study period, total area of study site, geographic coordinates of study site, number of camera-trap stations used, distance between camera-trap stations, area covered by camera-trap polygon, mean maximum distance moved (MMDM) by individuals, effective sampled area (ESA), survey period, sampling effort, number of recorded individuals, estimated abundance and its associated variation measures (standard error and/or confidence interval), estimated capture probability, estimated population density and associated variation measures (standard error and/or confidence interval), and estimation method (SECR, CR-MMDM or CR-hMMDM).

Some references reported more than one density estimate due to being conducted at distinct study sites, in more than one period (years or seasons) or using distinct estimation methods. Thus, the same reference could contribute with more than one density estimate to the dataset, so it received the same code to indicate the non-independence of data. The resulting dataset (dataset I) was filtered for estimates reporting standard errors (dataset II) to be used in the meta-analysis model testing for differences in estimate methods. A further filtered dataset (dataset III) was derived from dataset II, where each reference contributed with only one density estimate per study site, per method, reported by the authors of the original study as the main result. General findings of the systematic review are derived from analysis of dataset I. To evaluate if there were significant differences in the methods used to generate estimates, we used dataset II in a multilevel meta-analysis. Dataset III was used in a multivariate meta-analysis of moderator variables effects on ocelot density estimates. All density estimates and respective variation measures were converted to individuals/100 km².

3.2.3. Data analysis

We used descriptive statistics to summarize study design parameters and the main results reported in references using dataset I. The study design parameters evaluated were: (1) number of camera-trap stations used in surveys; (2) distance between camera-trap stations; (3) minimum convex polygon formed by camera-trap stations; (4) survey period in days; and (5) sampling effort. Results reported included in the analysis were: (1) number of individuals registered; (2) abundance estimated; (3) effective sampled area (for non-spatial methods); (4) mean maximum distance moved (MMDM) by ocelots (for non-spatial methods); (5) sigma (for SECR); (6) probability of capture (for non-spatial methods); (7) encounter rate (for SECR); (8) density estimated; (9) standard error of the density estimate; and (10) confidence intervals for the density estimates.

We ran one-way ANOVA to test for differences in mean ocelot densities reported using the three estimation methods and performed multiple Tukey pairwise comparisons to see if the mean differences between pairs of methods were statistically significant using dataset I. We used Pearson chi-square statistic to test if there were significant differences between proportions of parameters reported among the three methods.

We performed linear regressions to test if there was significant correlation between: (1) MMDM and camera-trap polygon; (2) MMDM and effective sampled area; (3) ocelot density and camera-trap polygon; (4) ocelot density and effective sampled area. Where necessary data was log-transformed to achieve normality. All analyses were run in R (R Core Team 2021) using R Studio (RStudio Team 2022).

3.2.4. Meta-analytical model construction and heterogeneity

The dependent variable (effect size) used in the models were the reported ocelot density estimates, converted to ocelot-individuals/100 km². Meta-analytic models require variability measures of the effect sizes to be included, so we used the standard errors originally reported in the studies reviewed. An important characteristic of capture-recapture models is that derived confidence intervals do not fit a normal distribution, with the lower tail always shorter than the upper (Cooch & White 2019). Using the formula provided in Cooch and White (2019: 20.3) to transform available CIs back to standard errors to increase our number of effect sizes did not produce reliable figures, so we decided to use only original density estimates with their respective reported SEs (Appendix A; Cooch & White 2019).

In all meta-analytical models built, study identity entered as random variable, as more than one estimate were extracted from the same study in some cases. To control the effect of spatial correlation between estimates, we entered a random term in the models for the geographic coordinates of study area centroids. To proper evaluate the variation caused in the density estimates, we quantified heterogeneity through the I^2 statistics (Viechtbauer 2010; Nakagawa & Santos 2012). Using I^2 we can partition the heterogeneity found in the model to understand the distinct sources of variance that are not related to sampling error (Nakagawa & Santos 2012; Booksmythe et al. 2017).

3.2.5. Multilevel meta-analytical models

We ran a multilevel random-effect meta-analysis using dataset II and setting study and location as random effects to obtain a mean ocelot density estimate for the whole distribution (model A). We extended this model to a multilevel mixed-effects meta-analysis including method (CR-hMMDM, CR-MMDM and SECR) as moderator to investigate its effect on reported densities and to extract mean density estimates for each method (model B).

To investigate the effect of primary productivity, extent of forested habitats and ocelot body mass on ocelot density estimates, we used dataset III in a multilevel meta-regression model (model C). In this model, besides study identity and location, we also included estimation method in the random term of the model formula to control its effect on reported estimates. We used the seasonal variation in Gross Primary Productivity (hereafter ‘variation GPP’; Radeloff et al. 2019) and Global Forest Canopy Height (hereafter ‘GFCH’; Potapov et al. 2021) as abiotic moderators in the meta-regression. The other moderator variable used in this model was the average weight of ocelots, extracted from the literature review or from references cited therein (Table A2). We used the average sampling area extracted from our literature review to buffer the centroid of study sites and calculate average values of abiotic variables. The expected effects of these variables on ocelot density are shown in Table 1. For details in selection of covariates and construction of the models see the Appendix A. We used the ‘metafor’ package (Viechtbauer 2010) to build models and run the meta-analysis in R (R Core Team 2021) using R Studio (RStudio Team 2022).

Table 1. Summary of moderator variables used in multilevel meta-regression models and expected relationships with ocelot density.

Moderator Variable	Description	Relation to ocelot density	Expected Effect	Source
Variation GPP	Average yearly seasonal variation in Gross Primary Productivity	Seasonality in primary productivity limits ocelot prey availability	Negative	Radeloff et al. 2019
GFCH	Estimates forest aboveground biomass and timber volume.	Ocelots are considered forest dependent species and should be more abundant in pristine forest	Positive	Potapov et al. 2021
Ocelot average body mass	The average weight of ocelot for the area	Increased population biomass decreases densities	Negative	Literature review

3.3. Results

3.3.1. Attrition of studies

We screened titles and abstracts of all 2,172 references generated by our systematic search of databases to identify potential studies to enter the final dataset. We read and appraised the methods and results sections of the short-listed studies (n = 199) to establish their eligibility for inclusion. This resulted in 42 references through database search (Figure 1). The other methods used for searching studies yielded 20 new records, which after assessing methods and results, resulted in nine additional references for inclusion in the final dataset (Figure 1). The resulting 51 references reported 228 ocelot density estimates referring to 65 study sites distributed in 13 countries (Figure 2).

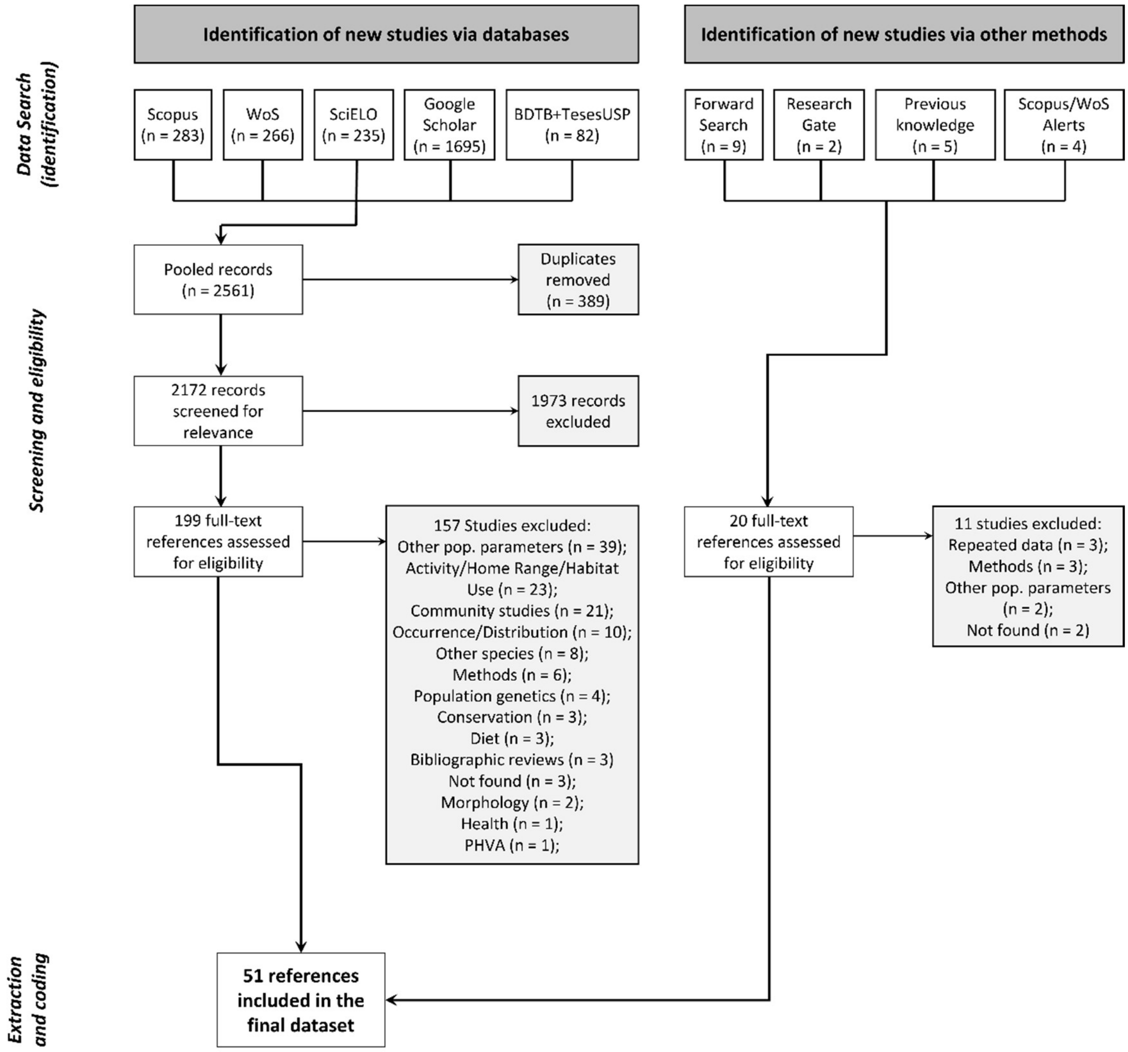

Figure 1. Flow chart of the literature search and data collection process, following PRISMA (Preferred reporting items for systematic reviews and meta-analysis) guidelines (Page et al. 2021).

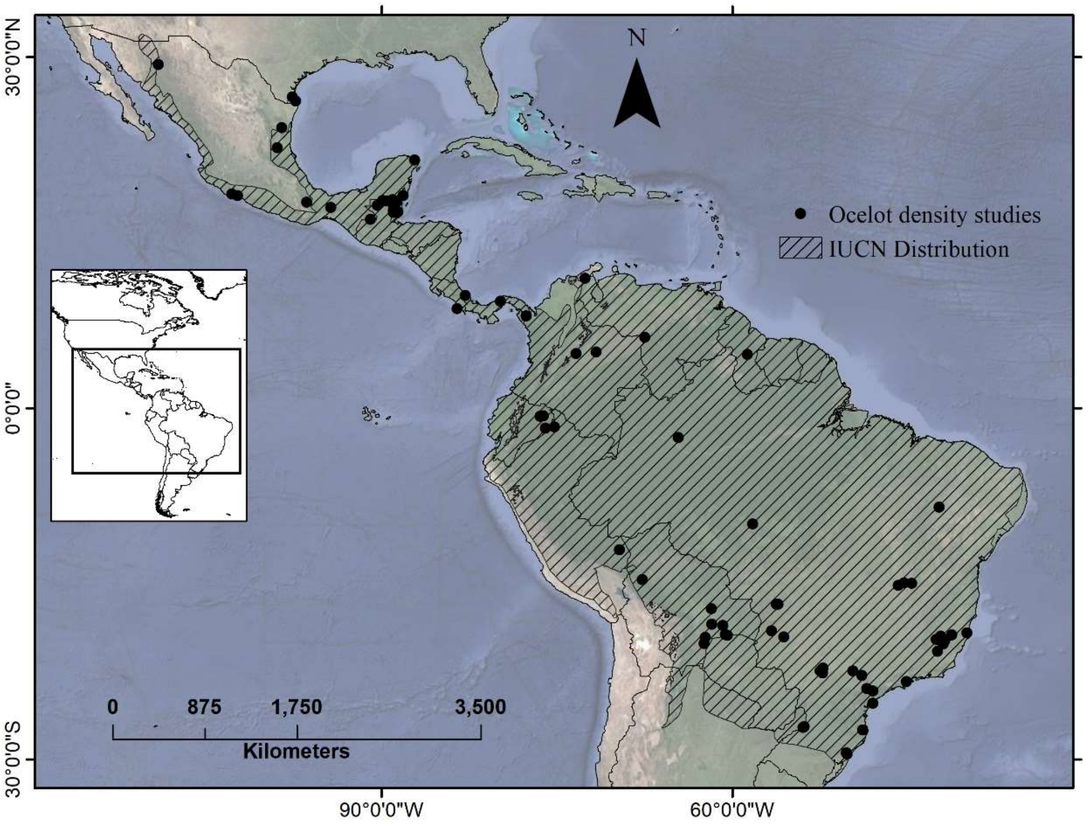

Figure 2. Location of the 65 study sites with ocelot density estimates reported in 51 references reviewed (full list of references and sites in Table 2).

3.3.2. Density estimation methods

The first ocelot density estimate found in the search is from a master dissertation of 2002 (Jacob 2002) and the first estimate published in a peer-review journal was in 2003 (Trolle & Kéry 2003), both using non-spatial capture-recapture models, with the former using MMDM and the latter using hMMDM to establish the effective sampled area. These two methods are still used, which can be observed by a cumulative total of 37 references until 2019. The first estimate using SECR models was published in 2010 (Ayala et al. 2010), with a steady increase in the use of this method since then, with 22 references until 2021 (Figure 3).

Our systematic review revealed that four references (Mendonça 2014, Ávila-Nájera et al. 2015, Villareal 2016, Rocha et al. 2016) used all the three methods considered herein, 29 references estimated ocelot density using only non-spatial methods and 14 studies used only the spatially-explicit method (Table 2). As a result, only six sampled sites present ocelot density estimates with the three methods, hampering direct comparisons between estimates throughout the species' distribution (Figure 2). The simple mean ocelot density, 20.2 individuals/100 km² (± 1.5 SE; 95% CI: 17.3–23.2; n = 228), and the meta-analytical mean density (model A), 20.3 individuals/100 km² (± 2.2 SE; 95% CI: 16–24.6; n = 158), were very similar.

Analyzing the full dataset (dataset I), we found significant differences in mean ocelot density estimates according to the estimate method (F(2) = 4.04, p = 0.02). The Tukey *post-hoc* test revealed significant pairwise differences only between ocelot density estimates obtained through CR-hMMDM ($\bar{x}$ = 25.5 ± 21.9 SD; n = 89) and CR-MMDM ($\bar{x}$ = 16.3 ± 23.9 SD; n = 68; p = 0.03). Pairwise differences between CR-hMMDM and SECR were only marginally significant ($\bar{x}$ = 17.4 ± 21.9 SD; n = 71; p = 0.06), while there were no significant differences between ocelot densities using CR-MMDM and SECR (p = 0.95; Figure 4). However, the multivariate mixed-effect meta-analytic model (model B) detected differences between average estimates among all three methods (Figure 4).

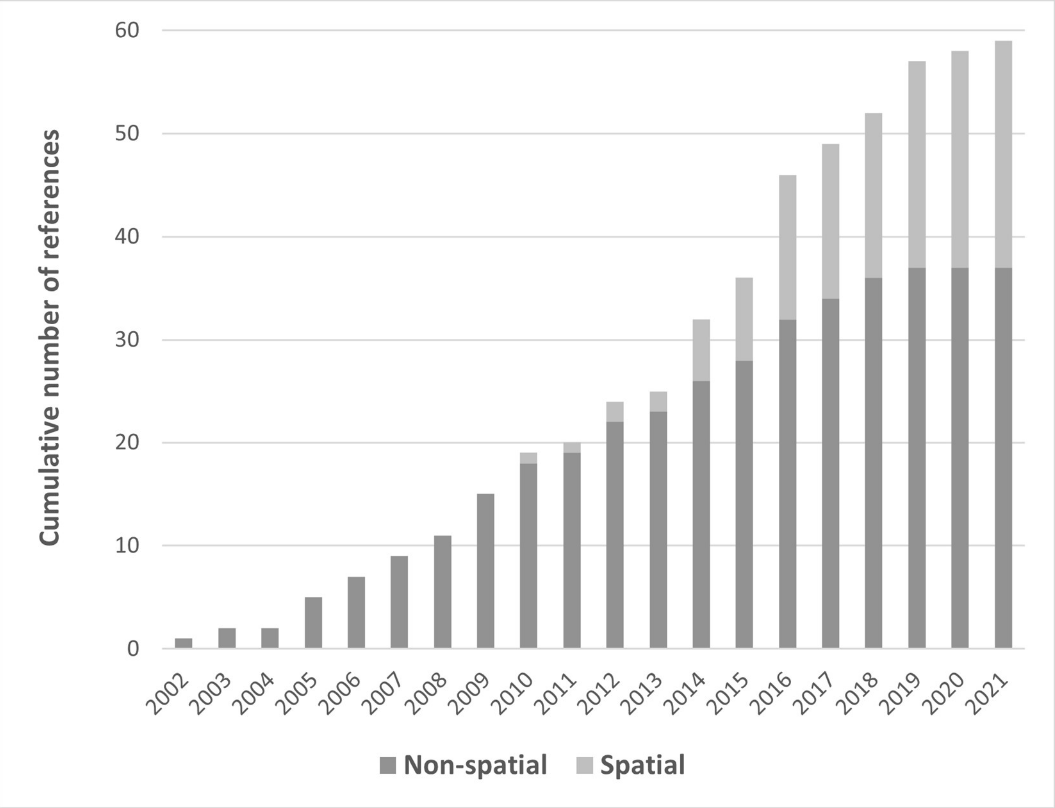

Figure 3. Temporal trend in studies addressing ocelot density estimates with the use of non-spatial and spatial methods.

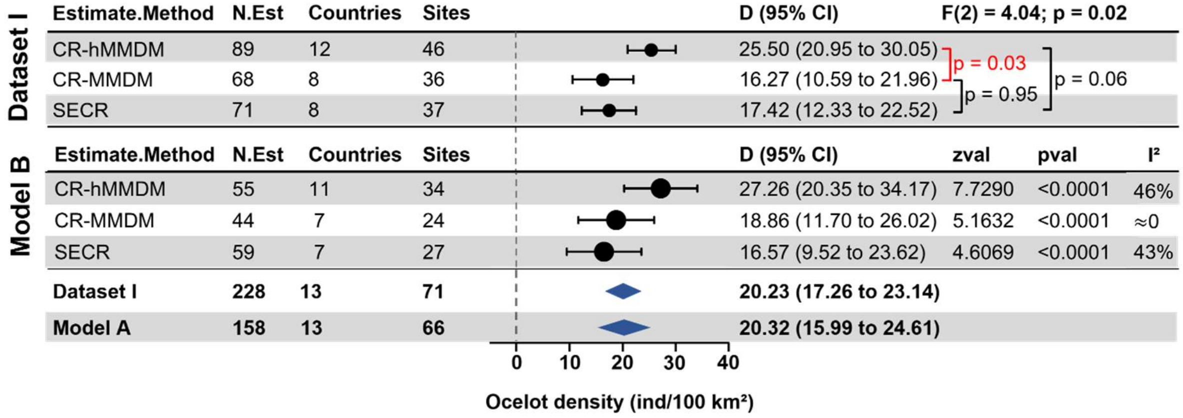

Figure 4. Differences between mean ocelot density estimates reported in references obtained through the systematic review, comparing Dataset I (full set) and Dataset II (estimates reporting SE; models A and B). Dataset I (n = 228) was used in one-way ANOVA and Tukey *post-hoc* test. Model A refers to the random effect meta-analytic mean. Model B refers to multi-variate meta-analysis model with estimate method as moderator. Whiskers refer to standard errors.

3.3.3. Sampling design

We identified a great variation in study design and values reported (Table 2). On average, surveys used 27 stations with one or two camera-traps (n = 206, SD = 24.5, Figure 5a) set at an average distance of 1610 m (n = 200, SD = 621, Figure 5b). The mean area formed by camera station polygons was 90 km² (n = 188, SD = 144.9, Figure 5c), although the median was considerably smaller (49 km²). All ocelot density estimates using non-spatial capture-recapture models (n = 157) reported the effective sampled area ($\bar{x}$ = 157 km² ± 232 SD, Figure 5d), although not all (82%) reported the camera-trap polygon area ($\bar{x}$ = 90 km² ± 145 SD, Figure 5c). Most estimates (89.5%) reported survey period, which lasted a mean of 76.4 days (n = 204, SD = 31.2, Figure 5e) and the majority (93%) also reported the sampling effort ($\bar{x}$ = 1628 camera-trap-days ± 1357 SD; Figure 5f). Of the 228 ocelot density estimates gathered, 69% were obtained through non-spatial capture-recapture using hMMDM (CR-hMMDM; n = 89) or MMDM (CR-MMDM; n = 68) to set the effective sampled area, and 31% used SECR modelling.

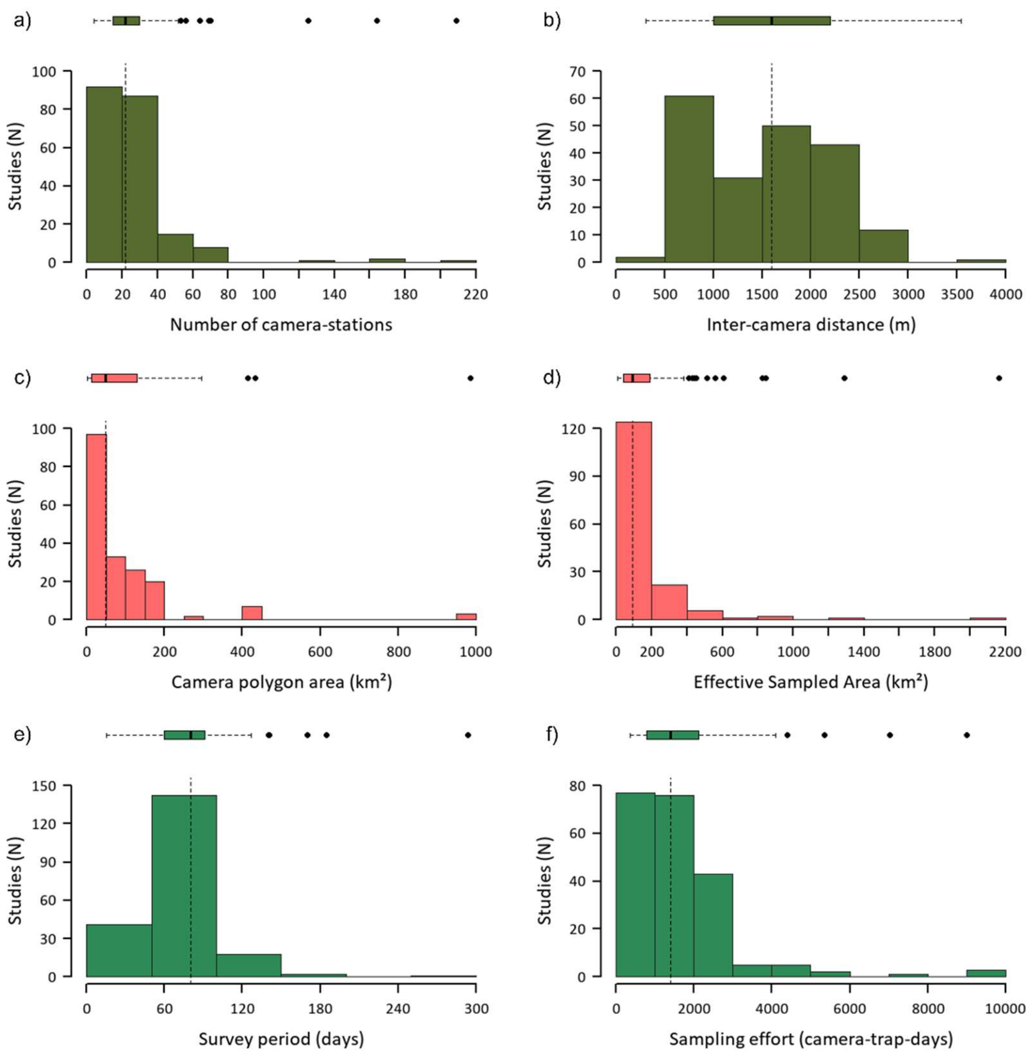

Figure 5. Study design information reported in original studies of ocelot density estimates: a) number of camera-trap stations used in surveys; b) distance between camera-trap stations; c) area of polygons formed by outermost camera-trap stations; d) effective sampled areas calculated for estimating ocelot density using non-spatial capture-recapture models; e) survey periods; f) sampling effort. Boxplots on top of each histogram showing median (vertical line), inter-quartile range (box), spread of data (whiskers) and outliers (dots). Dashed line in histograms indicate median values.

3.3.4. Parameters reported

Eighty-five percent of the estimates reported the number of individual ocelots recorded during surveys, which was on average 20 (n = 194) but decreased to a mean of 15 individuals when we removed outliers (n = 180, Figure 6a, b). As for abundance, 89% of estimates reported it, with an average of 24.4 individuals (n = 202), decreasing to 20.1 individuals when outliers are removed (n = 189, Figure 6Figure 6c, d). Finally, the mean ocelot density reported was 20.2 individuals/100 km² (SD = 22.8), which decreased to an average of 15.2 individuals/100 km² (SD = 11.7) when 18 outliers were removed (Figure 6e, f).

Of the total estimates found in the systematic review, 69.3% (n = 158) reported the standard error (SE), although SECR estimates reported SE more often (83%) than either of the non-spatial methods (CR-hMMDM = 62%, χ^2 = 7.52, p = 0.003; CR-MMDM = 65%, χ^2 = 4.97, p = 0.013). Only 35% of estimates presented the confidence interval (95% CI), without any significant differences between methods. And just 30 estimates (13.2%) were presented with both SE and 95% CI, while 19 didn't present variance, precision or any dispersion estimate, although this represented only 5.8% (n = 4) of the study sites.

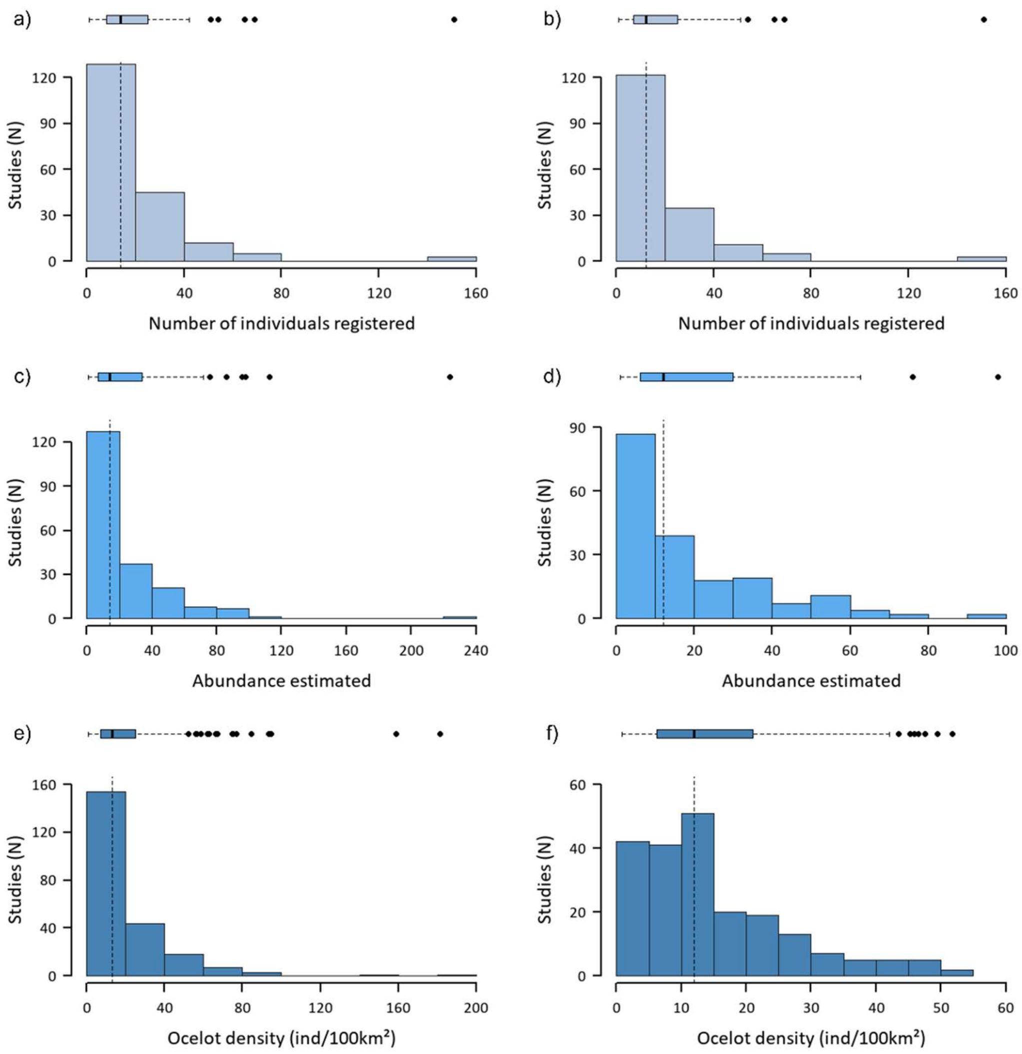

Figure 6. Distribution of estimates in relation to the number of individual ocelots registered (top), abundance (middle) and density (bottom), including (left panels) and excluding (right panels) outliers. Boxplots on top of each histogram showing median (vertical line), inter-quartile range (box), spread of data (whiskers) and outliers (dots). Dashed line in histograms indicate median values.

3.3.5. Study design effects on density estimates

We found significant positive correlations between MMDM and both camera-polygon area (Figure 7a) and effective sampled area (Figure 7b), and a significant negative correlation between ocelot density estimates and ESA (Figure 7d), but no correlation between ocelot density estimates and camera-polygon area (Figure 7c).

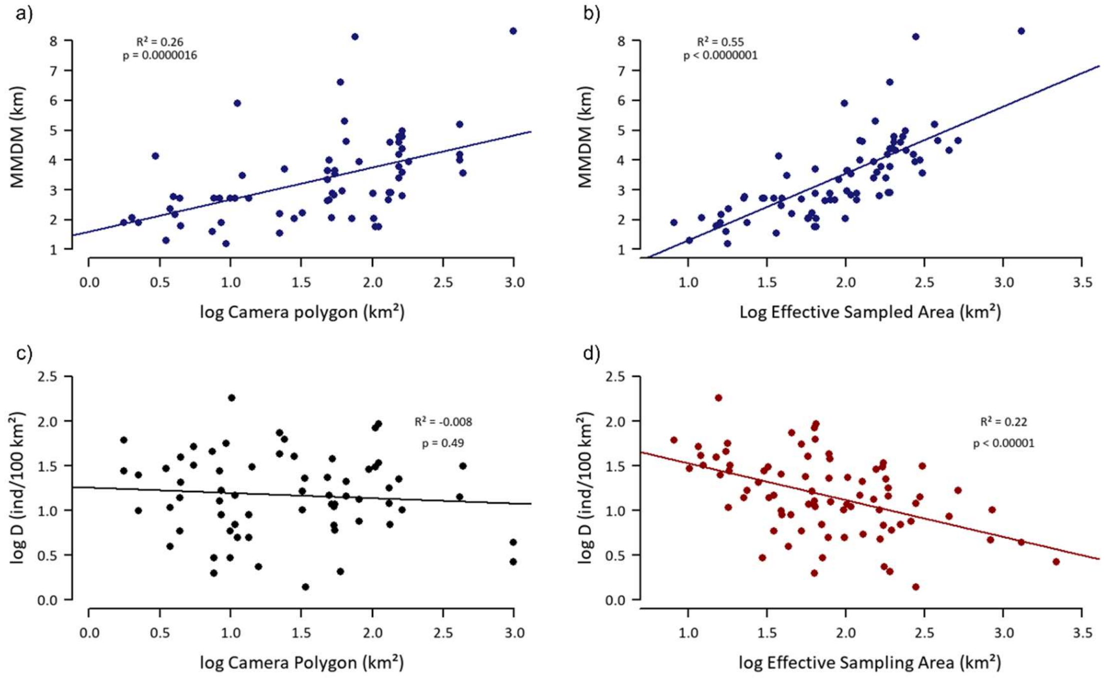

Figure 7. Data reported in ocelot density estimates obtained through non-spatial capture-recapture models showing relationship between mean maximum distance moved (MMDM) and camera-trap polygons (a); MMDM and effective sampled areas (ESA)(b); ocelot density and camera-trap polygons (c); and ocelot density and ESA (d). Significative relationships are show in blue (positive) and red (negative).

3.3.6. Effect of moderator variables on ocelot density

The range of GFCH values in our dataset was from 0.8 to 29.3 m ($\bar{x}$ = 12.4 m ± 9 SD), while 'variation' GPP varied between 0.1 and 0.6 ($\bar{x}$ = 0.3 ± 0.1 SD) and ocelot adult body mass ranged from 6.0 to 12.3 kg ($\bar{x}$ = 10.0 kg ± 1.9 SD; Appendix A). Our multilevel meta-analysis model constructed using the three moderator variables (model C), setting estimation method as a random variable, and controlling for the spatial correlation of study sites showed a significant positive effect of GFCH, a significant negative effect of the average ocelot weight, and a marginally significant negative effect of the 'variation GPP' on ocelot population density (Figure 8-10; Table 3).

The I^2_{Method} is the variance due to the estimation method used and could be further partitioned in I^2_{hMMDM}, I^2_{MMDM} and I^2_{SECR}, for CR-hMMDM, CR-MMDM or SECR, respectively. $I^2_{Spatial}$ represents the heterogeneity due to spatial correlation of study sites and accounted for a small amount of the total variance (3.68%). The sum of all these values (I^2_{Total}) represented 92% of heterogeneity. Most of this variance is due to estimation methods (89%), especially CR-hMMDM (46%) and SECR (43%).

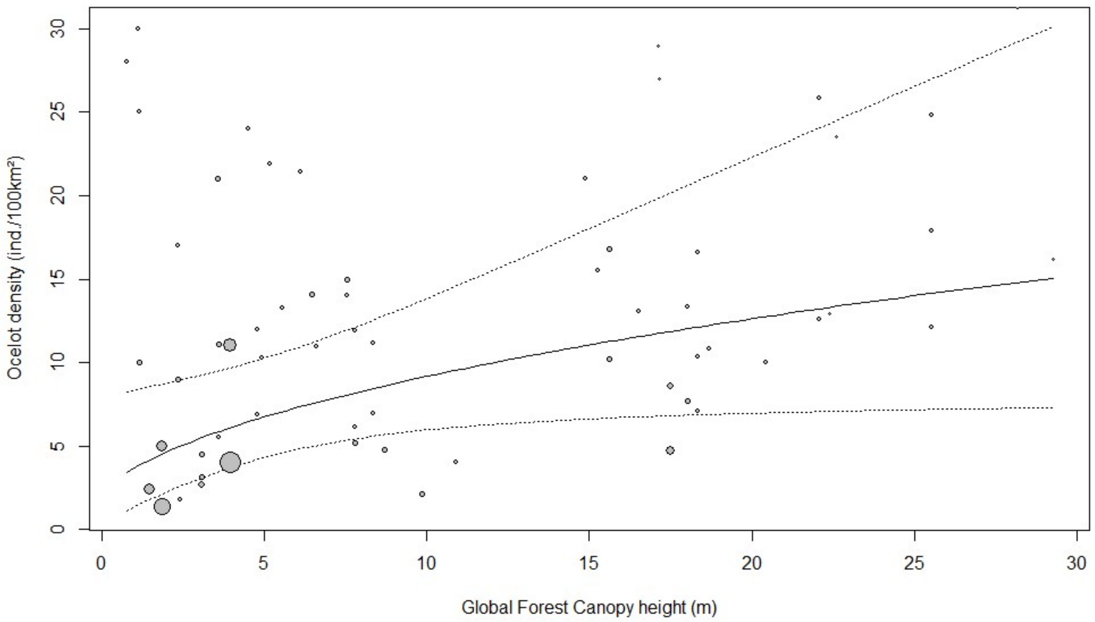

Figure 8. Relationship between ocelot population density and Global Forest Canopy Height. Thick line corresponds to the fitted meta-regression values and dotted lines to 95% confidence intervals. Grey circles are the original ocelot density estimates recovered in literature review; size is related to the precision (inverse standard error) of original estimates.

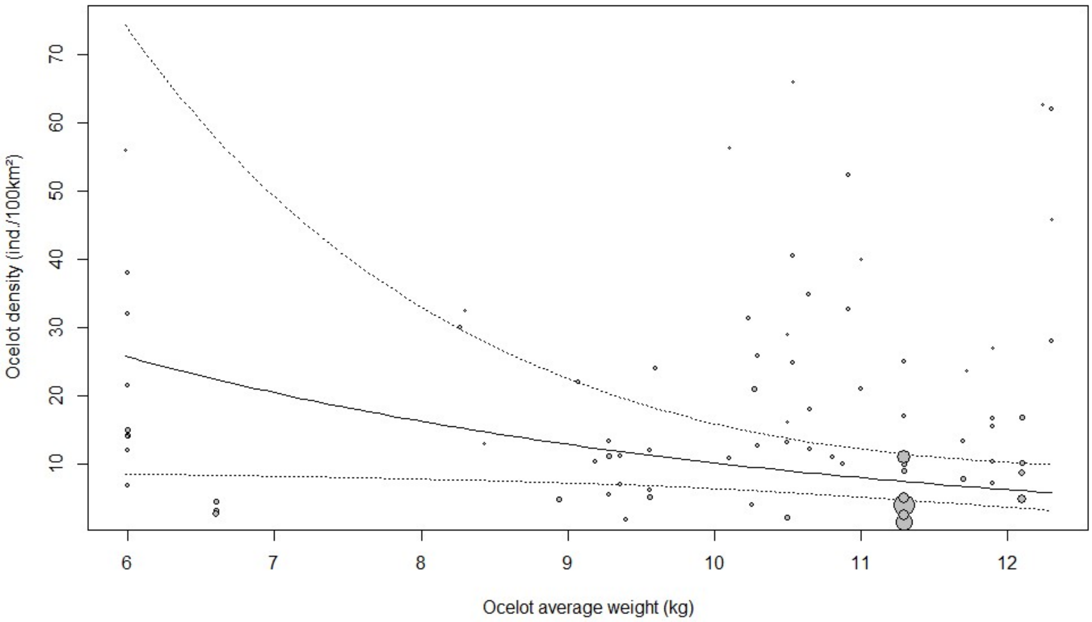

Figure 9. Relationship between ocelot population density and average weight. Thick line corresponds to the fitted meta-regression values and dotted lines to 95% confidence intervals. Grey circles are the original ocelot density estimates recovered in literature review; size is related to the precision (inverse standard error) of original estimates.

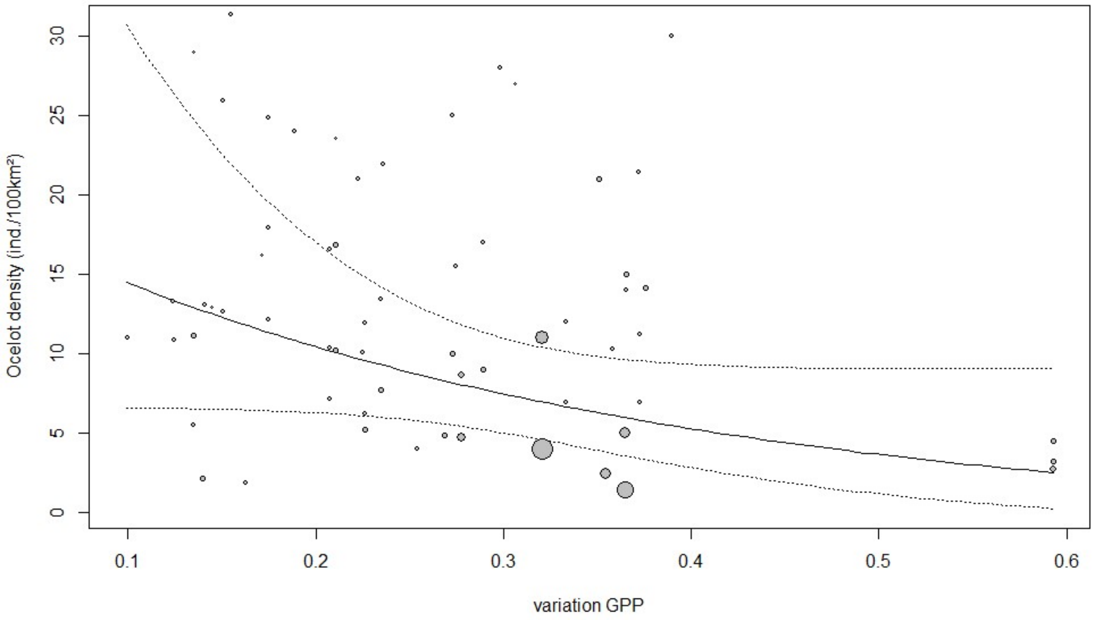

Figure 10. Relationship between ocelot population density and average yearly seasonal variation in Gross Primary Productivity. Thick line corresponds to the fitted meta-regression values and dotted lines to 95% confidence intervals. Grey circles are the original ocelot density estimates recovered in literature review; size is related to the precision (inverse standard error) of original estimates.

Table 2. Parameters reported in references from the systematic literature review on capture-recapture modelling associated with camera-trapping data to estimate ocelot density, ordered by country. Ocelot density is reported in individuals per 100 km^2. CR-M = non-spatial capture-recapture model where the Effective Surveyed Area is estimated by buffering the survey grid with the mean maximum distance moved by all individuals captured in more than one camera-trap station; CR-h = non-spatial capture-recapture model where the Effective Surveyed Area is estimated by buffering the survey grid with half the mean maximum distance moved by all individuals captured in more than one camera-trap station; SECR = spatially-explicit capture-recapture models; Cam = number of camera-trap stations used to estimate ocelot density; Surv = period of survey in days; Dist = distance between camera-trap stations (m); Poly = area of the polygon made by camera-trap stations (km^2); Buff = distance used to buffer camera-trap polygon to establish ESA (km); ESA = Effective Sampling Area (km^2); Ind = number of individual ocelots registered in studies; $\widehat{N}$ = ocelot abundance estimated; Rang = range of density estimates in each study site; Est = number of density estimates available for the same study site. Countries: Argentina (ARG), Belize (BLZ), Bolivia (BOL), Brazil (BRA), Colombia (COL), Costa Rica (CRI), Ecuador (ECU), Guatemala (GTM), Guyana (GUY), Mexico (MEX), Panama (PAN), Peru (PER), United States (USA).

References	Country	Study Site	Estimate Method			Cam	Surv	Dist	Poly	Buff	ESA	Ind	$\widehat{N}$	Rang	Est
			CR-M	CR-h	SECR										
Di Bitetti et al. (2006, 2008)	ARG	Iguazu National Park	x	x		11-47	42-43.8	2500-2580	180*	1.97-4.67	122-843	11-65	12-86	4.70 - 19.99	8
DiBitetti et al. (2006)		Uruguaí Provincial Park	x	x		34	42	2000	80	1.98-3.96	150-259	17	20	7.71 - 13.36	2
DiBitetti et al. (2008)		Yaboti Biosphere Reserve	x	x		18-42	44.5	2430	NA	2.17-4.34	206-825	10-33	12-39	2.70 - 10.80	6
Davis (2009); Satter (2017); Augustine et al. (2018); Satter et al. (2019a)	BLZ	La Milpa (RBCA)		x	x	19-40	72-98	1000-2300	61-153	1.48-2.40	100-200	14-37	15-41	2.72 - 38.80	12
Davis (2009); Satter et al.		Mountain Pine Ridge Forest Reserve		x	x	35*	72*	1500*	59-295	3.31-10.2	189.2	3*	4*	0.90 - 2.11	2

(2019a)															
Dillon& Kelly (2008); Satter et al. (2019a)	BLZ	Chiquibul Forest Reserve and National Park	x	x	x	15*	30*	1342*	149*	1.24-2.47	39-79	9*	10*	2.30 - 25.88	3
Satter (2017); Satter et al. (2019a)		Fireburn Reserve		x	x	33	127	2300	132	2.3	221	14	16	7.00 - 9.30	2
Satter (2017); Satter et al. (2019a)		Gallon Jug Estate		x	x	30-35	85-92	2200-2400	413**	2.0-2.6	267-362**	41-51*	42-58*	13.00 - 18.20	4
Satter (2017); Satter et al. (2019a)		Hill Bank (RBCA)		x	x	19-31*	70-98*	1900-2400*	162	1.4-2.4	156-238	11-22*	13-24	6.40 - 14.60	7
Satter et al. (2019a)		Cockscomb Basin Wildlife Sanctuary			x	NA	NA	NA	139	NA		NA	NA	9.20	1
Ayala et al. (2010)	BOL	PNANMI-Madidi		x	x	69	15-59	700	28	1.03*	57	17	23	40.50 - 66.00	2
Maffei et al. (2005)		San Miguelito		x		28	60	NA	NA	1.35	52	23	29	56.00	1
Noss et al. (2012)		Cerro Cortado		x	x	30	60	1600	49-52	1.34-6.00	79-80	15-25	20-30	11.70 - 38.00	6

Noss et al. (2012)	BOL	Estación Isoso		x	x	NA	NA	NA	48-51	1.68-6.00	58-90	6-7	7-9	1.67 - 12.00	5
Noss et al. (2012)		Palmar-Ravelo		x	x	29*	60*	2280*	71-434	1.02-6.00	64-303*	21-69	49-96	14.10 - 77.00	12
Noss et al. (2012)		Tucavaca		x	x	6-32	60*	1000-1940*	2-130	1.04-6.00	12-122	5-34	6-39	2.98 - 52.00	17
Trolle & Kéry (2005); Alves (2016)	BRA	SESC Pantanal	x	x	x	21-209	21-36	1000-1012	54*	1.4-2.9	107-173	9-151	3-224	1.21 - 20.99	5
Bolze (2019); Bolze et al. (2021)		CPCN Pró-Mata			x	20	60	1000	NA	NA	NA	4	NA	27.00	1
Kasper (2007); Bolze (2019); Bolze et al. (2021)		Turvo State Park	x		x	4-20	60-65	300-1000	NA	2.5*	32-111	5-14	5-15*	8.00 - 23.00	5
Fusco-Costa (2007); Fusco-Costa et al. (2010)		Ilha do Cardoso State Park	x	x		13	45	650	4.4	0.9-1.8	15-28	6	6	21.00 - 40.00	2
Jacob		Morro do	x			4	NA	NA	14	0.94	32	9	10	31.00	1

(2002)	BRA	Diabo State Park													
Lima (2009)		ESEC MLP - Ponte Branca	x	x		16	60	1000	8.5	0.96-1.92	24-45	3	4	9.00 - 17.00	2
Lima (2009)		Santa Mônica	x	x		6	60	1000	1.76	0.96-1.92	8-18	4	5	28.00 - 62.00	2
Lima (2009)		Seis R	x	x		6	60	1000	2.21	0.96-1.92	16-39	3	4	10.00 - 25.00	2
Massara et al. (2015)		RPPN Fazenda Macedônia	x	x		20	80	1000	11	1.4-2.7	34-70	NA	4-5	6.00 - 15.00	4
Massara et al. (2015)		RPPN Feliciano Miguel Abdala	x	x		20	80	1000	7.5	1.4-2.7	29-63	1	1	2.00 - 3.00	4
Massara et al. (2015)		RPPN Mata do Sossego	x	x		20	80	1000	4.3	1.4-2.7	22-52	NA	1-3	2.00 - 14.00	4
Massara et al. (2015)		Rio Doce State Park	x	x		20	80	1000	8.3	1.4-2.7	30-63	NA	8	13.00 - 29-00	4
Massara et al. (2015)		Serra do Brigadeiro State Park	x	x		20	80	1000	13	1.4-2.7	39-76	NA	3-5	5.00 - 12.00	4
Massara et al. (2015)		Sete Salões State Park	x	x		20	80	1000	9.8	1.4-2.7	35-71	NA	2	3.00 - 6.00	2
Mendonça (2014)		Serra do Mar State Park	x	x	x	24	96	1087	32	1.12-6.00	60-272	8	10-30	7.10 - 16.57	4
Oliveira (2009)		Veredas do Peruaçu State	x	x		7	60	1000	3.8	1.2-2.4	18-43	2	2	4.00 - 11.00	2

		Park													
Oliveira (2009, 2018)	BRA	Grande Sertão Veredas National Park	x	x		7-21	60-170	1000	3-33	1.4-5.9	23-276	3-9	4-5	1.40 - 22.00	8
Oliveira (2018)		RPPN Porto Cajueiro	x			14	92-120	1000	16	5.1	174	7	3-4	1.80 - 2.40	2
Penido-Oliveira (2012); Penido et al. (2016)		Serra da Capivara National Park	x	x	x	70	140	2900	985	4.17-8.95	1289 - 2165	51	58	2.67 - 4.49	3
Rocha et al. (2016)		Amanã Sustainable Development Reserve	x	x	x	50-64	83-294	1250-1660	131-135	1.5-6.3	184-281	17-30	33-76	12.10 - 40.10	10
Trinca (2014)		Fazenda São Nicolau	x		x	10-11	89-98	2000-2200	33	2.1-8.4	77-415	8-17	7-18	7.36 - 23.30	8
Trolle & Kéry (2003)		Fazenda Santa Emília		x		6	84	900	9.3	0.6	17.7	9	10	56.40	1
Wolff et al. (2019)		Vale Natural Reserve			x	39	105	2600	291	3.2		42		45.84	1
Boron et al. (2022)		Serra do Amolar			x	39	43	1600	190	1.17		18		10.27	1
Diaz-Pulido & Garrido (2011)	COL	La Reserva Natural de la Sociedad Civil Palmarito	x	x		21	97	1200	NA	1.4-2.9	63-128	6	7	5.50 - 11.10	2
Garrote et		Reserva			x	9	40	1070	5.2	NA		2		1.80	1

al. (2019)	COL	Natural Bojonawi													
Padilla-Rivera et al. (2020)		Mina del Cerrejón	x			27	68	1000	NA	2.3	55	8	13	24.00	1
Valderrama-Vásquez (2013)		Medina		x		15	NA	850	7.3	0.8	17	NA	8	46.57	1
Boron et al. (2022)		Hato La Aurora			x	53	46	1600	151	1.42		25		13.24	1
Boron et al. (2022)		Magdalena River Valley			x	47	48	1600	155	1.38		21		10.97	1
Salom-Pérez (2005)	CRI	Corcovado National Park		x		12	45	3540	48	1.8	102	12	24	23.57	1
Mosquera et al. (2016)	ECU	Tiputini Biodiversity Station	x	x		10	112	1100	5.5	NA	11.5 - 26.4	6-8	6-11	32.70 - 74.60	4
Salvador & Espinosa (2016)		Yasuni National Park – Lorocachi	x	x		26	90	2600	110	0.9-1.8	64.3 - 172.4	36	60	34.80 - 93.30	2
Salvador & Espinosa (2016)		Yasuni National Park - Maxus Road	x	x		26	90	2500	104	0.9-1.8	62.7 - 169.2	35	53	31.30 - 84.50	2
Contreras et al.	GTM	Asociación Forestal Integral San			x	20	38	1560	16.7			21	63	13.06	1

(2016)		Andrés Petén													
Palomo-Muñoz et al. (2014)	GTM	Biotopo Protegido Dos Lagunas			x	25	46	1500	38.9			18	33	10.83	1
Moreira-Ramírez et al. (2012)		Mirador Río Azul National Park		x		33	46	2000	94	NA	155	32	45	29.00	1
Roopsind et al. (2017)	GUY	Iwokrama Forest			x	52	31	1250	NA			NA		16.20	1
Ávila-Nájera et al. (2015)	MEX	Reserva Ecológica El Eden	x	x	x	22-27	48-82	1200-2250	48-75	1.3-8.1	73-561	9-12	7-19	1.42 - 26.02	12
De La Torre et al. (2016)		Reserva de la Biosfera Montes Azules			x	33	60	1920	82	4.4***		14	34	12.90	1
Martínez-Hernández et al. (2015)		Sierra Abra-Tanchipa Biosphere Reserve			x	22-27	82-84	1500	46	3.05		6	9-21	3.00 - 4.00	2
Monterrubio-Rico et al. (2018)		El Naranjal	x			9	87-89	1840	NA	2.1-4.9	49-164	7-8	8-10	4.80 - 20.20	3
Monterrubio-Rico et al. (2018)		Playa del Venado	x			9	81-88	1840	NA	1.2-1.7	12-20	4-5	4-6	29.40 - 47.60	3
Villareal (2016)		Caracol-Camotal Ranch Complex	x	x	x	30	92-185	1600	65	2.3-4.6	126-185	34	18-27	9.70 - 21.90	5

Greenspan et al. (2020)		Nacori Chico			x	164	141	800	80	2.3-2.5 ***		17	98	4.33 - 4.66	2
Moreno & Bustamante (2009)	PAN	Estación Biológica de Cana		x		14	35	1450	24	1.85	64	11	40	62.70	1
Rodgers et al. (2014)		Barro Colorado Island	x		x	21	99	NA	NA	1.5	15	24	28	158-70 - 181.5	2
Kolowski & Alonso (2010)	PER	Block 39	x	x		23	44-96	1100	22	0.8-2.2	36-78	22-27	34	43.50 - 94.70	4
Haines et al. (2006)	USA	Yturria Ranch		x		15	77	1700	3.5	0.6	10	3	3	30.00	1

Table 3. Multilevel meta-analysis model results

Model Parameters	Estimate	se	Lower CI	Upper CI	Z val	p val	
Intercept	4.18	1.61	1.03	7.33	2.5976	0.0094	**
‘variation’ GPP	-3.01	1.68	-6.31	0.28	-1.7932	0.0729	.
Log (GFCH)	0.45	0.21	0.03	0.87	2.1010	0.0356	*
Ocelot average body mass	-0.22	0.10	-0.42	-0.02	-2.1603	0.0308	*

Signif. codes: ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1

3.4. Discussion

3.4.1. General findings

Although ocelots are present in 22 countries spanning through almost 35 million km² across the neotropics (Paviolo et al. 2015), we found no estimates for nine countries (41%) and five (Argentina, Belize, Bolivia, Brazil and Mexico) respond for 88% (n = 200) of the estimates surveyed, suggesting regional bias. Moreover, summing the size of the areas where estimates were carried out, a total of 120 thousand km² is reached, which is less than 1% of the potential distribution range of the species.

3.4.2. Sources of ocelot population density variability

The systematic and thorough bibliographic review that we carried out showed a large variation in ocelot population density throughout its distribution, ranging from below 2 individuals/100 km² (Noss et al. 2012; Ávila-Nájera et al. 2015; Satter et al. 2019; Garrote et al. 2019) to more than 70 individuals/100 km² (Kolowski & Alonso 2010; Rodgers et al. 2014; Mosquera et al. 2016; Salvador & Espinosa 2016). Using primary productivity (‘variation GPP’) and habitat heterogeneity (GFCH) as surrogates for availability of potential prey, we used a meta-regression model to test whether those variables and ocelot body mass are important drivers of ocelot population densities throughout its distribution. The variation detected was due to different methodologies used and to the ecological variables investigated herein. We discuss these two main sources of variation, disentangling the methodological effect off the ecological variables responsible for the extensive variability in ocelot densities.

3.4.3. Global Forest Canopy Height (GFCH)

Looking at the data we observe the highest reported densities occurring mainly in tropical and subtropical moist evergreen forests (Dinerstein et al. 2017), such as the Amazon forest in Bolivia and Ecuador (Kolowski & Alonso 2010; Salvador & Espinosa 2016). Our multilevel meta-regression model detected well this tendency, as higher ocelot densities are seen as GFCH increases, confirming our expectations. More interestingly yet, the range of expected densities in the upper and lower limits of GFCH values are very distinctive. The ocelot distribution comprises a broad range of GFCH reflecting a variety of forest and non-forest habitats (Potapov et al. 2021) suggesting a species highly flexible in habitat requirements as it is present in a variety of biomes and ecoregions (Paviolo et al. 2015). Although indeed ocelots inhabit from dry thorn scrublands to evergreen broadleaved forests (Harveson et al. 2004; Oliveira et al. 2010), they are considered forest dwellers because of the strong association to habitats with a well-structured vegetation cover, and thus occupy a much narrower range of microhabitats than expected by its large distribution (Emmons 1988; Di Bitetti et al. 2008; Paviolo et al. 2015). Even in areas of high GFCH, ocelots may not achieve very high densities because of other ecological factors such as habitat conditions or prey availability (Rocha et al. 2016). Hence, the broader range of expected densities in higher GFCH is probably due to these areas being able to support larger populations if local conditions allow it, while in the lower limit of GFCH the narrower range of suitable ecological conditions forces maximum population densities to much lower figures (Penido et al. 2016; Garrote et al. 2019).

3.4.4. Ocelot body mass

According to our prediction, we found a negative, although small, effect of body mass on ocelot population densities. Previous studies show consistent patterns and a strong relationship of population densities decreasing as average body mass increases for animals in general, irrespective of habit (terrestrial or aquatic), metabolism (endotherm or ectotherm) or taxonomy (Damuth 1987; Currie 1993; White et al. 2007). Even when looking specifically at distinct trophic levels in the same taxonomic group such as herbivore or carnivore mammals, the same tendency was observed, revealing strong ecological and evolutionary forces connecting energy requirements and population densities (Damuth 1981; Robinson & Redford 1986; Carbone & Gittleman 2002). However, such strong relationships were found mostly when looking at broad spatial and temporal scales and often lumping species that do not necessarily coexist at reported densities (Carbone & Gittleman 2002; White et al. 2007). Moreover, discussions are brought as why such global size-density relationships do not always hold true in local size-density relationships, or at least why not as strong (Lawton 1989; Jennings et al. 2007; White et al. 2007). It seems that global size-density relationships reflect or indicate possible maximum population densities and that the range of body masses used spans several orders of magnitude (Lawton 1989; Jennings et al. 2007; White et al. 2007).

We have compiled the most extensive dataset on ocelot population densities to date, also gathering information on average body masses across its distribution. Using regressions reported in the literature for carnivore mammals (Robinson & Redford 1986; Damuth 1987; Carbone & Gittleman 2002) and the range of ocelot body masses in our datasets (6.0-12.3 kg) the expected ocelot density ranged between 22 and 70 individuals/100 km^2, which fell in the upper bound of the estimates reviewed in this article. Very high ocelot densities (> 70 individuals/100 km^2) reported in some of the areas are most likely equivalent to maximum values, artificial results from methods, absence of competitors or predators, or a combination of those (Kolowski & Alonso 2010; Rodgers et al. 2014; Mosquera et al. 2016; Salvador & Espinosa 2016). The small range of body masses in our dataset was the probable cause for the rather small effect detected in our meta-regression model, although, interestingly, the relationship held true (Lawton 1989; Currie 1993).

3.4.5. Seasonality in gross primary productivity

While the effect of seasonality was only marginally significant, it still showed an important negative tendency (95% CI: -6.31–0.28) as expected by our predictions. The range of expected ocelot density estimates in more seasonal areas was much narrower and with much lower maximums than in areas where seasonality was not as pronounced. For instance, in Serra da Capivara National Park, located in the Brazilian Caatinga, where the 'variation' GPP was highest, ocelot density estimates varied from 2.7 to 4.5 individuals/100 km², depending on the estimation method used (Penido-Oliveira 2012; Penido et al. 2016). On the other hand, ocelot density estimates from areas with low 'variation' GPP extended from below two to more than 80 individuals/100 km² (Salvador & Espinosa 2016; Garrote et al. 2019). Ocelot density estimates on the lower bound of 'variation' GPP values that were smaller than 6 individuals/100 km² (Davis 2009; Diaz-Pulido & Garrido 2011; Garrote et al. 2019) are from areas where GFCH was lower than 10m, corroborating our model.

We argue that areas of higher seasonality limit ocelot population size due to high variation in potential prey populations. Ocelots are medium sized terrestrial carnivores that prey on a great array of food items, relying heavily upon small mammals in most areas (Oliveira et al. 2010). Small mammal populations fluctuate due to annual and seasonal ecological and environmental changes, and in areas of marked seasonality this can produce dramatic changes in their numbers (Bronson & Perrigo 1987; O'Connell 1989; Bronson 2009). There seems to be an increase in reproductive activity of some small rodent species due to an increase of food resources such as arthropods and fruits during or just after the seasonal rains typical of tropical regions (O'Connell 1989; Bergallo & Magnusson 1999; Becker et al. 2007; Santos-Filho et al. 2008). Similar patterns of increased abundance correlated with resource abundance and rainfall seasonality have been reported for marsupials and neotropical bird communities as well (Fleming 1972; Blake & Loiselle 1991; Poulin et al. 1993; Gentile et al. 2000). Hence, variation in prey communities and populations are intensified in more seasonal environments, where harsher ecological and climatic conditions prevail during part of the year acting as resource bottlenecks and constraining density of ocelot populations.

3.4.6. Estimation methods and study design effects on ocelot density

Since the first studies on ocelot density (Jacob 2002; Trolle & Kéry 2003), there has been an increase in both our knowledge about the species and the understanding of methods used for estimating animal population density (Royle et al. 2014; Royle & Converse 2020). The overwhelming majority of studies related to ocelot density use camera-trapping in association with capture-recapture models, with very few estimates using distinct methods (Ludlow & Sunquist 1987; Emmons 1988; Desbiez et al. 2010), and it could be inferred that our knowledge about population sizes for this species is quite consolidated. However, an important portion of the heterogeneity in our meta-regression model was detected by the inclusion of methodology in the random term, expressed specially by CR-hMMDM (I^2_{hMMDM} = 46%) and SECR (I^2_{SECR} = 43%) estimating methods. Furthermore, our multilevel mixed-effects meta-analysis model detected significant differences among the three methods evaluated, with CR-hMMDM consistently overestimating ocelot densities in comparison to both other methods. The SECR method provided more conservative ocelot densities than the other methods, consistent to what is expected in the literature (Efford 2004; Royle et al. 2014). The main reason why both non-spatial methods produce higher estimates compared to SECR becomes clear when we observe the significant positive relationships between camera-polygon area and MMDM and between MMDM and ESA, a pattern also observed in jaguar density estimates (Tobler & Powell 2013). In non-spatial capture-recapture models, the parameter estimated is abundance, which is then translated to density dividing it by the *ad-hoc* ESA (Karanth & Nichols 1998; Efford 2004; Royle et al. 2014). In SECR, locations of captures and recaptures are input in the model allowing the estimation of a movement parameter for the population, and this will be integrated in the modelling framework to establish the area of inference from where density will be derived (Efford 2004; Royle et al. 2014). Hence, SECR models are more robust to changes in the inference area while non-spatial methods are very sensitive to changes in ESA (Foster & Harmsen 2012; Royle et al. 2014).

Looking at the perspective of management and conservation, an important issue rises if distinct methods for estimating population sizes yield such contrasting results. While the overall average ocelot density estimate using simple means from reported studies (20.2 individuals/100 km²) did not differ from our multilevel random-effect meta-analysis model (20.3 individuals/100 km²), mean density estimates from the three methods differed significantly, with the most used method (CR-hMMDM) consistently overestimating values, posing a relevant question whether we indeed have reliable ocelot density estimates across its range. Furthermore, most reviewed estimates are from protected areas or from what is considered prime ocelot habitat, and should be interpreted as probable maximum local densities, with special care when using them in extrapolations. Lastly, there are considerable issues regarding variation in study designs, such as sampling period, camera-trap polygon area, number of stations and distance between them that further influences resulting estimates (Foster & Harmsen 2012). In face of our recent and thorough review, the urging request made by Foster and Harmsen (2012) ten years ago never seemed so actual:

> *"We urge field biologists to plan their camera surveys carefully in order to collect data of high quality that are suitable for analysis. (...) We encourage field biologists to carefully review the range of available estimators when designing their camera surveys so they can consider the assumptions and limitations."*

Nonetheless, while the magnitude of point estimates may vary due to differences in study designs and methods, our meta-regression model was still capable of detecting the ultimate ecological effects that drive ocelot population density variation, evidencing the importance of dense forest canopy and seasonality for the species and how these interplay with the intrinsic morphological differences among populations, allowing ocelots to be one of the most successful neotropical cats.

3.5. Final considerations and guidelines for sampling design and results reporting

Evaluating the causes for variation in population densities of species distributed across an extensive latitudinal range such as the ocelot is vital to better understand how ecological and environmental factors affect persistence of distinct species. Furthermore, separating and evaluating methodological sources of such variation are crucial for better planning conservation actions and monitoring protocols.

Many studies reviewed didn't present all parameters related to study designs and resulting estimates that should have been reported for a proper appraisal of results by readers. Furthermore, the lack of variance measures such as standard errors precluded the use of many estimates in the modelling framework used herein. Future studies would benefit from reporting more precise data on study areas, such as georeferenced maps, showing trap-stations location, disposition and MCP. Most journals encourage the presentation of supplemental materials to overcome issues related to publication space and transparency, so providing more precise and detailed information regarding study designs, methods and additional parameters related to general results should be a routine followed by authors and editors.

Finally, we present suggestions regarding reporting of study designs and results that should be followed by any studies using capture-recapture models irrespective of the species focused. Considering the study design, it should always be reported:

1 – Number of trapping stations and detectors by station.

2 – Distance between stations.

3 – Camera-trap station minimum convex polygon area (MCP).

4 – Survey period and sampling effort.

5 – Coordinates of MCP centroid.

As for reporting results and associated parameters, authors should present:

1 – Density estimates with respective standard errors (SE) and confidence intervals (CI), stating clearly how variance measures were computed.

2 – Number and sex of individuals recorded.

3 – Number of captures/recaptures of individuals by trap-station.

4 – Abundance estimates with respective SE and 95% CI.

5 – Effective sampling areas (ESA), state-space or mask area, stating clearly how these were calculated.

6 – Mean maximum distance moved (MMDM).

7 – Capture probability (for non-spatial capture-recapture models).

8 – Detection function and associated parameters (encounter rate, movement parameter; for SECR models).

3.6. Conclusions

Significant portion of variation found in ocelot densities can be explained by distinct methods and study designs used. Controlling the effects of methods used, spatial correlation, and non-independence of estimates coming from the same reference, our multivariate meta-regression model allowed the detection of significant effects of environmental variables (i.e., GFCH and ‘variation GPP’) as well as intrinsic factors (i.e., ocelot body mass) in determining most of the variation found in ocelot density estimates across its range. Ocelot populations thrive in more forested habitats, with higher canopies, but this relationship seems to be restrained by the seasonality of the environment. It is not the primary productivity per se that allows higher density, but rather its stability. Last, further variation in ocelot densities is defined by variation in morphology in such a way that even in some more seasonal areas with lower canopy the species could attain fairly high densities because of smaller body sizes.

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4. OCELOT DENSITY IN AN AGROECOSYSTEM IN THE ECOTONE OF PANTANAL AND CERRADO OF BRAZIL

Resumo

Densidade populacional de jaguatiricas em um agroecossistema no ecótono Pantanal - Cerrado do Brasil

Paisagens agropastoris estão se tornando mais comuns ao longo da distribuição da maioria dos felinos, ameaçando diversas espécies com a perda e fragmentação de habitats, doenças, caça, atropelamentos e isolamento genético. No Brasil, esta é uma questão urgente, com boa parte da conversão de habitats naturais ocorrendo no Cerrado e Pantanal. A jaguatirica é um felino neotropical de porte médio, predador especialmente de pequenos roedores, os quais, por sua vez, tem grande importância ecológica, podem causar extensos danos em plantações e são hospedeiros de diversos agentes etiológicos de zoonoses de preocupação para o homem e a fauna. Usando modelos de captura-recaptura espacialmente explícitos, nós investigamos uma população de jaguatiricas que habita um agroecossistema no ecótono Pantanal-Cerrado, avaliando a variação espacial na densidade de jaguatiricas em função de covariáveis de uso e cobertura do solo. Testamos a hipótese de que campos abertos de agricultura na área de estudo podem ajudar a manter a população de jaguatiricas, levando em conta características intrínsecas da espécie que podem afetar sua detecção e o uso do espaço. Amostramos 60 estações de armadilhas-fotográficas pareadas com espaçamento médio de 815 m, cobrindo uma área amostral mínima de 48 km^2, com um esforço amostral total de 3.796 armadilhas-dia. Modelos SECR de densidade levaram em conta variação nos parâmetros da função de detecção. Depois de fixar o modelo SECR mais ajustado para a função de detecção, nós permitimos que o parâmetro de densidade variasse de acordo com um processo Poisson não-homogêneo para avaliar a variação espacial na densidade da jaguatirica em função do tipo de habitat. Obtivemos um sucesso de 15,9 capturas de jaguatiricas a cada 100 noites, e identificamos 41 indivíduos com uma razão sexual de 3,1F:0,1M. A taxa basal de encontro com estações colocadas em estradas ($\lambda 0 = 0.173 \pm 0.011$ SE) foi nove vezes mais alta do que com estações em trilheiros, independente do sexo da jaguatirica. O parâmetro de movimento dos machos foi mais alto ($\sigma = 926$ m ± 38 SE) do que das fêmeas ($\sigma = 614$ m ± 19 SE), resultando em densidade mais alta de fêmeas do que de machos (37,9 vs 8,8, respectivamente). A densidade de jaguatiricas na área de estudo foi de 46,7 indivíduos/100 km^2. Embora o modelo para variação espacial tenha tido menos suporte, ele mostrou estimativas mais altas para os habitats de floresta nativa e agricultura, do que nas pastagens de gado e campos nativos. Nossos resultados revelaram padrões de uso do espaço variando entre os sexos, resultando em diferenças significativas nas densidades por sexo e na razão sexual da população. Além disso, existe de fato uma população residente de jaguatiricas no agroecossistema investigado, e a inclusão de covariáveis de uso e cobertura do solo nos modelos SECR permitiu detectar diferenças no uso dos habitats que são importantes de serem consideradas quando se monitora populações em áreas modificadas pelo homem e que merecem mais investigação.

Palavras-chave: agroecossistema; armadilha-fotográfica; Cerrado; jaguatirica; *Leopardus pardalis*; Pantanal; SECR.

Abstract

Agropastoral landscapes are becoming more common over most felid's distribution ranges, threatening many species with habitat loss, fragmentation, diseases, poaching, roadkills and genetic isolation. In Brazil, this is an urgent matter, as most of the conversion of natural habitats advances over the Cerrado and Pantanal biomes. The ocelot is a medium-sized neotropical cat, preying especially on small rodents, which, in turn, have great ecological importance, can also make extensive damage to distinct crops and are hosts to diverse etiological agents of zoonotic diseases of human and animal concern. Using spatially-explicit capture-recapture models, we investigated an ocelot population inhabiting an agroecosystem in the Pantanal-Cerrado ecotone, evaluating the spatial variation in density related to land use and cover covariates. We tested the hypothesis that open agriculture fields in the study area can help supporting this ocelot population, considering intrinsic characteristics of the species that can affect its detection and space use. We sampled 60 double-camera-trap stations spaced 815 m apart, covering a minimum sampling area of 48 km^2, for a total sampling effort of 3,796 camera-trap-days. SECR density models accounted for variation in parameters of the detection function. After fixing the best SECR model for the detection function, we allowed the density parameter of the model to vary according to an inhomogeneous Poisson point process to evaluate spatial variation in ocelot density as a function of habitat type. We had an overall trap-success of 15.9 ocelot captures/100 nights, and identified 41 ocelots, with a sex-ratio of 3.1F:1M. The estimated baseline encounter rates with on-road stations ($\lambda 0 = 0.173 \pm 0.011$ SE) were nine times higher than with off-road stations, irrespective of sex of the ocelot. Movement parameter was higher for males ($\sigma = 926$ m $\pm$ 38 SE) than for females ($\sigma = 614$ m $\pm$ 19 SE), resulting in higher female ocelot density than male's (37.9 vs 8.8, respectively). Ocelot density in the study area was 46.7 individuals/100 km^2. Although the model for spatial variation in ocelot density had lower support, it showed higher estimates for native forest habitats and agriculture than livestock pastures or natural open vegetation types. Our results revealed distinctive space use pattern among sexes, resulting in significant differences in density estimates and sex-ratio of the population. Furthermore, there is indeed a resident ocelot population in the agroecosystem investigated, and the inclusion of land use and cover covariates in SECR models allowed detecting differences in habitat use that are important to acknowledge when monitoring populations in human-modified landscapes and deserves further investigation.

Keywords: agroecosystem; camera-trapping; Cerrado; *Leopardus pardalis*; ocelot; Pantanal; SECR.

4.1. Introduction

The conversion of natural areas for human use is considered one of the main causes of the decline of different felid populations around the world (Loveridge et al. 2010). Indeed, at the beginning of the 2000s, agropastoral landscapes already corresponded to about 40% of the planet's surface (Foley et al. 2005; Ramankutty et al. 2008), while, in Brazil, the expected increase for the next ten years in areas destined for agriculture and cattle production is from 82 million hectares to 93.3 million in 2030/31 (MAPA 2021). In general, felids are considered keystone species in ecosystems because they control other animal populations through predation (Macdonald et al. 2010). Thus, the extinction or even the reduction of their populations can lead to an increase in herbivory and a consequent change in the composition of vegetation and landscape structure (Loveridge et al. 2010). Therefore, the current habitat loss and conversion scenario makes the situation of these cats worrisome.

The ocelot is a medium-sized neotropical cat (7 to 15 kg) that naturally occurs from southern USA, across Central and South America, to northern Argentina (Murray & Gardner

1997; Paviolo et al. 2015). The species is an important predator of small and medium-sized species, especially small rodents (Emmons 1987; Concone 2004), which have great importance in seed consumption and dispersion (DeMattia et al. 2004; Godó et al. 2022), can make extensive damage to distinct crops (Gonçalves et al. 2015), and are hosts to diverse etiological agents of zoonotic diseases of human and animal concern (Muylaert et al. 2019; Prist et al. 2021). Because it is considered a relatively more resilient species and with more robust populations than other neotropical cats, it is listed as “Least Concern” (LC) by the International Union for Conservation of Nature (IUCN; Paviolo et al. 2015). Despite this, the species was included in the official list of endangered species of the Ministry of the Environment (MMA) until 2014 (Brasil 2014) and it is included in the National Action Plan for the Conservation of Small Cats (ICMBio 2014), indicating that more information is necessary to ensure its status on the MMA endangered list.

In Brazil, robust populations of this species are found mainly in the Amazon rainforest (Oliveira et al. 2013; Paviolo et al. 2015). However, ocelots are present in other Brazilian biomes such as the Pantanal, an area considered of extreme importance as a natural refuge for several species considered endangered in the country (Harris et al. 2005); and the Cerrado, the most threatened biome by agriculture expansion in Brazil and the most biodiverse savannah of the world (Strassburg et al. 2017; da Silva & Lacher 2020). Even so, less than 5% of the Pantanal is formally protected under public or private areas (Called Conservation Units in Brazil; Brasil 2010; Tomas et al. 2019), while the scattered Cerrado’s conservation units cover only 8.6% of this vast region (da Silva & Lacher 2020). The number of protected areas in the Pantanal and Cerrado are not enough to ensure the protection of biodiversity and, therefore, conservation basically depends on the action of private landowners, who retain about 95% and 90% of the use of the areas, respectively (Zimmermann et al. 2005; Bonanomi et al. 2019). Knowing this, research needs to be developed in areas of human use in these biomes to identify the factors that influence the survival of the species.

Studies of habitat use by ocelots show that the species is highly dependent on dense forest cover (Harveson et al. 2004; Jackson et al. 2005; Chapter 1), as these habitats provide shelter and food resources, while open habitats are avoided as they do not provide shelter (Horne et al. 2009). At the northern limit of the species' distribution, in southern Texas (USA) and northern Mexico, the conversion of areas of native vegetation into agricultural fields has fragmented ocelot habitat, isolating populations and reducing genetic diversity (Janečka et al. 2007; 2011). Research conducted in that region revealed that ocelots avoided using open areas and that home ranges were established where dense cover was predominant, even though bare ground associated to agriculture were almost 50% of the available habitat in the landscape (Horne et al. 2009), suggesting that the species is negatively impacted by habitat fragmentation due to agriculture.

However, observations in the study area investigated in this article indicated a high population density of ocelots and the use of areas considered inappropriate, such as open irrigated rice fields and other agricultural landscapes (Concone 2004, Concone & Giordano 2013, Fraga 2020). In two years of surveying night outings (75 outings in the period) in search of wildlife, there were 225 (two hundred and twenty-five) ocelot sightings in irrigated rice fields (Concone & Giordano 2013), while in two years of camera-trapping almost 53% of ocelot records were taken in crop areas (Fraga 2020). Other studies conducted in human-modified landscapes have found an increase in the average relative abundance of ocelots related to an increase of sugarcane crops, but only where large tracts of native forest remain (Paolino et al. 2018). Thus, the species presents itself as a good model for studying the effects of land use changes, as it is considered a species with a wide geographic distribution and with relatively high demographic densities, compared to other small cats (Oliveira et al. 2013). In this chapter we evaluated the spatial variation in ocelot population density in relation to land use and cover covariates, testing the hypothesis that open agriculture fields in the study area can help supporting the ocelot population. Considering intrinsic characteristics of the species that can affect its detection and space use, we investigated an agroecosystem in an ecotone formed by the southern Brazilian Pantanal and the Cerrado using spatially-explicit capture-recapture (SECR) models.

4.2. Methods

4.2.1. Study area

The study was carried out at Fazenda San Francisco (FSF; Figure 11; 20°05'10"S and 56°36'57"W), an area of 8,970 hectares (ha) located in an ecotone between Pantanal and Cerrado biomes of Brazil. More than 80% of this ranch is inserted into an ecoregion of the southern portion of the Brazilian Pantanal subject to seasonal inundation due to floodwater from Miranda and Salobra rivers and rainwater from the central part of Bodoquena Hills (Concone 2004; Azevedo & Murray 2007). According to Köppen's classification, predominant climate type is Am, tropical monsoon (Alvares et al. 2013), with almost 75% of the annual average rainfall of 1366 mm falling between October and March, characterizing a rainy season. Average temperature is 27.6°C, although it varies greatly during the year, with lowest temperatures of 8°C in July and August and highest temperatures reaching more than 40 °C in eight months.

This ranch has been used for livestock raising since 1975, when 2,100 ha of Cerrado were converted into cultivated pastures, adding to existing native pastures. Intense conversion of natural habitats for irrigated rice cultivation started in 1984, occupying as much as 3,200 ha, including infrastructural improvements such as dirt roads and irrigation canals. Since 2013, part of the areas destined for cultivated pastures and rice fields were converted to the rotational planting of soybean and corn, which today encompass about 1,000 ha. The area still harbors 3,600 ha (40% of the area) of native vegetation, in a mosaic of open fields, swamps, semi-deciduous seasonal forests and the riparian forest of Miranda River and an intermittent tributary.

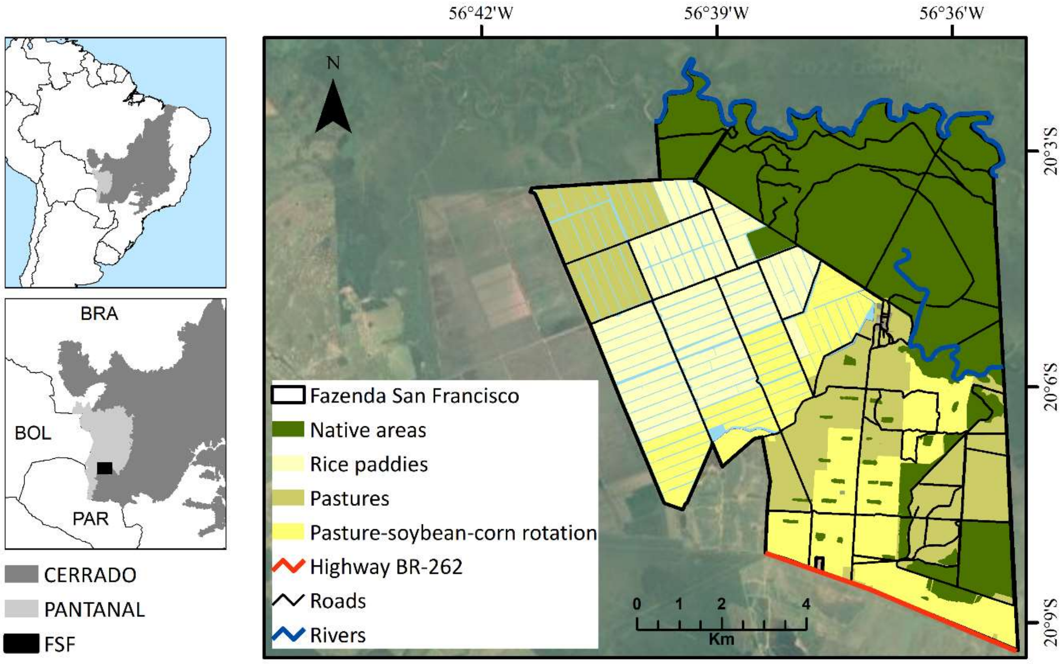

Figure 11. Map of Fazenda San Francisco (FSF) located in an ecotone of Pantanal-Cerrado. Human-modified and natural vegetation areas are depicted.

4.2.2. Study design and data analysis

To evaluate the appropriate distance between sampling stations, as well as the use of the SECR model, we established a pilot study with 54 sampling days between the months of September and November 2018. Sixteen paired camera-trap stations were set in two adjacent blocks with eight stations each. The average distance between pilot stations was 1261 m and the minimum area covered by the grid was 26.4 km². After evaluating results, we have adjusted the average distance between stations and increased the total number of sampling points and area covered by the final grid. A full description of the pilot study is presented in the Appendix B.

For the main survey of the study, we sampled 60 stations consisting of two camera-traps facing each other (Reconyx HC500; Cuddeback E.; Scoutguard SG565), establishing a 1 x 1 km grid over the study area, using a stratified sampling where the number of camera-trap stations were proportional to native and agricultural areas. The maximum distance of 1 km was used based on the smallest ocelot home ranges to ensure that all animals in the area had a theoretical capture probability > 0 (Karanth & Nichols 1998; Oliveira et al. 2010) and the final mean distance between camera-trap stations after deploying the grid was 815 m. We adjusted station locations in the field to maximize the number of camera-traps in dirt roads to maximize capture probability (Karanth & Nichols 1998; Sollmann et al. 2011). Stations that were not in roads were set in wildlife trails. The grid covered a minimum convex polygon of 48 km² (Figure 12). Due to logistic constraints, the 60 sampling stations were split in two adjacent blocks of 30 trap stations (Royle et al. 2014). Each block was sampled for an average of 53 (± 2.6 SE) and 58 (± 4.0 SE) days, respectively, and the capture histories of the two blocks were combined at the end (Soisalo & Cavalcanti 2006; Royle et al. 2014). The first block of 30 stations started in July 2019 and ended in late August 2019, and the second block started in late August and ended in mid-November 2019. Individual ocelots were identified from their unique coat patterns (Trolle & Kéry 2003) and spatialized individual capture histories were created using the camtrapR package (Niedballa et al. 2016) in software R (R Core Team 2021) using R Studio (RStudio Team 2022).

To build spatial detection histories, first we used the freely available software Timelapse 2 (Greenberg Consulting Inc.), to identify and fetch all ocelot images to a new working directory. This batch of ocelot images was then screened for individual identification, comparing to a database of ocelot images from the study area constructed in the past fifteen years. After all images were identified to species and individual level, we created individual folders for each ocelot, and then we ran the function '*recordTableIndividual'* of camtrapR package, setting an interval of 24 hours between images of the same animal in the same station as an independent record. Finally, for each capture occasion of one day we recorded in which stations an individual ocelot was detected.

We estimated ocelot population density using maximum likelihood SECR models, which input the spatial information of trapping devices directly in the model and are more robust than *ad-hoc* approaches to establish effective sampling areas (Borchers & Efford 2008; Foster & Harmsen 2012). SECR modelling assumes that individuals have roughly circular and randomly distributed home ranges in a state-space (S) and use the locations of individual captures and recaptures to estimate home range centers (Royle et al. 2014). The model assumes that the encounter rate of an individual j with station i (λ_{ij}) decreases as the distance to the home range center increases, according to a detection function (Efford 2019). We used the half-normal detection function which is defined by the basal encounter rate λ_0 and the movement parameter σ. The first parameter can be understood as the encounter rate at a station hypothetically placed in the center of the home range, and the second is related to the average home range radius, and it is estimated from captures of the same individual in more than one station (Royle et al. 2014, Efford 2019). We defined S by buffering trap-stations by 4,100 m resulting in an area of 208 km² (Figure B1). This buffer corresponds to more than 4 x σ and it is expected to cover all potential home range centers exposed to our sampling grid (Royle et al. 2014; Figure B1).

We have built distinctive SECR density models accounting for variation in parameters of the detection function and evaluated their fit through Akaike's Information Criteria corrected for small sample sizes (AIC_c) to select the best model (Burnham et al. 2011). Ocelots present distinctive space use behavior between sexes, with males having significant larger home ranges than females (Gonzalez-Borrajo et al. 2017; Azevedo et al. 2019) and there is evidence of sex influencing their capture probabilities (Massara et al. 2015), so we included 'sex' as a covariate in the detection function to estimate both λ_0 and σ (Sollmann et al. 2011; Rocha et al. 2016). Furthermore, to account for differential use of roads against game trails, we also built models including location of trap stations (on/off road) and allowed for variation in sampling effort in all models (Royle et al. 2014).

After, selecting the best detection model, we fixed those parameters, and built a new SECR density model to evaluate the hypothesis of spatial variation in ocelot as a function of habitat type (natural vs anthropized; Appendix). For this model, we assume that home range centers are not uniformly distributed in *S*, but rather respond to an inhomogeneous Poisson point process allowing variation in the density parameter (Royle et al. 2014). *S* space is a discretized grid generated when building SECR models, and cell size is calculated internally by the function when setting the buffer around stations (Efford 2019; Figure B3). We quantified the proportion of land use and cover for each S cell using data from the Brazilian Annual Land Use and Land Cover Mapping Project (Souza et al. 2020; https://mapbiomas.org). We then grouped the predominant classes in broader categories of anthropized and natural habitat areas. We used the package secr (Efford 2021) in software R (R Core Team 2021) using R Studio (RStudio Team 2022) to run all ocelot density models and geoprocessing was performed in ArcMap 10.2 (ESRI 2014).

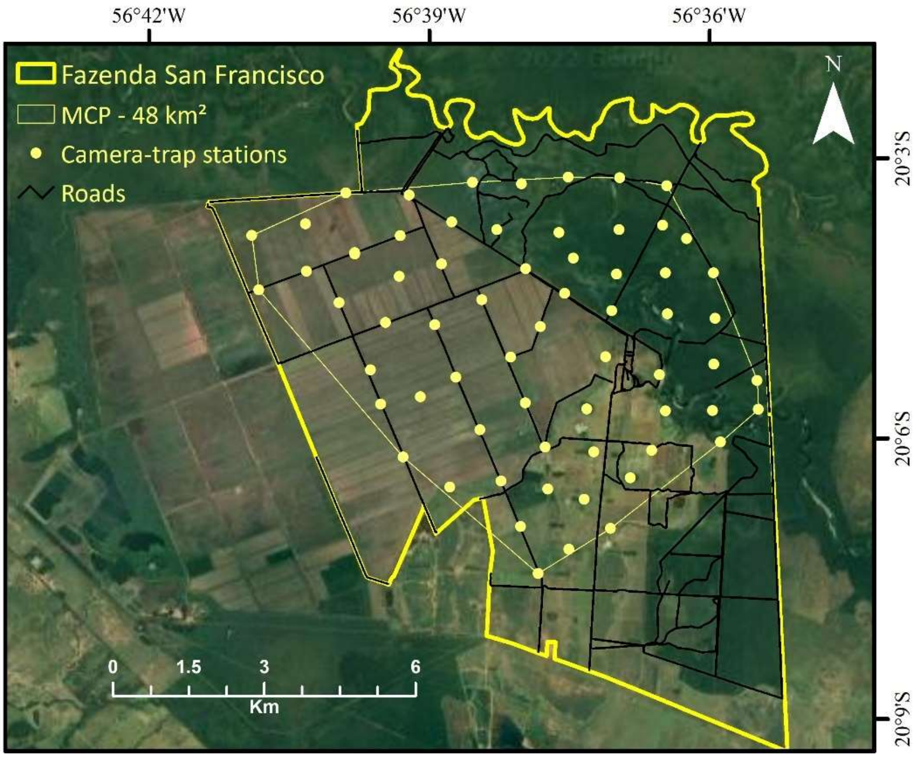

Figure 12. Study area with the grid of 60 camera-trap stations, showing the minimum sampled area (MCP) of 48km².

4.3. Results

The sixty camera-trap stations were operational for an average of 63 (± 2.3 SE) days, totaling 3,796 camera-trap-days. We recorded 2,913 ocelot pictures of 43 individuals, being 31 females, 10 males and two that we couldn't confirm the sex, generating a sex ratio of 3.1F:1M. There were 126 records where individual recognition was not possible. Eight ocelots were recorded only once during the sampling (3F, 3M and 2 unidentified), and the other 35 individuals were recorded between two and 64 times during the sampling period, with most of them (n = 27) being recorded in two or more stations (Tables B2, B3).

Twenty-six ocelots have been recorded in years before this survey (18 females and 8 males), nineteen of which (13 females and 6 males), also recorded in the pilot study. Five animals recorded in the previous year were not recorded during the 2019 survey, and for one the fate was known (Appendix B). Three females were recorded with one small cub (± 3 months old) each, with the first record of cubs being in late October (females LP040 and LP052) and mid-November (female LP053). A female cub of similar estimated age was recorded with the mother (LP003) in early December 2018 and then photographed alone in one of the stations as a sub-adult (HC43F01) between September and October 2019. Her mother was recorded also alone in the same station two weeks after (Figure B3, B4). Another female recorded in December 2018 as a large cub (> 6 months old) still moving close to the presumed mother (LP011) was recorded in the 2019 survey (LP026).

The final dataset of individual ocelots has 604 independent records, with an average of 22 records for the ten males, who were recorded on average at 5 distinct stations. The 31 females were recorded a mean of 12 times each and recorded on average at three stations (Table 4). Mean maximum distance moved by all individuals captured in more than one station was 2166 m and the overall trap success was 15.9 ocelot captures per 100 nights. Females shared camera-trap stations an average of 2.3 (± 1.3 SD) with other females and an average of 1.8 (± 0.8 SD) with males. Males, on the other hand, shared camera-trap stations an average of 5.4 (± 4.1 SD) with females and 1.4 (± 0.9 SD) with other males.

Our best ranked density model included sex of individuals and location of trap stations in the detection parameters and showed an overall ocelot density in FSF of 46.7 (±7.4 SE; 95% CI: 34.3-63.6) ocelots per 100 km². Female ocelot density was higher (37.9 ± 6.9 SE; 95% CI: 26.7-53.9) than male ocelot density (8.8 ± 2.8 SE; 95% CI: 4.8-16.2). The estimated baseline encounter rates with on-road stations ($\lambda0 = 0.173 \pm 0.011$ SE) were nine times higher than with off-road stations, irrespective of sex of the ocelot. On the other hand, the movement parameter was higher for males ($\sigma = 926$ m ± 38 SE; 95% CI: 855-1002 m) than for females ($\sigma = 614$ m ± 19 SE; 95% CI: 578-653 m; Figure 13). The estimated proportion of females to males in the population was 0.76F:0.24M. The model for variation in ocelot density in relation to land use and cover had lower support than the anterior, but it showed higher estimates for native forest habitats and agriculture than livestock pastures, while estimates for natural open vegetation types were extremely low (Table 5). The results of the other detection models are presented in Table B4 (Appendix B).

Table 4. Summary of spatial capture histories separated by sex, showing the number of independent records and the number of stations in which individuals were recorded. N = number of individuals; Nsr = number of individuals with spatial recaptures; MMDM = mean maximum distance moved by individuals recorded in more than one station (in meters).

Sex	N	MMDM (N_{sr})	Independent Records			Stations	
			Mean	Range	Total	Mean	Range
Female	31	1840 (21)	12	1-54	384	3	1-7
Male	10	3307 (6)	22	1-64	218	5	1-11

Table 5. Density estimates (in ocelots/100 km^2) for each land use and cover class.

Land use and cover	Density	SE	Lower 95% C.I.	Upper 95% C.I.
Natural forest	51.57	± 12.93	31.78	83.67
Agriculture	49.29	± 11.74	31.10	78.12
Pasture	26.83	± 22.09	6.55	109.88
Natural open vegetation	<< 0.0001			

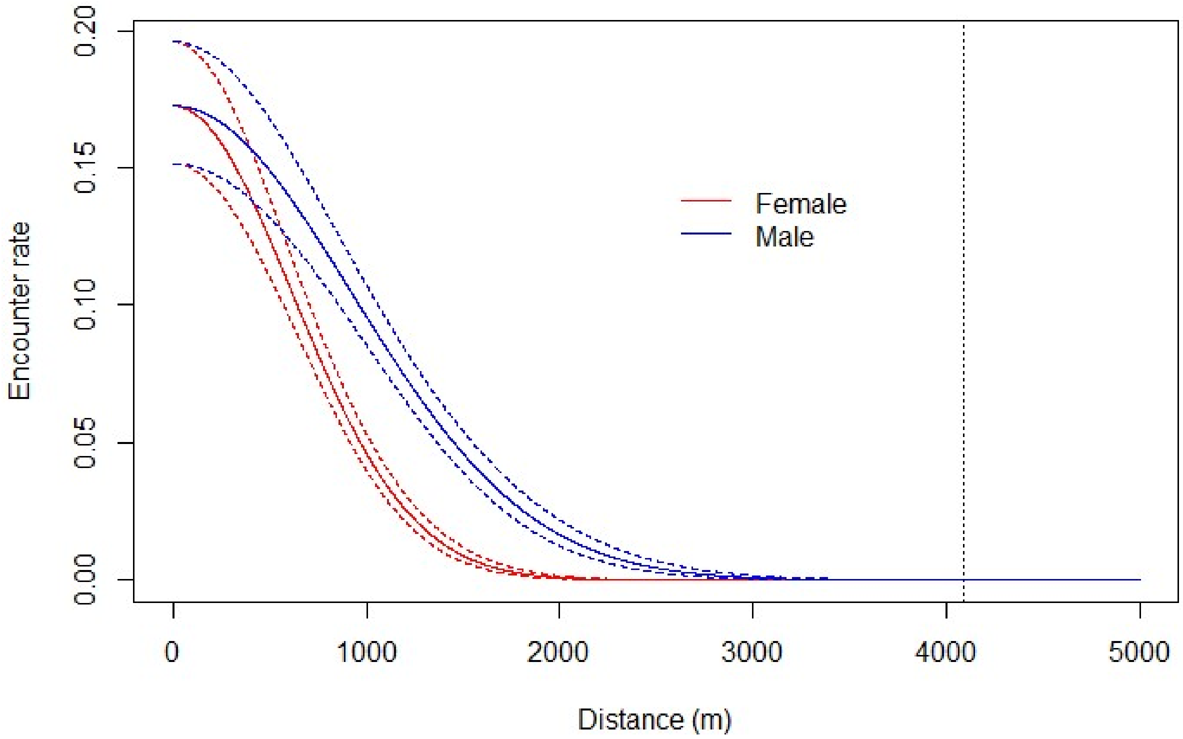

Figure 13. Half-normal detection function of best ranked detection model for ocelot density. Encounter rate (λ) decreases with increased distance from estimated home range centers. Steeper decrease in female curve is due to the smaller movement parameter (σ = 614 m), compared to males (σ = 926 m). Colored dashed lines represent confidence intervals (95%). Vertical dotted black line indicates buffer used to establish *S* state-space.

4.4. Discussion

4.4.1. Density Estimates

We have performed one of the most intense sampling efforts (60 stations and 3796 camera-trap-days) to estimate ocelot density available in the literature (mean of 27 stations and 1628 camera-trap-days; Chapter 1) and the overall ocelot density estimate for our study area, 46.7 individuals/100 km^2 (± 7.4 SE; 95% CI: 34.3-63.6), figures above the average for the entire distribution of the species (20.3 ± 2.2 ocelots/100 km^2; Chapter 1), irrespective of the method used. Looking at other density estimates in the Pantanal and Cerrado biomes, just one area located in the central Brazilian Pantanal has reported a higher ocelot density of 56.4 individuals/100 km^2 (95% CI: 17-96; Trolle & Kéry 2003), while other estimates ranged from 1.2 to 22 ocelots/100 km^2 depending on the modelling framework utilized (e.g., Trolle & Kéry 2005, Boron et al. 2022; Table 2 – Chapter 1). However, the authors of the former study note that the large variation in confidence intervals are related to the limited sampling area, small population size and low capture probability (Trolle & Kéry 2003). Furthermore, the adoption of non-spatial capture-recapture models using half of the mean maximum distance moved by individuals to estimate the effective sampling area inflates density estimates, and hence, care is needed with some estimates (Foster & Harmsen 2012, Royle et al. 2014; Chapter 1).

Although SECR modelling is generally considered a better approach for robust density estimation, results ultimately depend upon the adequacy of the data provided to models (Quigley & Hornocker 2010; Foster & Harmsen 2012). The overall number of individuals recorded, the mean number of independent records by individuals and the number of spatial recaptures in total and by individuals obtained during our survey allowed for a precise estimate of the detection function parameters needed for a robust density estimation using SECR modelling (Royle et al. 2014). It is important to note that our sampling design was adjusted after the pilot study revealed that the distance between sampling stations was too high, affecting the number of spatial recaptures, especially of females. The inclusion of covariates related to the detection parameters, i.e., location of stations and sex of individuals, affecting encounter rate and sigma, respectively, have further improved the fit of the models, allowing to disentangle the effect of roads in the detection of ocelots and to provide density estimates for each sex in the study area. Furthermore, we detected differences in ocelot density related to distinct land use and cover that are important when considering managing and conservation in private lands that dominate both the Pantanal and Cerrado biomes of Brazil.

4.4.2. Effect of roads on encounter rates

The fact that ocelots have much higher encounter rates at on-road stations is consistent with other studies (e.g., Di Bitetti et al. 2006; Paolino et al. 2018) and highlights the importance of incorporating this information when modelling detection parameters of the species (Trolle & Kéry 2005). In our study area, there are around 170 km of dirt roads, trails and boardwalks used for transport of agriculture and livestock goods, employees and tourists, and ocelots are often observed moving and hunting along these pathways. Roads can be important travel routes for carnivores (Muhly et al. 2019) and this large network of linear infrastructures, especially prevalent in the areas of intense human activity of the study area, might also act as landmarks for territorial species like ocelots (Di Bitetti et al. 2006). During fieldwork we have documented 12 distinct latrines, which are important sites for communication between ocelots (Ludlow & Sunquist 1987, Emmons 1988, Moreno & Giacalone 2006). Most of these sites were in very conspicuous human structures like bridges, observation towers or pumping stations, or at the intersection of roads. Moreover, major roads are aligned with an array of water canals used for irrigating and draining agriculture fields, and shrub and arboreal vegetation grows along those canals, forming micro-habitat conditions for many potential prey species of ocelots to thrive (Silva 2020). On the other hand, it is also important to note that roads have known negative impacts on wildlife populations (Van Der Ree et al. 2015) and are a major source of mortality for ocelots (Abra et al. 2021; Blackburn et al. 2021; Appendix B).

4.4.3. Effect of sex on movement

Despite some evidence that sex might influence ocelot detection probability (Massara et al. 2015), we did not detect this effect on the basal encounter rate λ_0 of the species in our study area, although detection probability and basal encounter rates are somewhat distinct concepts (for a better comprehension of this differences we refer readers to Sollmann et al. 2011; Royle et al. 2014; Cooch & White 2019). This is a striking difference to larger cats, of which females are much less detected than males (Sollmann et al. 2011; Gray & Prum 2012; Singh et al. 2014). It is a common practice of large cat density studies to set up camera-trap stations at roads and large trails to increase capture probability and improve estimates (Karanth & Nichols 1998). However, female large cats avoid human-made trails and roads seemingly to decrease chances of encountering larger and more mobile adult males (Salom-Pérez et al. 2007; Gray & Prum 2012; Singh et al. 2014). In case of ocelots, even considering that males also move farther than females (Emmons 1988; Dillon & Kelly 2008), both are active similar amounts of time during their activity periods (Emmons 1988; Azevedo et al. 2019), and this seems to explain why they are equally likely to be detected in their estimated activity centers, irrespective of stations placed in roads or not.

On the other hand, in agreement with our expectations, the effect of sex of individuals on the movement parameter σ was very significant (as seen by largely distinct confidence intervals) and essential in honing the density estimates. Sigma in the SECR modelling framework adopted herein can be directly related to a circular home range radius according to

$r_{0.95} = \sigma\sqrt{5.99}$,

where $r_{0.95}$ is the home range radius of the area around the estimated activity center which contains 95% of the movement outcomes during the sampling period (Royle et al. 2014). Although circular home range areas might be a simplification of space use, it still holds true for the relationship between home ranges sizes and the movement parameter of the detection function (Royle et al. 2014). For instance, using estimated sigma in the above equation gives circular 95% home-range contours of 16.1 and 7.0 km^2 for males and females, respectively, corroborating expected sex-differences in ocelot home range areas (Gonzalez-Borrajo et al. 2017; Azevedo et al. 2019). In summary, male and female ocelots have equal basal encounter rates λ_0, but because females have smaller home range areas the decay in detection is more accentuated in relation to movement parameters.

Another aspect of the distinction in space use between sexes detected by different movement parameters is that it allowed for estimating separately density for both sexes, revealing that female ocelot density in the study area is around four times that of males, without confidence interval overlap in neither density nor sex-ratios estimated. This pattern may emerge not only because of distinct space use and home range behavior, but also because dispersal movements are expected mostly for sub-adult males, while females usually are philopatric (Sunquist & Sunquist 2002). Although female-skewed sex-ratio in adult population is common among cats (Sunquist & Sunquist 2002), and other ocelot populations showed similar patterns (Di Bitetti et al. 2006), there has been variation in overall sex-ratio in some ocelot populations. For instance, in the dry forests of eastern Bolivia, ocelots presented sex-ratios closer to 50% and one population showed a strongly male-skewed sex-ratio (Maffei et al. 2005). Similarly, long-term monitoring in Belize revealed most populations with overlapping density estimates for the sexes and sex-ratios slightly female-biased, except for two sites that presented strong opposing trends (Satter et al. 2019). Authors argue that male-biased sex-ratio was observed in the site with less suitable habitat areas, and males there were likely surplus individuals living in the edge of broadleaf forest habitats, leaving the more abundant pine forests mostly vacant (Satter et al. 2019).

4.4.4. Habitat effect on density estimates

Even though the results for density in relation to land use and cover had confidence intervals largely overlapping, they revealed that ocelot density in the native forested areas and agriculture are very similar and much greater than either livestock pastures or natural open habitats, giving some support to our hypothesis of agriculture being able to help maintaining a viable ocelot population in this agroecosystem. These evidences are further supported by results of spatial capture-recapture data showing several activity centers located in the agricultural areas (Appendix). Results of ongoing investigations on small-mammal community and population in the study area can help shed some light on the matter. Of the ten species of small mammals recorded, one species of small rodent, the Chacoan marsh rat (*Holochilus chacarius*), is dominant in the rice crops where ocelots are often recorded hunting (Silva 2020). The estimated density of Chacoan marsh rats in rice fields varied from 60 to 114 individuals/km^2, following the crop cycle from sowing to harvesting (July-December) and coinciding with the ocelot camera-trapping period (Silva 2020). Emmons (1987) estimated a daily flesh consumption of 60 to 90 g/kg of ocelot. Considering that the mean body mass for female and male ocelots in the study area were 9.4 and 11.9 kg, respectively (Braga 2019), and that mean body mass of live-trapped Chacoan marsh rats was 130g (Silva 2020), it means that females in the study area needs to catch between 4 to 6 Chacoan marsh rats per day, while males would require around 5-8 *H. chacarius* per day. Pondering that other potential ocelot prey, such as cavy (*Cavia aperea*), reptiles and birds, are also present in agriculture fields, it is likely that prey biomass is not a limiting factor for the estimated high ocelot density (Concone 2004; Silva 2020).

On the other hand, prey resources are not the only requirements sought by ocelots for thriving in an area, and questions remain in relation to how this species strongly dependent of forest cover copes with large areas of presumably unsuitable habitat such as open crops. It is likely that human structures in the area (e.g., bridges, culverts) and the shrub and arboreal vegetation that grows alongside the array of irrigation canals provide enough shelter and secure sites for ocelots (Ludlow & Sunquist 1987; Emmons 1988). The fact that we have recorded adult females with small cubs and many of the same mature individuals in the area for several years indicate a resident population that uses this human-modified landscape as habitat (Quigley & Hornocker 2010).

Nonetheless, it is important to highlight that about 40% of the study area remains with native vegetation cover, extending to the north well beyond the limits of the property. Ocelot population density in this land cover was higher than in agriculture (although overlapping) and in pastures and, therefore, shows that native habitats are fundamental for the maintenance of the species in the agricultural landscape (Paolino et al. 2018). Furthermore, the amount of native area on this property is twice what the legislation requires for both the Pantanal and the Cerrado (Law Number 12,651/2012; Brasil 2012), reinforcing the importance that private properties that dominate these two biomes have not only in agricultural production, but also its crucial role in the maintenance and conservation of species. Hence, robust ocelot populations can be supported in areas destined to agriculture in the Pantanal-Cerrado ecotone, as long as considerable areas of native forest are maintained.

4.5. Final considerations

There are though, many important questions that require further investigation and consideration. Recent research regarding the health of wild carnivores in our study area evaluated the presence of hemoparasites, including some of importance to public health like the etiological agents of leptospirosis and leishmaniosis, as well as others that might pose threat to species conservation, like the rabies virus (Braga 2019). That author has detected high prevalence and coinfection rates among the thirteen ocelots evaluated in 2018, and most did not present good health conditions (Braga 2019). Of the 13 ocelots captured by Braga (2019), eleven (85%) were recorded during our camera-trapping survey in 2019. Hence, the high ocelot density in agriculture fields and intense social contact among ocelots evidenced by the number of camera-trap stations shared by several individuals of both sexes might exacerbate health issues. Also, some hemoparasites detected are transmitted through oral infection (e.g., *Trypanosoma cruzi*) and can be bioaccumulated by ocelots due to their strict carnivore diets and high consumption of rodents known as natural hosts (Emmons 1987; Concone 2004; Rocha et al. 2013; Roque & Jansen 2014; Braga 2019). Moreover, the common and widespread use of agrochemicals in crops (Bombardi 2019) can further contribute to worsen human and wildlife health conditions (Galloway & Handy 2003; Medici et al. 2021). For instance, organophosphate pesticides of use in rice and soybean production

(Bombardi 2019), the two major crops in the study area, can cause immunotoxicity and reduce infection resistance (Galloway & Handy 2003). Thus, on the one hand, the agroecosystem seems to favor the maintenance and abundance of ocelots, due to high population density of small rodents. On the other hand, it seems to negatively affect their health and increase contact between host populations of parasites – both prey and predators – enhancing transmission rate and prevalence.

Therefore, population size must not be the only parameter to be considered when discussing the role of private areas in species conservation (Hoogesteijn & Chapman 1997; Haines et al. 2006; Tomas et al. 2019). Health data on the ocelot population in the study area indicate possible negative effects of pesticide use in plantations and warrant further investigation. Long-term monitoring of populations inhabiting agroecosystems must therefore not only assess possible changes in population density, but also monitor the health of individuals and their relationship with parameters such as survival and fertility.

4.6. Conclusions

There is a resident ocelot population in the agroecosystem investigated, evidenced by the presence of breeding females with cubs, and of adult individuals recaptured in distinct years. Adjustment of the sampling design after the pilot study was essential to improve the accuracy of estimates. By decreasing distance between stations, and increasing their numbers, we were able to record a greater number of individuals and enhance spatial recaptures, which are fundamental conditions for honing the fit of SECR models.

Accounting for station-specific covariates (i.e., on/off roads) was important for adjusting encounter rates, and to determine that this landscape feature does not have an effect related to sex of individuals of the study area. Ocelot space use pattern differ among the sexes, as evidenced by non-overlapping confidence intervals between movement parameters estimated for males and females, resulting in significant differences in density estimates and sex-ratio of the population. Males move through larger areas than females, resulting in a lower density of individuals of that sex compared to females.

Finally, including land use and cover of the study area as spatial covariates influencing ocelot density estimate helped to detect differences in habitat use and deserves further investigation.

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5. CONSIDERAÇÕES FINAIS E CONCLUSÕES

Embora existam diversos estudos sobre populações de jaguatiricas disponíveis na literatura, o que permitiu a instituições como a IUCN determinar seu status de conservação global como pouco preocupante (LC), em realidade há forte um viés regional acerca do conhecimento de suas populações. Nove países de sua distribuição (41%) não possuem qualquer estimativa populacional e apenas cinco países respondem por 88% das estimativas disponíveis. A distribuição da espécie se estende por grande parte da região neotropical, abrangendo oito biomas e 141 ecorregiões[2]. Entretanto, não foram encontradas estimativas populacionais para 110 dessas ecoregiões (78%) distribuídas por sete biomas (Apêndice 3). Isto revela uma grande lacuna de conhecimento acerca de populações da espécie na maior parte de sua distribuição. Olhando unicamente para o Brasil, apesar de ser um dos países com mais estimativas (Tabela 2, Capítulo 1), é notável também os vieses regionais encontrados e a grande lacuna de estudos na maior parte do território brasileiro. Existe apenas uma área amostrada em toda a Caatinga, o Parque Nacional da Serra da Capivara, duas na Amazônia (Reserva de Desenvolvimento Sustentável do Amanã e Fazenda São Nicolau), três no Cerrado (Parque Nacional Grande Sertão Veredas, Reserva Particular do Patrimônio Natural Porto Cajueiro e Parque Estadual Veredas do Peruaçu), três no Pantanal (Fazenda Santa Emília, SESC Pantanal e Serra do Amolar) e nenhuma no Pampa. A Mata Atlântica tem estimativas em 15 locais diferentes, porém concentrados nos estados de São Paulo (n = 6) e Minas Gerais (n = 6), sendo os outros três locais no Rio Grande do Sul (Parque Estadual do Turvo e Reserva Particular do Patrimônio Natural Pró-Mata) e no Espírito Santo (Reserva Natural Vale). Desta forma, é importante que esforços futuros para obter estimativas de densidade populacional de jaguatiricas sejam direcionados para áreas pouco estudadas ao longo da região neotropical e, no Brasil em específico, em mais áreas da Amazônia, Caatinga, Cerrado, Pampa e Pantanal.

Além disso, é importante que sejam estabelecidos estudos de longo prazo em Unidades de Conservação e paisagens modificas pelo homem, como agroecossistemas, para que seja possível monitorar como populações variam ao longo do tempo. Isso permitirá determinar as causas e a magnitude dessas variações e avaliar efeitos oriundos das

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[2] Dinerstein et al. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6): 534-545.

mudanças na paisagem. O avanço do agronegócio sobre o Cerrado e Pantanal vem levando a rápidas e profundas mudanças na paisagem, em especial causadas pelo aumento das áreas destinadas às lavouras temporárias em detrimento de áreas de vegetação nativa. Embora a espécie possa habitar também esses agroecossistemas, ainda é necessário investigar os efeitos do uso de agroquímicos sobre a saúde dos animais e como a espécie utiliza essas paisagens. Essas informações são fundamentais no planejamento de ações visando o manejo e conservação de fauna em propriedades privadas que detêm a maior parte do uso da terra no Pantanal e Cerrado brasileiros.

APÊNDICES

Appendix A. Supplementary Material of Chapter 1

Calculating standard errors of density estimates

Based in the formula provided by Cooch and White (2019; Chapter 20, section 20.3) to estimate confidence intervals:

$$\widehat{D} \pm exp\left[log\left(\widehat{D}\right) \pm 1.96\left(\frac{SE\left(\widehat{D}\right)}{\widehat{D}}\right)\right]$$

where $\widehat{D}$ was the reported density, we calculated standard errors ($SE\left(\widehat{D}\right)$) using reported confidence intervals, under:

$$SE\left(\widehat{D}\right) = \frac{\left(\left(\widehat{D} * log\left(95\%CI_{UB} - \widehat{D}\right)\right) - \left(\widehat{D} * log\left(\widehat{D}\right)\right)\right)}{1.96}$$

where $95\%CI_{UB}$ was the upper bound of the confidence interval reported in original studies.

Table A 1. Summary of searches performed between 18 and 25/December/2019. BDTD = Digital library of thesis and dissertations (Brazil).

Search Engine	Number of retrieved documents	Search terms
Scopus	283	ocelot* OR jaguatirica OR "Leopardus pardalis" OR "Felis pardalis" OR manigordo* OR cunaguaro* AND "camera-trap*" OR "camera trap*" OR densi* OR abund* OR occupan* OR ocupa* OR distribu* OR "capture-recapture" OR "captur* mark* recaptur*" OR "spatial* explic*" OR secr OR cmr OR scr OR captur* OR occur* OR ocorr* OR "home range" OR "space use"
Web of Science	266	
SciELO	235	
Google Scholar	1722	
BDTD	76	Leopardus pardalis OR Felis pardalis
Teses USP	19	Leopardus pardalis AND Densidade OR Leopardus pardalis AND Abundância

Table A 2. Mean ocelot weight used for the meta-regression model (Model C), ordered by female mass. Ecoregions follow Dinerstein et al. 2017.

Country	Ecoregion	Body mass (kg)		Source
		Female	Male	
Bolivia	Dry Chaco	5.6	6.4	1
Brazil	Caatinga	6.1	6.9	2
Mexico	Yucatan Moist Forest	7.4	11.0	3
USA	Western Gulf Coastal Grassland	7.5	9.8	4, 5
Brazil	Chiquitano Dry Forest	7.9	10.1	1, 6, 7, 8, 9, 10
Brazil	Pantanal, Cerrado	8.6	11.6	6, 7, 8, 9
Colombia	Llanos	8.8	10.0	4
Belize	Peten-Veracruz Moist Forest	9.1	11.9	3, 11, 12
Guatemala	Mesoamerican Gulf-Caribbean mangroves	9.1	11.9	3, 11, 12
Bolivia, Brazil, Ecuador, Guiana, Peru	Amazon Forest	9.4	11.7	13
Colombia	Magdalena-Uraba moist forests	9.6	11.6	4, 12
Argentina, Brazil	Atlantic Forest	10.2	13.6	14, 15, 16, 17, 18, 19
Panama	Isthmian Atlantic Forest	10.3	13.8	12

1. Maffei & Noss (2008); 2. Marinho et al. (2017); 3. Caso (1994); 4. Oliveira (1994); 5. Tewes (1986); 6. Crawshaw & Quigley (1989); 7. Rocha (2006); 8. Bianchi (2009); 9. Braga (2019); 10. Schaller 1983; 11. Konecny (1989); 12. Moreno et al. (2012); 13. Emmons (1988); 14. Crawshaw (1995); 15. Gonçalves et al. (2018); 16. Penteado (2012); 17. Widmer et al. (2017); 18. P. Estrela (pers. comm.; UFPB collection); 19. F. Peters (unpublished data)

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Appendix B. Supplementary Material of Chapter 2

Pilot study

To evaluate the appropriate distance between sampling stations, as well as the use of the SECR model, we established a pilot study with 54 sampling days between the months of September and November 2018. Sixteen paired camera-trap stations were set in two adjacent blocks with eight stations each. The first block was active for 25 days, and the second block for 21 days, totaling 654 traps/night. The average distance between the stations was 1261 m and the minimum area covered by the 16 stations was 26.4 km^2 (Figure B 2, left).

There were 98 independent records of 24 individuals, and eight records where identification was not possible. Of the total number of individuals, sixteen were females, seven were males and one was not able to determine the sex, generating a sex ratio of 2.29F:1M. Six individuals were recorded only once during the sampling (5F and 1 unidentified), and one of these females (LP046) was found run over and killed on the BR-262 highway three days after the end of the sampling, approximately 1500m from where she was recorded. The other 18 individuals were recorded between two and 16 times during the sampling period, with only half of them being recorded at more than one station (Table B 1).

The spatial capture history obtained from the pilot survey was used to fit a spatially explicit model (SECR) of maximum likelihood (Royle et al. 2014) using the secr package (Efford 2019) for software R (R Core Team 2019). Using the “half-normal” detection function, the estimated basal encounter rate λ_0 was 0.132 ± 0.023 SE, while the movement parameter σ was 592.5 m ± 39.6 SE. The estimated population density was 49.6 ocelots/100 km^2 (± 10.5 SE) for an area of just over 75 km^2.

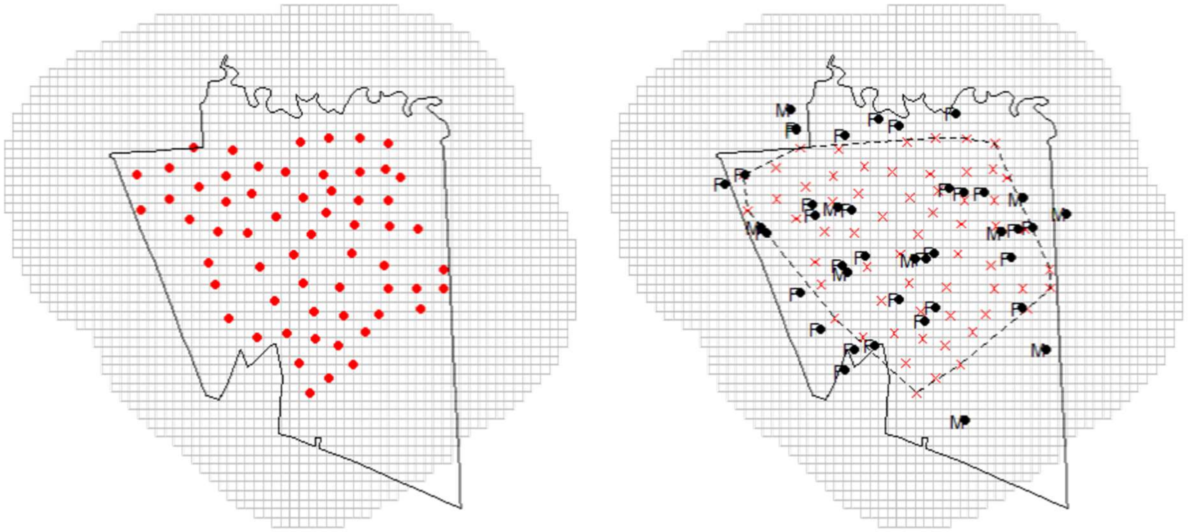

Figure B 1. Figure depicting the *S* space, formed by buffering camera-trap stations by 4,100 m, resulting in an area of 208 km². Red dots (left) and crosses (right) represent camera-trap stations. The figure in the right side shows the estimated activity centers of the 41 individual ocelots recorded (black dots), with letters indicating the sex. F = female; M = male.

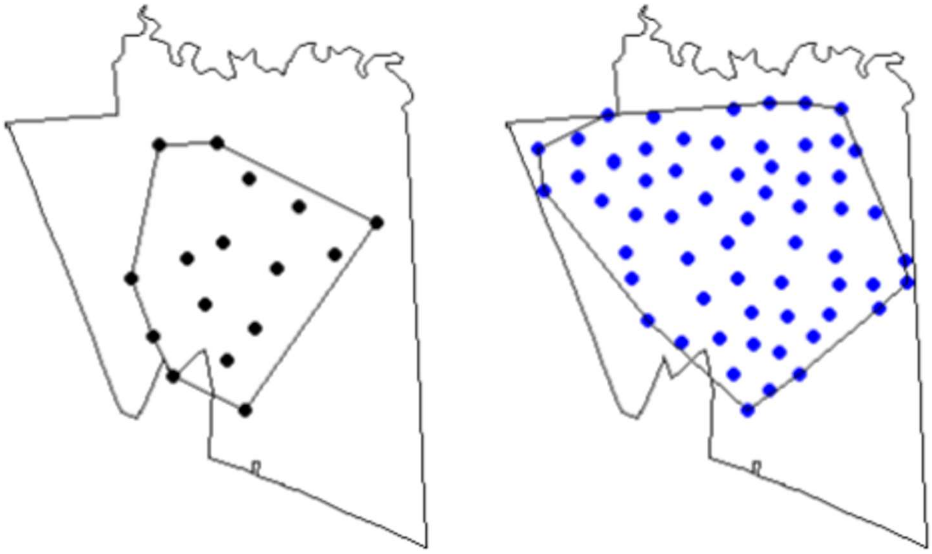

Figure B 2. Camera-trap station grid of pilot study (left) and final design (right) implemented for field work in 2019. Pilot study used 16 stations, spaced 1261 m, forming a minimum sampled area of 26.4 km². Final design used 60 stations, spaced 815 m, forming a minimum sampled area of 47.8 km².

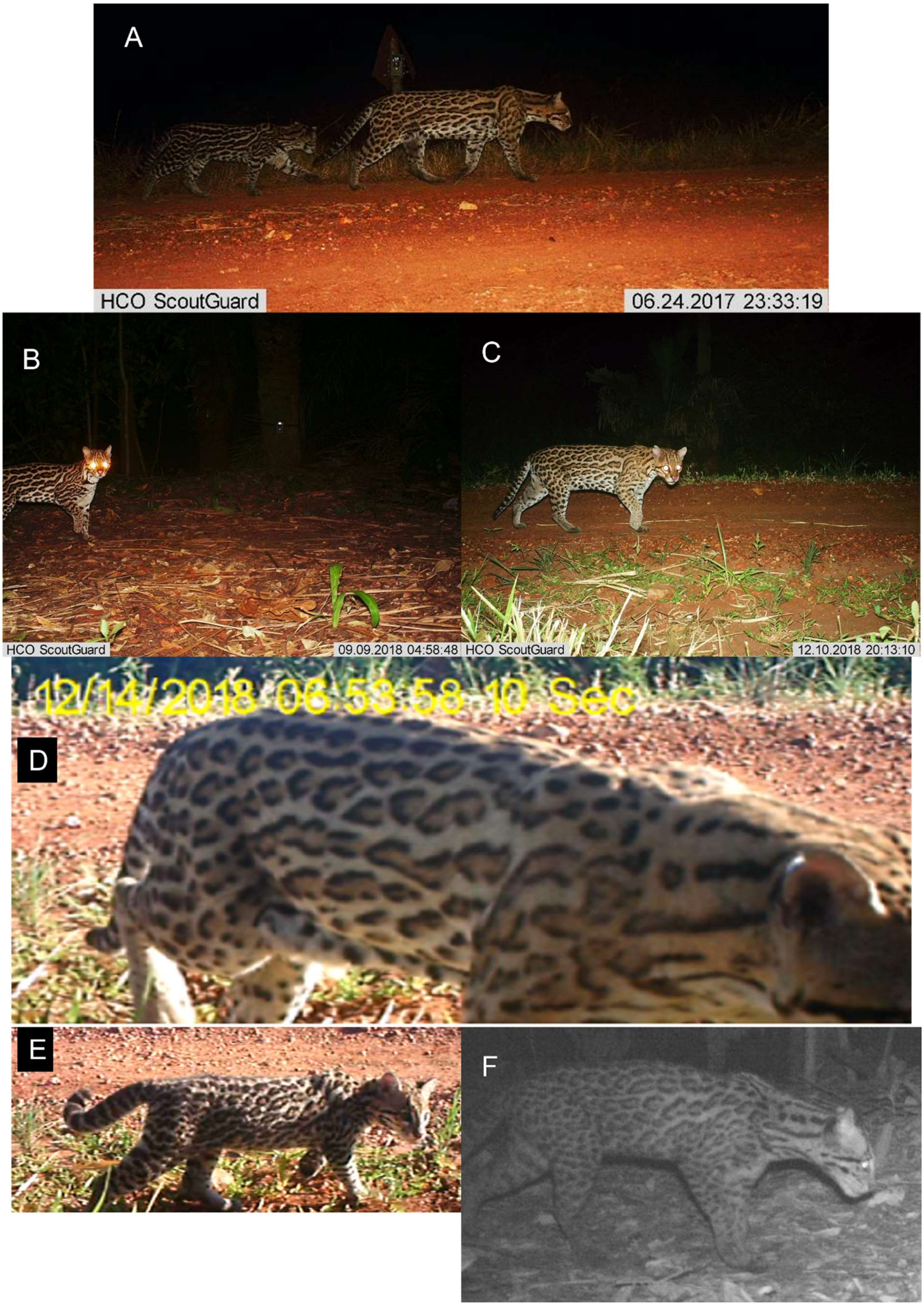

Figure B 3. Camera-trap records of female ocelot LP 003 in different moments with two distinct cubs. (A) LP 003 with male cub LP 061 in June/2017; (B) Sub-adult male LP 061 in September/2018; (C) LP 003 in December 2018, without LP 061; (D) Frame of video of LP 003 in late December/2018, followed by small cub HC43F01 (E); (F) HC43F01 in October/2019.

Figure B 4. Female LP 003 recorded with a new cub in January/2022. Photo courtesy: Allan G. dos Santos (A), Edir Alves (B).

Table B 1. Summary of ocelot records obtained during pilot study carried out between September and November 2018.

Individual	Sex	Independent Records	Stations
LP051	M	16	4
LP043	M	8	5
LP052	F	8	1
LP049	F	6	2
LP053	F	6	1
LP005	M	5	1
LP021	M	5	1
LP044	F	5	1
LP011	F	4	2
LP013	F	4	2
LP047	F	4	3
LP050	F	4	2
LP055	M	4	1
LP041	M	3	3
LP048	F	3	3
LP054	F	3	1
LP040	F	2	1

LP045	M	2	1
LP003	F	1	1
LP012	F	1	1
LP029	F	1	1
LP042	F	1	1
LP046	F	1	1
LP066	N.Id.	1	1

Table B 2. Summary of individual spatial capture histories obtained during full camera-trapping campaign in 2019, ordered by number of independent records.

Individual	Sex	Independent Records	Stations
LP051	M	64	10
LP021	M	55	11
LP048	F	54	5
LP053	F	51	7
LP043	M	44	10
LP040	F	28	4
HC49F01	F	26	5
LP030	M	20	5
LP052	F	19	4
LP049	F	17	4
HC11F01	F	15	3
LP003	F	13	4
LP041	M	13	6
LP044	F	13	2
HC46F03	F	13	1
LP038	F	12	4
LP011	F	11	4
HC08F01	F	11	2
HC46F01	F	11	1
HC46M02	M	11	1
LP039	F	10	3

HC48F01	F	10	2
LP012	F	9	3
LP050	F	9	1
LP005	M	8	6
LP042	F	8	3
HC63F01	F	8	2
HC50F01	F	7	5
LP018	F	6	4
LP026	F	5	2
LP029	F	5	2
HC36F01	F	4	1
HC08F02	F	2	1
HC25F01	F	2	1
HC43F01	F	2	1
LP013	F	1	1
LP025	M	1	1
LP045	M	1	1
HC09NI01	NI	1	1
HC15M01	M	1	1
HC26F01	F	1	1
HC53F01	F	1	1
HC09NI01	NI	1	1

Table B 3. Comparison between main study conducted in 2019 and the pilot study (2018) in terms of number of individuals recorded by number of stations. In 2019, there were 60 stations spaced 815m. The pilot study used 16 stations spaced 1261m. N.MS = number of individuals in the main study; N.PS = number of individuals in the pilot study; N Stations = number of stations individuals were recorded.

Sex	N.MS	N.PS	N Stations
Female	10	10	1
	6	4	2
	4	2	3
	7	0	4
	3	0	5
	1	0	7
Male	4	4	1
	0	1	3
	0	1	4
	1	1	5
	2	0	6
	2	0	10
	1	0	11

Table B 4. Distinct SECR models. Par = number of parameters; D = density; g0 = basal encounter rate (**λ0**); sigma = movement parameter (σ); pmix = sex-ratio; kcov = camera-trap covariate related to placement "on-road" (0) or "off-road" (1); h2 = mixture factor for sex (0 = female; 1 = male).

Name	Model	Par	AIC$_c$	dAIC$_c$	AIC$_c$wt
Sex.kCov	D~1 g0~kcov sigma~h2 pmix~h2	6	1452.317	0.000	0.8095
Sex_kCov	D~1 g0~h2 + kcov sigma~h2 pmix~h2	7	1455.210	2.893	0.1905
DSex.kCov	D~categ g0~kcov sigma~h2 pmix~h2	9	1456.375	8.058	0.0142
D Sex_kCov	D~categ g0~h2 + kcov sigma~h2 pmix~h2	10	1463.877	11.560	0.0000
SEX	D~1 g0~h2 sigma~h2 pmix~h2	6	1628.973	176.656	0.0000

Appendix C.

Table C 1. Countries of ocelot distribution without density estimates.

El Salvador	Nicaragua	Trinidad and Tobago
French Guiana	Paraguay	Uruguay
Honduras	Suriname	Venezuela

Table C 2. Ecoregions of ocelot distribution without density estimates, ordered by biome. Nomenclature and divisions follow Dinerstein et al. (2017)[3]. DXS = Deserts & Xeric Shrublands; FGS = Flooded Grasslands & Savannas; MGS = Montane Grasslands & Shrublands; Man = Mangroves; TSCF = Tropical & Subtropical Coniferous Forests; TSDBF = Tropical & Subtropical Dry Broadleaf Forests; TSGSS = Tropical & Subtropical Grasslands, Savannas & Shrublands; TSMBF = Tropical & Subtropical Moist Broadleaf Forests.

BIOME	ECOREGION
DXS	Araya and Paria xeric scrub
DXS	Chihuahuan desert
DXS	La Costa xeric shrublands
DXS	Meseta Central matorral
DXS	Motagua Valley thornscrub
DXS	Paraguaná xeric scrub
DXS	Sechura desert
DXS	Sonoran desert
DXS	Tamaulipan mezquital
FGS	Guayaquil flooded grasslands
FGS	Orinoco wetlands
FGS	Paraná flooded savanna
FGS	Southern Cone Mesopotamian savanna
MGS	Central Andean dry puna
MGS	Central Andean puna
MGS	Central Andean wet puna
MGS	Cordillera Central páramo
MGS	Cordillera de Merida páramo
MGS	High Monte
MGS	Northern Andean páramo
MGS	Santa Marta páramo
Man	Amazon-Orinoco-Southern Caribbean mangroves
Man	Northern Mesoamerican Pacific mangroves
Man	South American Pacific mangroves
Man	Southern Mesoamerican Pacific mangroves
TSCF	Central American pine-oak forests
TSCF	Sierra Madre de Oaxaca pine-oak forests
TSCF	Sierra Madre Oriental pine-oak forests
TSCF	Trans-Mexican Volcanic Belt pine-oak forests
TSDBF	Apure-Villavicencio dry forests
TSDBF	Balsas dry forests
TSDBF	Bolivian montane dry forests

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[3] Dinerstein et al. (2017). An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* 67 (6): 534-545.

BIOME	ECOREGION
TSDBF	Cauca Valley dry forests
TSDBF	Central American dry forests
TSDBF	Chiapas Depression dry forests
TSDBF	Ecuadorian dry forests
TSDBF	Lara-Falcón dry forests
TSDBF	Magdalena Valley dry forests
TSDBF	Maracaibo dry forests
TSDBF	Maranhão Babaçu forests
TSDBF	Panamanian dry forests
TSDBF	Patía valley dry forests
TSDBF	Sinaloan dry forests
TSDBF	Sinú Valley dry forests
TSDBF	Sonoran-Sinaloan subtropical dry forest
TSDBF	Southern Pacific dry forests
TSDBF	Tumbes-Piura dry forests
TSDBF	Veracruz dry forests
TSDBF	Yucatán dry forests
TSDBF	Brazilian Atlantic dry forests
TSGSS	Belizian pine savannas
TSGSS	Beni savanna
TSGSS	Campos Rupestres montane savanna
TSGSS	Guianan savanna
TSGSS	Humid Chaco
TSGSS	Miskito pine forests
TSGSS	Uruguayan savanna
TSMBF	Atlantic Coast restingas
TSMBF	Caatinga Enclaves moist forests
TSMBF	Caqueta moist forests

BIOME	ECOREGION
TSMBF	Catatumbo moist forests
TSMBF	Cauca Valley montane forests
TSMBF	Central American Atlantic moist forests
TSMBF	Central American montane forests
TSMBF	Chiapas montane forests
TSMBF	Chimalapas montane forests
TSMBF	Cordillera La Costa montane forests
TSMBF	Costa Rican seasonal moist forests
TSMBF	Eastern Cordillera Real montane forests
TSMBF	Eastern Panamanian montane forests
TSMBF	Guianan freshwater swamp forests
TSMBF	Guianan Highlands moist forests
TSMBF	Guianan piedmont moist forests
TSMBF	Gurupa várzea
TSMBF	Iquitos várzea
TSMBF	Isthmian-Pacific moist forests
TSMBF	Juruá-Purus moist forests
TSMBF	Magdalena Valley montane forests
TSMBF	Marajó várzea
TSMBF	Marañón dry forests
TSMBF	Mato Grosso tropical dry forests
TSMBF	Monte Alegre várzea
TSMBF	Negro-Branco moist forests
TSMBF	Northeast Brazil restingas
TSMBF	Northwest Andean montane forests
TSMBF	Oaxacan montane forests
TSMBF	Orinoco Delta swamp forests
TSMBF	Pantanos de Centla

BIOME	ECOREGION
TSMBF	Pantepui forests & shrublands
TSMBF	Pernambuco coastal forests
TSMBF	Pernambuco interior forests
TSMBF	Peruvian Yungas
TSMBF	Purus-Madeira moist forests
TSMBF	Purus várzea
TSMBF	Rio Negro campinarana
TSMBF	Santa Marta montane forests
TSMBF	Sierra de los Tuxtlas
TSMBF	Sierra Madre de Chiapas moist forests
TSMBF	Solimões-Japurá moist forests

BIOME	ECOREGION
TSMBF	Southern Andean Yungas
TSMBF	Southwest Amazon moist forests
TSMBF	Talamancan montane forests
TSMBF	Tapajós-Xingu moist forests
TSMBF	Uatumã-Trombetas moist forests
TSMBF	Ucayali moist forests
TSMBF	Venezuelan Andes montane forests
TSMBF	Veracruz montane forests
TSMBF	Western Ecuador moist forests
TSMBF	Xingu-Tocantins-Araguaia moist forests
TSMBF	Tocantins/Pindare moist forests