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Modelagem de abundância com drones: detectabilidade, desenho amostral e revisão automática de imagens em um estudo com cervos-do-pantanal

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Modelagem de abundância com drones: *detectabilidade, desenho amostral e revisão automática de imagens em um estudo com cervos-do-pantanal*

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RESUMO

Entender como a abundância de uma espécie se distribui no espaço e/ou no tempo é uma questão fundamental em ecologia e conservação e ajuda, por exemplo, a elucidar relações entre a heterogeneidade de paisagens e populações ou compreender influência de predação na distribuição de indivíduos. Informações de tamanho populacional também são essenciais para avaliar risco de extinção, monitorar populações ameaçadas e planejar ações de conservação. Modelar a abundância de cervos-do-pantanal (*Blastocerus dichotomus*), sendo um grande herbívoro da América do Sul, pode ser importante para entender relações da espécie com a variação espacial da produtividade primária, das áreas úmidas que a espécie ocupa e do seu principal predador, a onça-pintada. Além disso, por estar ameaçado de extinção, estimar a abundância de cervos pode contribuir para avaliar populações relictuais da espécie, assim como monitorar populações após grandes eventos, como os incêndios de 2020 no Pantanal. Porém, acessar estimativas de abundância confiáveis de maneira eficiente requer métodos robustos que levem em conta os possíveis erros nas contagens e que forneçam as estimativas em tempo hábil, além de um desenho amostral otimizado para aproveitar os recursos geralmente escassos. Os drones tem aparecido como uma ferramenta versátil e custo-efetiva para amostragem de populações animais e vêm sendo aplicados para várias espécies diferentes nos mais variados contextos ecológicos. Como um método emergente, o uso de drones na ecologia fornece oportunidades para explorar novas possibilidades de amostragem e análise de dados, ao mesmo tempo em que pode apresentar novos desafios. Nesta tese, i) exploro oportunidade e desafios na utilização de drones para modelagem de abundância de animais, abordando questões de erros de detecção, desenho amostral e como lidar com os grandes bancos de imagens gerados; e ii) aplico os métodos desenvolvidos para estudar a variação na abundância de cervo-do-pantanal, assim como estabelecer uma abordagem para monitoramento robusto e efetivo dessa espécie. Assim, no primeiro capítulo, conduzo uma revisão na literatura descrevendo os potenciais erros de detecção que podem enviesar estimativas de abundância com drones, buscando soluções atuais para lidar com esses erros e identificando lacunas que precisam de desenvolvimento. Nessa revisão, destaco o potencial dos modelos hierárquicos para estimar abundância em amostragens com drone. No segundo capítulo, aplico amostragens espaço-temporalmente replicadas com drone, analisadas com modelos hierárquicos *N-mixture*, para entender o efeito de processos topo-base (distribuição de onças-pintadas) e base-topo (disponibilidade de forragem de qualidade e corpos d’água) na distribuição da abundância de cervos-do-pantanal. Nesse estudo, encontrei que, na época seca, os cervos se concentram em áreas de alta qualidade (maior disponibilidade de forragem e próximas a corpos d’água), mesmo sendo a região em que é esperado maior efeito da predação. No capítulo 3, em um estudo com simulações, avalio o desempenho de modelos *N-mixture* para estimativas de abundância a partir de amostragens espaço-temporalmente replicadas, explorando otimização de esforço amostral e o impacto de um protocolo com observadores duplos na acurácia das estimativas. No capítulo 4, desenvolvo uma abordagem para estimar abundância com drone usando observadores múltiplos na revisão das imagens, sendo um dos observadores baseado em um processamento semiautomático usando algoritmos de inteligência artificial. Nesse estudo, exploro técnicas de aprendizado profundo de máquina, com redes neurais convolucionais, acessíveis para ecólogos, treinando algoritmos para detectar cervos nas imagens de drone. Além de ajudar a elucidar questões sobre as relações do cervo-do-pantanal com aspectos diferentes da paisagem do Pantanal, as abordagens exploradas e desenvolvidas aqui têm um grande potencial de aplicação, ajudando a estabelecer os drones como uma ferramenta eficiente para modelagem e monitoramento populacional de diversas espécies animais, e particularmente de cervos.

Palavras-chave: computação visual, detecção imperfeita, ecologia de populações, levantamento aéreo, modelos hierárquicos, monitoramento populacional, redes neurais convolucionais, veículos aéreos não-tripulados

ABSTRACT

Abundance modeling with drones: detectability, sampling design and automated image review in a study with marsh deer

Understanding how abundance distributes in space and/or time is a fundamental question in ecology and conservation, and it helps, for example, to elucidate relationships between landscape heterogeneity or predation and populations. Information on the population size also is essential to evaluate extinction risk, monitor threatened species and plan conservation actions. Abundance modeling of marsh deer (*Blastocerus dichotomus*), as a large herbivore of South America, may be important to understand the relationships of this species with spatial variation in primary productivity, in the availability of wetlands that the species inhabits, and in the distribution of its main predator, the jaguar. Moreover, since marsh deer threatened to extinction, estimating its abundance can be contribute in assessments of relictual populations, as well as in monitoring the species after big events, such as the Pantanal 2020 megafires. However, efficiently assessing reliable abundance estimates require robust methods that account for possible sources of error in counts while providing the estimates timely. An optimized sampling design is also important, in order to make the best use of the usual scarce resources. Drones have raised as a versatile and cost-effective tool for sampling animal populations, and they have been applied for several species in a wide variety of ecological contexts. As being an emergent method, the use of drones in ecology provides opportunities to explore novel possibilities of sampling and analyzing data, while potentially presenting new challenges. In this thesis I: i) explore opportunities and challenges in the use of drones for animal abundance modeling, approaching issues about detection errors, sampling design and how to deal with the huge image sets generated from drone flights; and ii) apply the developed methods to study the spatial variation in marsh deer abundance and to establish an approach to monitor this species robustly and efficiently. Thus, in the first chapter, I carry on a literature review describing potential sources of errors that may bias abundance estimation with drones and the current solutions to address them, identifying gaps that need development. In this review, I highlight the potential of hierarchical models for abundance estimations from drone-based surveys. In the second chapter, I apply spatiotemporally replicated drone surveys, analyzed with N-mixture models, to understand the influence of bottom-up (forage and water) and top-down (jaguar density) variables on the spatial variation of marsh deer local abundance. In such study, I found that, in the dry season, the deer concentrate in high quality areas (high-quality forage available and close to water bodies), even these regions being expected to present higher predation risks. In chapter 3, in a simulation study, I evaluate the performance of N-mixture models for abundance estimation from spatiotemporally replicated surveys, exploring optimization of sampling effort and the impact of a double-observer protocol on estimation accuracy. In chapter 4, I develop a pipeline to estimate abundance from drone-based surveys using a multiple-observer protocol in which one of the observer is a semiautomated procedure based on deep learning algorithms. In such study, I explore deep learning techniques with convolutional neural networks that are accessible for ecologists, and train algorithms to detect marsh deer in drone imagery. Besides helping to elucidate questions about the relationships of marsh deer with landscape variables in Pantanal, the approaches explored and developed here have a great potential of application in order to establish drones as an efficient technique for population modeling and monitoring of several wildlife species, and particularly the marsh deer.

Keywords: computer vision, imperfect detection, population ecology, aerial surveys, hierarchical models, population monitoring, convolutional neural networks, unmanned aerial vehicles.

SUMÁRIO

INTRODUÇÃO GERAL

Estimativa e monitoramento de tamanho populacional

Abundância ou tamanho populacional é uma variável fundamental na ecologia e na conservação. Estimar a abundância e acompanhar sua variação no tempo são aspectos essenciais na avaliação de riscos de extinção e na detecção ou previsão de declínios populacionais, embasando a maioria dos critérios de avaliações de status de conservação (IUCN, 2019). Em tempos de rápidas mudanças ambientais causadas por altas taxas de conversão e degradação dos habitats e pelas mudanças climáticas antrópicas, o monitoramento contínuo de espécies ameaçadas se torna um aspecto importante no planejamento de ações de conservação e manejo. As técnicas de coleta, processamento e análise de dados utilizadas no monitoramento de populações precisam apresentar rapidez e robustez na obtenção dos resultados, subsidiando ações efetivas.

Porém, raramente é possível observar e medir a abundância de maneira completa, sem influência dos potenciais ruídos, ou erros, que podem surgir durante uma coleta de dados. Alguns indivíduos, por exemplo, podem estar escondidos durante a amostragem e, portanto, não serem contabilizados ou, mesmo quando disponíveis, um observador pode falhar na detecção. Alguns indivíduos podem se movimentar durante a amostragem fazendo com que sejam contabilizados duas vezes. Essas fontes de erro nas amostragens podem gerar vieses positivos ou negativos nas contagens. A maioria das técnicas de coleta de dados em ecologia, na maior parte dos sistemas biológicos estudados, está sujeita a fontes de erro que, se não levadas em conta nas estimativas, podem resultar em padrões ou relações enviesadas.

Os modelos hierárquicos têm se estabelecido como uma abordagem integradora predominante em estudos populacionais e mais recentemente também de comunidades (Kery & Schaub, 2012; Kéry & Royle, 2016; Mackenzie et al., 2018; Royle et al., 2014; Royle & Dorazio, 2008). Por serem abrangentes e flexíveis, permitem explorar processos espaciais e temporais de diversas variáveis ecológicas (e.g. ocorrência, abundância e riqueza), enquanto incorporam aspectos do processo de observação que podem gerar erros na estimativa dessas variáveis (i.e. erros de detecção). A estrutura de um modelo hierárquico consiste basicamente em uma sequência interligada de modelos lineares generalizados com pelo menos dois níveis: um nível correspondente ao processo biológico, que governa a variável latente de interesse (e.g. abundância, ocorrência, sobrevivência, colonização); e outro para o processo de observação (Dénes et al., 2015; Guillera-Arroita, 2017). Este último acomoda o ruído que ocorre durante a coleta de dados, mascarando a variável latente. Em cada um dos níveis, as variações nos processos biológico e observacional podem ser ajustadas através de equações lineares usando covariáveis (espaciais, temporais, individuais, entre espécies, etc.). Assim, a modelagem hierárquica fornece uma estrutura básica flexível e robusta para estimativa e monitoramento de tamanho populacional.

Grandes herbívoros

Populações de grandes herbívoros são basicamente influenciadas por processos base-topo (*bottom-up*), relacionados a produtividade primária dos ambientes, e por processos topo-base (*top-down*), referentes a predação por grandes carnívoros, além de aspectos menos estudados como competição e parasitismo. Estudar a influência relativa dessas forças tem sido um tópico de interesse em estudos ecológicos e de conservação desse grupo (Anderson et al., 2010; Hopcraft et al., 2010; Owen-Smith, 2010; Riginos, 2015). Além da produtividade primária por si só, a distribuição dos ungulados é influenciada pela disponibilidade de forragem de alta qualidade. Visto que biomassa vegetal pode conter muita matéria seca ou de difícil digestão (grande quantidade de lignina e metabólitos secundários), os grandes herbívoros tendem a preferir vegetação em estágios iniciais de crescimento, ou seja, plantas jovens e brotos, facilmente digeríveis e com alto teor proteico. O balanço entre quantidade e qualidade de biomassa (geralmente inversamente proporcionais) faz com que os herbívoros tendam a otimizar seu ganho energético em quantidades intermediárias de biomassa (hipótese da maturação da forragem; (Fryxell, 1991; Hebblewhite et al., 2008; Hobbs & Gordon, 2010). Essa busca por forragem de qualidade, especialmente em ambientes sazonais e heterogêneos, é considerada o principal fator responsável por movimentos migratórios de grandes herbívoros em diversos ecossistemas. Dessa forma, os grandes herbívoros acompanhariam gradientes fenológicos na época de crescimento da vegetação. Por exemplo, gradientes latitudinais de chuva no fim da estação seca provocam gradientes fenológicos que seriam responsáveis por movimentações sazonais de grandes mamíferos africanos, como os elefantes (Purdon et al., 2018) ou as grandes migrações de gnus no Serengueti (Boone et al., 2006). Em ambientes temperados da América do Norte e Eurásia, ungulados acompanham, durante a primavera, gradientes de vegetação nova gerados após o derretimento de neve em regiões montanhosas (Aikens et al., 2017;

Bischof et al., 2012; Hebblewhite et al., 2008; Jakes et al., 2018; Rivrud et al., 2016; Sawyer & Kauffman, 2011). Esse comportamento de seguir gradientes de vegetação brotante em ambientes heterogêneos é conhecido como Hipótese da Onda Verde (Armstrong et al., 2016; Merkle et al., 2016).

A predação por grandes carnívoros pode ser um fator importante afetando populações de grandes herbívoros, modulando os efeitos das suas preferências por forragem de qualidade (Hopcraft et al., 2010; Rivrud et al., 2018). Os efeitos da predação podem ser dar a partir de dois tipos de processo: efeitos consumptivos e não-consumptivos. Efeitos consumptivos se referem a remoção direta de indivíduos pela predação e são uma causa potencial de extinções locais de ungulados, mesmo em situações de baixas taxas de predação (Festa-Bianchet et al., 2006). Os efeitos não-consumptivos são aqueles relacionados a respostas comportamentais que os herbívoros apresentam de modo a evitar o que percebem como risco de predação (Lima & Dill, 1990; Say-Sallaz et al., 2019). Esses efeitos podem ter influências distintas, e até mesmo maiores, do que efeitos consumptivos nas populações de grandes herbívoros. Quando expostos ao risco de predação, herbívoros podem aumentar seu comportamento de vigilância, tamanho de bando ou modificar seus padrões tanto de atividade diária quanto de ambiente utilizado (Creel et al., 2014). As alterações comportamentais de ungulados causadas pelo risco de predação podem acarretar consequências em seus hábitos alimentares com potenciais consequências em toda a cadeia trófica, processo bem documentado a partir da introdução de lobos no Parque Nacional de Yellowstone, noroeste dos EUA (Ripple & Beschta, 2012).

Entender a influência relativa de fatores base-topo e topo-base em populações de grandes herbívoros pode ser importante também para ações de conservação e manejo desse grupo. Por exemplo, para antever as consequências das mudanças climáticas globais na disponibilidade de forragem de alta qualidade, prever os efeitos de extinções ou reintroduções, tanto de ungulados quanto de grandes predadores nas funções ecossistêmicas ou manejar ungulados exóticos invasores ou espécies com interesse de caça. Os grandes herbívoros são considerados o grupo trófico mais ameaçado de extinção no mundo e a perda de espécies desse grupo pode ter consequências ao longo da cadeia trófica afetando ecossistemas inteiros (Atwood et al., 2020). As características de história de vida dos grandes herbívoros, como grandes áreas de vida, baixas taxas reprodutivas e muitas espécies com comportamento migratório (Gnanadesikan et al., 2017), tornam esse grupo particularmente sensíveis a conversão e modificação de ambientes, caça e doenças causadas pelo gado doméstico (Ripple et al., 2015).

A amostragem de populações de grandes herbívoros pode ser bastante desafiadora devido às dimensões e acessibilidade das áreas a serem amostradas. O desenvolvimento de tecnologias para amostrar vida silvestre tem facilitado muito nesse sentido. No nível de indivíduos, a biotelemetria tem ajudado a entender como os grandes herbívoros se movimentam e utilizam o espaço em relação a variáveis de paisagem associadas a disponibilidade de forragem e risco de predação (Hopcraft et al., 2014; Merkle et al., 2016; Owen-Smith, 2010). Para estudar os grandes herbívoros no nível populacional, armadilhamento fotográfico e amostragens aéreas são métodos comumente usados (Caughley, 1974; Vucetich & Peterson, 2004), este último particularmente interessante para áreas extensas e remotas.

Cervo-do-pantanal

Os cervídeos colonizaram a América do Sul com o soerguimento do Istmo do Panamá (2,5-3 milhões de anos atrás) e logo se diversificaram nos distintos ambientes do continente (Merino & Rossi, 2010). Ao longo dessa diversificação, duas principais variações morfológicas surgiram: enquanto as espécies de ambientes densamente florestados convergiram a um menor tamanho e chifres simples (gêneros *Mazama* e *Pudu*), as espécies de áreas abertas possuem um porte maior e chifres ramificados (gêneros *Odocoileus, Hippocamelus, Ozotoceros* e *Blastocerus*) (Duarte et al., 2008). Contudo, mesmo com a disponibilidade de extensas áreas de campos e savanas com grande proporção de gramíneas, nenhuma das espécies adotou estratégias de forrageio do tipo “pastador não-seletivo” (Merino & Rossi, 2010), assim como ocorreu com outros grupos de ungulados (e.g. bovídeos, Gordon & Prins, 2008). A lacuna desse tipo de forrageio nos cervídeos é atribuída a um sistema digestório menos desenvolvido, o que limita seus hábitos alimentares a uma forragem com menor teor de lignina e celulose, geralmente presentes em folhas novas e brotos, e não amplamente disponível nas pastagens (Gordon & Prins, 2008; Hanley, 1982). Como consequência, a busca por forragem de qualidade deve ser o fator determinante no uso do espaço por cervídeos de áreas abertas, embora o risco de predação também possa exercer um papel importante (Frair et al., 2005; Kie, 1999).

O cervo-do-pantanal (*Blastocerus dichotomus*), o maior cervídeo da América do Sul (até 150kg), é uma espécie associada a áreas úmidas que habita regiões de banhados, pântanos, planícies de inundação, savanas e campos (Piovezan et al., 2010). Possui características morfológicas atribuídas a adaptações aos ambientes úmidos que ocupa e parte de sua dieta é composta por plantas aquáticas. Também pode ser encontrado em menores densidades em ambientes de campos e savanas onde se alimenta de brotos, folhas novas e flores (Costa et al., 2006; Marin et al., 2020). Grande parte dos ambientes que o cervo-do-pantanal habita sofrem de variações sazonais associadas a pulsos de inundação de rios de planície. Os cervos são conhecidos por apresentarem mudanças sazonais na sua distribuição relacionadas a esses de forma que na seca se concentram nas áreas mais úmidas e na cheia se espalham pelas áreas inundadas pulsos (Tomas et al., 2001). Acredita-se que a espécie possa se beneficiar do pico de produtividade primária produzido ao longo dos pulsos de inundação de alguns ambientes que ocupa (Tomas et al., 2001).

Por conta de sua especificidade de habitat, a distribuição atual do cervo-do-pantanal está altamente fragmentada. A espécie está classificada internacionalmente como ameaçada de extinção na categoria Vulnerável devido a conversão e modificação do seu habitat, principalmente para agricultura e barragens hidrelétricas, caça ilegal e doenças causadas pelo gado doméstico (Duarte et al., 2016). As maiores e mais contínuas populações de cervo estão localizadas no Pantanal. Porém, recentemente até mesmo essas populações vem sofrendo ameaças, principalmente devido ao aumento da frequência de eventos climáticos extremos, como secas severas e grandes incêndios, como consequência das mudanças climáticas globais (Leal Filho et al., 2021; Marengo et al., 2016).

Devido a extensão e dificuldade de acesso das áreas de ocorrência do cervo-do-pantanal, o método de levantamento aéreo tem sido comumente usado para acessar o tamanho populacional da espécie (Andriolo et al., 2005; Mourão et al., 2000; Ríos-Uzeda & Mourão, 2012; Tomas et al., 2001). Grande parte dos estudos que estimaram populações de cervos não considerou completamente os possíveis erros de detecção que podem enviesar as estimativas, particularmente o erro de disponibilidade.

Amostragem aérea com drones

O uso de drones (formalmente conhecidos como aeronaves remotamente pilotadas ou veículos aéreos não-tripulados) para amostrar populações animais tem apresentado um rápido e amplo crescimento em estudos ecológicos e de conservação ao longo da última década. Os drones têm sido sugeridos como o futuro do monitoramento de vida silvestre (Linchant et al., 2015), por permitirem amostragens com alta resolução espacial (centimétrica) e temporal (alta frequência de voos), além de muitos modelos permitirem o uso de diferentes sensores, como termais e multiespectrais. Adicionalmente, as imagens coletadas fornecem registros permanentes que podem ser revisitados.

Os modelos de aeronave são divididos em duas categorias principais: os de asa fixa, que apresentam maior autonomia, capacidade de carga de sensores, mas menos flexibilidade; e os multirrotores, que apresentam maior flexibilidade e facilidade logística na operação. Assim, os drones tem prometido revolucionar a amostragem de animais para diversas espécies em variados contextos. Contagens feitas em imagens de drone tem se mostrado mais precisas e acuradas em comparação com outros métodos (Hodgson et al., 2016, 2018).

Inicialmente as amostragens com drone surgiram como uma alternativa mais acessível e segura em comparação com levantamentos aéreos convencionais em aviões tripulados, como por exemplo de grandes mamíferos (e.g. ungulados, Barasona et al., 2014; hipopótamos, Linchant et al., 2018; cervídeos, Preston et al., 2021; elefantes, Vermeulen et al., 2013), animais marinhos (pinípedes, Goebel et al., 2015; cetáceos e sirênios, Hodgson et al., 2013, 2017; tartarugas, Rees et al., 2018), aves aquáticas (Sardà-Palomera et al., 2012) e crocodilianos (Ezat et al., 2018). A partir do grande potencial dessa ferramenta (flexível e com capacidade para diferentes sensores), o uso de drones tem se expandido para amostrar espécies que antes seriam inimagináveis de se amostrar pelo ar. É o caso, por exemplo, de levantamentos aéreos de espécies pequenas como tartarugas de água doce (Bogolin et al., 2021), tubarões e raias (Kiszka et al., 2016) ou amostragens usando câmeras termais de canídeos (Bushaw & Ringelman, 2019), além de primaras (Melo, 2021) e coalas em áreas florestais (Hamilton et al., 2020).

Com todo método emergente para estudos ecológicos, surgem oportunidades de explorar novas possibilidades de amostragem e análise de dados, assim como também novos desafios. Na coleta de dados em levantamentos aéreos com drones, a escolha do tipo de tecnologia utilizada (i.e. drone multirrotor ou de asa-fixa; sensor de luz visível ou termal) influencia as dimensões da área amostrada (Christie et al., 2016), a resolução das imagens coletadas e a capacidade de detecção dos indivíduos amostrados (Chrétien et al., 2016). A definição do desenho amostral (e.g. configuração das linhas de voo, horário de amostragem e número de repetições) é muito importante para atingir resultados confiáveis (i.e. acurados e precisos) (Baxter & Hamilton, 2018). A flexibilidade dos drones permite explorar diferentes configurações de desenho dos voos, além das tradicionais transecções em linha usadas em amostragens aéreas. As imagens podem ser tratadas separadamente, assim como coletadas, ou podem ser fundidas em uma única imagem georreferenciada (i.e. ortomosaicos).

Pela capacidade de replicação e a disponibilidade de um banco de imagens permanente, as amostragens com drone fornecem um grande potencial para lidar com os erros de detecção comumente considerados em amostragens aéreas (indisponibilidade do indivíduo no momento do voo e falha de detecção pelo observador). Por outro lado, outros tipos de erro podem ser potencializados, como contar duas vezes o mesmo indivíduo ou confundir com outra espécie, dependendo da configuração de voo utilizada e de como a revisão das imagens é conduzida. Durante a etapa de compilação dos dados, o momento mais crítico é a revisão das imagens. As amostragens com drones têm gerado bancos de imagens cada vez mais volumosos, transformando a revisão manual em uma tarefa quase impraticável. Nesses casos, a utilização de métodos de busca automáticos nas imagens se torna imprescindível. Assim, a consolidação dos drones para amostragem de fauna silvestre ainda depende da exploração dessas novas oportunidades, bem como da superação de alguns desafios para garantir a rapidez e a robustez necessárias na coleta, compilação e análise de dados.

Computação visual com redes neurais (deep learning) na ecologia

O uso cada vez mais amplo de tecnologias para amostrar sistemas biológicos tem facilitado a coleta de dados em pesquisas ecológicas e de conservação, permitindo inclusive responder perguntas que antes não eram possíveis (Lahoz-Monfort & Magrath, 2021). Porém, juntamente com a facilidade na coleta de dados, o uso de tecnologias tem gerado bancos de dados cada vez maiores, impondo desafios em como lidar com eles. Grande parte desses bancos de dados são compostos por imagens, como no caso dos gerados por armadilhas fotográficas, drones ou satélites, ou processados como imagens, como sonogramas derivados de amostragem com gravadores acústicos. Diversas técnicas de computação visual já foram exploradas para detectar, identificar ou contar animais, plantas ou habitats em imagens (Christin et al., 2019; Corcoran et al., 2021; Dujon & Schofield, 2019; Weinstein, 2017). Essas técnicas variam desde simples classificações baseadas em características dos pixels até algoritmos mais complexos de aprendizado de máquina (*machine learning*) como análises de imagem baseada em objetos (OBIA) ou máquina de vetores de suporte (*support vector machine*).

Recentemente, uma técnica de inteligência artificial na área da computação visual tem se destacado notavelmente pelos resultados atingidos em tarefas com imagens, inclusive em contextos bastante complexos: as redes neurais convolucionais (*convolutional neural networks*, CNNs) (LeCun et al., 2015). As CNNs podem ser empregadas em tarefas de computação visual para três objetivos gerais: i) classificação de imagens: atribuir uma classe à uma imagem; ii) segmentação de imagens: segregar conjuntos/regiões em uma imagem à diferentes classes; e iii) detecção de objetos: localizar e classificar objetos em uma ou mais classes numa imagem. Para os três objetivos, as redes neurais convolucionais tem uma mesma estrutura básica, que consiste em uma sequência de camadas interligadas que são compostas por nós (parâmetros), os quais são ajustados a partir de amostras rotuladas de modo a diminuir o erro de predição entre a amostra e sua classificação verdadeira (LeCun et al., 2015). Uma CNN é composta por basicamente dois tipos de camadas: as camadas convolucionais, que contém vários filtros que varrem a imagem mapeando padrões regionais; e as camadas de agrupamento (*pooling*) que reduzem a dimensão (*down-sampling*) das camadas mapeadas pelos filtros convolucionais. No final da rede, há camadas densas (totalmente conectadas) que terminam com uma última camada de classificação (o *output* da rede). A partir da passagem de amostras rotuladas na rede, a primeiras camadas “aprenderiam” a identificar padrões mais localizados nas imagens (e.g. bordas, pequenos contrastes), enquanto as camadas mais para o final da rede aprenderiam, a partir do conjunto de padrões localizados, atributos mais abstratos e complexos (Chollet & Allaire, 2017; LeCun et al., 2015). Uma das grandes vantagens das redes neurais profundas com relação a outros algoritmos de aprendizado de máquina é a capacidade das redes de aprenderem por conta própria os atributos das imagens que determinam sua classificação, fazendo com que não seja necessário construir manualmente diferentes extratores de atributos específicos para as diferentes tarefas.

Apesar da concepção das CNNs ser bastante antiga, o potencial dessa técnica só pôde ser realmente explorado a partir do grande poder computacional provido pelas atuais placas gráficas (GPUs), aliado com a estruturação de gigantescos bancos de dados para treinamento. O marco temporal considerado chave no desenvolvimento das redes neurais em tarefas com imagens foi quando a primeira rede neural profunda (AlexNet) venceu uma famosa competição *ImageNet Challenge* em 2012 (Krizhevsky et al., 2012), apresentando um considerável aumento na performance em comparação com algoritmos anteriores. A partir disso, uma grande diversidade de redes neurais surgiu, produzindo uma sequência de quebra de recordes, eventualmente superando o que era considerado o limiar de acurácia humana em 2015. Com a diversificação das CNNs, suas aplicações também começaram a se difundir em estudos ecológicos e de conservação. Por exemplo, o uso de CNNs já foi explorado para: classificação de uso e cobertura do solo (Stupariu et al., 2021; Wagner et al., 2020); identificar, contar e descrever comportamento de animais em fotos de armadilhas fotográficas (Norouzzadeh et al., 2017; Tabak et al., 2019); identificar espécies em sonogramas (Dufourq et al., 2021; Mac Aodha et al., 2018; Ruff et al., 2019); reconhecimento individual (Hou et al., 2020); medir indivíduos (Gray et al., 2019); e detectar e contar indivíduos em imagens aéreas ou satelitais (Morales et al., 2018; Natesan et al., 2020).

Apesar dos avanços obtidos, o uso de redes neurais em imagens coletadas em sistemas biológicos ainda apresenta desafios para obtenção do grande número de registros necessários para treinar os algoritmos devido à complexidade e variabilidade dos alvos e sistemas estudados. No contexto de coleta de dados em campo, a presença da espécie de interesse nas imagens ou sonogramas coletados é geralmente rara, aparecendo em proporções muito baixas. Isso faz com que, além de um número relativamente baixo de registros da espécie, seja necessário lidar com uma grande quantidade de amostras “vazias” no banco de dados. Esse desafio se torna ainda maior no caso de espécies ameaçadas de extinção, as quais são comumente menos abundantes.

Objetivos e estrutura da tese

Esta tese de doutorado possui dois principais escopos de abordagem interligados. No primeiro, de contexto mais metodológico, exploramos as oportunidades e desafios na utilização de uma ferramenta emergente de coleta de dados na ecologia, os drones, para modelagem e monitoramento de populações animais. No outro escopo, com contexto mais teórico, buscamos aplicar essas técnicas para entender as relações de um grande herbívoro sul-americano, o cervo-do-pantanal (*Blastocerus dichotomus*), com as paisagens heterogêneas de planícies de inundação, assim como estabelecer métodos robustos e eficientes para o monitoramento de grandes herbívoros ameaçados de extinção.

Assim, no primeiro capítulo da tese (**Capítulo 1**: *Detection errors in wildlife abundance estimates from Unmanned Aerial Systems (UAS) surveys: Synthesis, solutions, and challenges*), conduzimos uma revisão na literatura descrevendo os potenciais erros de detecção que podem enviesar estimativas de abundância com drones, buscando soluções atuais para lidar com esses erros e identificando lacunas que precisam ser preenchidas com novas pesquisas. No segundo capítulo (**Capítulo 2**: *Drone Surveys Revealed Bottom-Up, And Not Top-Down, Effects On The Marsh Deer Local Abundance*), empregamos amostragens com drone para avaliar o efeito de processos topo-base (distribuição de onças-pintadas) e base-topo (disponibilidade de forragem de qualidade e corpos d'água) na distribuição da abundância de cervos-do-pantanal, explorando o uso de contagens espaço-temporalmente replicadas com um ou dois observadores para estimar abundância com drones levando em conta a detecção imperfeita. No terceiro capítulo (**Capítulo 3:** *Optimally designing drone surveys for wildlife abundance modeling with N-mixture models*), exploramos otimização de esforço amostral e o impacto de um protocolo com observadores duplos visando estimativas de abundância o mais acuradas possíveis com drones. Finalmente, no quarto capítulo (**Capítulo 4:** *Multiple-observer protocol for drone-based abundance estimation: integrating counts from manual review and accessible deep learning algorithms*), exploramos técnicas de inteligência artificial (redes neurais convolucionais) para detectar semi-automaticamente indivíduos de cervo-do-pantanal em imagens aéreas e como integrar esse processo nas estimativas de abundância. Como um resultado de todos os passos e ferramentas desenvolvidos, finalizo a tese com um *Protocolo de amostragem com drones para cervo-do-pantanal*, esperando facilitar a implementação dos métodos em diferentes populações da espécie ao longo de sua distribuição.

História e motivações desta tese

Desde a graduação tive um grande interesse em entender como os diferentes mecanismos influenciam a distribuição dos indivíduos e populações no espaço. No final da graduação surgiu a oportunidade de explorar novas ferramentas tecnológicas para amostrar animais. Assim, comecei a trabalhar com o uso de drones ainda no mestrado em 2014, no qual tinha como objetivo testar uma abordagem amostral e analítica para estimar abundância com drones em uma população de gado bovino de tamanho real conhecido. Além disso, tínhamos a expectativa de aplicar a abordagem desenvolvida para estimar abundância de uma população relictual de cervos-do-pantanal na região do Banhado Grande, próxima a Porto Alegre. O período todo do meu mestrado foi uma sequência de fracassos nas tentativas de realizar os voos com drone, entre treinamentos malsucedidos com um primeiro drone e inúmeras falhas técnicas e acidentes. Como havia muito pouco material na época sobre métodos de estimativa de abundância com drones, investi minha formação em pensar as possíveis maneiras de acessar tamanhos populacionais de maneira robusta. Fiz diversos cursos de modelagem hierárquica para ecologia e métodos para estudos populacionais. Através de algumas parcerias, também buscamos realizar uma sequência de voos no Banhado Grande para contagem de cervos. Porém, após várias horas de voo realizadas, não detectamos nenhum cervo nas imagens, provavelmente em decorrência do comportamento predominantemente noturno da espécie na região. O aprofundamento das explorações com modelos hierárquicos para estimar abundância com drone e uma sequência de três voos realizados com sucesso (embora no último, a aeronave tenha caído dentro de um lago...) sobre uma população de gado de tamanho real conhecido, culminaram na minha dissertação. Nessa etapa, explorei através de simulações computacionais a exequibilidade de amostragens aéreas espaço-temporalmente replicadas com drone e realizei um pequeno teste de detecção de gado bovino nas imagens obtidas durante aqueles três voos.

Em 2017 entrei no doutorado, com uma perspectiva mais otimista de utilização de um novo drone e um campo piloto realizado no Pantanal em 2016. A proposta inicial de projeto de doutorado tinha a ambiciosa missão de estudar três espécies de cervídeos em ambientes dinâmicos de planícies de inundação, utilizando amostragens aéreas com drone. A ideia inicial era: i) estudar mecanismos que influenciassem a dinâmica espacial do cervo-do-pantanal no Pantanal; ii) avaliar a distribuição espacial de uma população de veados-galheiros (*Odocoileus virginianus*) no contexto de expansão do Parque

Nacional do Viruá, RR; e iii) entender como a abundância de veados-campeiros se relaciona com as diferentes intensidades de produção bovina no Pantanal. Tudo isso, enquanto explorássemos o uso de drones para amostrar populações de ungulados. O estudo com os campeiros foi inviável logo de início pela falta de perspectiva de financiamento e o esforço extra que demandaria em campo.

A partir do aprendizado adquirido ao longo do mestrado, a principal motivação para escrever meu primeiro capítulo foi "o que eu gostaria de ter lido quando comecei a trabalhar com drones para estimar abundância?", artigo de revisão publicado em 2018. No segundo semestre de 2017, realizamos uma expedição para o Pantanal que resultou, finalmente, no primeiro campo bem sucedido que fizemos para estimar tamanho populacional com drone. Entre o primeiro ano de mestrado e essa expedição se passaram quase quatro anos. Os dados coletados nessa expedição geraram o segundo capítulo da tese, onde exploramos as relações da abundância de cervos-do-pantanal com variáveis de paisagem base-topo e topo-base no Pantanal. Enquanto isso, após duas longas expedições no PARNA do Viruá, Roraima, para coletar os dados de contagem de veado-galheiro, a perspectiva de obtenção de registros suficientes para a análise de dados começou a se mostrar pouco viável a partir da revisão das imagens. Isso fez com que o estudo dos veados-galheiros acabasse ficando de fora. Ao todo, realizamos duas expedições na seca no Pantanal (2017 e 2018) e duas expedições no Viruá, uma no final da vazante (2018) e outra na seca (2019). As dificuldades logísticas e financeiras de realizar mais expedições na época das chuvas, um acidente grave que tive com fratura no quadril durante atividade de campo no Viruá e a oportunidade de ir para o doutorado sanduíche no exterior, complicaram a possibilidade de conseguirmos conduzir expedições na vazante no Pantanal. Com isso, a ideia inicial de estudar a dinâmica espacial dos cervos não foi viabilizada.

Assim, a partir da primeira experiência empírica no Pantanal, usando os modelos hierárquicos para modelar a abundância dos cervos e com a iminência de novas expedições no Pantanal e Viruá, duas questões importantes surgiram. A primeira, relacionada com a precisão relativamente baixa das estimativas de abundância obtidas no capítulo 2, provocou a necessidade de planejarmos as amostragens espaço-temporalmente replicadas com drone de maneira otimizada para aproveitarmos da melhor forma possível o esforço empregado. A segunda questão que surgiu derivou do grande tempo despendido na revisão manual das imagens. A revisão do banco de imagens de 2017 do Pantanal (25 mil fotos) levou mais de um ano para ser concluída, enquanto a revisão da expedição de 2018 (50 mil fotos) demorou quase dois anos. Além disso, havia as fotos do PARNA Viruá para serem revisadas concomitantemente (70 mil fotos). Portanto, o desenvolvimento de um método de detecção automática de cervos-do-pantanal, possivelmente podendo ser depois adaptado para os galheiros, se tornou imperativo para a continuação dos projetos.

O grande incêndio que ocorreu no Pantanal em 2020, que atingiu aproximadamente um terço do bioma e mais de 90% da unidade de conservação onde fizemos as amostragens de cervo (RPPN Sesc Pantanal, MT), também suscitou a urgência de desenvolvermos maneiras mais ágeis de gerarmos as estimativas populacionais para a espécie. Essas duas questões de desenvolvimento metodológico (otimização de desenho amostral e detecção automática) acabaram se tornando o principal assunto do meu projeto de doutorado sanduíche no *Quantitative Applied Ecology Group* da Universidade de Melbourne, Austrália, resultando nos dois últimos capítulos da tese. Como é possível constatar, esta tese provavelmente é resultado mais de percalços do que sucessos. Mas acredito que o que foi desenvolvido aqui são passos essenciais para seguirmos tentando entender as relações dos cervídeos com as paisagens heterogêneas da América do Sul de maneira eficiente e robusta, além do potencial de embasar protocolos de monitoramento de ungulados ameaçados.

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CAPÍTULO 1

Detection errors in wildlife abundance estimates from Unmanned Aerial Systems (UAS) surveys: Synthesis, solutions and challenges

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Detection errors in wildlife abundance estimates from Unmanned Aerial Systems (UAS) surveys: Synthesis, solutions and challenges

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Headline: Detection errors in counts from drones

Abstract

1. Unmanned aerial systems (UAS) are emerging as an accessible and versatile tool for ecologists, promising to revolutionize the way abundance and distribution data are obtained in wildlife studies. Establishment of UAS as an efficient and reliable tool demands understanding how detection errors influence UAS-derived counts and possible solutions to address them.

2. We describe two types of false negative errors (availability and perception errors) and two types of false positive errors (misidentification and double count) that may bias abundance estimates from UAS surveys. Then, we discuss available methods to address detection errors in UAS surveys and point out challenges for future developments. We present hierarchical models as an integrative framework to account for multiple detection errors and data sets in UAS abundance modeling.

3. Methods to address detection errors in UAS surveys depend on how data are collected (flight plan, images processing and reviewing procedure). Conventional aerial surveys literature offers a set of solutions, especially to deal with false negative errors. Available auxiliary information (such as ground counts and telemetry data) facilitates estimating detection errors, although the versatility of UAS permits exploring novel approaches. Solutions involve planning separated strip transects, temporally replicating flights, carrying out counts in orthomosaics and multiple observer protocol. When automatic image review is used, sub-sample manual reviewing, trial experiments and semiautomated procedures might deal with algorithm errors.

4. UAS surveys need to be consciously planned, thinking on what kind of errors can significantly affect counts and the use of raw counts and indices should be avoided. Approaches that formally account for false positives are needed, particularly for double counts. Hierarchical modeling (especially *N*-mixture models) offers a fruitful framework to explore and combine solutions, integrating multiple data sets and accommodating different detection errors.

Portuguese Abstract

1. Os sistemas aéreos não-tripulados (SANT) estão surgindo como uma ferramenta acessível e versátil para ecólogos, prometendo revolucionar a maneira como dados de abundância e distribuição são obtidos. O estabelecimento dos SANT como uma ferramenta eficiente e confiável requer o entendimento de como os erros de detecção influenciam as contagens a partir de SANT, além das possíveis soluções para lidar com esses erros.

2. Nos descrevemos dois tipos de erro falso negativos (erros de disponibilidade e percepção) e dois tipos de erro falso positivos (erro de identificação e contagem dupla) que podem enviesar estimativas de abundância geradas a partir de amostragens com SANT. Além disso, nós discutimos os métodos disponíveis que permitem acessar erros de detecção em amostragens com SANT e apontamos desafios para desenvolvimentos futuros. Nós apresentamos os modelos hierárquicos como uma abordagem integradora para acomodar múltiplos erros de detecção e conjuntos de dados na modelagem de abundância com SANT.

3. Métodos para acessar erros de detecção em amostragens com SANT dependem de como os dados são coletados (plano de voo, processamento das imagens e tipo de revisão). A literatura de amostragens aéreas convencionais oferece um conjunto de soluções, especialmente para lidar com erros falso negativos. Informações auxiliares disponíveis (como contagens de solo e dados de telemetria) facilitam a estimativa dos erros de detecção, embora a versatilidade dos SANT permita explorar novas abordagens. As soluções envolvem planejar faixas de transecção separadas, voos replicados temporalmente, realizar as contagens em ortomosaicos e protocolo de observadores múltiplos. Quando se utiliza uma revisão automática das imagens, uma revisão manual de uma subamostra, experimentos de verificação e procedimentos semiautomáticos podem lidar com os erros de detecção do algoritmo.

4. Amostragens com SANT precisam ser planejadas conscientemente, pensando em quais os tipos de erro de detecção podem afetar significativamente as contagens; e o uso de índices ou contagens brutas deveria ser evitado. São necessárias abordagens que acomodem explicitamente erros falso positivos, principalmente contagens duplas. A modelagem hierárquica (especialmente modelos de mistura para abundância) oferece uma abordagem frutífera para explorar e combinar soluções, integrando múltiplos conjuntos de dados e acomodando diferentes erros de detecção.

Key-words

aerial surveys, count data, drones, false negatives, false positives, hierarchical models, imperfect detection, population size

Introduction

Unmanned aerial systems (UAS), popularly known as drones, have been consolidated as an accessible and versatile tool for ecologists for fine-scale mapping (Zweig *et al.* 2015), vegetation studies (Getzin, Wiegand & Schöning 2012), environmental monitoring for control and management actions (Koh & Wich 2012; Mulero-Pázmány *et al.* 2014) and animal population research and monitoring (Linchant *et al.* 2015; Christie *et al.* 2016). UAS are promising to revolutionize the way abundance and distribution data are obtained in wildlife studies (Anderson & Gaston 2013; Christie *et al.* 2016). The use of UAS for investigating and monitoring wildlife populations has been proposed for several species, from elucidating basic ecological questions to assisting conservation and management issues (Linchant *et al.* 2015; Christie *et al.* 2016; Hodgson *et al.* 2016).

UAS tend to replace traditional aerial surveys with manned aircrafts to study wildlife abundance, especially for sampling large terrestrial mammals in open areas (Vermeulen *et al.* 2013; Barasona *et al.* 2014), marine mammals (Hodgson, Kelly & Peel 2013; Goebel *et al.* 2015; Hodgson, Peel & Kelly 2017), waterbirds (Sardà-Palomera *et al.* 2012; Chabot *et al.* 2015), crocodiles (Evans *et al.* 2016) and marine turtles (Rees *et al.* 2018). Despite some drawbacks with regulatory issues (e.g. line-of-sight and 120 m above ground level flights) and relatively low autonomy of current available equipments, UAS versatility permits collecting data with higher spatial and temporal resolution, while allowing the use of multiple sensors (e.g. RGB, thermal infrared, and near infrared) and permit safe, cost-effective fieldwork (Christie *et al.* 2016).

During UAS surveys, sampling errors, such as not detecting an individual present in the area or counting the same individual twice, may produce biases in abundance estimates, if not properly addressed. Further, the effects of these errors may often vary in both time and space, challenging the use of corrected indices as surrogates of abundance. Reliable abundance estimates require considering these sources of bias for making strong inference about ecological patterns and basing sound decisions for conservation and management actions (Anderson 2001; Yoccoz, Nichols & Boulinier 2001).

Although abundance estimates are still incipient in UAS published literature, several studies have carelessly assessed abundance with raw counts (e.g. Chabot & Bird 2012; Chabot *et al.* 2015; Goebel *et al.* 2015; Hodgson *et al.* 2016) or corrected indices (e.g. Barasona *et al.* 2014; Mulero-Pázmány *et al.* 2015), ignoring possible biases caused by detection errors. In order to establish UAS as an effective and reliable tool for monitoring wildlife, it is imperative to understand how sampling processes can affect counts, taking advantage that such UAS application is still on the rise. Furthermore, the recent development and advances in statistical methods for unmarked populations (i.e. hierarchical models; Dénes *et al.* 2015; Kéry & Royle 2016) offer a fruitful field to explore the use of UAS for estimating and monitoring wildlife abundance.

Here, we i) review potential types of detection errors that may arise in UAS surveys and bias estimates using count data and ii) discuss solutions that have emerged to address detection errors in UAS surveys and identify challenges for future developments, focusing on the potential role of hierarchical models as an integrative and robust approach.

Detection errors in UAS surveys

Detection errors can be roughly categorized as either false negatives or false positives. False negatives errors (i.e. not detecting an individual present in the area) are commonly addressed in wildlife studies, including aerial surveys, and there is a vast literature about how to deal with them (e.g. Williams *et al.* 2002; Mackenzie *et al.* 2006; Royle & Dorazio 2008; Kéry & Royle 2016). False positives (i.e. counting an individual twice or recognizing another target as an individual) are typically assumed insignificant; and the development of methods to deal with this error type is still nascent (Dénes, Silveira & Beissinger 2015).

In addition to species traits (e.g. color and shape) and site features (e.g. arboreal cover), characteristics of sampling design (e.g. separated strip transects or orthomosaic from overlapped strips) and image processing (e.g. manual count or automated review) might determine how detection errors will affect counts in different stages of sampling process. Next, we highlight potential sources of bias in abundance estimates specifically in the context of UAS surveys (Fig. 1). We consider only detection errors in direct counts of individuals, not including possible extra errors that may arise in indirect methods, such as tracks or nest counts.

Availability error

In aerial surveys, availability bias commonly refers to when an individual is present in the sampled area but unavailable for detection (Fig. 1.1) by, for example, being hidden below vegetation, into a burrow or submerged under water. When sample units are not closed, availability can also refer to individuals that temporarily move outside the sampling unit during data collection. Availability error has been considered a matter of concern in aerial surveys for both terrestrial and aquatic fauna (e.g. Pollock *et al.* 2006; Edwards *et al.* 2007; Terletzky & Koons 2016). Availability may basically be influenced by characteristics of the sampled area, for example, sample unit size or arboreal cover; and behavioral patterns of target species, such as habitat preference or diving and daily activity. It could be possible to minimize availability bias by prioritizing flights in period that individuals might be more exposed, although this would rarely be sufficient. It is conceivable that in some specific situations the number of unavailable individuals is insignificant, such as when sampling aggregation sites of, for example, waterbirds or pinniped colonies (but see Rodgers *et al.* 2005).

Perception error

Given that an individual is available for detection (i.e. visible in the image), an observer or a detection algorithm could miss it (Fig. 1.2), leading to negative biases in estimates. Intensive manual reviewing may produce many failures to detect individuals by observer fatigue, while, in automated reviews, the algorithm can fail in detecting an individual that is, for example, partially hidden or with a different shape. Perception bias, for both manual and automated reviews, becomes particularly significant when contrast between individuals and background is low (Chabot & Bird 2012; Chabot & Francis 2016; Patterson *et al.* 2016). Ground sampling distance (i.e. projection in the ground of pixel resolution), resulting from flight height and camera resolution, could also influence perception probability.

Misidentification

Misidentification may occur by classifying another species or a background feature as the target species (Fig. 1.3). While avoidable in manual reviews by discarding uncertain individuals, misidentification may become more noteworthy in fully automated detection reviews, where detected targets are not post-checked by an observer (Mejias *et al.* 2013; Chrétien, Théau & Ménard 2016). In studies where populations are classified in categories, such as juveniles and adults (e.g. Seymour *et al.* 2017) or males and females, individuals can be misclassified between categories.

Likewise, in multispecies studies, similar species may be mismatched (Conn *et al.* 2013).

Double count

In UAS surveys, an individual can be counted more than once by appearing in more than one image. Double counts may occur for at least two reasons: i) individuals present in overlapping parallel strips or overlapping successive images (Fig.1.4a); or ii) individuals might move between neighboring flight lines during a survey (Fig. 1.4b). Obviously, double counts in overlapped areas are a matter of concern when counts are carried out in separated pictures instead of orthomosaics.

Double counts caused by animal movement may be more problematic when flight strips overlap or are adjacent, especially for highly mobile species. In fact, movement could also produce false negative errors (in this case, similar to unavailability), if an individual moves from a non-sampled line to a sampled line (i.e. opposite movement than in Fig. 1.4b). Thereby, if individuals move independently at random in the flight area, effects of individuals “appearing” (false positive) and individuals “disappearing” (false negative) would cancel each other. Furthermore, animal movements caused by UAS disturbance during flight need to be carefully avoided, as it might produce huge biases in estimates, especially when surveying bird flocks.

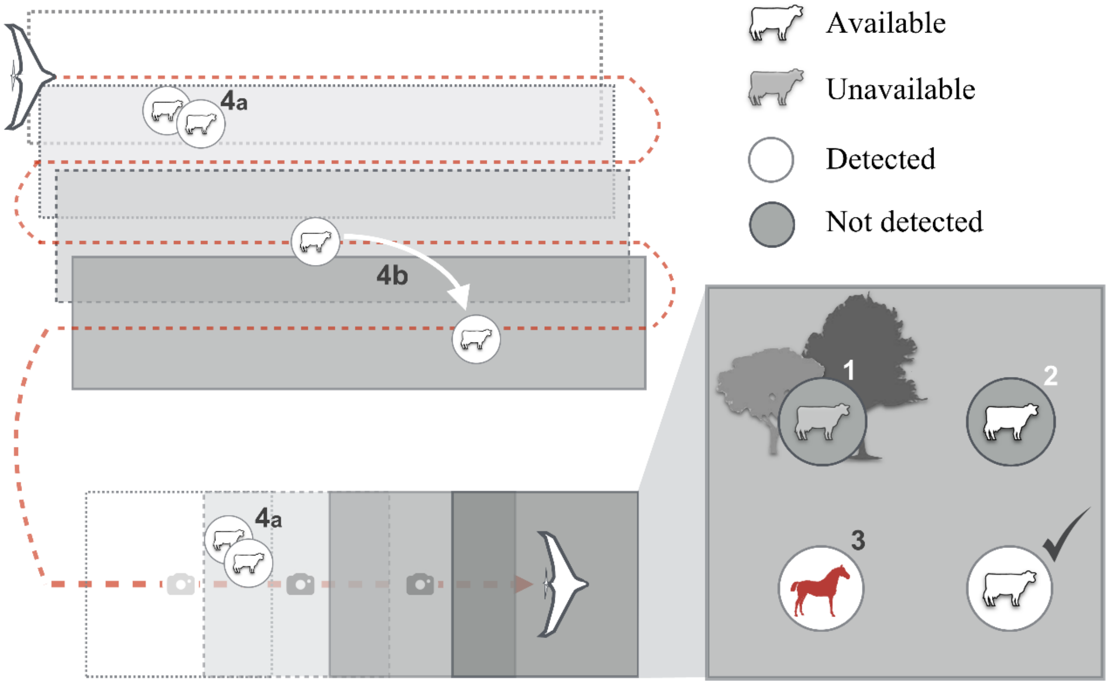

Fig. 1. Detection errors that may bias abundance estimates from UAS surveys. White numbers are false negative errors and black ones are false positives. 1) Availability error; 2) Perception error; 3) Misidentification; 4) Double count: a) in overlapped areas between images or strips, b) individual movement between flight strips. Check symbol corresponds to a correct detection.

Current solutions and future challenges

At first, dealing with detection errors lies in identifying the potential sources of error that may affect counts in order to plan sampling design and following image processing and data analysis. Possible solutions to address detection errors in UAS counts include adjusting flight plans, collecting (or using available) auxiliary data, temporally replicating flights and adapting image review process. Accumulated knowledge from conventional aerial surveys offers a set of solutions for UAS studies, especially for dealing with false negatives. In this session, we discuss available methods to deal with detection errors in UAS surveys (summarized in Table 1) and identify challenges for further development in the near future. Thus, we present hierarchical models as an integrative approach to combine methods and as a fruitful field for exploring future solutions.

Availability error

To correct aerial counts accounting for unavailable individuals, researchers typically use auxiliary data from telemetry marked individuals (e.g. diving and surfacing profile, Pollock *et al.* 2006; Martin *et al.* 2015; or sightability models, Terletzky & Koons 2016) or ground-based counts (e.g. land, boat or platform) (Chabot, Craik & Bird 2015; Hodgson, Peel & Kelly 2017). The use of ground-based counts as a surrogate for truth to correct aerial counts can be problematic because perfect detection is assumed, which is an unrealistic assumption in several sampling situations (e.g. Chabot & Bird 2012; Hodgson *et al.* 2016). When telemetry data are available, it can be used as auxiliary information. If it is not available, dependence on telemetry data to address availability could limit UAS usability. Hodgson *et al.* (2017) show an example of collecting auxiliary data with UAS for estimating availability, by following and video recording whale groups. For each group followed, they recorded the proportion of time that each group remained visible and the number of individuals, and thus they could estimate availability of the group and its heterogeneity according to group size. With this approach, they argue estimates would be more effective in estimating availability bias than with other auxiliary information (such as land-based count or telemetry data), because it provides a direct and more representative assessment in the same place and time. Moreover, availability bias can be addressed without the need of auxiliary information, in a hierarchical modeling framework, by temporally replicating flights (see later).

Barasona *et al.* (2014) and Mulero-Pázmány *et al.* (2015) accounted for availability bias in UAS surveys caused by ungulate individuals hidden by canopy cover using what they called “detection coefficients”. For this, they randomly placed points in a subset of images for two different land covers, and then they classified points as “not detectable” if located in vegetation canopy and as “detectable” if not, using the proportion of detectable points to correct counts. This approach has severe limitations because it assumes that individuals are randomly distributed in space and that availability is constant in time. Thus, if, for example, individuals avoid or prefer tree shadows (and this vary along day time), abundance estimates could be biased.

Perception error and misidentification

Perception bias, well-known in conventional aerial surveys (Pollock & Kendall 1987; Laake, Dawson & Hone 2008), is commonly assessed using a multiple observer protocol (Nichols *et al.* 2000; Pollock *et al.* 2006). By combining information collected by two or more observers from a plane or reviewing images, it is possible to estimate the probability of each observer to detect an individual available as in a capture-recapture approach and thus estimate missing individuals. This technique is easily applicable for estimating observer error in manual reviews of UAS imagery but it has been scarcely used (e.g. Vermeulen *et al.* 2013).

Misidentification in count data can be simply avoided by removing uncertain matches (e.g. Hodgson *et al.* 2013). Hence, individuals excluded by uncertainty would be accommodated in perception error or, if partially hidden, in availability error. Moreover, misclassification between similar species can be addressed by conducting a trial experiment in which species identity is known for some observations or with a multiple observer protocol, likewise estimating observer perception error (Conn *et al.* 2013).

In automated procedures, when choosing criteria and selecting thresholds, there is commonly a trade-off between detecting individuals (perception errors, also named omission) and making misidentification (also named commission error). Narrow thresholds might produce several failures in detecting individuals, while broader thresholds encompass many misidentifications. One possible solution is to prioritize the improvement of algorithm perception (i.e. choosing broader thresholds) and then post-check outcomes to discard false positives (i.e. semiautomated procedure; Andrew & Shephard 2017). Even so, automatic algorithms might still fail in detecting some individuals. Thus, the probability of an automatic algorithm detecting an individual present in imagery could be estimated by manually reviewing a sub-sample of images and comparing with targets found automatically (e.g. Conn *et al.* 2014). In fully automated procedures, both perception and misidentification rates of the algorithm can be estimated using this sub-sample manual review.

The use of thermal sensors has been shown to be particularly promising in detaching target species from background, significantly decreasing perception and misidentification errors (Chabot & Francis 2016; Christie *et al.* 2016; Seymour *et al.* 2017). Apparently, combining images of flights with simultaneous thermal and common RGB sensors can produce accurate estimates of available individuals, as found in an experiment conducted by Chrétien *et al.* (2016).

Double counts

Double counts of individuals in overlapped sequential images seems to be easily avoidable, because the time interval between successive pictures is usually very short (Hodgson, Kelly & Peel 2013; Hodgson, Peel & Kelly 2017). However, avoiding double counts by comparing successive images involves a careful reviewing process that can be time consuming. Another strategy to avoid double counts is to conduct counts in orthomosaics, since all overlapped areas are excluded when images are merged. Notwithstanding, it is very impractical to build orthomosaics for aquatic surveys, because it is extremely difficult to find sufficient matching points between different pictures for merging them. So, counts from aquatic surveys, especially based on flight plans with overlapped strips, should be treated carefully to avoid double counts. Additionally, overlapped areas can offer valuable cross-check information during review to solve some potential doubts in identifying individuals, because pictures are taken from different angles and moments. For example, Hodgson *et al.*

(2013) found that overlap between images helped to identify dugongs hidden by sun glitter.

Few studies mention the possibility of double counts by animal movement and approaches for quantifying this potential bias are urgently needed, as well as testing possible solutions to validate them. One simple solution could be designing flight plans in separated strips (e.g. Vermeulen *et al.* 2013; Chrétien *et al.* 2015). Seymour *et al.* (2017) commented that they corrected mosaics for individual movements, but did not mention how. Hodgson *et al.* (2017) offer an interesting solution for correcting directional movements of whales perceived in their study area. They quantified movement bias simulating individual movements (using land-based observations) and UAS passes. Auxiliary data from telemetry may provide useful information about movements to correct double counts (Terletzky & Koons 2016). In another way, if it is possible to identify the same individual in two or more pictures of a flight, distance between locations could be used to calculate individuals' movements and thus estimate double counts by movements. An advantage of such approach is to avail of the same images collected in flights.

Table 1. Summary of current methods to address detection errors that may bias abundance estimates from counts of UAS surveys.

Detection error	Method	Examples
False negatives		
Availability	Auxiliary data	
	Ground-based counts	Hodgson *et al.* 2017
	Telemetry data	Pollock *et al.* 2006; Conn *et al.* 2014; Martin *et al.* 2015
	UAS focal follow	Hodgson *et al.* 2017
	Temporally replicated flights	Williams *et al.* 2017
Perception	Manual review: multiple observers	Vermeulen *et al.* 2013; Martin *et al.* 2015
	Automated review: sub-sample manual review	Conn *et al.* 2014
False positives		
Misidentification	Manual review	
	Avoid/discard uncertainties	Hodgson *et al.* 2013;
	Trial experiment	Conn *et al.* 2013
	Uncertain species modeling	Conn *et al.* 2013; Chambert *et al.* 2016*
	Automated review	
	Sub-sample manual review	Conn *et al.* 2014
	Semiautomated procedure	Andrew & Shephard 2017
Double count		
Overlapped areas	Manual check	Chabot & Bird 2012; Chabot, Craik & Bird 2015; Adame *et al.* 2017
	Count in orthomosaic	Chabot, Craik & Bird 2015; Chrétien, Théau & Ménard 2016
Movement	Separate strip flights	Vermeulen *et al.* 2013
	Simulate movements and flights	Hodgson *et al.* 2017
	Telemetry data	Terletzky & Koons 2016

Spatially correlated counts	Chandler & Royle 2013*

* Example not applied in the context of aerial surveys.

Hierarchical modeling as an integrative approach

Methods to address detection errors in aerial surveys commonly do this in a two- (or multi-) step approach, first estimating detection probabilities and then correcting counts (e.g. Pollock *et al.* 2006; Edwards *et al.* 2007; Terletzky & Koons 2016). Such approaches often do not deal with heterogeneity in detection parameters and present constraints to fully accommodate uncertainty in estimates (Link 1999; Link & Barker 2004; Royle & Dorazio 2008).

Hierarchical models have been widely used in wildlife studies to explicitly model distribution and abundance (and associated demographic parameters), while formally accounting for multiple sources of error in a single model structure (Mackenzie *et al.* 2006; Royle & Dorazio 2008; Kéry & Royle 2016). To that end, hierarchical models handle variation in data as result of two (or more) hierarchically connected processes: i) an underlying ecological process which determines the latent variable (e.g. abundance); and ii) the observation process which is conditioned, but masks, the ecological process due to detection errors. Thus, variation in detection parameters and in latent variable can be explicitly modeled by including covariates in each part of the model. Available tools to fit hierarchical models permit conducting analysis in both statistical inferential paradigms, frequentist (e.g. the R package unmarked, Fiske & Chandler 2011) and Bayesian methods (e.g. Kery & Schaub 2012).

In the context of modeling abundance from count data, the so-called *N*-mixture models are considered an emerging approach for unmarked population surveys (Royle 2004; Chandler, Royle & King 2011; Dénes, Silveira & Beissinger 2015). In *N*-mixture models, spatial (and temporal) variation in abundance *N* (latent variable) is modeled with a distribution for non-negative integer values (usually Poisson or negative binomial) and observed count data *C*, conditional on *N*, is usually modeled as a binary observation process for each individual with binomial or multinomial distributions (but see Stanley & Royle 2005 for a Poisson observation process). The general basic sampling design for *N*-mixture models is sampling multiple spatial units with repeated visits (Royle 2004; Kéry, Royle & Schmid 2005). This sampling scheme fits with UAS characteristics of short and replicated flights, overcoming limitations of flight durations and availing of high UAS versatility.

Hierarchical modeling has been used with spatially replicated conventional aerial surveys, mostly to account for perception error with a multiple observer protocol (e.g. Langtimm *et al.* 2011; Conn *et al.* 2012; Ver Hoef *et al.* 2013) or distance sampling methods (e.g. Buckland *et al.* 2012). Availability error can be addressed in aerial surveys without the need of auxiliary data by temporally replicating flights (e.g. Martin *et al.* 2012; Williams *et al.* 2017). However, since replicating flights with manned aircrafts in the same spatial units is sometimes unfeasible due to financial constraints, availability bias is often accommodated in models by incorporating probabilities derived from telemetry data (e.g. Conn *et al.* 2014; Martin *et al.* 2015).

In one of the first studies using a hierarchical framework to UAS surveys, Martin *et al.* (2012) highlight the potential of such approach to predict distribution and abundance in relation to environmental spatial covariates. They conducted an experiment with tennis balls in a grid cell (motivated to apply it in abundance estimates of manatees), where in each UAS pass a proportion of balls were hidden to simulate unavailability. Then, they estimated abundance by summing occupancy state of cells. As the authors point out, one of the limitations of this approach is that it relies on assumptions of non-movement of individuals between small and adjacent sampling units.

Williams *et al.* (2017) suggest an application of a binomial *N*-mixture model for estimating abundance from surveys with aerial images, in which each picture is a spatial unit that can be temporally replicated. They also propose an adaptation in which overlapped areas of subsequent images could be used as temporal replicates. The authors point out two potential caveats of this approach: i) given that spatial unit area can be small (i.e. a single picture), closure assumption could be violated by individuals moving in and out between temporal replicates and ii) especially for cases where overlapped pictures are used, lack of independence between temporal replicates could preclude individuals of switching between unavailable and available states. Indeed, this may produce a trade-off between shorten interval between temporal replicates (to avoid the violation of closure assumption) and increase time between replicates (to ensure changes in availability).

The great majority of hierarchical models that addresses detection errors in wildlife surveys only account for false negatives errors. Models for false positive errors, especially for count data, are still in their infancy. Existing approaches for modeling false positives mainly account for misidentification errors when similar species are likely to be confounded (e.g. Conn *et al.* 2013, 2014). Chambert *et al.* (2016) present a *N*-mixture model to explicitly deal with misidentification when there is uncertainty in classification between similar species. Approaches for modeling double counts have remained unexplored. One possible way to address double counts could be modeling spatially correlated counts (Chandler & Royle 2013; Royle *et al.* 2014).

A powerful application of hierarchical modeling, especially within a Bayesian approach, is that it offers a flexible framework for integrating different sources of information (e.g. ground counts or telemetry data with UAS counts) to assess a variable of interest (Schaub & Abadi 2010; Gopalaswamy *et al.* 2012). Combination of multiple data sets to inform model parameters can be done by informing strong priors or formally accommodating them in the model structure. For example, Martin *et al.* (2015) combined repeated aerial counts with i) information collected in a visibility experiment and diving data from telemetry to estimate availability and ii) an independent double observer protocol to estimate perception probability. They included these probabilities as priors in a binomial *N*-mixture model to predict abundance of manatees in Florida coast. Auxiliary data could also be considered in a hierarchical framework with a double sampling design (Pollock *et al.* 2002), using ground counts to estimate detectability of aerial counts. Since ground counts generally involves more effort and are more time consuming, only a subset of the aerial sampled sites is sampled from the ground. Ground counts need to be considered a surrogate of truth and representative of the entire set to get a reliable estimation of detection errors.

One example of how hierarchical modeling can be used to accommodate many sources of detection error in aerial surveys is given by Conn *et al.* (2014). They present a framework to estimate multi-species abundance using automated detections in thermal images, a double sampling scheme where an observer reviewed a random subsample of digital photos to estimate perception error, an experiment with multiple observers to estimate misclassification rates and telemetry data to estimate availability.

The flexible framework of hierarchical (*N*-mixture) models offers several extensions that may be useful in future UAS studies, for example, to accommodate other sources of variation, such as correlated detection of individuals (i.e. group detection; Martin *et al.* 2011) or spatial autocorrelation in abundance (Royle *et al.* 2007); for modeling abundance dynamics (Dail & Madsen 2011; Zipkin *et al.* 2014; Williams *et al.* 2017b); or in multispecies (community) studies (Yamaura *et al.* 2012; Dorazio, Connor & Askins 2015; Sollmann *et al.* 2016). Furthermore, although basic sampling design of *N*-mixture models requires multiple spatial units, long-term monitoring could be led in a single unit using the time-for-space substitution, in which surveys are conducted in both short- and long-term temporal replications (Yamaura *et al.* 2011). This approach may be very useful to estimate trends of spatially restricted populations, such as waterbirds colonies.

Conclusions

Use of UAS is rapidly expanding in wildlife research to assess abundance estimates for investigating and monitoring populations. Main regulatory drawbacks for UAS use are expected to be overcome soon (Kakaes *et al.* 2015), as well as their autonomy limitations. Thus, a large replacement of manned aircraft for UAS in aerial surveys is a matter of time. Successful establishment of UAS as an effective tool in wildlife studies depends on acquisition of reliable estimates, taking into account possible sources of error in UAS-derived counts. Most of wildlife studies with UAS still focus on testing effectiveness of different methods to detect and count species and just a few studies actually estimate abundance for a meaningful area (Linchant *et al.* 2015). It is important that trials and development of techniques address how to deal with potential detection errors that may arise in all variety of contexts UAS are being applied.

Although knowledge accumulated in conventional aerial surveys offers a set of already available solutions for false negative errors, advantages of UAS plasticity for fieldwork allow exploring novel approaches. Available auxiliary information, such as telemetry data or ground-based counts, may facilitate addressing detection errors, especially availability, and make estimates more precise. However, auxiliary data can be unavailable or impractical to collect. Therefore, the high versatility of UAS platforms permits overcoming traditional (and possibly novel) problems of aerial surveys without resorting to auxiliary data, by for example, replicating flights (Williams *et al.* 2017a) or using focal follows (Hodgson, Peel & Kelly 2017).

Solutions available to address false positives are not yet well established. With the emergence of false positives in UAS surveys, assumed to be insignificant in most conventional aerial surveys, novel formal modeling procedures to account for these error types are particularly necessary, especially double counts.

With the widespread use of UAS (allied with the capacity of multiple sensors), data sets will commonly become enormous, resulting in the impossibility of manually reviewing images and so demanding the use of automatic detection algorithms. Hence, it will be imperative to test, and possibly develop, approaches that formally incorporate algorithm errors.

Hierarchical models stand out as a natural choice for modeling count data from UAS surveys, allowing the integration of multiple data sets and formally accommodating many sources of errors. Hierarchical modeling, especially *N*-mixture models, offers a flexible framework to be extensively explored in future studies to address solutions to account for detection errors in UAS-derived abundance estimates. Sampling scheme of *N*-mixture models permits overcome UAS limitations of flight range and duration to investigate populations and predict abundance at large spatial scales (e.g. Martin *et al.* 2015), an approach that is still lacking in UAS studies (Linchant *et al.* 2015). Furthermore, future researches may explore different flight designs in order to meet model assumptions, for example, how to get replicated passes over replicated sites or how to configure flight lines. In this way, we agree with Linchant *et al.* (2015) that different possibilities of flight plan designs, beyond conventional strip transects used in manned aerial studies, remain underexplored.

UAS surveys need to be consciously planned, thinking in what kind of error can significantly affect counts and sampling designs should optimize detection probabilities (e.g. time of day, flight height, flight scheme, image resolution, sensor type). Raw counts and indices as surrogates for abundance should be avoided as possible, and when used, should be interpreted with care (Anderson 2001).

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Authors' contributions

IVB conceived the main idea of the manuscript and all authors discussed and contributed to develop it. All authors reviewed drafts and gave approval for final version.

Data accessibility

No data was used in this review.

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CAPÍTULO 2

Drone surveys revealed bottom-up, and not top-down, effects on the marsh deer local abundance

Este capítulo está sob revisão no periódico ***Landscape Ecology****.*

Drone surveys revealed bottom-up, and not top-down, effects on the marsh deer local abundance

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Abstract

Spatial variation in large herbivore populations can be highly affected by the availability of resources (bottom-up) but modulated by the presence of predators (top-down). Studying the relative influence of these forces has been a major topic of interest in ecological and conservation research of this group, while it has also been challenging to sample large herbivores, especially at large spatial scales and remote areas. Here, we i) explore the use of spatiotemporally replicated drone-based counts analysed with *N*-mixture models to estimate the abundance of large herbivores and ii) evaluate the relative influence of bottom-up (forage and water) and top-down (jaguars) processes on the local abundance of the threatened marsh deer (*Blastocerus dichotomus*), for the dry season in the Pantanal wetland (Brazil). We conducted 25 fixed-wing drone flights (763km) in 6 planned paths (32-42km each) and the 25,000 images collected were reviewed by either one or two observers. We obtained deer counts, vegetation greenness, distance to water bodies, and jaguar density (from camera traps) for each 1km-site derived from the flight paths and fitted data using Binomial and Multinomial *N*-mixture models (for the single and double observer protocols respectively). We found a positive relationship of marsh deer local abundance with vegetation greenness, a negative relationship with distance to water bodies but no relation with jaguar density. Total marsh deer abundance was 1856 (95%CI = 951-3710) with most of the population concentrated in the lower and wetter region, even though it is the area expected to be more lethal from jaguar predation. Bottom-up processes are shaping the distribution of marsh deer individuals in the dry season. The benefits of accessing high-quality areas, that are expected to provide high-quality forage and are close to water bodies (as a habitat specialist associated with wetlands), outweigh predation risk from jaguars. Spatiotemporally replicated drone-based counts may serve as an accessible and cost-effective protocol to estimate abundance and monitor large herbivores while accounting for imperfect detection.

Key-words: aerial surveys, imperfect detection, large herbivores, *N*-mixture models, Pantanal wetland, predation, vegetation greenness

Introduction

Large herbivore populations can be highly affected by resource availability (i.e. bottom-up) and the predator presence (i.e. top-down). Assessing the relative effect of these forces has been a major topic of interest in ecological studies of this group (e.g. Anderson et al., 2010; Hopcraft et al., 2010; Owen-Smith, 2010; Riginos, 2015). As both resource availability and predator presence may commonly vary in space, the local abundance of large herbivores is expected to be heterogeneous in landscapes. Furthermore, individuals can avail of this heterogeneity to access high-quality resources while avoiding predation (Armstrong et al., 2016; Hebblewhite & Merrill, 2009). Understanding these effects is important for wildlife conservation and management since herbivores are considered the trophic group at the highest extinction risk, with consequences for entire ecosystems (Atwood et al., 2020). The knowledge about bottom-up and top-down effects in large herbivores can be used to predict consequences of global climate changes in forage availability, to foresee possible effects of large herbivore or predator extinctions or reintroductions on ecosystem functions, and to manage exotic invasive herbivores or game species.

Beyond primary productivity itself, a major factor influencing large herbivore populations is the distribution of high-quality forage. Large herbivores usually seek vegetation with high nutritional quality, that is, young and fresh plants, easily digestible and rich in protein. As the plant biomass increases, forage quality reduces, thus herbivores tend to optimally choose intermediate forage biomass to maximize energy intake (Fryxell, 1991; Hebblewhite et al., 2008; Hobbs & Gordon, 2010). In heterogeneous landscapes, the variation in vegetation phenology can sustain high herbivore densities. Especially in seasonal environments, high-quality forage is considered the major factor influencing large herbivores migrations, for example, in African savannas (Boone et al., 2006; Purdon et al., 2018) and mountainous regions of North America (Aikens et al., 2017; Hebblewhite et al., 2008; Jakes et al., 2018; Merkle et al., 2016; Sawyer & Kauffman, 2011) and Eurasia (Bischof et al., 2012; Rivrud et al., 2016). The spatial distribution of herbivores in a specific time would be then strongly determined by plants' phenological stage, with higher densities in areas showing higher vegetation greenness values.

Predation is also an important process shaping large herbivore populations, usually modulating the effects of optimal foraging preferences (Hebblewhite et al., 2008; Hopcraft et al., 2010; Rivrud et al., 2018). Predation can be a potential cause of local extinction for large herbivores, even when kill rates are low (Festa-Bianchet et al., 2006). Beyond the direct effect of predation in removing individuals from the population (i.e. consumptive effects), prey species can show behavioural responses as they perceive the risk of predation (Lima & Dill, 1990; Say-Sallaz et al., 2019). When exposed to predation risk, large herbivores can increase vigilance behaviour or herd size, and even change used areas or time of activity (Creel et al., 2014). These non-consumptive effects may have different – and sometimes larger – effects in prey dynamics than direct predation (Creel & Christianson, 2008). Thus, the resulting spatial distribution pattern of large herbivore individuals would be a trade-off between foraging gains and predation effects.

Studying large herbivore populations is challenging, especially at large spatial scales and in remote areas. The influence of forage distribution and predators on herbivore individuals has usually been studied using biotelemetry, by evaluating how landscape variables associated with forage availability and predation affect individuals' movements and space use (Hopcraft et al., 2014; Merkle et al., 2016; Owen-Smith, 2010). Population-level studies of large herbivores are commonly carried out using aerial surveys with manned aircraft (e.g. Caughley, 1974; Vucetich & Peterson, 2004), which is often financially prohibitive and can prevent the necessary amount of spatial or temporal replications for accurate and frequent estimates needed for decisions in conservation (Ferreira & Aarde, 2009; Fritsch & Downs, 2020). Recently, drones (Unmanned Aerial Systems or Remotely Piloted Aircraft) have emerged as an accessible, safe, and cost-effective alternative for aerial surveys and have been tested to sample large herbivore populations (e.g. Barasona et al., 2014; Chrétien et al., 2016; Gentle et al., 2018; Linchant et al., 2018; Rey et al., 2017; Vermeulen et al., 2013).

As for other wildlife survey methods, aerial count data obtained from drone-based surveys are susceptible to imperfect detection. Some individuals present in the sampling area may be unavailable for detection (e.g. under a tree) or, even when available, an observer can fail to detect them when reviewing imagery (Brack et al., 2018). Addressing these sources of error in count data with a robust framework is imperative to obtain unbiased abundance estimates. Given the potential of hierarchical *N*-mixture models to estimate abundance accounting for imperfect detection and without the need of marking individuals (Royle, 2004), they have been proposed as a feasible approach for aerial surveys (Brack et al., 2018; Williams et al., 2017), especially for modelling abundance at large spatial scales (e.g. Martin et al., 2015). Moreover, the typical sampling design for *N*-mixture models matches the characteristics of drone surveys, that is, multiple and short flights in spatiotemporally replicated surveys.

Our objective here was two-fold: i) explore the potential of drone surveys and hierarchical *N*-mixture models to estimate large herbivore abundance and ii) use this innovative approach to evaluate the relative influence of bottom-up (forage and water) and top-down (predators) factors on the local abundance of marsh deer (*Blastocerus dichotomus*). The marsh deer is the largest cervid in the Neotropics (up to 150 kg), highly adapted to use marshes and swamps, living in low densities in South America's wetlands and savannas. Because of its association with wetlands, marsh deer's current distribution is highly fragmented and the species is listed as Vulnerable with extinction (IUCN; Duarte et al., 2016). Its main predator is the jaguar (*Panthera onca*) and, although marsh deer are considered a valuable prey for jaguars (Hayward et al., 2016), they only compose ≤10 % of the jaguar's diet (Cavalcanti & Gese, 2010; Azevedo & Murray, 2007; Perilli et al., 2016). Here, we specifically tested a positive influence of (1) vegetation greenness (as a proxy for high-quality forage availability) and (2) water bodies on the local abundance of marsh deer, and a negative effect of (3) jaguar density. We also tested a modulatory effect of jaguar density on the relation of deer local abundance with vegetation greenness, expecting higher jaguar densities to be associated with weaker positive effects of forage. We assessed these predictions during the dry season of the Pantanal wetland of Brazil. Additionally, we discuss the feasibility of spatiotemporally replicated drone surveys applied here, and compare two hierarchical *N*-mixture modelling approaches (single and double observer protocol) for estimating the abundance of large herbivore populations, which can also be employed for other wildlife species in different contexts.

Methods

Study area

The Pantanal wetland, the world's largest tropical floodplain, is an inner lowland region of Quaternary sedimentary deposits in central South America. With a seasonal rainy climate, it receives periodic flooding pulses from the rivers in the surrounding highlands (Junk et al., 2006). This study was conducted in the Sesc Pantanal Private Natural Reserve, a 108,000-ha private reserve created in 1997, located in the Northern Pantanal (16º 45’ S and 56º 15’ W), and designated as a Ramsar Site (number 1270). The area is characterized by a tropical savanna climate with a pronounced dry season, showing a mean annual temperature of 26ºC and an annual average rainfall of 1200 mm concentrated from November to March (Hofmann et al., 2016). The reserve is located between two of the major Pantanal rivers, Cuiabá and São Lourenço, receiving their overflows in the flooding season. The area is composed of a highly heterogeneous vegetation (grasslands, shrublands, and riparian, flooded, and seasonally dry forests) mainly structured by microrelief differences that receive different flooding regimes (Oliveira et al., 2013). We focused this study on two regions of the Sesc Pantanal Reserve dominated by open vegetation types: (1) the western portion, covered by shrublands, sometimes mixed with flooded forest patches of *Vochysia divergens*, located at lower altitudes and retaining more water in the dry season; and (2) the central region, covered by savannas (woody “cerrado” vegetation and grasslands) and seasonally dry forests, and containing some small artificial water ponds, built before the reserve creation (1997) for cattle watering in the dry season, that are used by marsh deer. Since the reserve creation in 1997, cattle were excluded from the area and wildfires have been fought.

N-mixture models for count data from drone surveys

N-mixture models are a family of hierarchical models used to estimate abundance from repeated counts of unmarked individuals while accounting for imperfect detection (Dénes et al., 2015; Royle, 2004). The typical sampling design for *N*-mixture models consists of multiple sites observed multiple times (i.e. spatiotemporally replicated surveys). These count data are modelled in a hierarchical way, as a result of (at least) two processes: i) the biological state process that governs the local abundance at sites, and ii) the observation process, affected by imperfect detection of individuals. In the application of *N*-mixture models for drone surveys we present here, each transect (a flight path) is split into segments, which represent the sites. Each site is flown multiple times and the aerial images captured from the drone are reviewed under a double independent observer protocol (Figure 1). Thus, the resulting dataset can be represented as a three-dimensional array containing, for each visit in each site, the counts summarized as different possibilities of encounter histories by the observers (i.e. number of individuals detected by both; only by the first observer; and only by the second observer). With this data structure, it is possible to estimate abundance while accounting for the two common sources of false-negative errors in aerial surveys: availability and perception errors (Brack et al., 2018). The availability error refers to individuals that are present in the sampling area but unavailable for detection at the time the image is taken due to, for example, being hidden below vegetation. Perception error occurs when an observer (or an algorithm) fails to detect an individual that is available for detection. Both errors, if not properly addressed, generate underestimation of population size.

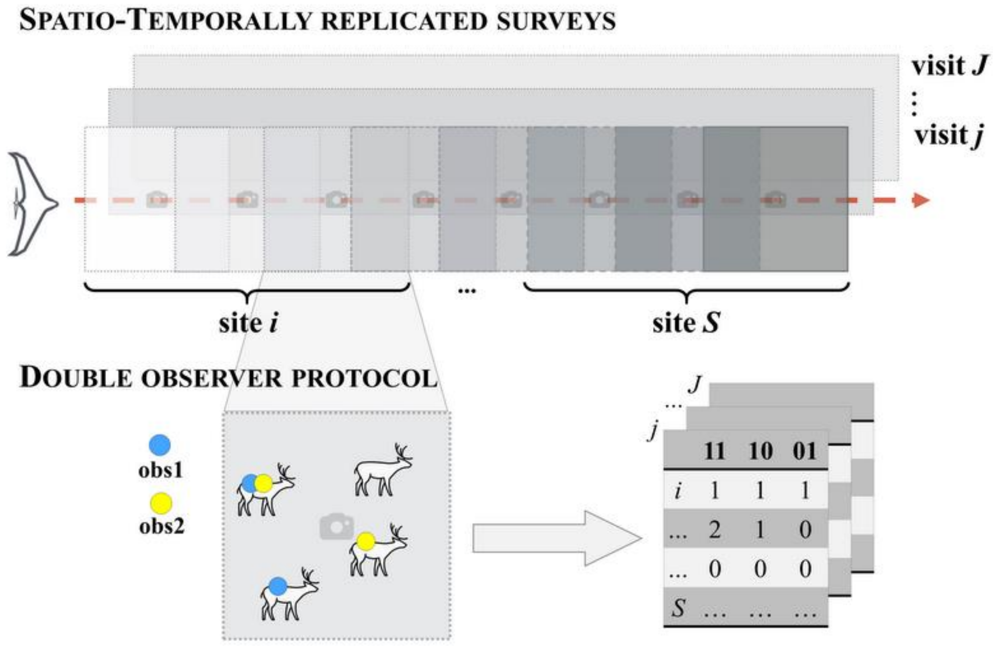

Figure 1. Sampling design and resulting count data to account for availability and perception errors in abundance modelling (for a multinomial N-mixture model with temporary emigration) from drone surveys. The sampling scheme presumes drone flights conducted at multiple sites (site i=1 to S, possibly from segmented flight paths) and with multiple visits (visit j=1 to J); and a double independent observer protocol for image review. The resulting data is a 3-d array count data (S,K,J ; in which K is the number of possible encounter histories, i.e. “11”=detected by both observers, “10”=detected only by the 1st observer, and “01”=detected only by the 2nd).

For modelling such count data, we used the three-level multinomial *N*-mixture model with a temporary emigration component proposed by Chandler, Royle, & King (2011). Under the assumption site abundance remains constant throughout independent visits, we model the local abundance M_i at sites $i \in \{1,..,S\}$ as a Poisson distribution (given counts are non-negative integer numbers):

$$M_i \sim \text{Poisson}(\lambda)$$

Then, in each visit $j \in \{1,..,J\}$, each individual from the population M_i at site *i* has a probability φ of being available for detection, resulting in the number of available individuals N_ij:

$$N_{ij} \sim \text{binomial}(M_i, \varphi).$$

If the sites are truly closed to changes in population (i.e. no departures nor entries), the availability parameter φ corresponds to the probability of an individual present at a site not being hidden, for example, below vegetation, inside a burrow, or, in the case of marine surveys, submerged. However, if there is some movement of individuals in and out of the surveyed area between visits, the availability parameter would correspond to both processes: the probability of the individual being present on the site at the time of survey and not being hidden.

In the last observation level, each individual available for detection N_ij has a probability p of being detected by each observer independently (i.e. perception probability). With a double independent observer protocol, there are four possible encounter histories for each available individual: detected by both observers ("11"), detected only by the 1st observer ("10"), detected only by the 2nd ("01"), and not detected ("00"). Then, the counts Y under each observable encounter history k $\in \{1,2,3\}$ are modelled as a function of multinomial conditional cell probabilities π_k, in which $\text{k}_{11} = p^2$; $\text{k}_{10} = p(1 - p)$; $\text{k}_{01} = (1 - p)p$:

$$Y_{ijk} \sim \text{multinomial}(N_{ij},\ \pi(p)_k).$$

Alternatively, it is possible to estimate abundance with a single observer protocol for image review using the classic binomial *N*-mixture model (Kéry et al., 2005; Royle, 2004, and proposed for drone-based surveys in Williams et al., 2017), but forgoing the possibility of segregating both observation processes. In this case, the single observer counts *Y* for each site *i* in each visit *j* are modelled under a binomial distribution in which each individual of the population M_i has an overall detection probability $p*$ that is the product of availability (φ) and perception (p):

$$Y_{ij} \sim \text{binomial}(M_i, p^*), \text{ where } p^* = \varphi.\, p$$

The use of a double observer protocol for image review is not necessary for the entire image set: a mixed single and double observer protocol (i.e. double observer only in a subset of the imagery) is enough to separately estimate perception and availability probabilities (Brack et al., 2018; Kéry & Royle, 2016).

Further to this constant model, parameters can be estimated as a function of covariates using linear regressions with appropriate link functions (e.g. log for λ and logit for φ, p, and $p*$).

Drone flights and marsh deer counts

Aerial marsh deer surveys were carried out in preprogramed flight paths using the drone Echar 20B (XMobots®, http://xmobots.com/). Echar 20B is a battery-propelled fixed-wing drone (2 m wingspan, 7 kg) with a flight time of about 1h15min and a cruise speed of 70 km/h. It is launched by a catapult and lands with a parachute. The drone was equipped with either a Sony Alpha500 (24Mpix) or a Sony A7R (36Mpix) RGB sensors. Flight height and lens focal distance were adjusted for each camera in order to keep a ground sample distance (GSD) of approximately 2 cm/pix (e.g. Sony Alpha A7R, 110 m above ground and 22 mm focal distance). Resulting strip width (photo) was approximately 180-200 m.

We planned six flight paths, ranging from 32 to 42 km in length (Figure 2 and Table 1). We first defined a 1x1 km grid with a random origin in the study area to guide the flight lines and planned flight paths preferably in separated strips (to avoid deer movements between lines), perpendicular to the flooding pulse (to minimize intra-site and maximize inter-site vegetation and water heterogeneity). Flight paths avoided highly forested areas seldom used by marsh deer and where the availability of individuals for detection would be close to zero. As flight time is a limiting factor for drone surveys (especially battery-propelled), we planned the flight paths to start and finish nearby to minimize wasted flight time outside planned lines. The drone was programmed to take photos with a frontal overlap of 50-60 %, meaning that each point in the ground would appear in 2-3 pictures. We conducted a total of 25 drone flights (2-6 visits in each flight path) in September and October of 2017, resulting in 763 km flown. To define the sites for the *N*-mixture models, we split the six flight paths into segments of 1 km length, expecting to reduce effects of movement of individuals between sites during our sampling window (daily movements of marsh deer intra-season are expected to be short; Piovezan et al., 2010). This resulted in 203 sites with 1-6 visits per site. Flights were operated preferably in the mildest hours of the day (i.e. 6-9 h and 16-18 h) when marsh deer are more active. We first repeated flights in the same path to then go to the next flight path, in order to minimize the effect of individuals entering and leaving the sites between visits (i.e. avoid temporary emigration by movement). Intervals between visits for each flight path are presented in Table 1.

For the approximately 25,000 images collected, the first observer reviewed the entire imagery and the second only 20 % of the flights. Observers were instructed to conduct a careful review of each image with free zooming and to mark each marsh deer found (Fig. 2c) using the software ClickPoints (Gerum et al., 2017). For each site, we got the total marsh deer counts under each observable encounter history for each visit (Fig. 1). The first observer took more than 100 hours to review the entire imagery, with a mean time of 18 seconds per image. Given that the pictures were frontally overlapped, we used only the first appearance of each record and excluded the double counts. The overlapped areas between pictures increased the chance of detection by the observers and were helpful to solve identification uncertainties. We only included a marsh deer as a certain record after all detections were reviewed by experts. Thus, we are confident our dataset does not include false-positive records (which are not accounted for in our modelling approach). We had only two uncertain detections excluded by experts, since the size, shape, and colour of the marsh deer records are usually very conspicuous and differ from any other species or background feature.

Covariates

We tested the effects of bottom-up (vegetation greenness and distance to water) and top-down (jaguar density) covariates on the local abundance of marsh deer at the sites. Vegetation greenness was calculated using the Normalized Difference Vegetation Index (NDVI) as a proxy for the availability of high-quality forage (Appendix S1: Figure S1). The NDVI has been widely used as a proxy for primary productivity and forage quality for large herbivores (Garroutte et al., 2016; Pettorelli et al., 2005, 2011), presenting a well-documented relation with protein content in vegetation and in herbivores faeces (Hamel et al., 2009; Ryan et al., 2012). We calculated the NDVI from

Sentinel-2 satellite images (10 m spatial resolution), obtained in the same period of the drone flights (September/2017). As we avoided flying over forested areas, we assume that NDVI calculated is, at a reasonable extent, related to green and fresh vegetation available for marsh deer at the sites. On the same satellite image, we identified water pixels using low NDVI values, and we calculated, for each 10x10 m cell, the Euclidean distance to the nearest water pixel, resulting in a raster map of distance to water (Appendix S1: Figure S2). The jaguar density map (500 m spatial resolution; Appendix S1: Figure S3) was derived from a spatial capture-recapture (Royle et al., 2014) study conducted in the same reserve (unpublished data, more info in Appendix S1: Figure S3). We do not expect an effect of marsh deer abundance on the distribution of jaguars, which could preclude interpretations of causal relations in this study, because marsh deer are generally not a major prey item of jaguars. Although the cougar (*Puma concolor*), the other large predator in Pantanal, could potentially influence marsh deer, we did not investigate these effects since we did not find any evidence of cougar predation on marsh deer in the literature.

To account for heterogeneity at the observation level, we considered air temperature during flights and forest cover as sources of variation on the availability of individuals. Since temperatures during the day in Pantanal can be high (sometimes close to 40º C), marsh deer probably avoid exposure to sunlight during the hottest times of the day by being hidden below vegetation. Thus, we expect the higher the temperature, the lower the availability of marsh deer for detection. In the same way, in areas where tree cover is higher, there is more chance of marsh deer being hidden below vegetation, and thus we expect the higher the forest cover, the lower the availability of marsh deer for detection. Air temperature was recorded during flights approximately every 10 minutes with a thermometer Incoterm® 7665.02.0.00 (precision = 1º C) about one meter above ground. The forest cover in sites was obtained from a land cover map derived from Landsat satellite scenes of 2016 (30 m resolution), using a supervised classification of images from 3 periods of the year: flooded, discharging and dry seasons.

For each 1km-site, we summarized NDVI, distance to water bodies, and jaguar density by calculating the mean pixel value, and extracted forest cover as the percentage of forest pixels within the site. We obtained a single value of air temperature for each site in each visit.

Model fitting

We modelled marsh deer drone-based counts in relation to the covariates using the two model structures presented in the modelling description section: i) the single observer binomial *N*-mixture model, and ii) double observer multinomial *N*-mixture model. We built the models with a maximum of two covariates in the biological process (local abundance λ), considering the interaction (i.e. modulatory effect) between jaguar density and vegetation greenness and avoiding the inclusion of jaguar density and distance to water bodies in the same model (because jaguar density was modelled in relation to water). In the observation level (availability φ for the multinomial and overall detection *p** for the binomial *N*-mixture), we compared all combinations of forest cover and temperature. For the multinomial *N*-mixture model, we only considered the perception probability *p* as constant. This resulted in 28 candidate models for each *N*-mixture model structure (Appendix S2: Tables S1-S2).

We fitted the models under a maximum likelihood approach (Appendix S5) using functions *pcount* (single observer) and *gmultmix*, (double observer) from package *unmarked* (Fiske & Chandler, 2011) in the programming language R (R Core Team, 2020). We performed model selection with the Akaike Information Criteria adjusted for small sample sizes (AICc). We chose only a Poisson distribution for the local abundance parameter since the use of the Negative Binomial distribution has been unrecommended because it can provide unreliable very high abundance estimates in *N*-mixture models (Joseph et al., 2009; Kéry et al., 2005). All covariates were standardized by subtracting their mean and dividing by their standard deviation. No pairwise correlation between covariates was higher than $|r| = 0.7$. We applied a visual check of residuals and goodness of fit test for the binomial *N*-mixture model using *nmixgof* package (there is no GOF test readily available for the multinomial *N*-mixture model), which indicated an adequate fit and presented an estimated overdispersion parameter $\hat{c} < 1.1$. Using the best-ranked model for the double observer approach, we produced an abundance map of the marsh deer in the Sesc Pantanal Reserve from the predicted covariate relations and excluding pixels we considered to be non-habitat for the species (i.e. forest cover > 80 %).

We also checked whether the choice to segment the flight paths in 1km-sites affected our abundance estimates and if we could detect any effect of spatial temporary emigration. For this, we segmented the flight paths using different site length definitions, ranging from 400 to 2000 m in steps of 50 m, and fitted a null multinomial

N-mixture model (λ, φ, and *p* constants) for each of these 33 scenarios. To be able to compare the abundance estimates between these scenarios with different segment lengths for sites, we added an offset using the logarithm of the segment length in the abundance parameter (λ).

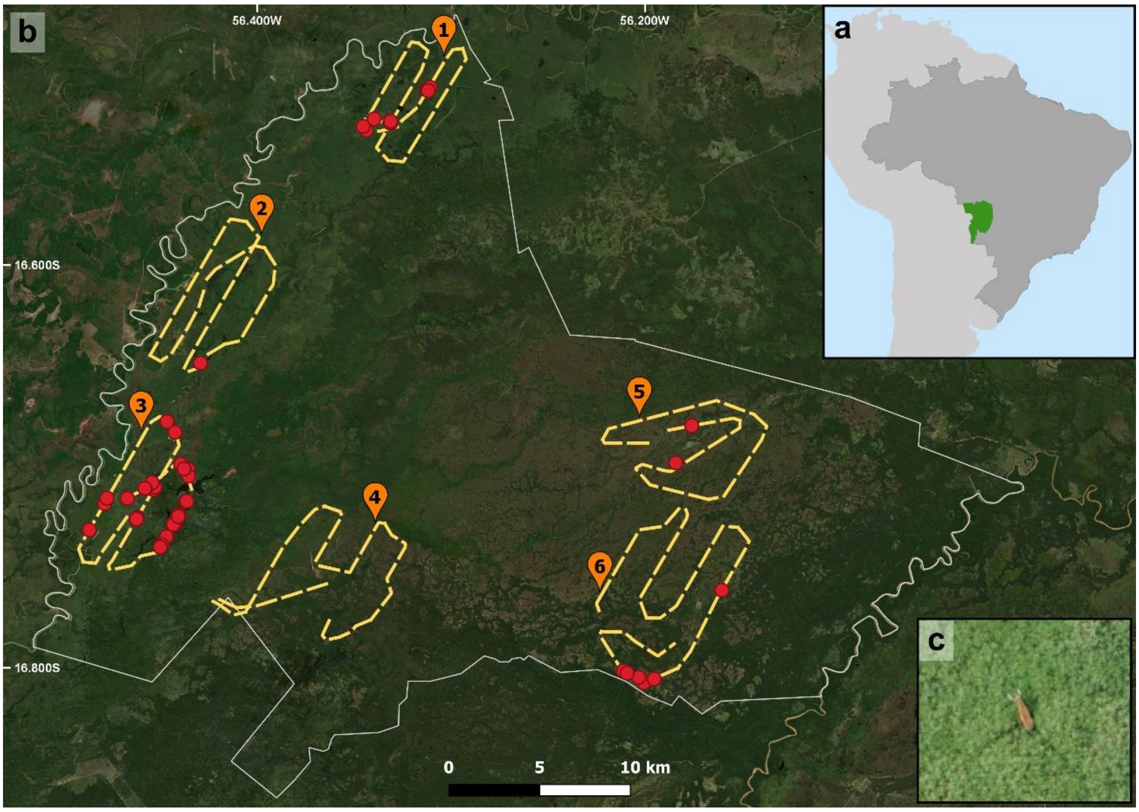

Figure 2. (a) Pantanal wetland, Western Brazil; (b) Sesc Pantanal Reserve (white contour) and marsh deer records (red dots) obtained from drone surveys at six flight paths (yellow dashed lines). Detailed information of the flight paths (orange numbered icons) is presented in Table 1. (c) Example of marsh deer record from drone imagery.

Results

From the approximately 25,000 images collected in the 25 flights, we obtained a total of 66 unique marsh deer records by both observers (Figure 2, Table 1) that appeared in 137 images (the same record usually appeared in more than one image because the pictures were overlapped). For the five flights that have a double observer protocol, 20 deer were detected by both observers, two detected only by the first observer, and two only by the second (Table 1). Marsh deer were detected in 26 of the 203 1km-sites and the maximum count for a visit was four and occurred in two sites.

For those 26 sites that presented any marsh deer detection, the mean count per visit was less than one (0.72).

Table 1. Length, number of flights (visits), and marsh deer counts by the 1st and the 2nd observers for the six flight paths planned at Sesc Pantanal Reserve (Brazil). Visits intervals present the median time between visits and maximum time between the first and the last visit. The first observer reviewed the entire imagery and the second only 20% of the flights.

Path ID	**Length** (km)	**N visits**	**Visits intervals** median (max) in hours	**Counts obs1**	**Counts obs2**
1	32	2	1 (1)	4 / 7	3 / -
2	38	3	8 (15)	1 / 0 / 0	- / - / -
3	35	5	10 (49)	6 / 5 / 10* / 15 / 7	- / - / 10* / - / 8
4	36	5	16 (200)	0 / 0 / 0 / 0 / 0	- / - / - / - / -
5	34	6	5 (23)	1 / 0 / 0 / 1 / 0 / 0	1 / - / - / - / - / -
6	42	4	24 (72)	3 / 1 / 1 / 2	3 / - / - / -

* total number of detected individuals in this flight was 11 (9 detected by both and 1 by each one).

Model selection picked up the same covariates for both model structures (single observer binomial and double observer multinomial *N*-mixture; Appendix S2: Tables S1-S2) and both approaches presented very similar coefficient estimates in the top-ranked models (Appendix S2: Table S3). We found a negative effect of the distance to water bodies and a positive effect of vegetation greenness (NDVI) on marsh deer local abundance (Fig. 3). We did not find evidence of an effect of jaguar density on the local abundance of marsh deer. Sites with a higher proportion of forest cover and flights conducted at higher air temperatures had lower detection probabilities (Fig. 3c and 3d). The estimated perception probability of detecting a deer available on the imagery by an observer (*p*) was very high: 0.93 (95 % CI = 0.82–0.97).

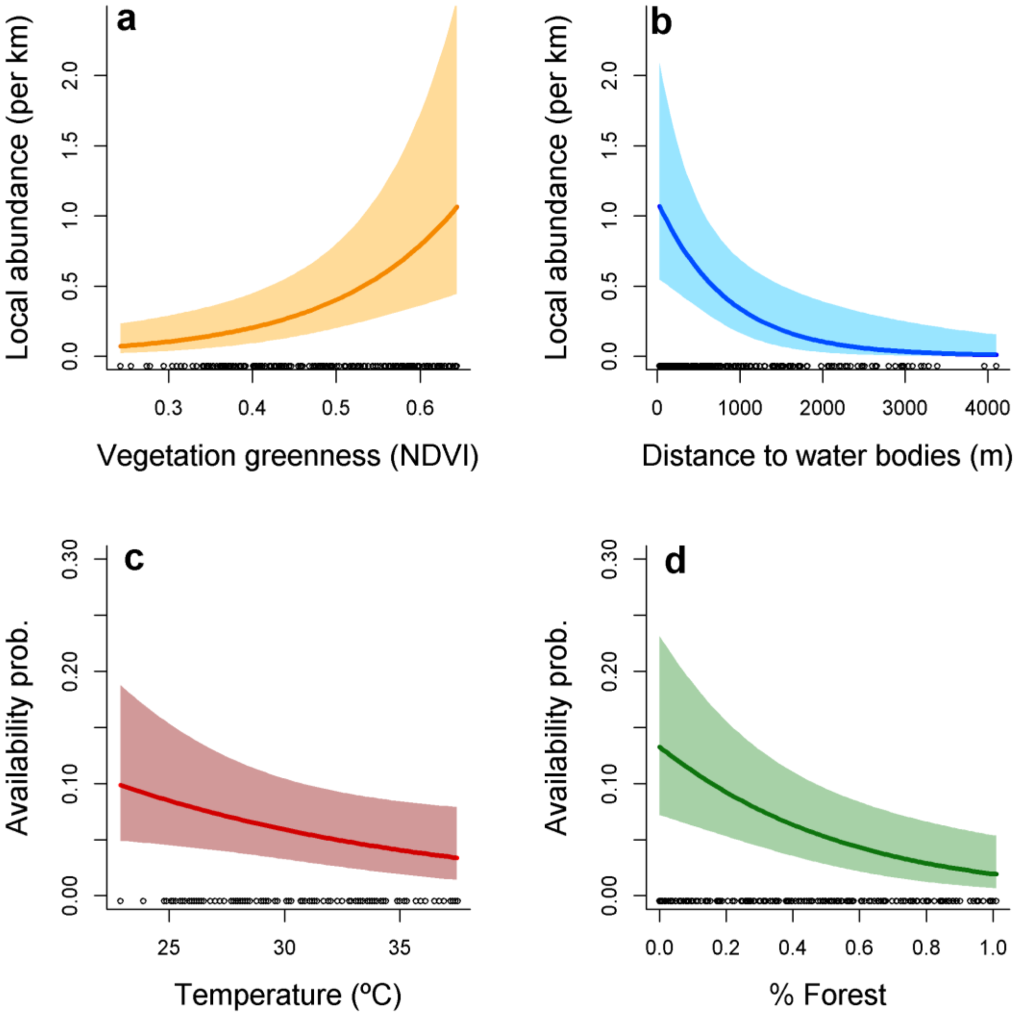

Figure 3. Predicted relations of marsh deer local abundance with (a) vegetation greenness, and (b) distance to water bodies; and individuals' availability with (c) temperature during flight, and (d) proportion of forest in sampled sites. Relations were predicted by modelling counts from spatiotemporally replicated drone surveys with a double observer protocol, using a Multinomial N-mixture model. Shaded areas represent the 95% confidence interval and the dots in the x-axis indicate the covariate values.

Estimated mean marsh deer abundance (λ) ranged from close to zero (sites with low values of NDVI or with a mean distance of water bodies greater than 2 km) to about one (sites near to water bodies or with high values of vegetation greenness); keeping the mean value of one covariate when varying the other (Fig. 3a and 3b). Predicted abundance for sites near water bodies and with high NDVI values was 3.2 (95 % CI =

1.5–6.7). The total abundance estimated for all 203 sampled sites was 150 individuals (95 % CI = 43–445). The spatial distribution of marsh deer local abundance obtained from the predicted relations indicates consistently higher densities of the population in the western part of the reserve (Fig. 4; lower and upper 95 % CI local abundance maps are provided in Appendix S3: Figure S4). The resulting total abundance predicted for the Sesc Pantanal Reserve was 1856 (95 % CI = 951–3710) marsh deer.

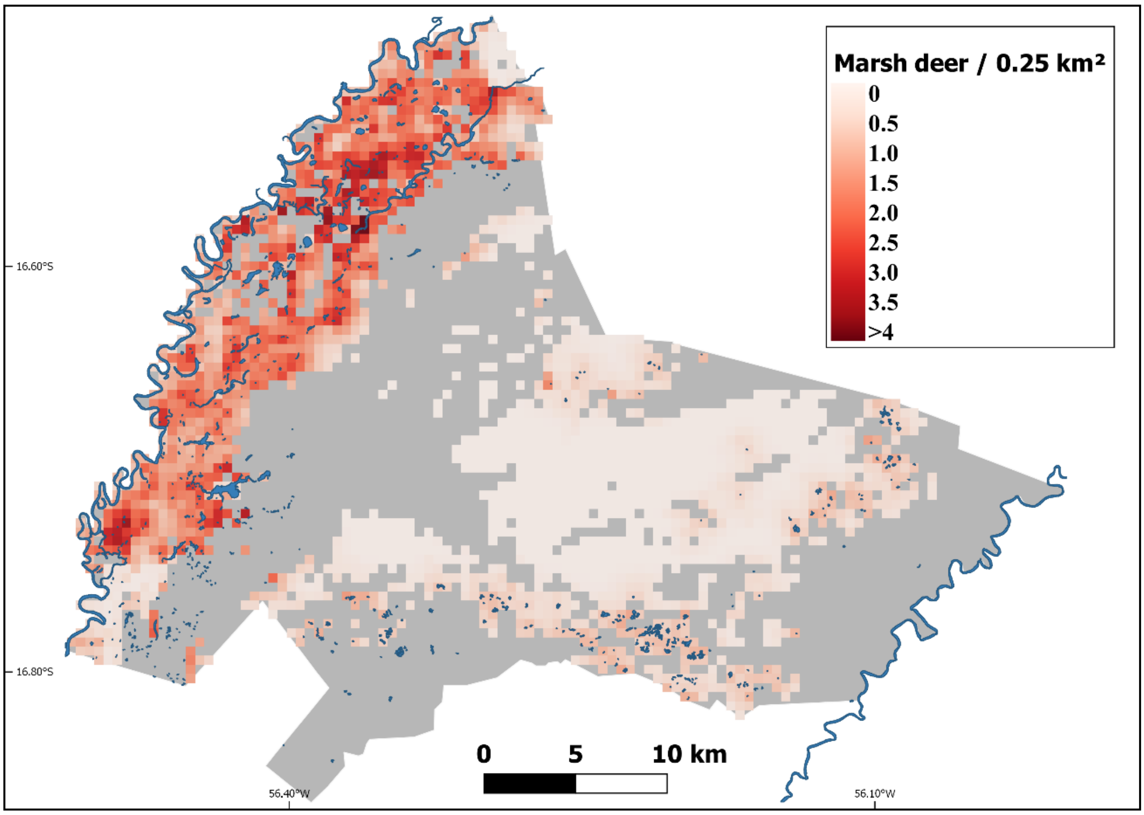

Figure 4. Spatial prediction of marsh deer local abundance for the dry season of 2017 in Sesc Pantanal Reserve, derived from spatially replicated drone-based counts. Blue polygons represent water bodies and grey areas correspond to highly forested areas (>80%) for which local abundance was not predicted.

For the analysis comparing different choices of site length, we obtained a considerable variation in the precision among scenarios, but the estimates overlapped consistently (Appendix S4: Figure S5). Highly uncertain estimates correspond to scenarios where some deer records were excluded by the way flight paths were segmented.

Discussion

We were able to reveal the effects of bottom-up (forage and water) and top-down (predators) landscape variables on the spatial variation of marsh deer local abundance using spatiotemporally replicated drone flights while accounting for detection errors. We first discuss the methodological implications of our results and then explore the biological interpretations of the tested hypotheses.

Modelling abundance with spatiotemporally replicated drone surveys

Count data obtained from spatiotemporally replicated drone surveys and analysed with *N*-mixture models has proven to be a straightforward method to estimate abundance and its relationship with landscape variables for a low-density large herbivore at a relatively large spatial scale (especially for studies using drone surveys). We were able to reach a coefficient of variation for the mean local abundance estimate $CV(\bar{\lambda}) = 35\ \%$ with 66 records collected in 25 flights that surveyed an area of 1080 km^2 in less than 20 days of fieldwork. With this approach, we assessed marsh deer abundance accounting for the two main detection errors in aerial surveys: availability and perception. This is particularly interesting for the availability error, which is rarely addressed in aerial surveys or estimated by using costly auxiliary data, such as from biotelemetry (e.g. Martin et al., 2015). The nature of this method (multiple short flights) can overcome a common limitation of population assessments by drone surveys: the short flight time and range. Finally, local abundance estimates were robust (i.e. no evidence of bias) to the choice of segment length we made to split the flight paths.

The use of single observer counts in image review, instead of a double observer protocol, did not compromise abundance estimates or the relationship of detection parameters with covariates (assumed to affect only the availability process). Both modelling structures (single and double observer) provided very similar estimates for all parameters. This result is due to the very high perception probability we had for the observers (*p* = 93 %; 95 % CI = 82–97 %). In our case, a double observer protocol in image review could be considered unnecessary. However, this is possibly not the case for many other species, which are, for example, less conspicuous in drone images, or in the case of thermal imagery with lower sensor resolution and often low contrast between background and individuals (Burke et al., 2019). In this case, a double observer protocol could improve abundance estimates by providing more precise estimates in the observation process. The double observer protocol can be applied to a subset of the imagery; we were able to estimate both observation processes (perception and availability) with confidence using a second observer review in only 20 % of the flights. With the increase of automated algorithms for drone image reviews (e.g. Gray et al., 2018; Kellenberger et al., 2018), this double observer protocol could be applied manually to an image subset to address the algorithm error. Other situations to apply a double observer protocol to segregate the detection processes include having different hypotheses for availability and perception covariates or when the same covariate is expected to affect both processes in different ways. For example, in drone surveys with thermal cameras under cold weather, temperature may positively affect availability (individuals seeking sunlight) and negatively affect perception (lower contrast in thermal signature).

One limitation of the approach presented here is that spatial temporary emigration (i.e. individuals entering and leaving the site between visits), if it exists, would bias the estimation of abundance. In such cases, the local abundance parameter should not be used to obtain absolute density numbers (Kéry & Royle, 2016) and could be more adequately interpreted as the intensity of use by the population, that is, the number of individuals of the population that use that site. It is possible to reduce the effects of spatial temporary emigration on abundance estimates by shortening the time between visits, but avoiding a temporal autocorrelation between visits (Brack et al., 2018; Williams et al., 2017). Another factor that can affect the influence of the spatial temporary emigration is the relative magnitude of the individuals' movements in relation to the site size, depending on the site size itself and the home range size of the species (Chandler et al., 2011). In this study, we did not find any trend of the abundance estimates in relation to the choice of segment length (i.e. site size). Although this analysis could not directly detect spatial temporary emigration effects, it apparently indicates no positive bias in abundance estimates. Even though absolute abundance numbers derived from this method should be treated carefully in the presence of spatial temporary emigration, this approach is widely useful for studying the relationship of abundance with spatial variables and as relative abundance estimates for long-term monitoring of population trends.

Spatial variation in marsh deer abundance

We found evidence of bottom-up related processes (water bodies and vegetation greenness as a proxy for available forage) affecting the distribution of marsh deer local abundance in the dry season. Even it is not possible to affirm that there are no predation effects on marsh deer abundance, its relative influence is certainly weaker than the bottom-up processes we studied. Interestingly, the high-quality areas that sustain higher densities of marsh deer in the dry season (i.e. near water bodies and higher levels of vegetation greenness) are the areas that would be expected to be more lethal (i.e. higher jaguar density). Moreover, areas close to water bodies are considered riskier in the dry season because large predators tend to hunt in such regions (Owen-Smith, 2014; Valeix et al., 2011). Although top-down factors (i.e. predation) are expected to significantly affect the distribution of ungulates (McArthur et al., 2014), our result may not be very surprising. In seasonal rainy savannas, remaining areas with available forage in the dry season are considered a major factor limiting large herbivore populations (Owen-Smith, 2014), sometimes overshadowing high risks of predation (Riginos, 2015). Thus, the benefits of accessing high-quality areas (with more food and water) for marsh deer in the dry season may outweigh predation risk from jaguars, resulting in higher marsh deer local abundance. Also, to reduce risks in these areas, marsh deer may present some behavioural mechanisms to prevent predation by, for example, avoiding being active at night, when predation success is higher, or increasing vigilance while foraging (Creel et al., 2014). Furthermore, the presence of predators could influence the local abundance of marsh deer at finer scales than we evaluated here, or the influence of predation on marsh deer may be related to other variables than jaguar density such as the amount and distribution of safe and risky patches in the landscape (Laundré et al., 2014; Moll et al., 2017). Finally, as marsh deer is not a common prey for jaguars (Cavalcanti & Gese, 2010; Azevedo & Murray, 2007), jaguars may not impose strong predation risks for marsh deer.

The positive relation we found between marsh deer abundance and vegetation greenness corroborates the known pattern that primary productivity is a major factor shaping the distribution of large herbivore populations in landscapes. This relationship is well studied for ungulates in temperate regions of Eurasia, where, with the beginning of the spring season, herbivores track gradients of green and fresh vegetation produced after snow melting in heterogeneous topographic landscapes (Bischof et al., 2012; Hebblewhite et al., 2008; Merkle et al., 2016; Rivrud et al., 2016). In tropical areas, large herbivores in African savannas follow a green-up gradient produced by differences in precipitation among regions (Boone et al., 2006; Cornélis et al., 2011; Purdon et al., 2018). In South America, a similar pattern was found for guanacos in the temperate environments of Patagonia (Schroeder et al., 2014). Similarly, the results presented here suggest that the seasonal dynamics of tropical floodplains may also produce forage quality heterogeneity for large herbivores (in this case, marsh deer). Although we did not evaluate the relation of local abundance and vegetation greenness for the wet season, in the dry season, the marsh deer population was concentrated on the remaining patches of green vegetation in wetter areas of the reserve. Then, we could expect an expansion of the marsh deer population following a vegetation green-up with the rain and the floods of the wet season. While this mechanism was proposed to influence variation in marsh deer abundance in the Pantanal wetland (Tomas et al., 2001), it remains unevaluated.

As expected, we found a strong relationship of marsh deer abundance to water bodies, with the local abundance of marsh deer drastically reduced along the first two kilometres from water bodies. Access to water, especially in the dry season, can be an important factor in shaping ungulate spatial patterns (Owen-Smith, 2014) and severe droughts are a potential cause of local extinctions (Spinage & Matlhare, 1992). Marsh deer is known to be a habitat specialist associated with wetlands: they present long limbs with interdigital webbing to move in flooded areas (Nowak, 1991). Since aquatic macrophytes and other flood-tolerant plants compose a significant part of marsh deer's diet (Costa et al., 2006; Tomas & Salis, 2000), this relationship with water bodies is probably also a consequence of foraging opportunities, beyond water supply. However, marsh deer may occur in low densities in drier areas, since some individuals were found away from wet areas, where small water bodies may be sufficient to sustain low densities. Interestingly, some areas of intermediate local abundance predicted to the central region of the reserve are close to the artificial water ponds (cattle watering holes remnant of the former ranches). These artificial water bodies can play an important role in the maintenance of marsh deer populations in dry areas, especially in severe drought years.

The predicted spatial pattern shows that the population is concentrated in the western portion of the Sesc Pantanal Reserve, the lower and wetter region, presenting incredibly high densities for the species in this area (more than 8 individuals per km² in contrast with <2 ind./km² in the drier central region). Most other studies that estimated marsh deer density in different regions obtained a maximum of one individual per km² (Andriolo et al., 2005; Mourão et al., 2000; Peres et al., 2017; Ríos-Uzeda & Mourão, 2012; Tiepolo et al., 2010), with Tomas et al. (2001) reporting a maximum of 1.85 ind./km² in some areas of Pantanal in the dry season. Although we should treat our density estimates carefully because of potential spatial temporary emigration, these apparent high densities for marsh deer could be justified by the fact that these previous studies did not account for the availability bias in estimates. As it is clear from our low estimates of the availability parameter ($\varphi < 0.3$), the availability error might have an important influence on aerial counts of marsh deer (and potentially other ungulate species). It is not uncommon to find studies that ignore or poorly address the availability error in aerial surveys (e.g. Barasona et al., 2014; Mourão et al., 2000), providing a biased estimation of abundance. This result highlights the importance of accounting for imperfect detection (here, particularly the availability error) – and modelling its heterogeneity – in large herbivores population assessments.

Conclusions

Large herbivores are highly threatened because of habitat conversion, overhunting, and livestock diseases and competition, combined with usually large home ranges, migratory behaviour in many species (Gnanadesikan et al., 2017), and low reproductive rates (Ripple et al., 2015). Methods to efficiently estimate population size are important to monitor and evaluate the status of threatened large herbivore populations. Counts from spatiotemporally replicated drone-based surveys analysed with hierarchical *N*-mixture models may serve as an accessible and cost-effective protocol for modelling the abundance of large herbivores (and certainly other wildlife species observable from aerial images) accounting for imperfect detection, especially in open vegetation and remote areas.

Marsh deer local abundance in the dry season presented a strong relation with what is expected to be the high-quality areas for the species: high levels of vegetation greenness (that are expected to provide high-quality forage) and close to water bodies (as a habitat specialist associated with wetlands). The distribution of marsh deer abundance was not influenced by its main predator, the jaguar, and the higher densities of the population overlapped with the higher densities of jaguars. Small water bodies (even the artificial ones) may sustain some individuals in drier areas and may be an important resource for the species in severe years. As primary productivity and availability of water bodies present a very contrasting seasonal dynamics associated with flood pulses in Pantanal (and in other marsh deer occurrence areas), it would be interesting to evaluate how the trade-off between these bottom-up and top-down forces behaves in the wet season. Effective conservation actions (e.g. delimitation of protected areas) can be improved by the understanding and prediction of these dynamics to encompass the entire range of high-quality areas for marsh deer.

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Supporting Information

APPENDIX S1: Spatial distribution of covariates and 1km-sites segmented from flight paths.

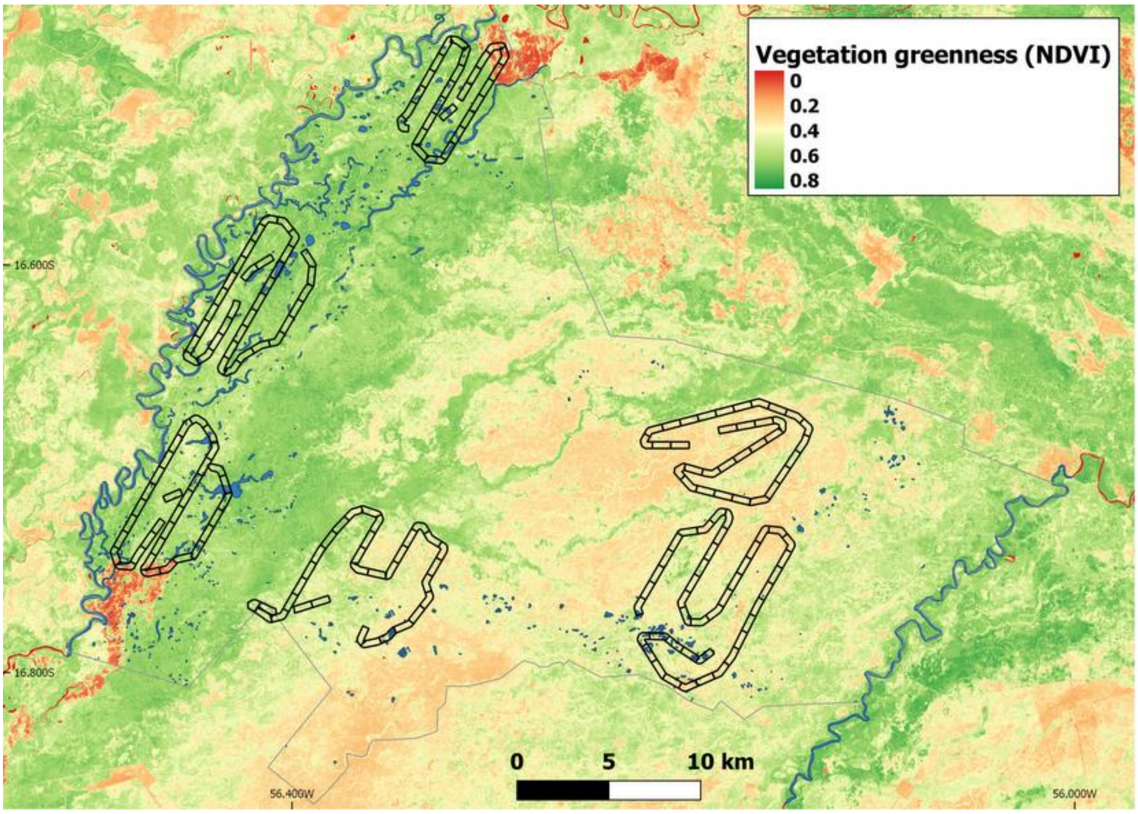

Figure S1. Spatial distribution of vegetation greenness (from Normalised Difference Vegetation Index) for the dry season (2017) in Sesc Pantanal Reserve (gray contour) as a proxy for quality forage for marsh deer. The NDVI was extracted from images of the Sentinel-2 satellite (10 m pixel resolution).

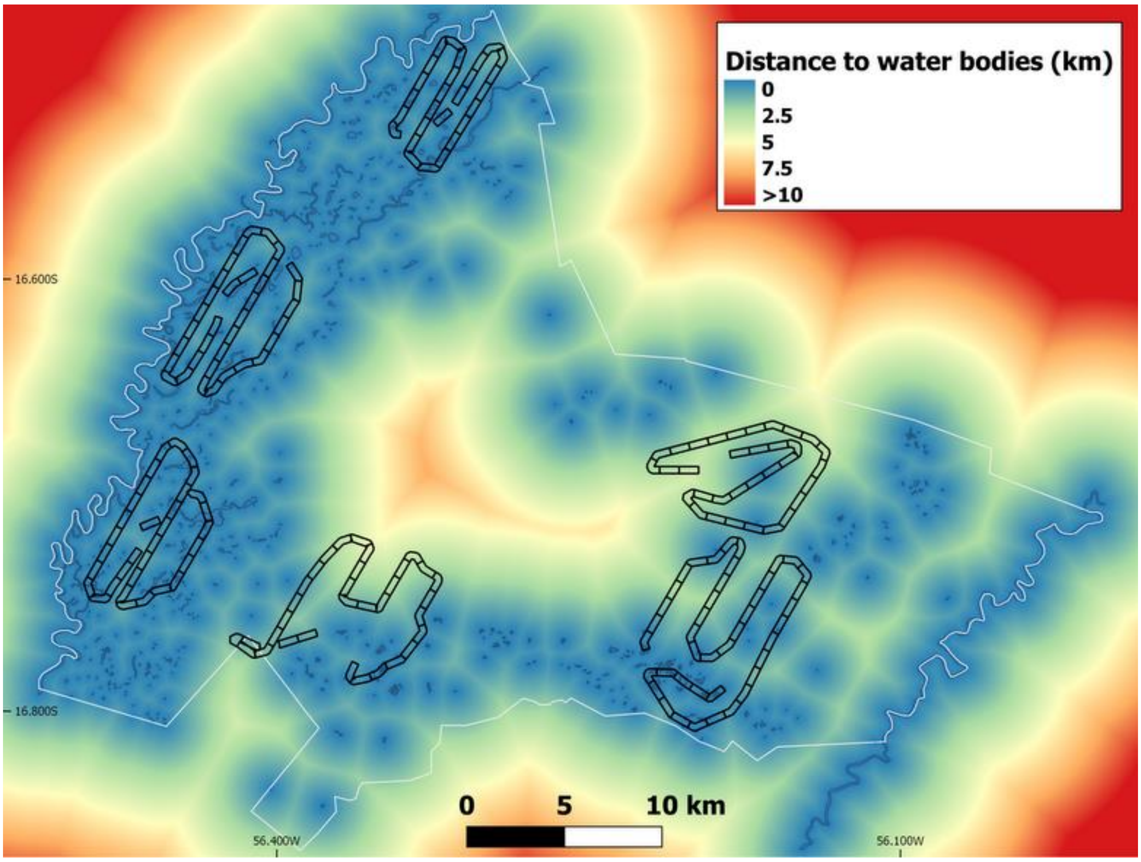

Figure S2. Distance to water bodies in the dry season (2017) of the Sesc Pantanal Reserve (white contour). The water bodies were extracted from images of the Sentinel-2 satellite (10 m pixel resolution) and the distance to the nearest water body was calculated for each pixel.

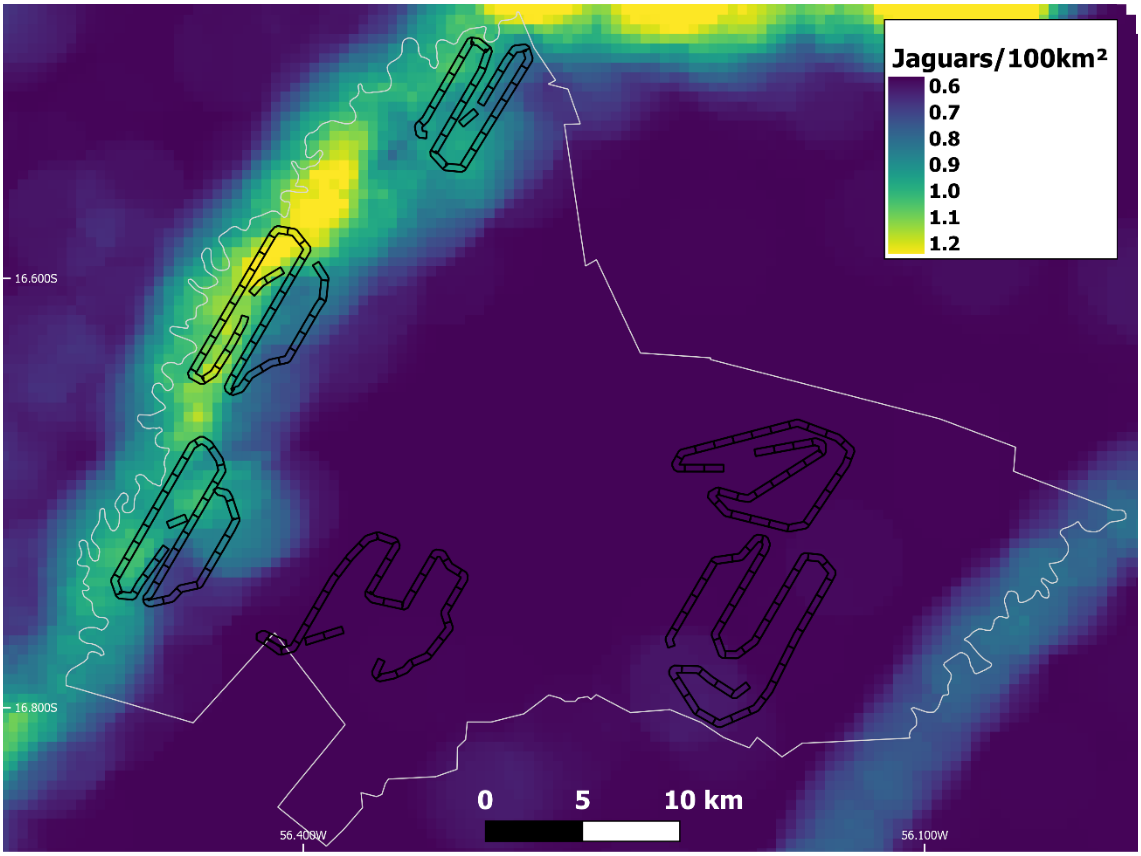

Figure S3. Density map of jaguars (*Panthera onca*) for the dry season (2016) in the Sesc Pantanal Reserve (white contour). Jaguar density was estimated using spatial captures of individuals from 355 camera trap stations in 2010-2012 that were fitted with closed population spatially explicit capture recapture models (SECR). The AICc best-ranked model presented the intensity of activity centers positively related to water amount in a 3000m-radius buffer. Then, we predicted this density map of jaguars to 2016, using the class water from a land cover map produced under a supervised classification of Landsat scenes (30 m spatial resolution).

APPENDIX S2: Model-selection results and coefficient tables

Table S1. Single observer (Binomial *N*-mixture) model selection results for local abundance (λ) and detection probability (p^*) of marsh deer in Pantanal wetland (Brazil). We tested the effects of vegetation greenness (ndvi), distance to water bodies (dist2water) and jaguar density (jaguars) on local abundance, and the effects of temperature (temp) and proportion of forest (forest) on detection probability, using drone surveys.

Model	***K***	**AICc**	**ΔAICc**	***w*AICc**
λ(ndvi+dist2water) p^*(temp+forest)	6	369.89	0	0.75
λ(ndvi+dist2water) p^*(forest)	5	372.26	2.37	0.23
λ(ndvi+dist2water) p^*(temp)	5	379.33	9.44	0.01
λ(ndvi) p^*(temp+forest)	5	379.94	10.05	0
λ(ndvi+dist2water) p^*(.)	4	380.17	10.28	0
λ(ndvi+jaguar) p^*(temp+forest)	6	381.94	12.05	0
λ(ndvi) p^*(forest)	4	382.45	12.56	0
λ(dist2water) p^*(temp+forest)	5	383.70	13.81	0
λ(ndvi*jaguar) p^*(temp+forest)	7	383.97	14.08	0
λ(ndvi+jaguar) p^*(forest)	5	384.42	14.53	0
λ(dist2water) p^*(forest)	4	385.40	15.51	0
λ(ndvi*jaguar) p^*(forest)	6	386.40	16.51	0
λ(dist2water) p^*(.)	3	390.31	20.42	0
λ(dist2water) p^*(temp)	4	390.41	20.52	0
λ(ndvi) p^*(temp)	4	392.30	22.41	0
λ(ndvi) p^*(.)	3	392.79	22.90	0
λ(ndvi+jaguar) p^*(temp)	5	394.03	24.14	0
λ(ndvi+jaguar) p^*(.)	4	394.64	24.75	0
λ(ndvi*jaguar) p^*(temp)	6	396.10	26.21	0
λ(ndvi*jaguar) p^*(.)	5	396.69	26.80	0
λ(jaguar) p^*(temp+forest)	5	401.20	31.31	0
λ(jaguar) p^*(forest)	4	402.97	33.08	0
λ(jaguar) p^*(temp)	4	406.70	36.81	0
λ(jaguar) p^*(.)	3	406.74	36.85	0
λ(.) p^*(temp+forest)	4	413.21	43.32	0
λ(.) p^*(forest)	3	413.65	43.76	0
λ(.) p^*(.)	2	417.19	47.30	0

λ(.) p*(temp)	3	418.37	48.48	0

K = number of estimated parameters; **AICc =** Akaike's Information Criteria adjusted for small sample size; **ΔAICc =** difference in the AICc values between top model and the current model; ***w*AICc =** AICc model weight.

Table S2. Double observer (Multinomial N-mixture) model selection results for local abundance (λ), availability probability (φ), and perception probability (p) of marsh deer in Pantanal wetland (Brazil). We tested the effects of vegetation greenness (ndvi), distance to water bodies (dist2water) and jaguar density (jaguars) on local abundance, and the effects of temperature (temp) and proportion of forest (forest) on availability, using drone surveys.

Model	***K***	**AICc**	**ΔAICc**	***w*AICc**
λ(ndvi+dist2water) φ(temp+forest) p(.)	7	469.89	0	0.74
λ(ndvi+dist2water) φ(forest) p(.)	6	472.12	2.23	0.24
λ(ndvi+dist2water) φ(temp) p(.)	6	478.62	8.73	0.01
λ(ndvi+dist2water) φ(.) p(.)	5	479.56	9.67	0.01
λ(ndvi) φ(temp+forest) p(.)	6	481.93	12.04	0
λ(dist2water) φ(temp+forest) p(.)	6	482.65	12.76	0
λ(ndvi+jaguar) φ(temp+forest) p(.)	7	484.08	14.19	0
λ(dist2water) φ(forest) p(.)	5	484.22	14.33	0
λ(ndvi) φ(forest) p(.)	5	484.25	14.36	0
λ(ndvi*jaguar) φ(temp+forest) p(.)	8	486.24	16.35	0
λ(ndvi+jaguar) φ(forest) p(.)	6	486.37	16.48	0
λ(ndvi*jaguar) φ(forest) p(.)	7	488.51	18.62	0
λ(dist2water) φ(.) p(.)	4	488.73	18.84	0
λ(dist2water) φ(temp) p(.)	5	488.75	18.86	0
λ(ndvi) φ(temp) p(.)	5	493.5	23.61	0
λ(ndvi) φ(.) p(.)	4	494.01	24.12	0
λ(ndvi+jaguar) φ(temp) p(.)	6	494.84	24.95	0
λ(ndvi+jaguar) φ(.) p(.)	5	495.55	25.66	0
λ(ndvi*jaguar) φ(temp) p(.)	7	496.95	27.06	0
λ(ndvi*jaguar) φ(.) p(.)	6	497.63	27.73	0
λ(jaguar) φ(temp+forest) p(.)	6	500.95	31.05	0
λ(jaguar) φ(forest) p(.)	5	502.56	32.66	0

λ(jaguar) φ(temp) p(.)	5	505.78	35.88	0
λ(jaguar) φ(.) p(.)	4	505.93	36.04	0
λ(.) φ(temp+forest) p(.)	5	514.25	44.36	0
λ(.) φ(forest) p(.)	4	514.51	44.62	0
λ(.) φ(.) p(.)	3	517.43	47.54	0
λ(.) φ(temp) p(.)	4	518.57	48.68	0

***K* =** number of estimated parameters; **AICc =** Akaike's Information Criteria adjusted for small sample size; **ΔAICc =** difference in the AICc values between top model and the current model; ***w*AICc =** AICc model weight.

Table S3. Coefficient estimates for marsh deer local abundance and detection using the single observer (Binomial *N*-mixture) or double observer (Multinomial *N*-mixture) top-ranked models, analyzed from drone-based counts in Pantanal wetland (Brazil). ndvi = vegetation greenness; dist2water = distance to water bodies; temperature = air temperature during flight; %forest = proportion of forest. All covariates were scaled.

	SINGLE OBSERVER (Binomial *N*-mixture)				**DOUBLE OBSERVER** (Multinomial *N*-mixture)			
	Est.	**SE**	**-95%**	**+95%**	**Est.**	**SE**	**-95%**	**+95%**
Local abundance (λ)								
λ (Intercept)	-1.08	0.35	-1.76	-0.39	-1.04	0.36	-1.74	-0.34
ndvi	0.72	0.20	0.33	1.11	0.68	0.19	0.30	1.06
dist2water	-1.02	0.36	-1.74	-0.31	-1.09	0.37	-1.81	-0.37
Detection processes								
p^* (Intercept)	-2.05	0.34	-2.71	-1.39	-	-	-	-
φ (Intercept)	-	-	-	-	-2.79	0.32	-3.41	-2.16
temperature	-0.34	0.16	-0.65	-0.02	-0.30	0.14	-0.58	-0.01
forest	-0.72	0.21	-1.14	-0.30	-0.63	0.19	-1.00	-0.25
p (Intercept)	-	-	-	-	2.57	0.53	1.53	3.62

APPENDIX S3: Confidence intervals (95%) in marsh deer local abundance map

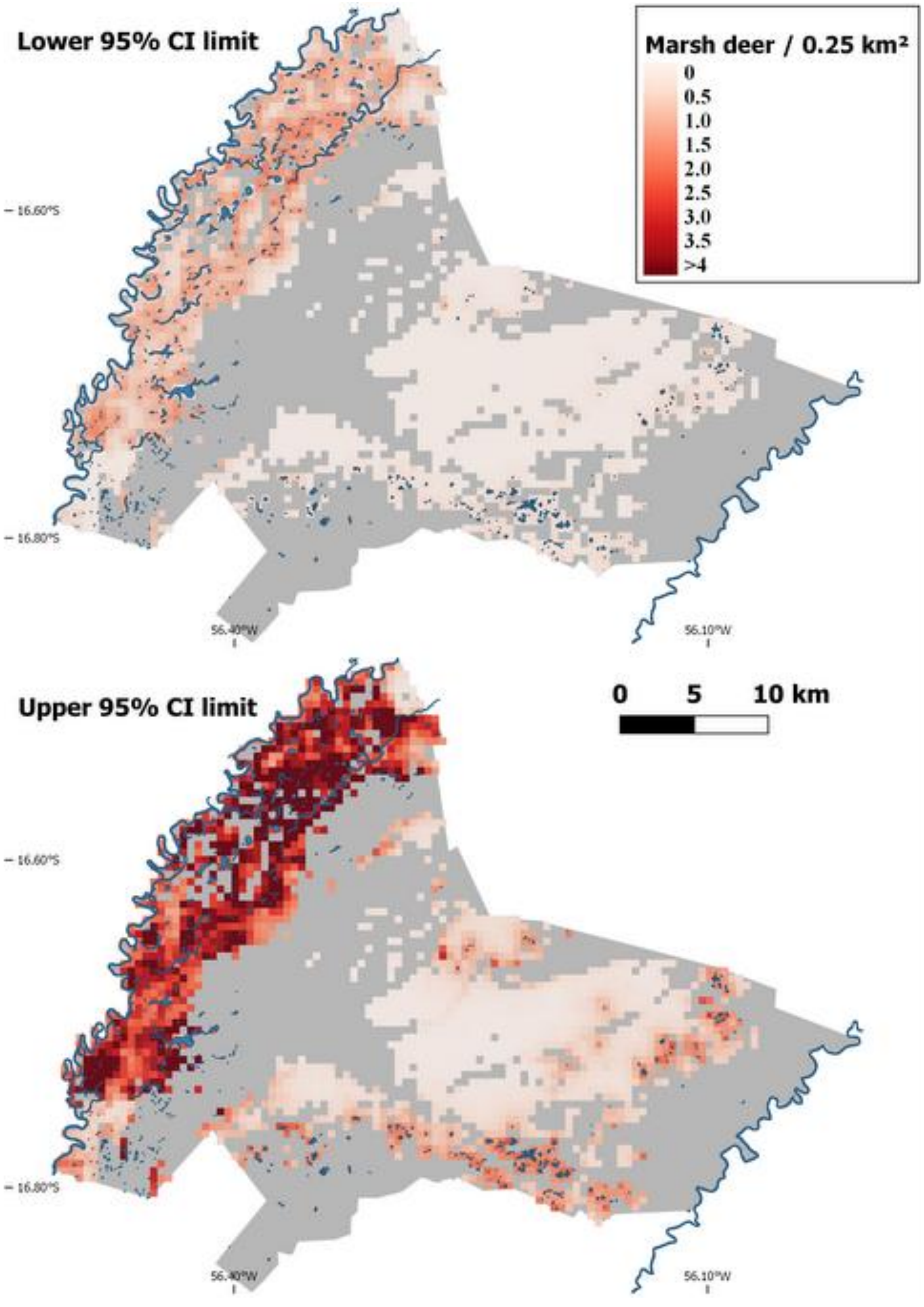

Figure S4. 95% confidence intervals marsh deer local abundance for the dry season of 2017 in Sesc Pantanal Reserve, derived from spatially replicated drone counts. Blue polygons indicate water bodies and gray areas correspond to highly forested areas (>80%) for which local abundance was not predicted.

APPENDIX S4

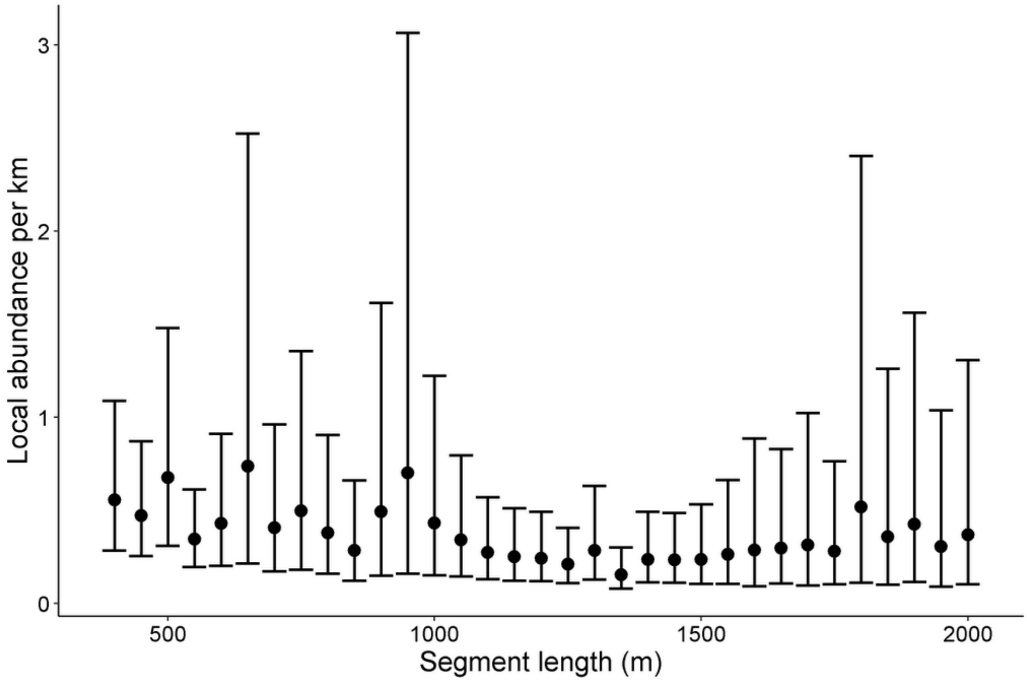

Figure S5. Marsh deer local abundance estimates for different segment lengths for the flight paths in Pantanal wetland (Brazil), using a constant double observer Multinomial *N*-mixture model, analyzed from drone-based counts.

APPENDIX S5: Count data, covariates, and R script for analysis.

Data in “CountDataCovariates_Bracketal2021.RData”, available at https://figshare.com/s/3b392fce55d83b43cdc1

CAPÍTULO 3

Optimally designing drone surveys for wildlife abundance modeling with N-mixture models

Douglas Berto

Este capítulo será submetido ao periódico ***Methods in Ecology and Evolution***.

Optimally designing drone surveys for wildlife abundance modeling with N-mixture models

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Abstract

1. Hierarchical N-mixture models have been suggested for abundance estimation from spatiotemporally replicated drone-based count surveys, since they allow modeling abundance of unmarked individuals while accounting for detection errors. However, it is still necessary to understand how these models perform in the wide variety of contexts and species drone surveys are being used. This knowledge is fundamental to plan study designs with optimal allocation of scarce resources in ecology and conservation.
2. We conduct a simulation study to address N-mixture model (binomial and multinomial) performance and optimal survey effort allocation in different scenarios of local abundance and detectability of individuals, focusing on their application for drone-based surveys. We also investigate the benefits of using a double-observer protocol in image review to decompose the detection process in availability and perception. Finally, we illustrate our simulation-based survey design considerations by applying them to abundance estimation of marsh deer in Pantanal wetland (Brazil).

3. Accuracy of abundance estimation with N-mixture models increases with local abundance in sites and especially with the availability of individuals. An optimized design requires more visits in fewer sites when availability probability is lower, and the optimal design is more flexible as local abundance increases. Two observers checking images can increase the estimator performance even at very high perception probabilities. The use of a double-observer protocol in image review can reduce fieldwork effort while achieving the same accuracy.
4. N-mixture models can deliver accurate abundance estimates from spatiotemporally replicated drone surveys in a wide variety of contexts while accounting for imperfect detection. The improvements achieved by a consciously planned design, rearranging survey effort among sites and visits, as well as using a second observer in image review, can be crucial to detect trends when monitoring a population or to categorize a species as threatened or not.

Key-words: abundance estimation, aerial surveys, count data, double observer, effort allocation, hierarchical models, imperfect detection, sampling design

Introduction

The use of drones (a.k.a. Unmanned Aerial Vehicles or Remotely Piloted Aircrafts) to survey wildlife populations has spread to many different species in many different contexts. Drones are replacing conventional aircrafts to survey for instance large herbivores (e.g. Barasona et al., 2014; Rey et al., 2017; Vermeulen et al., 2013), waterbirds (e.g. Hodgson et al., 2018; Hong et al., 2019), marine mammals (e.g. Goebel et al., 2015; A. Hodgson et al., 2013, 2017), and crocodiles (e.g. Ezat et al., 2018). Furthermore, given the flexibility of this tool, drone surveys are being explored for situations where conventional aircrafts were unsuitable before, expanding the ability of aerials surveys to sample smaller species (e.g. canids, Bushaw & Ringelman, 2019; sharks and rays, Kiszka et al., 2016) and in forested areas (e.g. primates, Melo, 2021; koalas, Hamilton et al., 2020). Thus, drone surveys are improving the way we collect abundance data for ecological studies (e.g. population dynamics) or conservation/management issues (e.g. threatened or invasive species monitoring).

To estimate the abundance of wildlife populations using drones, counts need to be carried out by searching a species of interest on the images or footage obtained along with the flights. Errors in these counts might bias estimation of abundance if not properly addressed. Some individuals may be hidden (e.g. below vegetation, inside a burrow, or underwater) and therefore are not visible on images, or may be indistinguishable from the background making them difficult to detect. An individual can thus be missed, yielding false-negative errors in counts (i.e. imperfect detection), by two different processes: i) it is unavailable for detection or ii) given that it appears on an image, it can be missed by a human observer or an algorithm during reviewing (Brack et al., 2018). As in other wildlife survey methods, processes driving these detection errors in drone-based counts can vary in space and time, and may depend on species characteristics (e.g. conspicuity and behavior), habitat features (e.g. tree coverage or water turbidity), and conditions when surveying (e.g. weather) (Guillera-Arroita, 2017). Furthermore, some characteristics specific to drone surveys could also affect detectability, such as sensor type (e.g. thermal or visible), pixel resolution, and flight height.

Hierarchical N-mixture models have been suggested to model abundance from spatiotemporally replicated aerial counts since they are a valuable framework for studying unmarked populations while accounting for the sources of imperfect detection

(Brack et al., 2018; Christensen et al., 2021; Martin et al., 2015; Williams et al., 2017). In such approach, count data obtained for each visit (i.e. repeated flight) in each site are modelled as a result of (at least) two hierarchically connected processes: local abundance at sites and observation process of individuals in each visit for each site (susceptible to imperfect detection). Moreover, a double-observer protocol can be applied to image review to permit decomposing the detection process in two components: *availability* of individuals to detection in the images and *perception errors* (not detecting those available individuals in the images). By fitting these double-observer count data on spatiotemporally replicated surveys, it is possible to address the two common sources of false-negative errors in aerial surveys – availability and perception – without resorting to auxiliary data such as biotelemetry marked individuals (Brack et al., 2018).

The accuracy of hierarchical models for estimating abundance depends on several factors, including population density, sample size, and detectability (e.g. availability and perceptibility), so their efficient use depends on an adequate sampling design. Furthermore, the reliability of drone surveys to assess abundance in different contexts relies on assessing how these abundance estimators perform in a wide variety of scenarios of population densities and detection probabilities of individuals. Since the total effort in fieldwork is commonly limited by a fixed budget B, the sampling design of hierarchical models must distribute this budget in a specific combination of number of sites S and visits J so that $B = S*J$. A survey design could be planned to spend the budget by visiting more sites but with less visits; this gives more sampling units to better estimate abundance, but fewer records per site and hence less information to estimate detection probabilities. On the other hand, one could choose to characterize the detection process more thoroughly by spending the budget with more repeated visits to fewer sites, but possibly forgoing the ability to capture variations in abundance. Thus, for each scenario of population density and detectability, there is an optimal combination of survey design elements in this trade-off (i.e. prioritize more sites and less visits, or more visits in fewer sites) that produces the most accurate estimation of abundance.

As different scenarios demand different effort allocations, it is important to optimize the available budget to an efficient spending of the usually scarce resources for ecological studies (i.e. conscious sampling design) (e.g. Conn et al., 2016; Knights et al., 2021). Simulation experiments are a powerful approach to address the performance of estimators in different contexts and assess optimal survey allocation to assist sampling design decisions (Kéry & Royle, 2016; Zurell et al., 2010). In short, this kind of experiment encompasses a computer-based stochastic simulation of the data collection process over a simulated population for which the true underlying parameters are known in both levels (biological and observational). Then, simulated data are fitted to the respective (or an alternative) model structure, and the capacity of the estimator to rescue true parameter values is evaluated (performance).

Performance of N-mixture models, particularly the binomial N-mixture model for single observer counts, has been evaluated before but in limited scenarios of abundance, detection probability, and number of sites and visits, or evaluating model performance in the presence of assumption violations (Duarte et al., 2018; Kéry & Royle, 2016; Veech et al., 2016; Yamaura, 2013). Here, we provide a very wide scan of N-mixture models performance and survey effort allocation (as for occupancy-detection models in Mackenzie & Royle, 2005) in different scenarios of population abundance and detectability of individuals, focusing on their application for drone-based surveys. We also investigate the benefits of using a double-observer protocol to decompose the detection process in availability and perception. We conducted three experiments creating simulated count data from spatiotemporally replicated surveys and fitting N-mixture models to the data aiming to:

1) Assess the performance of N-mixture models using double and single observer counts under different scenarios of local abundance and detection probability, and address the optimal survey effort allocation in terms of spatial vs. temporal prioritization for each scenario.
2) Investigate how the use of a double-observer protocol increases model performance and affects optimal survey effort allocation.
3) Evaluate if the use of a double-observer protocol can reduce the fieldwork effort required to match the performance of the single observer approach in the same circumstances.

Finally, we showcase our simulation-based survey design considerations by applying them to estimate the abundance of marsh deer (*Blastocerus dichotomus*) in Pantanal wetland (Brazil).

N-mixture models for spatiotemporally replicated drone surveys

To estimate abundance with N-mixture models, drone flights are conducted with repeated visits in multiple sites (i.e. spatiotemporally replicated) and counts are carried out in the collected imagery by either one or two observers (human and/or an algorithm) (Figure 1). Assuming abundance M_i at sites $i \in \{1, \ldots, S\}$ is constant along visits $j \in \{1, \ldots J\}$, we can model this local abundance at sites under a Poisson distribution (or other distribution for count data) with mean (and variance) λ:

$$M_i \sim \text{Poisson}(\lambda).$$

With a single observer reviewing imagery, counts Y_{ij} for each visit j at each site i are determined by a binomial distribution in which each individual of the local population M_i has a probability p^* of being detected:

$$Y_{ij} \sim \text{binomial}(M_i, p^*), \text{ where } p^* = \varphi.\ p.$$

In this case, it is not possible to decompose the detection probability p^*, assumed to be the product of two processes: availability probability φ and perception probability p. This two-level model for single observer counts is called binomial N-mixture model (Kéry et al., 2005; Royle, 2004).

When using a double-observer protocol for image review, the observation process can be segregated into two levels. Then, each individual of M_i has a probability φ of being available for detection in (the image correspondent to) each visit j, so de facto of the M_i individuals, only N_{ij} will be available for detection in the imagery:

$$N_{ij} \sim \text{binomial}(M_i, \varphi).$$

When sampled sites are truly closed throughout visits (no entries nor departures of individuals), the availability process described by φ corresponds to the probability of an individual present at the site i to not being hidden. However, not rarely when sampling wildlife species, individuals could move in and out the surveyed sites. Then, availability would correspond to two processes: i) the probability of the individual (that has its home range overlapping the sampled site) to being present at the site i in visit j and ii) not being hidden (Brack et al., 2018; Chandler et al., 2011; Kéry & Royle, 2016).

Finally, each individual from the available pool N_{ij}, has a probability p of being detected by each observer (independently), resulting in four possible *encounter histories* (as in a capture-recapture procedure): k_1 = ‘11’ detected by both observers; k_2 = ‘10’ only detected by the first observer; k_3 = ‘01’ only detected by the second observer); and k_4 = ’00’ not detected by any observer. Thus, the resulting count data Y_{ijk} for each visit j, at each site i, and under each observable encounter histories $k \in \{1,2,3\}$ is modeled as a function of multinomial conditional cell probabilities π_k:

$$Y_{ijk} \sim \text{multinomial}(N_{ij},\ \pi(p)_k)$$

in which, the probability of each observable encounter history is determined as $k_{11} = p^2$; $k_{10} = p(1 - p)$; and $k_{01} = (1 - p)p$. This three-level model for independent double observer counts is known as multinomial N-mixture model with a temporary emigration component, hereafter “multinomial” (Chandler et al., 2011). The double-observer protocol can be applied in only a proportion (i.e. subset) of the imagery (flights), still being possible to segregate the two observation levels by modeling the data from the mixed double and single observer protocols.

For each of the presented levels, heterogeneity in the basic parameters (λ, φ, p, p^*) can be modeled as a function of explanatory variables through linear regression and an appropriate link function (log for λ and logit for probabilities).

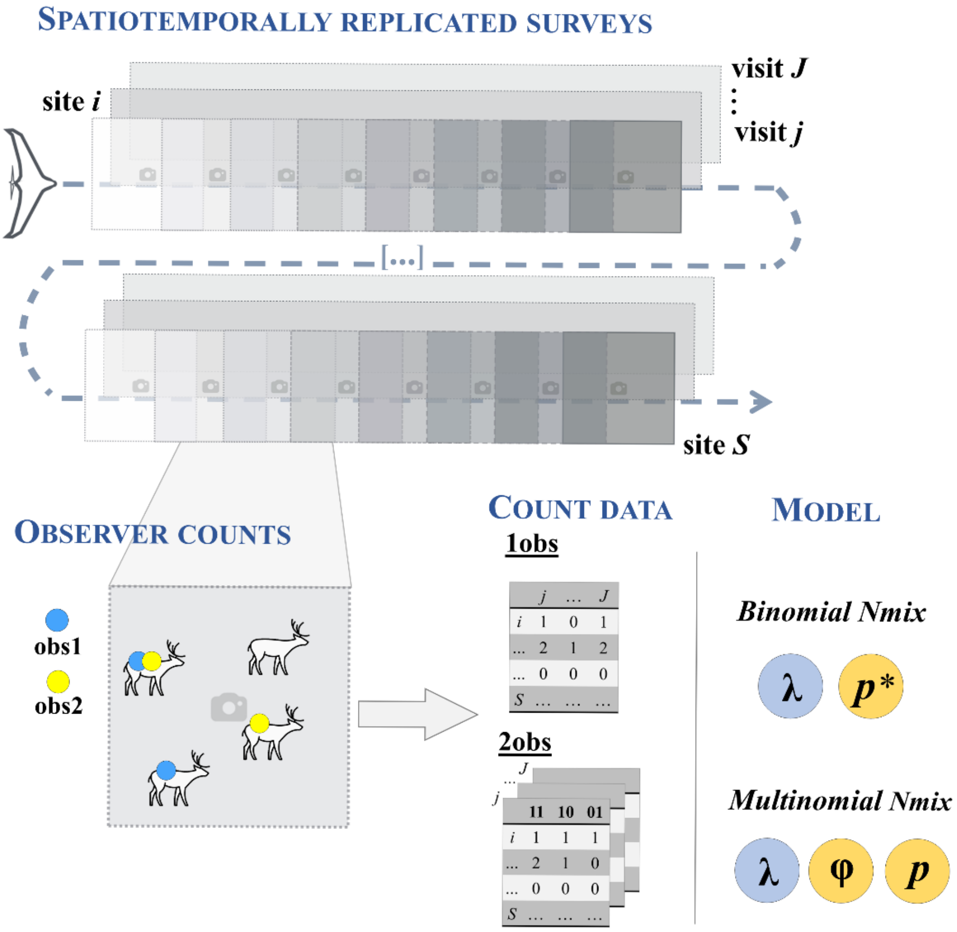


Figure 3. Sampling design, count data and N-mixture models for spatiotemporally replicated drone-based surveys with a single or multiple observers reviewing images. Single observer counts are fitted with binomial N-mixture models and multiple observer counts under a Multinomial N-mixture model with a temporary emigration component. Parameters: λ = local abundance; p* = overall detection probability; φ = availability probability; and p = perception probability. Figure adapted from Brack et al. (2021).

Simulations General Design

To assess the performance and optimal design of N-mixture models for drone-based surveys, we simulated count data under single and double observer review protocols and analyzed them with the correspondent N-mixture model structure (binomial or multinomial). In software R (R Core Team, 2020), we simulated the local abundance as Poisson distributed, a binomial outcome for available individuals (in the multinomial model) and for the single observer counts under overall detection (in the binomial model), and a multinomial outcome derived from the perception probability by the observers for the double observer counts. For each simulation, we defined the number of sites, visits, and observers and the true local abundance, availability, and perception probabilities. We considered all model parameters constant (i.e. no covariates), a common practice in survey design studies that aim to find general design principles (e.g. Guillera-Arroita et al., 2010; Mackenzie & Royle, 2005; Yamaura, 2013). We fitted simulated data using maximum likelihood estimation with the R package *unmarked* (Fiske & Chandler, 2011), utilizing the *pcount* function for the single observer data and *gmultmix* for the mixed- and double-observer protocols.

All simulation results and code to reproduce the simulations and results of this paper are available at https://github.com/ismaelvbrack/designNmix4droneSurveys. We provide R code to simulate and analyze data under both modeling structures (single binomial and double multinomial N-mixture models, including the mixed-protocol model) using maximum likelihood estimation, as well as BUGS code to conduct Bayesian analysis for the same models using JAGS software (Plummer, 2003) from R (*jagsUI* package; Kellner, 2015). As supplementary material, we provide an interactive "ready-to-consult" website (https://ismaelvbrack.github.io/designNmix4droneSurveys) to assist future studies with planning drone-based surveys according to specific scenarios of expected local abundance and detectability. There, it is possible to explore all results of this study on the performance of N-mixture models with single and double observers and the optimal survey effort allocation in a user-friendly interface, besides simulating examples of these models.

For each simulation study, we defined different scenarios considering local abundance, availability, and perception probability. For each of these, we simulated data collection and analysis for different combinations of number of sites, visits and observers, and calculated the estimator accuracy for the local abundance parameter based on 2000 iterations of the simulation using the root mean squared error relative to the true parameter value ($\text{rel.RMSE} = {}^{1}\!/_{\lambda} \sqrt{\frac{1}{n} \sum_{i=1}^{n} (\hat{\lambda}_i - \lambda)^2}$; in which *n* is the number of iterations, $\hat{\lambda}$ is the estimated local abundance and λ is the true known local abundance). The lowest rel.RMSE value for each scenario of {λ, φ} was used to define the optimal survey design $J_{\text{opt}} = B/S_{\text{opt}}$. From the 2000 iterations of each scenario, we excluded those with no convergence or with infinite abundance estimates (upper 95% confidence intervals > 200 individuals, associated with detection probabilities near zero). To the purpose of using N-mixture models for drone-based counts, we fixed the perception probability *p* at 0.8, considering what we have seen as a moderately low perception threshold in studies with drone surveys (e.g. Brack et al., 2021; Patterson et al., 2016; Preston et al., 2021; Vermeulen et al., 2013). However, for other applications of N-mixture models with availability and perception observation processes (e.g. auditory bird point counts, terrestrial strip transects of burrowing species, or boat-based counts of marine mammals), scenarios with lower perception probabilities should be explored (with just slight modifications in the code provided). We also note that, if the study focus is not on the local abundance level but other parameters (e.g. availability or detection), defining optimality with respect to these parameters is likely to lead to different optimal survey designs (Guillera-arroita et al., 2010).

Simulation Study 1: optimal design of count surveys for N-mixture abundance estimation

We assessed the performance and optimal effort allocation of N-mixture models for drone surveys in 73 scenarios defined from the combination of 11 mean local abundances in sites λ {0.1; 0.2; 0.3; 0.5; 1; 2; 4; 8; 12; 20; 40} and eight availability probabilities φ {0.1; 0.2; 0.3; 0.4; 0.5; 0.6; 0.7; 0.8}. For the last three values of local abundance, we only combined them with availabilities of {0.1; 0.2; 0.5} to check general tendencies for higher local abundances and because simulations can be highly time-consuming. Perception probability *p* was fixed at 0.8. We defined a fixed total effort (budget) of B = 2000 flights (i.e. 2000 site-visits); we purposely chose a high number here to represent a case where data are not a limiting factor for analysis (large sample dataset) and hence ensure that large-sample approximations from maximum likelihood estimation hold in scenarios of low local abundance and/or detectability. For each scenario, we tested different combinations of this total effort on the distribution of sites *S* and visits *J* so that B = *S*J* (e.g., 1000 sites with 2 visits, 250 sites with 8 visits, 100 sites with 20 visits and so on). We ranged the number of visits from *J* = 2 until either *J* = 10 visits or until being sure that the rel.RMSE was rising up (i.e. the estimator accuracy was decreasing).

We then assessed the accuracy of the estimator of local abundance (based on the rel.RMSE from the 2000 iterations) for each number of visits in each scenario of {λ, φ}. We found the optimal survey design for each scenario based on the lowest rel.RMSE value. Because of the difference in rel.RMSE between numbers of visits was very low for many scenarios, we also obtained the range of designs ($S*J$) for which the rel.RMSE was lower than 0.5% and considered the accuracy inside this range as equivalent. This means that a range of designs results in very similar performance and thus other criteria (e.g. travel times between sites) could be used to choose among those possibilities to design studies.

We repeated this procedure on the 73 scenarios considering the single observer counts (binomial N-mixture model) and the (full) double-observer protocol (multinomial N-mixture model). Finally, we checked whether the pattern we found for optimal designs across scenarios was consistent for a different total survey effort using B = 4000 flights, that is, if the pattern for J_{opt} is independent of the total effort as it is observed for the related occupancy-detection models (Mackenzie & Royle, 2005). For this last analysis, we only considered six scenarios using local abundances {0.2; 1} and availability probabilities {0.2; 0.4; 0.6}.

Results

Both model structures – single observer binomial and double observer multinomial N-mixture models – presented unbiased estimations of local abundance for all evaluated scenarios. The rel.RMSE of N-mixture models under the optimal number of visits in each scenario of local abundance λ and availability φ ranged from 0.024 to 0.426 for the single observer model and from 0.017 to 0.378 for the double observer model. That is, under optimal survey effort allocation, the mean error of the estimator relative to the true local abundance ranged between ~2% and ~40%, depending on population density (local abundance in sites) and availability of individuals. Estimators reached much larger rel.RMSE values (near one) for designs with a small number of visits in scenarios of low local abundance ≤ 0.5 (Figures S1-S2). Only in one scenario ($\lambda = 0.1$; $\varphi = 0.1$), the rel.RMSE was higher than 30% (for both modeling approaches).

The loss of performance from the single to double observer approaches (i.e. difference in rel.RMSE) was 0.05 lower for the {$\lambda = 0.1$; $\varphi = 0.1$} scenario, and this difference reduced with the increase in local abundance and/or availability (Figures S1-S2). The accuracy of both model structures increased with local abundance λ and especially with the availability of individuals φ.

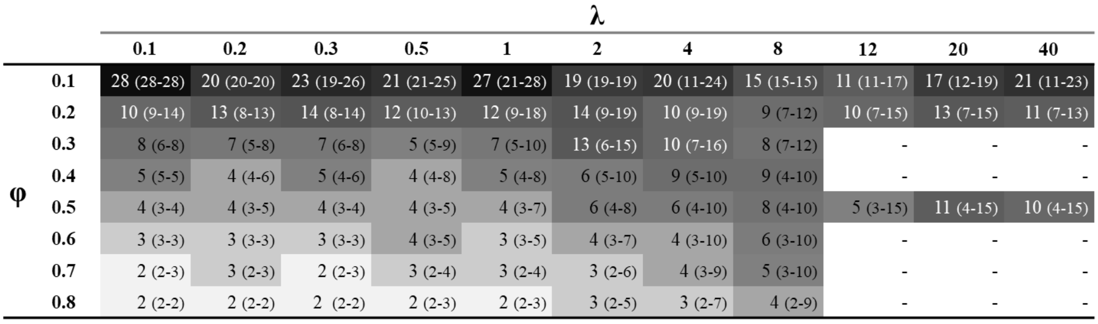
The optimal number of visits varied from $J = 28$ to $J = 2$ for the single observer model and from $J = 22$ to $J = 2$ for the double observer model depending on the scenario of local abundance and availability (Table 1). Generally, J_{opt} decreased especially with increasing availability φ, and it was lower for the double observer model than for the single observer one. The range of possible optimal number of visits J_{opt} (i.e. considered equivalent with a difference in rel.RMSE<0.5%) increased with local abundance λ (Table 1).

For the six scenarios we evaluated a different total effort B = 4000 ($\lambda = \{0.2; 1\}$; $\varphi = \{0.2; 0.4; 0.6\}$), we found a very similar J_{opt} (except for a few stochastic differences because of the number of iterations). We interpret this as supporting the idea that the optimal number of visits is independent of the total effort in large sample sizes for both binomial and multinomial N-mixture models (Figure S3).

Table 1. Optimal number of visits (J_{opt}) in spatiotemporally replicated drone-based surveys for abundance modeling with N-mixture models, under different scenarios of local abundance (λ) and availability probability (φ). **a)** Binomial N-mixture model for single observer counts. **b)** Multinomial N-mixture model for double observer counts. The optimal J is obtained from the lowest relative root mean square error (rel.RMSE) calculated from 2000 iterations for each combination of the number of sites S and visits J. In brackets, the range of visits J for which the performance can be considered

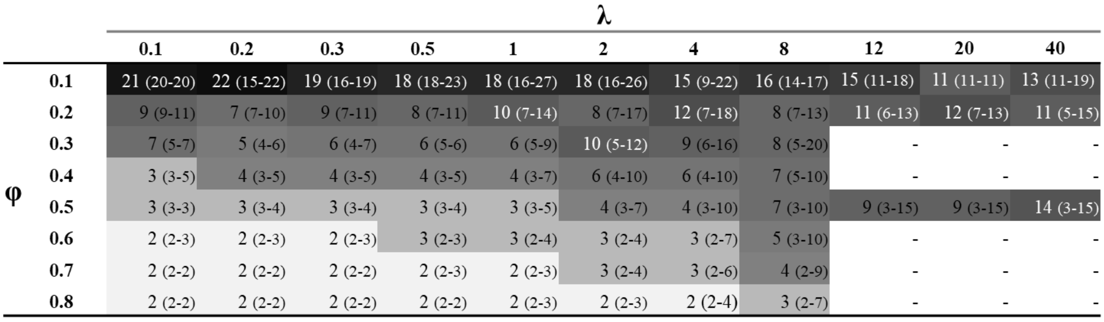
equivalent (i.e. rel.RMSE < 0.5%). Shading of the table cells (from light gray to black) indicates an increasing J_{opt}.

a. *Single observer (Binomial) N-mixture model*



		λ										
		0.1	**0.2**	**0.3**	**0.5**	**1**	**2**	**4**	**8**	**12**	**20**	**40**
φ	**0.1**	28 (28-28)	20 (20-20)	23 (19-26)	21 (21-25)	27 (21-28)	19 (19-19)	20 (11-24)	15 (15-15)	11 (11-17)	17 (12-19)	21 (11-23)
	0.2	10 (9-14)	13 (8-13)	14 (8-14)	12 (10-13)	12 (9-18)	14 (9-19)	10 (9-19)	9 (7-12)	10 (7-15)	13 (7-15)	11 (7-13)
	0.3	8 (6-8)	7 (5-8)	7 (6-8)	5 (5-9)	7 (5-10)	13 (6-15)	10 (7-16)	8 (7-12)	-	-	-
	0.4	5 (5-5)	4 (4-6)	5 (4-6)	4 (4-8)	5 (4-8)	6 (5-10)	9 (5-10)	9 (4-10)	-	-	-
	0.5	4 (3-4)	4 (3-5)	4 (3-4)	4 (3-5)	4 (3-7)	6 (4-8)	6 (4-10)	8 (4-10)	5 (3-15)	11 (4-15)	10 (4-15)
	0.6	3 (3-3)	3 (3-3)	3 (3-3)	4 (3-5)	3 (3-5)	4 (3-7)	4 (3-10)	6 (3-10)	-	-	-
	0.7	2 (2-3)	3 (2-3)	2 (2-3)	3 (2-4)	3 (2-4)	3 (2-6)	4 (3-9)	5 (3-10)	-	-	-
	0.8	2 (2-2)	2 (2-2)	2 (2-2)	2 (2-3)	2 (2-3)	3 (2-5)	3 (2-7)	4 (2-9)	-	-	-

b. *Double observer (Multinomial) N-mixture model*



		λ										
		0.1	**0.2**	**0.3**	**0.5**	**1**	**2**	**4**	**8**	**12**	**20**	**40**
φ	**0.1**	21 (20-20)	22 (15-22)	19 (16-19)	18 (18-23)	18 (16-27)	18 (16-26)	15 (9-22)	16 (14-17)	15 (11-18)	11 (11-11)	13 (11-19)
	0.2	9 (9-11)	7 (7-10)	9 (7-11)	8 (7-11)	10 (7-14)	8 (7-17)	12 (7-18)	8 (7-13)	11 (6-13)	12 (7-13)	11 (5-15)
	0.3	7 (5-7)	5 (4-6)	6 (4-7)	6 (5-6)	6 (5-9)	10 (5-12)	9 (6-16)	8 (5-20)	-	-	-
	0.4	3 (3-5)	4 (3-5)	4 (3-5)	4 (3-5)	4 (3-7)	6 (4-10)	6 (4-10)	7 (5-10)	-	-	-
	0.5	3 (3-3)	3 (3-4)	3 (3-4)	3 (3-4)	3 (3-5)	4 (3-7)	4 (3-10)	7 (3-10)	9 (3-15)	9 (3-15)	14 (3-15)
	0.6	2 (2-3)	2 (2-3)	2 (2-3)	3 (2-3)	3 (2-4)	3 (2-4)	3 (2-7)	5 (3-10)	-	-	-
	0.7	2 (2-2)	2 (2-2)	2 (2-2)	2 (2-3)	2 (2-3)	3 (2-4)	3 (2-6)	4 (2-9)	-	-	-
	0.8	2 (2-2)	2 (2-2)	2 (2-2)	2 (2-2)	2 (2-3)	2 (2-3)	2 (2-4)	3 (2-7)	-	-	-

Simulation Study 2: exploring the benefit of the double-observer protocol

To assess the improvement in accuracy with the use of a double-observer protocol, we defined six scenarios: local abundances λ {0.2; 1} and availability probabilities φ {0.2; 0.4; 0.6} and fixed $p = 0.8$. For each scenario, we tested different combinations of number of sites S and visits J using a fixed total effort of B = 2000 for different proportions of the flights checked by two observers (double-observer protocol): {0%; 20%; 40%; 60%; 80%; 100%}. The 0% corresponds to the single observer binomial model, the 100% corresponds to the full double observer multinomial model (both considered in simulation experiment 1), and the rest are mixed protocols with only a percentage of flights reviewed by a second observer.

The simulation procedure was as in simulation study 1 (rel.RMSE from 2000 iterations under each number of visits; total survey budget B = 2000 flights) for each proportion of the double-observer protocol. For each double observer proportion, we found the optimal design J_{opt} for each scenario of {λ, φ} with the lowest rel.RMSE. Because of the stochasticity from the 2000 iterations, we estimated a linear trend of the rel.RMSE in relation to the proportion of double observer review and calculated the linear decrease in rel.RMSE in relation to the single observer model (0%).

Results

The accuracy of the abundance estimator increased (decreasing rel.RMSE) with the proportion of images checked by two observers (Figure 2). The difference in accuracy reached almost 15% for the full double observer model in the {λ = 1; φ = 0.6} scenario (compared to the baseline performance of a single observer). The optimal allocation of effort showed a tendency to decrease the number of repeat visits (lower *J*), thus allowing visiting more sites (higher *S*), as the proportion of double-observer protocol increases (Figure S4).

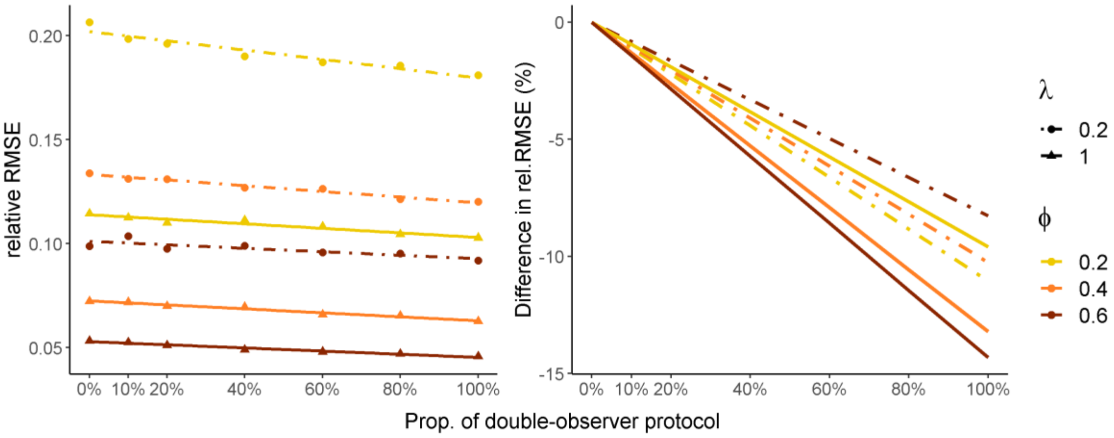


Figure 4. Accuracy (relative RMSE) and increase in accuracy (difference in rel.RMSE) in abundance estimation with N-mixture models in relation to the proportion of double-observer protocol in image reviewing, and under different scenarios of local abundance in sites (λ) and individual availability probability (φ). 0% = single observer binomial N-mixture model; 100% = full double observer multinomial N-mixture model; the others are mixed protocols of multinomial N-mixture models.

Simulation Study 3: reducing fieldwork effort by employing a double-observer protocol

We have seen how the double-observer protocol leads to an increased accuracy in the estimation of local abundance. Alternatively, double observers could be used to reduce the amount of fieldwork effort needed to match the same accuracy that is obtained from an optimal design of the single observer model. We explored this strategy using the same six scenarios of simulation study 2 ($\lambda = \{0.2; 1\}$; $\varphi = \{0.2; 0.4; 0.6\}$; $p = 0.8$) by calculating the proportional reduction of total fieldwork effort (B = 2000 flights) that can be achieved with a double-observer protocol while still matching the accuracy (lowest rel.RMSE) of the single observer model under optimal design J_{opt}.

To do this, we started with the full budget B = 2000 for the double observer model and reduced B (under its optimal number of visits, thus reduced the number of sites) until we reached an accuracy (rel.RMSE) similar to the target single observer rel.RMSE. Because of the long computational time, we conducted this search in only six incremental steps. In the first step we reduced the total effort to 50% (B = 1000 flights). Then for each subsequent search steps, the difference in B was reduced by 50% ("half-way" distance) between the last step and either the full reference effort (B = 2000) or the effort in the previous step, depending on if the rel.RMSE was over or under the target rel.RMSE, respectively. Because of small differences in rel.RMSE values and stochasticity from 2000 iterations, we provide an interval of survey effort B that is close to the target single observer rel.RMSE.

Results

If a full double observer protocol is used in image reviewing, the total fieldwork budget may be reduced from 9% to 37% (depending on the scenario of $\{\lambda, \varphi\}$), while still matching the best accuracy obtained with a single-observer protocol (Table 2, Figure S5).

Table 2. Proportion of the total effort (budget) of the double observer model (multinomial N-mixture) needed to obtain a similar performance to the single observer model (binomial N-mixture) for different scenarios of local abundance λ and availability of individuals φ.

		λ	
		0.2	**1**
φ	**0.2**	81-88%	75-83%
	0.4	75-81%	75-86%
	0.6	88-91%	63-72%

Case Example: marsh deer drone-based surveys in Pantanal wetland

The marsh deer (*Blastocerus dichotomus*), the largest cervid in South America (up to 150kg), is a habitat-specific species associated with wetlands (Piovezan et al., 2010) and threatened with extinction (IUCN; Duarte et al., 2016). Because of the inaccessibility of its habitat, marsh deer population estimates are usually obtained from aerial surveys (e.g. Andriolo et al., 2005; Mourão et al., 2000; Ríos-Uzeda & Mourão, 2012). In 2017, Brack et al. (2021) conducted spatiotemporally replicated drone-based count surveys to estimate the abundance of marsh deer in Pantanal wetland (Sesc Pantanal Private Natural Reserve; 108,000 ha) and explored the use of this method to monitor that species. Six flight paths (32-42km) were flown from two to six times each using a fixed-wing drone equipped with a RGB camera. The six flight paths were split into 203 1km-sites, and two observers carried out deer counts in a manual review of the collected imagery. The first observer reviewed the entire image set (~25,000 images) and the second observer reviewed only 20% of the flights. Count data were fitted using the three-level multinomial N-mixture model for the mixed single and double observer protocol. Average estimates of marsh deer local abundance λ was 0.33 (95% CI = 0.23-0.48), availability probability φ was 0.14 (0.10-0.19) and perception probability by observers p was 0.93 (0.82-0.97).

Aiming at improving accuracy in marsh deer abundance estimation and optimally plan survey design for upcoming assessments, we conducted a simulation study based on the previous population survey of 2017. We considered the point estimates of the 2017's population assessment ($\lambda = 0.33$; $\varphi = 0.14$; and $p = 0.93$), a total effort of B = 813 (from S = 203 and J = 4), and different proportions of the images checked by two observers (double-observer protocol): {0%; 20%; 50%; 100%}. We allocated the number of visits between J = 4 and J = 26 and, for each number of visits and each proportion of double observers, we ran 2000 iterations from which we calculated the relative RMSE.

Results

The optimal number of visits J_{opt} for the defined budget (B = 813) varied from J = 14 to J = 24 depending on the proportion of flights reviewed by double observers. In comparison to the survey design used in the 2017's marsh deer survey (J = 4), the rel.RMSE reduced around two-third (62-64%) under the J_{opt}. Under the optimal design, there was a reduction in rel.RMSE of about 11% between the single observer model and the full double observer, even with the high perception probability used ($p = 0.93$). For the proportion of 20% of double-observer protocol, as used in the 2017's assessment, the increase in accuracy of local abundance estimation (in comparison to the single observer model) is generally very small.

Discussion

We presented here a comprehensive assessment of N-mixture models performance and optimal effort allocation to assist sampling designs for estimating abundance with drone-based surveys. We found that spatiotemporally replicated drone-based counts analyzed with N-mixture models can be applied in a wide variety of contexts of population densities and availability of individuals. Interestingly, these results suggest that drone-based wildlife surveys can be suitable to estimate abundance even when the availability of individuals is low (e.g. forested areas, burrowing species, and marine animals that rarely remain at the water surface) and for low-density species (which are often threatened). Nonetheless, as already shown in previous simulation studies with binomial N-mixture models (Joseph et al., 2009; Yamaura, 2013), extra care should be taken in scenarios of very low local abundance and availability (here $\lambda = 0.1$; $\varphi = 0.1$, where abundance estimation performance was unstable). The results of this study are valuable until sample sizes are sufficient; for small sample sizes, the performance of N-mixture models is expected to be poorer (including biased abundance estimation), more particularly in scenarios of low detection probability (Kéry, 2018; Yamaura, 2013).

We found that consciously planning drone-based surveys by optimally allocating survey effort can have a great impact on the performance of N-mixture models for abundance estimation.   sites when availability probability is expected to be low, while more sites with fewer visits should be selected to optimally allocate effort in higher availabilities. For example, in the marsh deer study case shown, we found that an optimized sampling design can increase the accuracy in abundance estimation by up to two-thirds when compared to a non-optimal design. To optimize sampling designs, pilot studies or previous knowledge on the species are fundamental to provide guesses about the parameters for the simulations. From the comparison between the two N-mixture model structures (single and double observer counts), the single observer model generally demands allocating effort in more temporal replicates than the double observer model for the same scenario. Lastly, as abundance estimation accuracy notably increases with the availability of individuals, logistic adjustments in surveys to sample in moments that individuals are more available (e.g. time of the day, season) have a great potential to improve abundance estimation performance.

The optimal design becomes less sensitive to the choice of number of visits and sites when local abundance is higher (rel.RMSE curves become “flatter”). Therefore, there is a wider range of efficient designs with similar accuracy in the estimation of local abundance (i.e. close performance to the optimal design). This flexibility allows for other design considerations when planning surveys, for example, choosing to sample more sites if there is interest in the spatial variation of abundance (relationships with covariates) or more visits if travel cost to new sites is expensive. It is important to note that, in “real-case” studies such as the marsh deer example, when modeling the spatial variation in local abundance using covariates (e.g. Brack et al., 2021), the optimal number of visits would be pushed towards lower numbers of visits (and more sites).

There is a fundamental difference between fieldwork sampling design (number of visits and sites), which must be planned before data collection, and the reviewing procedure protocol (to use one or two observers to check images). The decision to use a double-observer protocol can be made after fieldwork and might improve the estimation accuracy. Notably, the accuracy in abundance estimation can be considerably improved even at very high perception probabilities by the observers, as illustrated in the marsh deer case study (11% increase at $p = 0.93$). Moreover, the improvement in the estimator performance can be achieved with the second observer only reviewing a proportion of the images. For the perception probability considered in the simulations ($p = 0.8$, representative of human observer counts from drone imagery), this benefit is more evident for >20% of the image set with double observer counts. This result is particularly interesting when an automated process is used in image review, when the algorithm counts could be considered the first observer and a human the second observer, reviewing only a subset of the drone imagery. In this case, the perception probability of both the algorithm and the human observer should be estimated separately.

We showed here that it is possible to reduce considerably the effort in fieldwork by doubling the effort in image reviewing in lab (i.e. double instead of single observer counts) while achieving a similar accuracy in abundance estimation. This consideration is particularly interesting when budget or conditions (e.g. weather, visibility or loss of equipment) are limited for fieldwork. However, depending on the time needed to manually review images, a double-observer protocol can be prohibitive. Here, we have limited the budget for optimal allocation only considering fieldwork effort, under the assumption that lab effort is more flexible and commonly less costly. However, if image review is also costly and can be budgeted in comparison to fieldwork expenses, the simulations of this study could be expanded to consider this extra aspect of survey design (e.g. proportion of images with a double-observer protocol). This would require including costs for the different units of effort (fieldwork and image review) explicitly in the evaluations of optimal effort allocation.

As a cautionary note on the use of N-mixture models, we point that there have been raised concerns on the sensitivity of these models to assumption violations and the claim that repeated counts have little information about the detection process for parameter identifiability (Barker et al., 2017). Evaluations of assumption violations in binomial N-mixture models have shown that unmodeled heterogeneity in detection probability (especially directional/non-random) can lead these models to produce biased abundance estimation (Duarte et al., 2018; Knape et al., 2018; Link et al., 2018). However, despite these recently raised worries, studies comparing N-mixture models with more traditional and well-established approaches (i.e. capture-recapture models or distance sampling) have generally shown similar results (Christensen et al., 2021; Ficetola et al., 2018; Keever et al., 2017; Kéry, 2018). To ensure more robustness against not accounted heterogeneity, additional information of some marked individuals may be collected (see Dunstan et al., 2020 for an example of drone surveys of marked individuals). In the context of drone-based surveys, Corcoran et al. (2020) have found that N-mixture models can overestimate abundance in comparison to an adapted Horvitz-Thompson estimator. However, we argue that, although showing an alternative to estimate abundance from drone-based surveys, authors conducted an inadequate comparison between the methods. In that study, they ignored basic recommendations for study design and analysis of N-mixture models: i) very few sites sampled; ii) large time interval between visits, which can prevent interpretations about temporary emigration processes and thus local abundance (Chandler et al., 2011; Williams et al., 2017); iii) use of a negative binomial distribution for the local abundance parameter, known to often provide unrealistic high abundance estimates (see Joseph et al., 2009; Kéry, 2018; Kéry et al., 2005; Knape et al., 2018); iv) did not provide any uncertainty for the N-mixture model estimates, which in itself precludes any comparison; and v) did not account for false-positive errors when known to occur.

Sampling design considerations of this study are directly applicable to other contexts for which N-mixture models can be used with a double-observer protocol to segregate the availability process from the ability to detect individuals by the observers, such as birds auditory point transect surveys (e.g. Amundson et al., 2014) or terrestrial strip transects of elusive species (e.g. burrowing animals, Zylstra et al., 2009). Differences in performance between the two modeling approaches used in this study are expected to be more pronounced if the perception probability by the observers is lower, or otherwise differences tend to zero as perception gets close to one. Furthermore, the basic structure of the presented N-mixture models (closed population, single-season, and single-species) could be expanded to accommodate other sources of variation (e.g. overdispersion in detection probability, Knape et al., 2018; group detection, Martin et al., 2011; spatial autocorrelation, Guélat et al., 2018; include multiple species (multi-species random effects, Dorazio et al., 2015; Sollmann et al., 2016), or incorporate dynamics in abundance (trend models, Kéry et al., 2009; models with explicit dynamics, Bellier et al., 2016; Dail & Madsen, 2011; Zipkin et al., 2014).

The use of drones to survey wildlife is quickly spreading for many species in different habitats. Nevertheless, few studies go further than simple tests of detecting species in drone-based images and apply drone surveys to model abundance of wildlife populations (Brack et al., 2018; Linchant et al., 2015). It is imperative to plan sampling designs considering sources of detection errors and, for this, spatiotemporally replicated flights and N-mixture models have proven to be a useful straightforward approach. Survey design efficiency to make the best use of available resources is a key consideration in wildlife monitoring and conservation, particularly given that these resources are usually limited. The improvements achieved by an optimized design, rearranging survey effort among sites and visits to obtain the most accurate abundance estimation can be crucial, for example, to detect trends when monitoring a population or to categorize a species as threatened or not.

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Data Availability

All simulation results, data, and code to reproduce the simulations and results of this paper are available at https://github.com/ismaelvbrack/designNmix4droneSurveys. We also provide a website (https://ismaelvbrack.github.io/designNmix4droneSurveys) to simulate scenarios and see the results of this paper.

Author Contributions

IVB and JJLM conceived the ideas e designed the experiments. IVB conducted the simulation experiments and analyzed the data. All authors discussed results and applications. All authors contributed critically to the drafts and gave final approval for publication.

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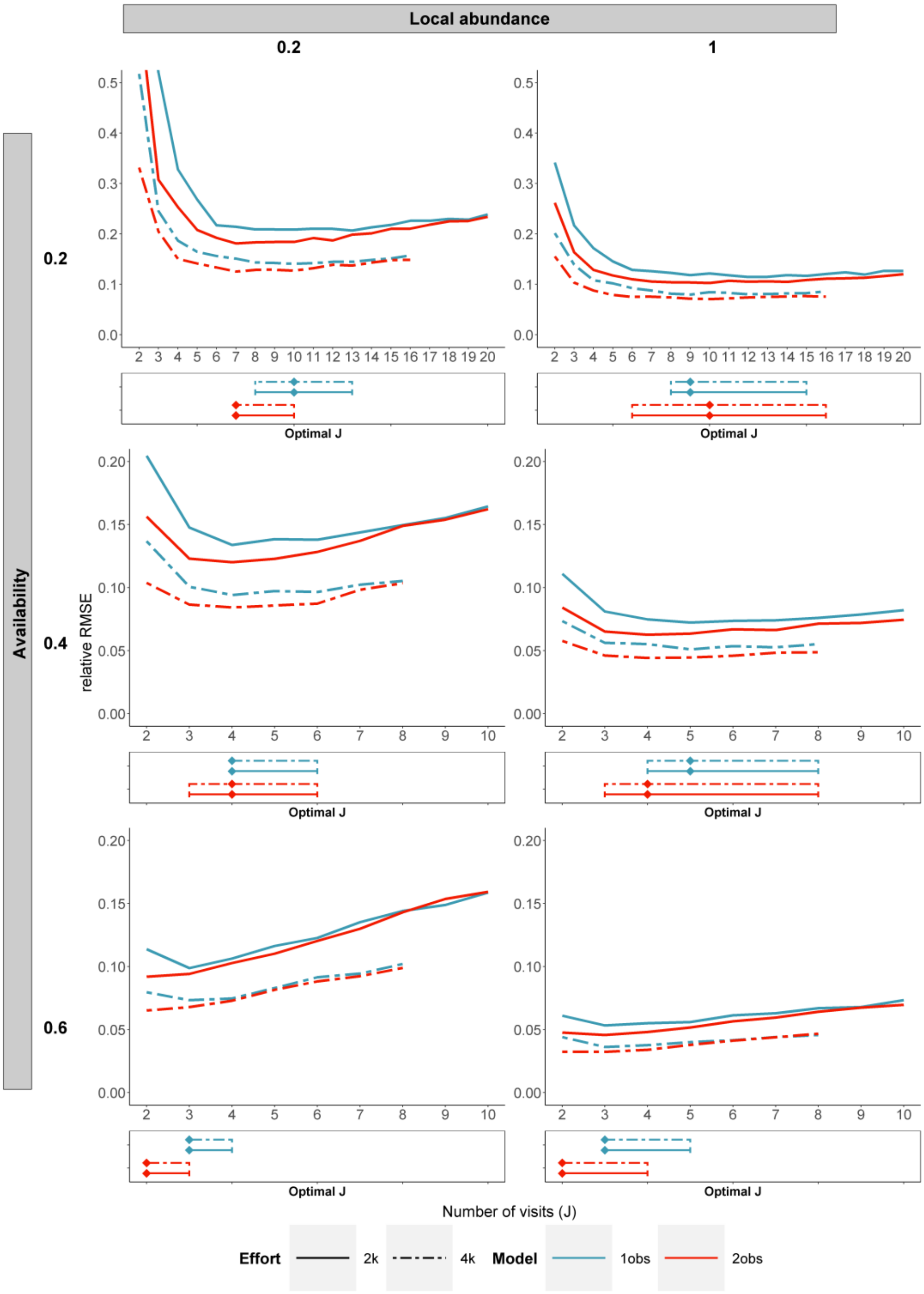
Supporting Information

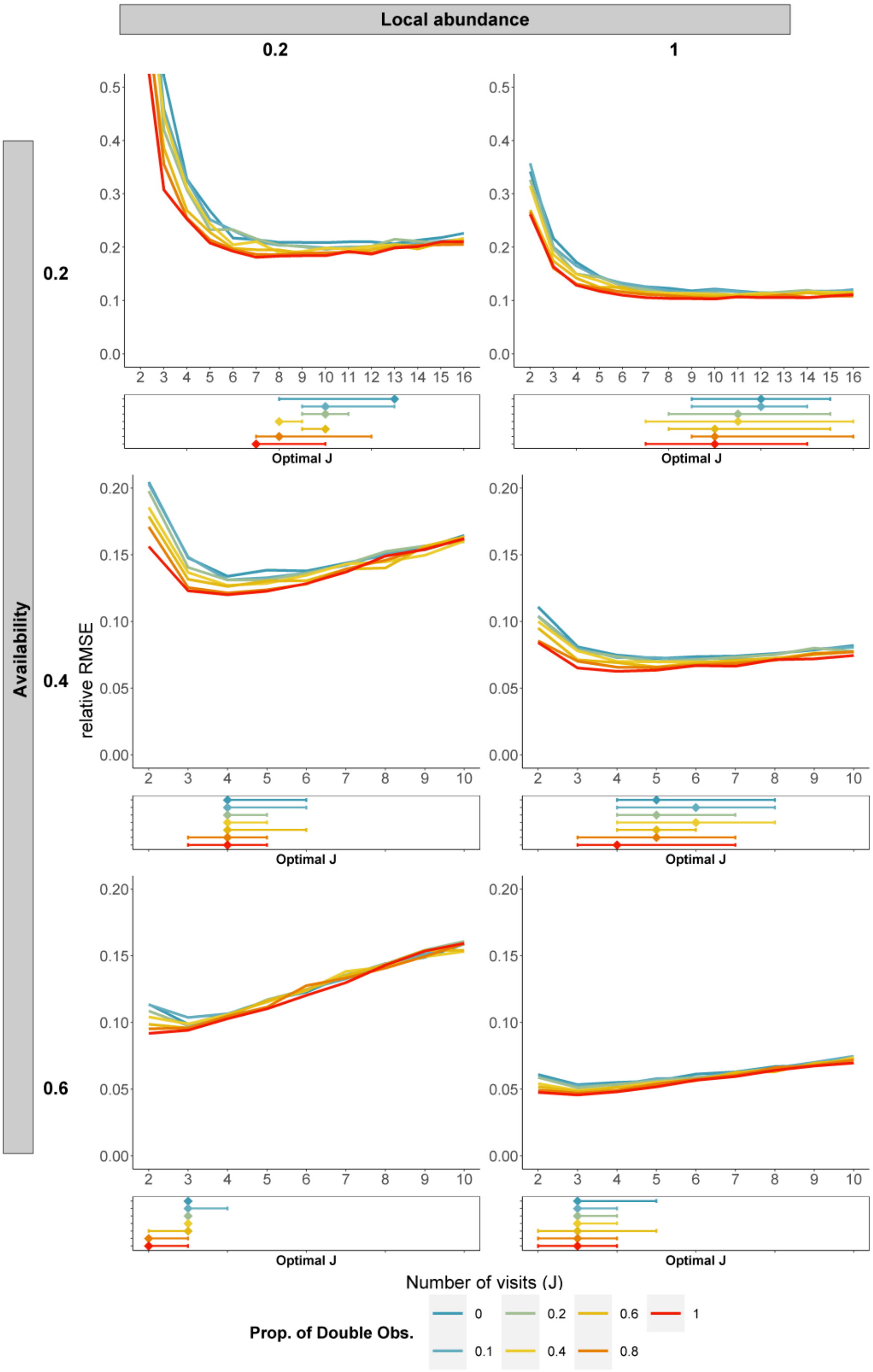
It is possible to see some of the supporting information at https://ismaelvbrack.github.io/designNmix4droneSurveys

Supplementary Figure S1. N-mixture model performance (relative RMSE curves) and optimal number of visits for single and double observer counts under different scenarios of local abundance and availability probability. Lower panels show the optimal number of visits (i.e. lowest rel.RMSE) and the bars correspond to the range of visits for which the performance can be considered equivalent (i.e. rel.RMSE < 0.5%). Available at: https://1drv.ms/b/s!AqbZVSnuy9hilepC2Nb8j4YmxpNGJA?e=NoN7Cd

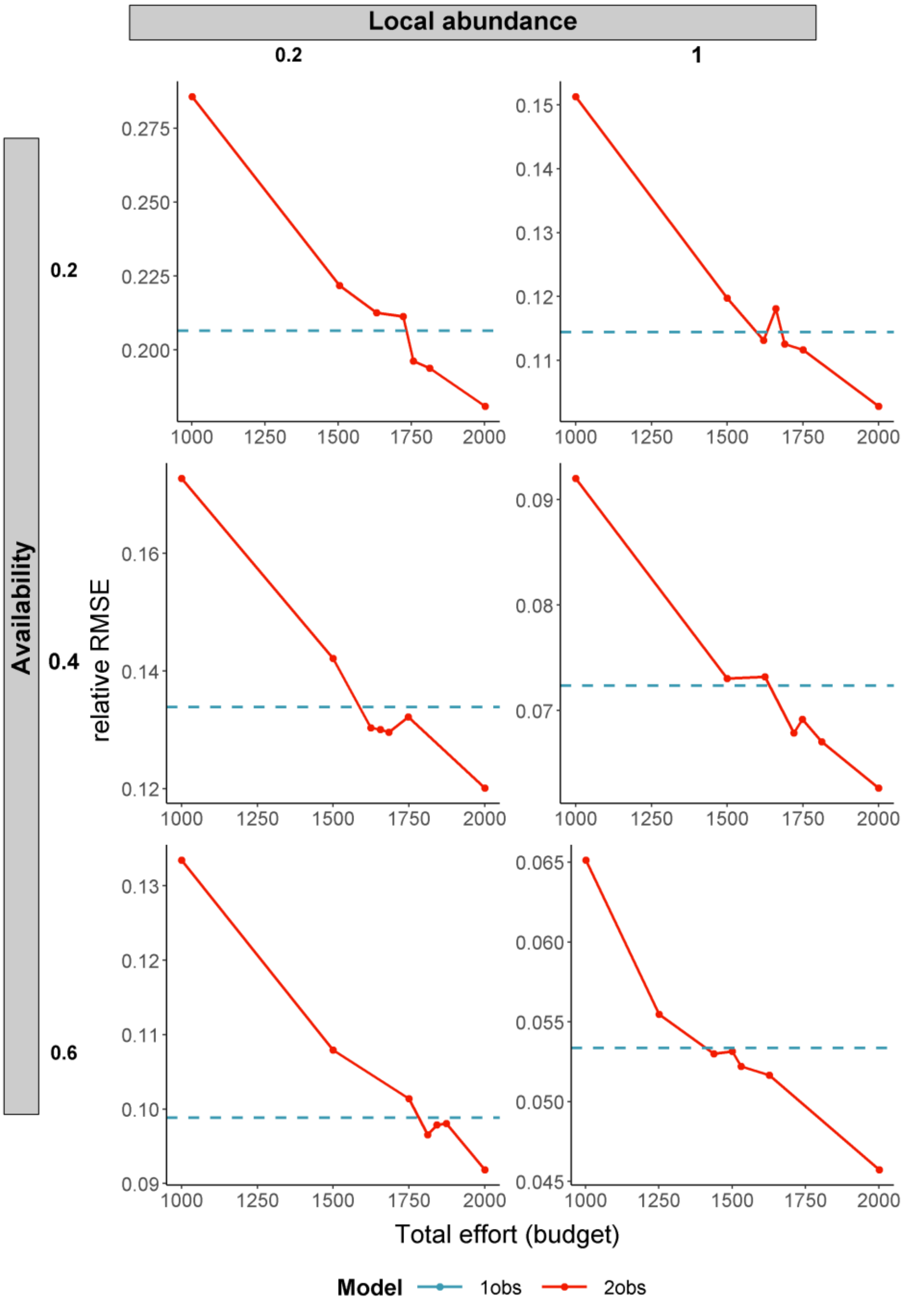
Supplementary Figure S2. N-mixture model performance (relative RMSE curves) and optimal number of visits for single and double observer counts under different scenarios of local abundance and availability probability. Lower panels show the optimal number of visits (i.e. lowest rel.RMSE) and the bars correspond to the range of visits for which the performance can be considered equivalent (i.e. rel.RMSE < 0.5%). Available at: https://1drv.ms/b/s!AqbZVSnuy9hilepBCwSpi6yygO2H-w?e=uN9BwW



Supplementary Figure S3. N-mixture model performance (relative RMSE curves) and optimal number of visits for two different total budgets (2k = 2000 flights, 4k = 4000 flights) in six scenarios of local abundance {0.2; 1} and availability probabilities {0.2; 0.4; 0.6}. Lower panels show the optimal number of visits (i.e. lowest rel.RMSE) and the bars correspond to the range of visits for which the performance can be considered equivalent (i.e. rel.RMSE < 0.5%).



Supplementary Figure S4. N-mixture model performance (relative RMSE curves) and optimal number of visits using different proportions of double-observer protocol for six scenarios, from the combination of local abundances {0.2; 1} and availability probabilities {0.2; 0.4; 0.6}. Lower panels show the optimal number of visits (i.e. lowest rel.RMSE) and the bars correspond to the range of visits for which the performance can be considered equivalent (i.e. rel.RMSE < 0.5%).



Supplementary Figure S5. Performance (relative RMSE) of the double observer (multinomial) N-mixture model for different total efforts (sites x visits) in comparison with the performance of a baseline single observer (binomial) N-mixture model with total effort = 2000.

CAPÍTULO 4

Multiple-observer protocol for drone-based abundance estimation: integrating counts from manual review and accessible deep learning algorithms

Este capítulo será submetido ao periódico ***Methods in Ecology and Evolution*** *ou*
Remote Sensing in Ecology and Conservation.

Multiple-observer protocol for drone-based abundance estimation: integrating counts from manual review and accessible deep learning algorithms

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Abstract

1. Reviewing large image sets remains a major challenge for wildlife abundance estimation from drone-based surveys, especially for rare and threatened species. Convolutional neural networks (CNNs) provide a straightforward framework to automatically detect wildlife in aerial imagery, although their implementation can be tricky for non-experts and small image sets. Motivated by the need to develop a pipeline for automated detection and abundance estimation of the threatened marsh deer, we i) explore deep learning techniques (convolutional neural networks) accessible to ecologists to detect rare wildlife species in drone imagery and ii) evaluate the

incorporation of algorithm detections through a semiautomatic procedure in multiple-observer models for wildlife abundance estimation from drone-based surveys.

2. We trained two CNNs using transfer learning and fine-tuning to classify drone image tiles into “deer” or “background” (non-deer). We evaluated algorithm performance in a test set for each trained CNN and with a consensus method. A human observer checked algorithm detections to discard false positives (semiautomated review). Manual and semiautomated individual detections were integrated under detection histories and fitted using a multiple observer closed-population capture-recapture model.

3. The consensus classification approach produced a 3.5-fold increase in precision while reducing only 0.09 the proportion of deer samples detected, when compared to each algorithm independently. Compared to manual reviewing, the semiautomated procedure greatly reduced the time needed to review images (from two months to 66 hours) while providing a similar detection probability of deer individuals available in the imagery. Planning drone flights with frontal overlapping in the images can enlarge the number of samples for training and improve algorithm detection.

4. Deep learning has become increasingly accessible for ecologists and conservationists to develop their own detection algorithms. A multiple-observer approach including manual and semiautomated reviewing can be used to address algorithms’ false-negative errors while avoiding false positives in abundance estimation. Monitoring programs of threatened species can greatly benefit from this to achieve timely assessments of abundance estimates from drone-based surveys in times of rapid environmental changes.

Keywords: aerial surveys, convolutional neural networks, detection algorithm, multiple observers, population size and monitoring, unmanned aerial vehicles

Introduction

Estimating population size and its variation through time is fundamental for many ecological and conservation studies. Abundance estimation and monitoring are essential to detect or predict population declines, evaluate species extinction risk and effectiveness of conservation/management actions, basing most criteria of conservation status assessments (IUCN, 2019). To provide useful and timely information for effective species conservation, abundance estimates need to be reliably and rapidly assessed. This becomes particularly challenging for rare species, that commonly present low densities and/or low detection rates and are often threatened to extinction.

Aerial surveys using drones (a.k.a. unmanned aerial vehicles) have been suggested as an efficient method to collect count data for abundance estimation of many wildlife species in several environments, including large mammals (e.g. Barasona et al., 2014; Vermeulen et al., 2013), canids (e.g. Bushaw & Ringelman, 2019), waterbirds (e.g. Hong et al., 2019; Sardà-Palomera et al., 2012), rays and sharks (e.g. Kiszka et al., 2016), marine turtles (e.g. Rees et al., 2018) and mammals (e.g. Goebel et al., 2015), and arboreal animals such as koalas (e.g. Hamilton et al., 2020) and primates (Melo, 2021). The versatility of drones allows accessing remote areas while forwarding spatial and temporal survey replication to achieve a representative population sampling at an adequate time interval for monitoring (Brack et al., 2018). Some approaches have been proposed to assess reliable estimates of abundance exploring drone-based survey designs (Baxter & Hamilton, 2018) and dealing with imperfect detection (Hodgson et al., 2017; P. J. Williams et al., 2017). However, reviewing drone-collected imagery after fieldwork to extract the count data, an important step to promptly achieve population estimates, still remains a major challenge. Manually reviewing image sets can be extremely time consuming and sometimes prohibitive given the often-huge number of images obtained in such drone flights. Hence, the use of algorithms to detect wildlife species in aerial imagery is imperative to a rapid compilation of count data and assessment of population size (Linchant et al., 2015).

Several computer vision methods have been applied to detect, count, or identify wildlife species in images, from pixel-based classifications to object-based image analysis and deep-learning algorithms (Chabot & Francis, 2016; Corcoran et al., 2021; Hollings et al., 2018; Weinstein, 2017). Among them, the recent rise of deep learning techniques with convolutional neural networks (CNNs), boosted by the availability of huge databases and the processing power of Graphics Processing Units (GPUs), has produced promising results in the performance of computer vision tasks (LeCun et al., 2015). CNNs are deep machine learning algorithms composed of sequences of connected “sliding-window” convolutional and pooling layers, in which regional features of input images are mapped through the network until the final classification layer (Chollet & Allaire, 2017; LeCun et al., 2015). Using labelled image samples to train the network weights, initial layers learn local features such as edges while subsequent layers, increasingly deeper into the network, learn more abstract and complex features. From the considered turning point in computer vision in 2012, when the first deep CNN (AlexNet, Krizhevsky et al., 2012) won the ImageNet Challenge (http://www.image-net.org/challenges/LSVRC/), there has been a rapid development of CNN architectures with impressive increases in performance, eventually surpassing human accuracy for some tasks. Subsequently, the use of CNNs has also increased in ecological and conservation studies (Christin et al., 2019; Corcoran et al., 2021), reducing the need of human labor in image processing. So far, CNNs have been used for: landscape classification (Stupariu et al., 2021); counting animals in satellite images (Gonçalves et al., 2020; Guirado et al., 2019); detect, identify and describe behavior of animals in camera trap imagery (Norouzzadeh et al., 2017; Tabak et al., 2019); detect animal vocalizations in audio records (Dufourq et al., 2021; Ruff et al., 2019, 2021); animal individual identification (Hou et al., 2020); and measure animal individuals (Gray, Bierlich et al., 2019). For detecting and counting individuals in aerial images, CNNs have been successfully applied for tree species (Morales et al., 2018; Natesan et al., 2020), marine animals (Dujon et al., 2021; Gray, Fleishman et al., 2019), waterbirds (Hong et al., 2019); koalas (Corcoran et al., 2019); and large mammalian herbivores (Eikelboom et al., 2019; Kellenberger et al., 2018; Torney et al., 2019).

Nevertheless, to reach useful performances (high accuracy), deep-learning models require large datasets (thousands or hundreds of thousands of images) for algorithm training while avoiding overfitting (i.e. algorithm memorizes training samples). Although the size of datasets in ecology and conservation has boomed in the last years thanks to the use of technologies for sampling (Lahoz-Monfort & Magrath, 2021), obtaining a large number of records can still be very difficult for many species, especially for the rare and threatened ones, for which the vast majority of images might be empty. In addition, implementing deep-learning algorithms can be restrictive for ecologists because it requires deep technical understanding to build the complex neural network architectures (Lamba et al., 2019). Furthermore, the predominant deep-learning language is Python, while the most popular programming language in ecology is R (Lai et al., 2019).

However, with the spread of deep learning, some techniques and tools have made the use of CNNs less cumbersome for non-specialist users and less demanding of large datasets. The development of application programming interfaces (APIs) such as keras (Chollet, 2015) has facilitated the implementation of deep-learning models, with some of its functionalities now readily available also for the R platform (Chollet et al. 2017, Chollet & Allaire, 2017). Moreover, using a technique so-called transfer learning, it is possible to skip the laborious and difficult process of building a CNN architecture from scratch. Transfer learning is the process of utilizing a pre-trained network (usually trained for a general classification task such as the ImageNet database) and then using a target image set to fine-tune only the final layers of the network. By applying transfer learning from a pre-built and -trained CNN, users can reduce training time and the number of samples needed, as well as avoiding overfitting (Christin et al., 2019; Lamba et al., 2019; LeCun et al., 2015). Another technique employed to enhance the usability of small datasets for CNNs is data augmentation (Christin et al., 2019; Kellenberger et al., 2018), which consists in inflating the image dataset by applying transformations on the original images (e.g. rotating, mirroring, brighten/darken, and distorting).

Even with a successfully trained CNN reaching high accuracy, the algorithm might still fail to detect some individuals (false negatives) and present some background features as individuals (false positives). Such false-negative and false-positive errors in counts, if not properly addressed, may produce biased abundance estimations, even when occurring at low frequencies. Under a fully automated procedure, it can be tricky to define an inclusion threshold that, at the same time, enhances the detection of individuals and reduces the chances of including a misdetection on counts. To prevent this error, a human observer could check every target provided by the algorithm and confirm if it is a true or a false positive (i.e. semiautomated procedure). Despite not completely benefiting from the time savings that a full automated approach may provide, a semiautomated review can already greatly reduce the reviewing time while avoiding false-positive errors. To deal with the eventual false negatives on abundance estimation, the semi-automated algorithm detections (checked by a human observer) could be integrated with human observer counts in a multiple-observer protocol (Brack et al., 2018; Conn et al., 2012).

Here, we i) explore deep learning techniques (convolutional neural networks) accessible to ecologists using transfer learning and R language to detect rare wildlife species in drone imagery; and ii) evaluate the incorporation of algorithm detections through a semiautomatic procedure in multiple observer models for wildlife abundance estimation from drone-based surveys. We develop this approach in the context of population monitoring of the rare marsh deer (*Blastocerus dichotomus*), in the heterogeneous landscape of the Pantanal wetland, western Brazil.

This study was motivated by the need to estimate and monitor marsh deer populations, particularly after the Pantanal 2020 megafires (Leal Filho et al., 2021; Marengo et al., 2021). The marsh deer is a threatened South American large herbivore (up to 150kg) associated with wetlands (Figure 2o). Its habitat has been severely reduced and fragmented in the last decades because of conversion to cattle ranching, agriculture, and hydroelectric dam lakes, and nowadays marsh deer presents a scattered distribution (Duarte et al., 2016; Piovezan et al., 2010). The largest and most continuous populations of marsh deer, located in the Pantanal wetland, are currently threatened by the increase in the frequency of megafires and severe droughts because of global climate changes (Marengo et al., 2016). Marsh deer population size is traditionally assessed using aerial surveys (e.g. Andriolo et al., 2005; Mourão et al., 2000; Ríos-Uzeda & Mourão, 2012) and drone-based surveys have been recently applied as a cost-effective alternative to manned flights (Brack et al., 2021). The reserve where our group has been monitoring marsh deer with drone surveys since 2017 had 93% of its area affected by the megafires of 2020 in Pantanal (José Cordeiro pers. comm.). So far, we have collected a large number of pictures in different years. The manual review of this image set has been extremely laborious and inefficient (taking several months or even a few years). Thus, the marsh deer monitoring program at our study site, or evaluations of other remnant and small populations, would greatly benefit from automation in drone image reviewing, allowing for a rapid assessment of abundance estimates before it is too late to take some management and conservation actions.

Materials and Methods

We used convolutional neural networks for image classification to detect marsh deer in drone imagery and support a semiautomated review procedure thereafter integrated with detections of human observers for estimation of algorithm detection probability and abundance (Figure 1). We first conducted a manual review in the collected drone imagery with annotation of detected deer. We separated the annotated samples in training and test sets, the first used for training the CNNs for binary classification and the last for evaluating algorithm performance. After defining a classification threshold, an observer checked all algorithm detections in a semiautomated review. Finally, deer detections from the semiautomated procedure were integrated with the manual detections under individual detection histories that were fitted using a multiple observer model to obtain abundance estimates.

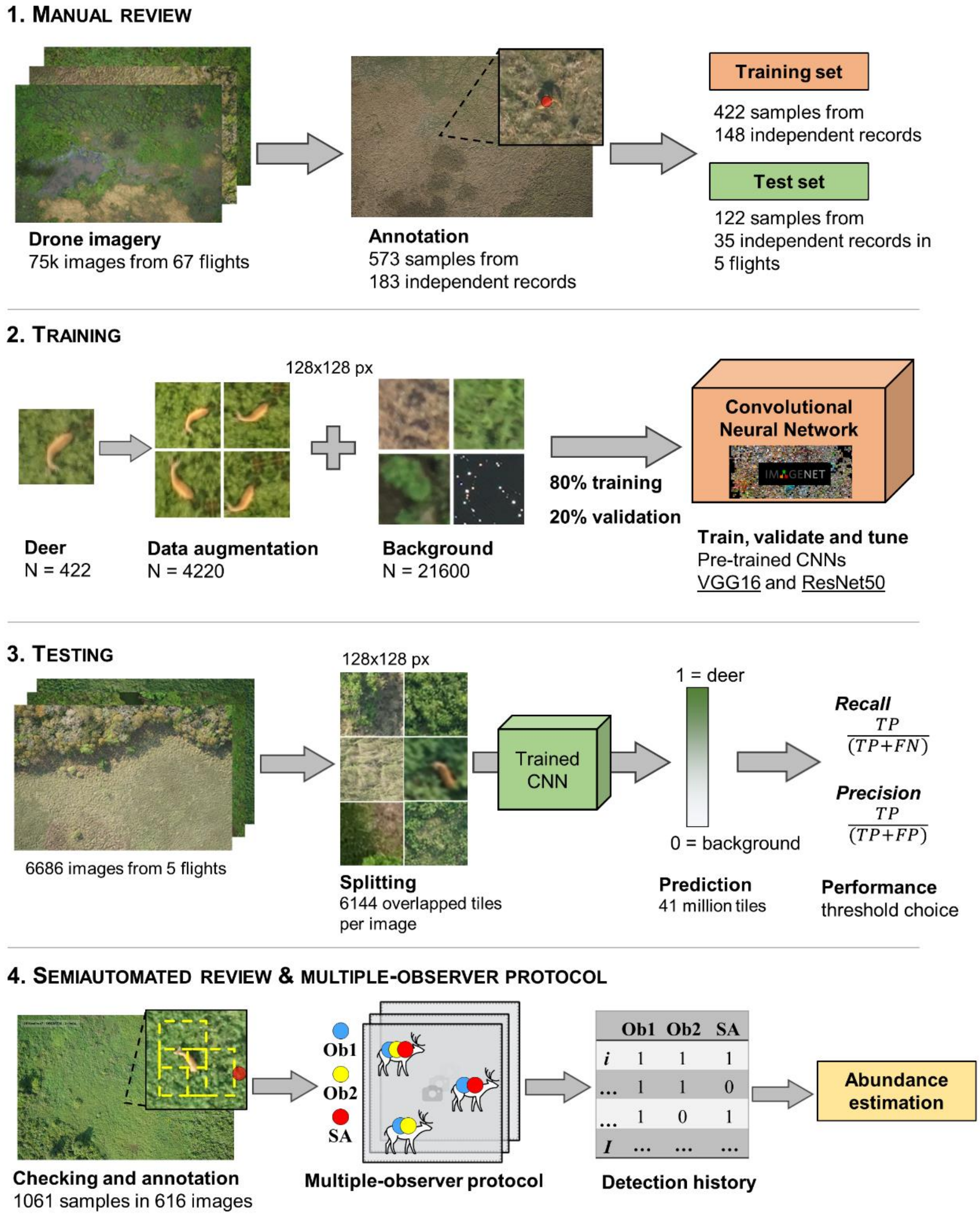

Figure 1. Overview of the main steps involved in the developed pipeline for training and testing convolutional neural networks for marsh deer detection in drone imagery, followed by the integration of manual and semiautomated detection histories under a multiple-observer protocol for abundance estimation. TP = true positives, FN = false negatives, FP = false positives. Ob1 and Ob2 = human observers; SA = semiautomated procedure.

Image collection and annotation: drone flights and manual review

We carried out marsh deer drone-based surveys in the dry season (September-October) of 2017 and 2018 at the Sesc Pantanal Private Natural Reserve (108,000 ha; 16º 45’ S and 56º 15’ W) in the Pantanal wetland, Western Brazil. We conducted a total of 67 flights (25 in 2017 and 42 in 2018) in seven preplanned flight paths using a fixed-wing drone (Echar 20B, XMobots) equipped either with a Sony A7R (7392x4920 px) or a Sony Alpha500 (6000x4000 px) oriented downwards (perpendicular to the ground). We set flight plan and payload to achieve a pixel resolution at the ground level (ground sampling distance) of about 2cm. Flights were planned to take frontal overlapped pictures (50-70%), making deer individuals to usually appear in more than one image. For more details on the flight specifications refer to (Brack et al., 2021).

From one to three independent human observers manually reviewed the 75,613 images collected in the 67 flights. For each marsh deer detected, the observers marked the individual with a central point using the ClickPoints software (Gerum et al., 2017). During revision, observers were instructed to group those deer records that appear in more than one overlapped image into a single independent record, that is, the detection is considered a new record at the first shot it appears, and as a repeated one in the subsequent images. The recognition of these records as correlated is easy since the time interval between successive pictures is ≤1s. Note that hereafter we consider as a deer sample all deer manual detections in the drone imagery that were used for training and testing, and as an independent record, only the first picture each individual is detected.

Image preparation

The manual review process resulted in 573 deer samples (found in 457 images) from 183 independent records (excluding overlapped images). We put aside 122 deer samples (35 independent deer detections) of five flights for testing and semiautomated reviewing (test set), remaining 451 samples (148 independent records) for training the algorithm (training set). We deleted 29 samples from the training set, that were in too dark pictures (taken in darkish hours) or containing individuals mostly hidden, to avoid confounding the algorithm.

For each of the training deer samples, we cropped a 128x128 px tiles around the central coordinates annotated during the manual review (we found this size to adequately fit marsh deer in our images). Then, we did data augmentation by applying random transformations to each sample (rotating, mirroring, range shifting, brighten/darken, and zooming in/out). We kept the original sample and augmented ninefold so that, for each deer sample, we ended up producing ten 128x128 px samples. This process resulted in 4220 deer samples for training. For the background samples ("non-deer"), we generated random points on the drone imagery (except in those images of the flights separated for testing) to crop 128x128 px windows around them. We did initial explorations in training the algorithm with balanced datasets (i.e. ~4k samples for background class) that ended unsuccessful, probably because of the lack of representativeness of 4k samples in a context of highly variable backgrounds (Kellenberger et al., 2018). We then produced five background samples for every deer sample (5:1), resulting in 21,600 samples. For the CNN training process, we split 80% of the samples for training and 20% for validation. As overlapped images might present similar shots of the same deer (autocorrelated records), we grouped sequential images to restrict the division in training and validation, so that these autocorrelated records were together in the same set to avoid overestimating validation metrics during training.

Neural network training

We used pre-existing popular CNN architectures for image classification and adapted them to classify drone image tiles as marsh deer or background. We explored networks pretrained on the ImageNet database (https://image-net.org/) available at the Keras API (e.g. ResNet50, VGG16, InceptionV3, Xception, InceptionResNetV2). Starting from the CNNs with pre-trained weights, we excluded the top dense layers (i.e. keeping the feature extraction blocks) and added new dense (fully-connected) layers with a final sigmoid classifier as output. The process of training a neural network consists in passing the training samples with their corresponding labels through the network to adjust model weights (i.e. parameters) aiming to reduce loss values. The training samples are passed in mini-batches (e.g. 32 or 64 mini-batch sizes) until completing an epoch (i.e. one pass of the entire training set). After each epoch, performance metrics are calculated after evaluating the predictions obtained on the annotated validation set. This process is iterated for several epochs until the metrics calculated for the validation set start decreasing in performance (i.e. presenting overfit on the training set). To fine-tune a pretrained model, we only adjusted weights of the top layers (final convolution and dense layers), while freezing all parameters of previous layers. Loss was calculated using binary cross-entropy (Chollet & Allaire, 2017). For training the different CNN architectures, we explored different: i) optimization algorithms (Adam and RMSprop); ii) learning rates (1e-3 to 1e-6); iii) mini-batch sizes (32, 64, and 128); and iv) number of unfrozen layers for adjusting weights (i.e. fine-tuning depth). We tuned these network settings (hyperparameters) based on validation loss. After an initial exploration in which we tested different CNN architectures, we ended choosing the two most promising models: VGG16 (Simonyan & Zisserman, 2015) and ResNet50 (He et al., 2016). VGG16 is a plain sequential network with 13 convolution layers, mostly composed of 3x3 filters, distributed in five blocks and three final dense layers. ResNet50 is a 50-layer network (only the last layer is fully connected) also with five general blocks of convolution layers, but each of them (except the first) composed of bottleneck blocks (three layers: 1x1, 3x3, and 1x1 filters) and presenting residuals shortcuts that skip the sequential connections between these blocks. Finally, after defining the settings for each model, we ran a final training to a determined number of epochs (ResNet50 = 11; VGG16 = 9) using both training and validation sets.

We conducted CNN training using Keras with TensorFlow backend engine (Abadi et al. 2016) on an Nvidia RTX 2080 GPU (8Gb), accessed from R software (R Core Team, 2020) utilizing the packages *keras* (Allaire & Chollet, 2021), *tensorflow* (Allaire & Tang, 2021) and *reticulate* (Ushey et al., 2021), that provide an interface to the Python libraries and environment.

Neural networks testing

As accuracy might not be the most adequate metric to evaluate the performance of an algorithm when there is interest in a single and infrequent class (i.e. marsh deer class), we used recall and precision for assessing CNNs performance. We did this for three situations: each of the two trained CNNs separately and as a consensus classification (i.e. we only considered a deer detection when both networks indicated a tile as deer using a single threshold). We used five drone flights containing 6,686 images and 122 deer samples detected by human observers. Each image was split into 6,144 tiles of 128x128 px with a 40% of vertical and horizontal overlap (to ensure the entire deer would appear in at least one tile; Gray et al., 2019). This resulted in approximately 41 million image tiles that we passed through the two trained CNNs to receive a class prediction probability. As our networks were trained for a binary classification, each tile received a probability of containing a deer by each model. Note that the same deer can be detected in more than one tile because of the overlap (Figure 2a-b).

We then classified each tile as “deer” or “background” defining different cutoff probabilities (i.e. confidence thresholds) from 0.5 to 1. For each threshold under each scenario (VGG16, ResNet50 and consensus), we calculated the recall and precision by computing the number of true positives, false negatives, and false positives (Figure 1, step 3). We treated these quantities in different ways for recall and precision. Recall is the proportion of known deer records detected by the algorithm, whether by one or more than one overlapped tile, and precision is the proportion of tiles assigned to deer class really containing deer. Thus, the meaning (and number) of “true positives” differed between the two metrics.

Semiautomated review

For the semiautomated procedure, we used the consensus classification and applied a confidence threshold of 0.995 for classifying the tiles of the test set as deer or background. We purposely selected a conservative high threshold value to reduce the number of false positives and to test the multiple observer method for the false negatives. We exported the entire images containing detections with the target tiles highlighted (see examples in Figure 2) and an observer, who had not previously seen the images, reviewed all tiles confirming whether or not they contained a marsh deer. For each deer detected, the observer accessed the entire drone imagery to verify the first image in which that deer appeared and marked the central pixel coordinates with ClickPoints to be used in the multiple-observer protocol.

Multiple-observer protocol for abundance estimation

In aerial wildlife surveys, it is common to use more than one (often two) independent observers (Magnusson et al., 1978; Pollock et al., 2006) and this method has been proposed to estimate the detection probability also in drone-based flights (Brack et al., 2018; Vermeulen et al., 2013). This method can be viewed as a capture-recapture approach in which the successful and failed detections of each observer are compiled in individual detection histories (Figure 1 step 4). By fitting the detection history matrix under a closed-population capture-recapture model (Williams et al., 2002), it is possible to estimate the detection probability by the observers and the number of individuals not detected by any observer to obtain unbiased abundance estimation. In the context of reviewing aerial imagery, the detection probability by an observer is well defined as perception probability, that is, the probability of an observer to detect an individual that is available on the imagery (Brack et al., 2018). Here, we considered two types of independent observers to build the detection histories: i) human reviewers; and ii) a semiautomated procedure (as described in the previous section). Assuming that an observer would not fail to detect a deer highlighted by an algorithm during the semiautomated checking, the perception probability of the semiautomated review can be assigned exclusively as the algorithm detection probability of an independent deer record.

The five flights used for the multiple-observer approach were reviewed by one to three human observers and the semiautomated reviewing. We built the detection histories using the annotated central pixel coordinates of each independent record (only the first picture, discarding overlapped records). This resulted in a 35x4 matrix (35 detected individuals; up to three humans plus one semiautomated observer).

We fitted the closed-population capture-recapture model under a Bayesian framework in software JAGS (Plummer, 2003) accessed from the package *jagsUI* (Kellner, 2015) in R (R Core Team, 2020). We used a data augmentation procedure by adding pseudo-individuals in the matrix (all-zero lines) and estimating the abundance parameter derived from an inclusion probability parameter (Royle et al., 2007). We checked if the number of added pseudo-individuals did not constrain estimates by adding more lines and seeing if posterior distributions changed. We estimated a single perception probability for all human observers and another for the semiautomated review. We assigned a uniform prior distribution between zero and one for the perception and the inclusion probabilities. We calculated the mean and 95% credible intervals for each parameter from samples of the posterior distributions obtained using Markov Chain Monte Carlo. We ran three parallel chains with 2,000 steps in the adaptive phase, followed by 10,000 steps from which the first 2,000 were discarded. This resulted in 24,000 samples of the posterior distribution. Model convergence was assessed by a visual inspection of the chains' traceplots and using the R-hat statistics (R-hat ≤ 1.1).

We provide R code for processing drone imagery (e.g. extract coordinates from ClickPoints project, crop and move samples, transform images in keras arrays, augment data samples, split image in overlapped tiles), training convolutional neural networks (fine-tune pretrained CNNs from ImageNet), evaluating algorithm performance, preparing images for semiautomated review, and fitting the multiple-observer model, at the GitHub repository https://github.com/ismaelvbrack/CervoNet.

Results

In model training, we reached performances for the validation set close to 1 (accuracy, precision and recall). As our validation set might underrepresent the algorithm performance for real problems (small image set and leak of information during training), we focus our interpretations on the test set metrics. From the 122 deer on the test set, 108, 109 and 104 were detected respectively by ResNet50 and VGG16 networks independently and the consensus at the threshold of 0.69; and 101, 105 and 98 at the 0.995 threshold (Figure 3a). Tiles with marsh deer samples corresponded to 1.9%, 2.1% and 7%, for ResNet50, VGG16 and consensus respectively, of all tiles classified at the 0.69 threshold; and 5.6%, 5% and 18.6% at the 0.995 threshold (Figure 3b). The false-positives detections were mainly composed by vegetation features of tree trunks (Figure 2j) and dead vegetation (Figure 2k) or other animal species such as horses (Figure 2g), capybaras (*Hydrochoerus hydrochaeris*) (Figure 2i) and jabiru birds (*Jabiru mycteria*; Ciconiidae) (Figure 2h).

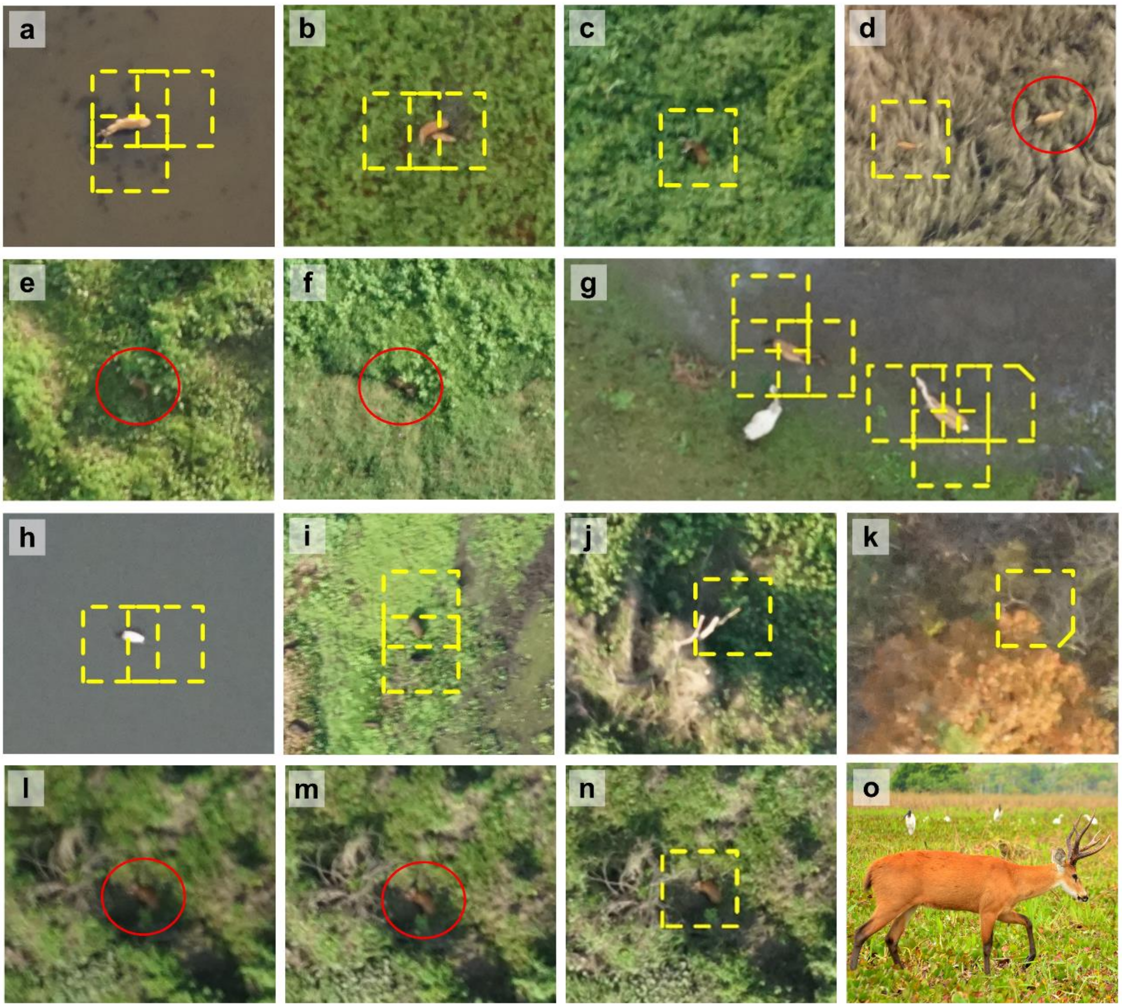

Figure 2. Drone image tiles classified as marsh deer (yellow boxes) by a consensus of two convolutional neural networks (ResNet50 and VGG16). a-d) contain true positive detections; d-f) present deer detection failures by the algorithms (red circles) and g-k) contain false positive detections. a) male marsh deer detected; b) female and young deer detected; c) partially hidden male detected; d) young detected and adult not-detected deer; e-f) partially hidden deer not detected by the networks; g) horses misdetected by the algorithm; h) jabiru bird and i) capybaras misdetected; and j-k) vegetation features misdetected. l-m-n) Deer individual (single independent record) shot in three overlapped images and detected only in the last one (n) by the algorithms. o) male marsh deer.

From the 35 independent deer records manually detected in the test set, 32 were present in more than one image (and 26 in more than two), composing the 122 deer samples. From the 41 million tiles of the 6,686 images of the five test flights, 1,061 tiles in 616 images remained to be checked under the semiautomated review (consensus method and 0.995 threshold), containing 98 deer samples. Most of these 98 deer samples available in the semiautomated review were detected by the algorithms in more than one overlapping tile, only 18 were detected on a single tile. Only three out of the 35 independent records were not detected under the semiautomated review (all of them shown in Figure 2d-f). The number of individuals detected by a single human observer was also 32. The probability of detecting a marsh deer available in the imagery (i.e. perception probability) was similar between the human observer and the semiautomated approaches (Figure 3c), 84.9% (95%CI = 77-91%) and 89.1% (95%CI = 77-97%) respectively. The estimated number of individuals available in the imagery was 35 (95%CI = 35-35), that is, we are 95% confident that all individuals available were detected by at least one observer.

The manual review of the 6,686 pictures in the test set took about 46 hours by one human observer (25 s per image), but distributed along approximately two months. The semiautomated procedure lasted a total of 66.3 hours (nearly 3 days): 65 uninterrupted hours to pass the entire test set in the two CNNs (35s per image) and 80 min for the observer to check the 616 images with algorithm detections (8 s per image).

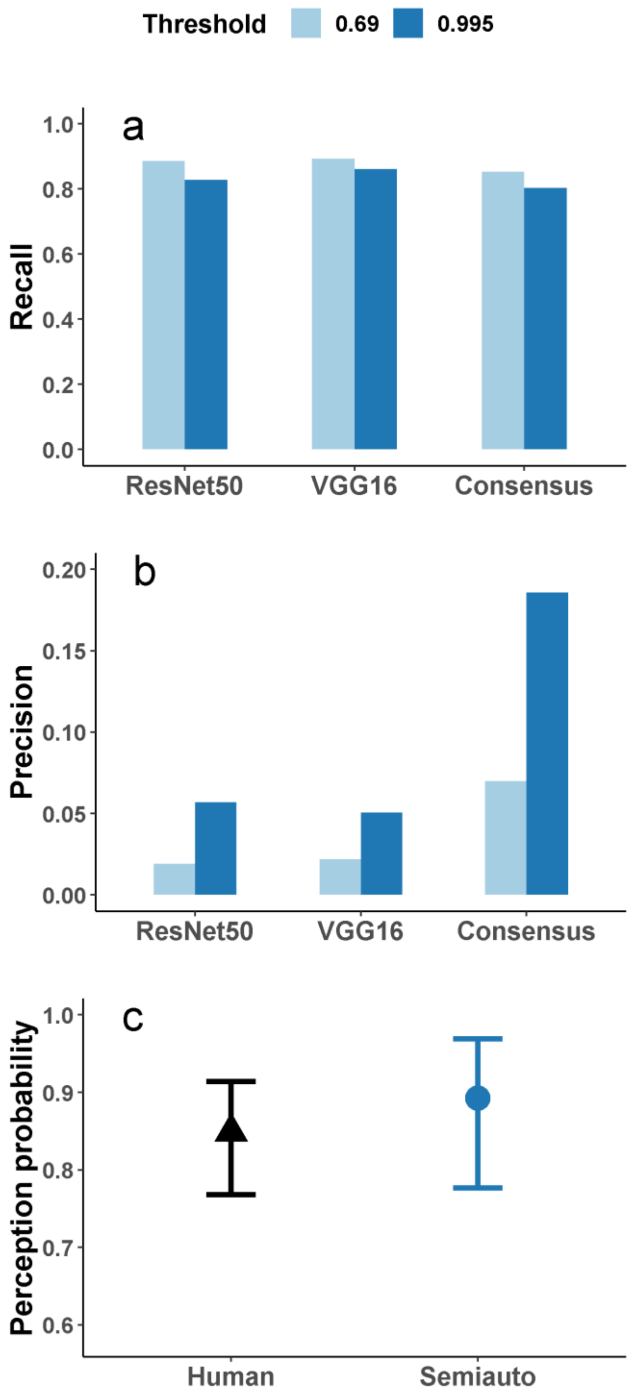

Figure 3. (a) Recall and (b) precision of the Convolutional Neural Networks (ResNet50, VGG16 and Consensus classification) trained to detect marsh deer in drone images for two choices of confidence threshold. (c) Estimated perception probability of human observers and semiautomated procedure to detect an individual available in drone images (with 95%CI). For the semiautomated procedure, we used detections from the consensus method and the 0.995 threshold.

Discussion

The increasing use of technologies to sample wildlife has facilitated data collection in ecology and conservation while generating huge databases that impose challenges in processing them. Deep learning (Convolutional Neural Networks) has proven to provide a straightforward approach to process images obtained from technological devices such as drone-acquired aerial images (Corcoran et al., 2021; Dujon & Schofield, 2019), satellite imagery (Duporge et al., 2020; Gonçalves et al., 2020; Guirado et al., 2019), camera trap image sets (Norouzzadeh et al., 2017; Tabak et al., 2019), and acoustic recordings (sonograms; Dufourq et al., 2021; Ruff et al., 2019). In this study, we tried to overcome two major obstacles to the use of CNNs by ecologists and conservationists: the demand for massive databases and a substantial knowledge to implement them (Christin et al., 2019; Lamba et al., 2019). We did this for detecting a rare and threatened species in drone imagery, the marsh deer in Pantanal (Western Brazil), to estimate abundance for monitoring purposes. To develop the pipeline for abundance estimation, we i) used deep learning techniques, such as transfer learning (with fine-tuning) and data augmentation, to deal with the small number of samples available for training the algorithm; and ii) integrated semiautomatically reviewed and human manual detections under a multiple observer model to estimate abundance while accounting for false-negative errors and avoiding false positives.

We reached a proportion of marsh deer detected by the algorithm (recall) of 89%, a performance comparable (or even higher) to other studies using CNNs on drone images (e.g. Corcoran et al., 2019; Dujon et al., 2021; Eikelboom et al., 2019; Gray, Fleishman et al., 2019; Kellenberger et al., 2018). Even when choosing a high confidence threshold (0.995) and applying a consensus classification of the two models, the recall remained relatively high (80%). This number is noteworthy considering the context of our aerial surveys of marsh deer: a species that appears at low frequencies in images (one deer sample every 132 pictures) with highly complex backgrounds. Data augmentation and fine-tuning pretrained networks for simpler and more specific tasks have shown to be very helpful here, especially with our relatively small image set. More interestingly, considering only independent records (marsh deer “individuals”), the semiautomated procedure (i.e. an observer checking the algorithm detections) detected the same number of deer as human observers and the estimated perception probability for the two approaches was similar.

Although being more time-consuming than fully automatic approaches, the semiautomated review is an efficient method since the false-positive detections (more difficult to address in statistical modeling of abundance) are prevented. Time savings are still great: by filtering images only with algorithm detections, we could reduce to 9% the number of images that needed reviewing. Moreover, as the algorithm detections were highlighted in these images, the average time needed to check each picture was threefold lower when compared to manual reviewing. By using a semiautomated review to integrate the algorithm detections in a multiple-observer approach for abundance estimation, it is possible to relax the requirement for high-accuracy performance in detection algorithms. Contrasting with previous studies that highlight the importance of choosing low classification thresholds to minimize losing individuals (Dujon et al., 2021; Gray, Fleishman et al., 2019; Mannocci et al., 2021), we showed that it may be preferable to prioritize the reduction of false positives, while addressing the false negatives with the multiple observer model. Moreover, with this approach, we were able to estimate the algorithm detection probability with its associated uncertainty. In contexts where the unavailability of individuals (i.e. individuals present in the image area but not available for detection by human or algorithm observers) can be considered insignificant (e.g. bird or pinniped colonies), an estimate of abundance is directly obtained from the multiple observer model. Otherwise, if the individuals' availability probability is less than one (as it may be in many cases, including ours), the modeling structure for multiple observers can be integrated into approaches that accommodate other sources of error, for example, as a level in hierarchical N-mixture models with repeated visits (Brack et al., 2021; Williams et al., 2017) or with auxiliary data (Martin et al., 2015). Obviously, a multiple observer approach can be time-consuming because it demands a person to manually review the imagery independently, but this can be done in only a subset of the images (Brack et al., 2021 and Chapter 3 of this thesis). Finally, the need of a human observer for image review can be dispensed under a spatiotemporally replicated survey design, in which the semiautomated counts are fitted under a single-observer N-mixture model (Brack et al., 2021 and Chapter 3 of this thesis). In this case, the perception probability by the algorithm compounds (together with the availability probability) an overall detection probability.

We obtained a large number of false-positive detections in our test set, although comparable to other studies that suggest that background heterogeneity negatively affects CNNs precision (Dujon et al., 2021; Dujon & Schofield, 2019; Kellenberger et al., 2018). The sources of these false positives we found (tree trunks, dead vegetation and other animal species) were similar to other examples of aerial image surveys of large mammals (e.g. Kellenberger et al., 2018). Although the networks were trained only with marsh deer samples, other species probably present more similar features to deer than to background, making them to be classified as marsh deer. One possible solution to reduce this type of error is to create another class (one or more) to comprise these other species and then retrain the algorithm. Furthermore, especially for rare species that appear in low frequencies in the imagery, the huge proportion of background area in images (in our test set, 122 deer in a context of 41 million tiles) hinders the generation of representative background samples. To avoid dealing with a very-large number of background samples (that can hamper training process), the trained CNNs could be retrained only with the false-positive tiles obtained in the first training. This process would potentially make the network to learn the specific features of common false positives (e.g. tree trunks and dead vegetation) and significantly increase algorithm precision.

Although the two CNNs presented independently a low precision, the consensus classification from the two architectures drastically reduced the number of false positives (3.5-fold increase in precision) without a great prejudice in the proportion of deer detected (reduction of 0.09 in recall). The considerable difference in the architecture of these two models may have favored the significant decrease in false positives, since the more dissimilar the architectures the more distinct will be the features learned (Brownlee, 2019). Hence, ensemble methods using distinct architectures may provide an avenue to achieve higher performances. A more straightforward approach than the simple classification consensus we used here would be training an ensemble algorithm that combines two or more CNN architectures in a unique framework (Brownlee, 2019).

Planning drone flights with frontal overlap between successive pictures can provide great benefits by i) enlarging the number of samples for training and ii) increasing the probability of an algorithm to detect an individual. This benefit was already perceived to improve detection by human observers in manual reviewing (Brack et al., 2021; Hodgson et al., 2013) and also to avoid effects of sun glitter in algorithm detections of aquatic animals (Dujon et al., 2021). In this study, the overlapping was particularly impactful to detect partially hidden individuals since pictures are taken from different angles (example in Figure 2l). In the case of video footage surveys, this overlap can be considered when extracting frames during the image preprocessing (Dujon et al., 2021). One important drawback that needs to be taken into account when planning frontal overlapping flight plans is the necessity of more storage and processing capacity. A 50% overlap is required to ensure each individual appears twice in the imagery; this percentage increases to 67% and 75% for three and four times respectively. The image set increases accordingly. Nevertheless, we strongly recommend planning flights with frontal overlap because of the benefits it provides, especially for rare species for which a large number of samples is usually more difficult to obtain.

Although interdisciplinary collaborations can improve speed and quality when using deep learning (Lamba et al., 2019; Weinstein, 2017), ecologists may benefit from training their own algorithms for specific purposes. Neural networks present a large advantage to other conventional machine learning algorithms that is the exemption of programming complex and problem-specific feature extractors. APIs such as Keras have smoothed learning curves for non-expert users, being now available from the most popular programming language used by ecologists (i.e. R). Furthermore, deep learning training is becoming more accessible without the need to build architectures from scratch by using transfer learning in networks pretrained in large databases for general tasks. The pipeline developed here including the use of accessible deep learning to detect animals in drone imagery and including algorithm counts in abundance modeling can greatly improve future assessments of population size and monitoring programs of threatened species, such as the marsh deer. We expect the accessibility of the presented approaches for ecologists to increase the use of deep learning in drone-based surveys, still quite restricted to “developed” countries (Dujon & Schofield, 2019).

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Data Availability

We provide R code for all the steps involved in this study at the GitHub repository https://github.com/ismaelvbrack/CervoNet. We do not readily provide the drone imagery neither the trained algorithms because of cloud storage limitations, but we are willing to share under requests.

Author Contributions

IVB, JJLM, AK, and LFBO conceived the study; IVB, DOB and LFBO conducted the marsh deer fieldwork; IVB, DOB, and GS processed flights' info and images and carried out the manual and semiautomated review; IVB prepared data for training and testing, trained the algorithms, analyzed the data, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONSIDERAÇÕES FINAIS

Esta tese traz contribuições em dois contextos detalhados abaixo: i) avanços em desenvolvimentos metodológicos para estimar e monitorar a abundância de populações animais; e ii) entendimento das relações de um grande herbívoro sul-americano, o cervo-do-pantanal (*Blastocerus dichotomus*), com diferentes aspectos da paisagem, assim como estabelecimento de uma abordagem para monitoramento dessa espécie ameaçada de extinção.

Modelagem de abundância em a partir de amostragem com drones

O estabelecimento dos drones como ferramenta de coleta de dados para amostragens de populações animais depende do desenvolvimento de abordagens metodológicas robustas e eficientes nos mais variados contextos em que eles têm sido utilizados. Nesta tese, exploramos possibilidades de desenho amostral e análise de dados para estimar abundância com drones, assim como tratamos de alguns dos principais desafios no seu uso, notadamente aspectos de detecção imperfeita e revisão de grandes bancos de imagens. Amostragens aéreas com drone devem ser cuidadosamente planejadas, com avaliações prévias dos possíveis erros de detecção. Esses erros devem ser levados em consideração no desenho amostral e na modelagem estatística, uma vez que podem afetar as contagens e consequentemente enviesar as estimativas de abundância. Os modelos hierárquicos fornecem uma abordagem flexível e robusta para modelar a abundância no espaço e no tempo, acomodando as possíveis fontes de erro durante as amostragens. O planejamento amostral consciente, de maneira a otimizar a alocação do esforço tanto no campo quanto no laboratório pode ter um grande impacto na acurácia das estimativas de abundância. A aplicação de algoritmos para detectar indivíduos nas imagens pode reduzir imensamente o tempo de processamento, sem comprometer as estimativas.

Contagens feitas a partir de amostragens com drone podem sofrer vieses a partir de quatro tipos principais de erro de detecção:

1. Erro de disponibilidade: indivíduos presentes na área de amostragem, mas indisponíveis para serem detectados por estarem escondidos (e.g. sob a vegetação ou mergulhados).

2. Erro de percepção: um observador humano ou um algoritmo pode falhar em detectar um indivíduo disponível nas imagens coletadas.
3. Erro de identificação: um observador humano ou algoritmo podem confundir uma feição da vegetação na foto ou outra espécie como um indivíduo da espécie de interesse.
4. Contagem dupla: o mesmo indivíduo pode aparecer duas ou mais vezes nas imagens devido a movimentação entre linhas de voo ou a sobreposição de imagens.

Os dois primeiros erros são considerados falsos negativos e geram vieses negativos nas contagens e os dois últimos são erros falsos positivos que geram vieses positivos. Enquanto os falsos negativos são considerados mais generalizados em amostragens aéreas (e também para outros tipos de métodos) e há mais abordagens disponíveis para lidar com eles, maneiras de corrigir falsos positivos em contagens ainda estão em etapas iniciais de desenvolvimento, embora sejam mais fáceis de evitar na amostragem. O erro de disponibilidade é comumente acessado em amostragens aéreas através de informações auxiliares (e.g. biotelemetria). O erro de percepção geralmente é estimado usando uma abordagem com observadores múltiplos. O erro de identificação pode ser evitado incluindo nas contagens apenas os indivíduos detectados com certeza, descartando as dúvidas. O erro de contagem dupla pode ser reduzido através da configuração dos voos e conferindo imagens sequencialmente sobrepostas. Os modelos hierárquicos oferecem uma abordagem integradora para acomodar as diferentes fontes de erro nas estimativas de abundância.

Amostragens espaço-temporalmente replicadas com drone, ou seja, voos repetidos em múltiplos sítios, analisadas através de modelos de mistura para abundância (*hierarchical N-mixture models*) se mostraram uma abordagem interessante para estimativas de abundância com drones, sem a necessidade de obtenção de dados auxiliares. Com essa abordagem é possível levar em conta as duas principais fontes de erros de detecção em amostragens aéreas, os erros de disponibilidade e os de percepção. Além disso, a partir do uso de observadores múltiplos revisando as imagens (em complemento a repetições de voo), é possível segregar o processo de observação em dois níveis que representam os dois erros de detecção (disponibilidade e percepção). Os sítios amostrados através dos voos repetidos de drone podem ser definidos a partir de segmentos de linhas planejadas de acordo com as características da espécie estudada, embora seja importante testar se diferentes configurações de tamanho de segmento afetam as estimativas. Notavelmente, as simulações que realizamos mostraram que os modelos *N-mixture* podem fornecer estimativas acuradas mesmo em cenários de baixa disponibilidade dos indivíduos, como no caso de ambientes florestais.

Dentro dessa lógica de amostragens espaço-temporalmente replicadas, diferentes combinações de número de sítios e repetições (partindo de um esforço total fixo) podem resultar em acurácias bastante distintas. A combinação ótima de sítios e visitas depende fortemente do contexto, particularmente da densidade e da detectabilidade da espécie. Por exemplo, usando como base as estimativas de abundância e detectabilidade de cervo-do-pantanal geradas a partir da expedição de 2017 na RPPN Sesc Pantanal, verificamos que um desenho otimizado pode produzir acurácias até dois terços maiores do que um desenho sem planejamento ótimo. Assim, um desenho amostral bem planejado deve levar em conta qual a combinação de sítios e repetições que otimiza o desempenho dos modelos *N-mixture* no contexto do sistema estudado. Em cenários de probabilidade de disponibilidade dos indivíduos mais baixa, o desenho amostral deve priorizar mais repetições do que sítios, enquanto em disponibilidades mais altas, priorizar mais sítios com menos visitas. À medida em que a abundância local da espécie aumenta, o desenho amostral ótimo se torna mais flexível com relação a escolha do número de sítios e visitas, permitindo que se leve em conta outros fatores no planejamento (e.g. priorizar mais sítios se há interesse em variação espacial da abundância ou priorizar mais visitas se o custo de amostrar novos sítios é muito alto).

A decisão entre utilizar um protocolo de revisão das imagens com apenas um único observador ou observadores duplos também pode afetar tanto o desempenho dos modelos *N-mixture* quanto a otimização do esforço amostral em campo. No caso de contagens de observador único, o desenho amostral ótimo tende a requerer um pouco mais de visitas do que com observadores duplos. À medida que se aumenta a proporção de voos com revisão de dois observadores, a tendência de otimização é diminuir o número de visitas necessários. Na comparação entre a performance de abordagens com observadores único (*binomial N-mixture*) e duplos (*multinomial N-mixture*), o emprego de um segundo observador pode aumentar a acurácia das estimativas mesmo em situações de alta probabilidade de percepção. Interessantemente, a decisão de usar um segundo observador na revisão das imagens, de modo a aumentar a acurácia das estimativas, pode ser feita após as amostragens de campo, em situações, por exemplo, de limitação de recursos para campo ou quando a precisão das estimativas é baixa. A revisão por um segundo observador pode ser aplicada em apenas uma parcela do banco de imagens, sem comprometer a capacidade de segregar os dois processos de observação (disponibilidade e percepção). Isso é particularmente interessante quando se tem contagens realizadas a partir de detecção automática. Dessa forma um segundo observador humano poderia apenas revisar uma parte das imagens.

Para detectar automaticamente animais em imagens aéreas, as redes neurais convolucionais tem se mostrado uma ferramenta poderosa (Christin et al., 2019; Corcoran et al., 2021; Wäldchen & Mäder, 2018; Weinstein, 2017). Porém, a implementação desses algoritmos em estudos ecológicos ainda apresenta algumas limitações. Redes neurais profundas são algoritmos com um grande número de parâmetros treináveis (na casa das dezenas de milhões) e, portanto, demandam bancos massivos de imagens para o treinamento sem que ocorra sobreajuste (i.e. o algoritmo "decora" as imagens usadas para treino). Outro possível obstáculo para o uso desses algoritmos por ecólogos é que construir suas arquiteturas é extremamente complexo, adicionalmente ao fato de que a principal linguagem de programação usada em *deep leaning* é Pyhton, enquanto a linguagem mais popular na área de ecologia é R (Lai et al., 2019). Aqui, nós desenvolvemos uma abordagem para detectar cervos-do-pantanal em imagens aéreas usando redes neurais convolucionais para classificação de imagens acessíveis para não-especialistas e lidando com pequenas amostras.

Para isso, nós aplicamos algumas ferramentas e técnicas recentes: i) transferência de aprendizado, no qual uma rede já existente e treinada para tarefas mais gerais é adaptada para uma tarefa mais específica; ii) inflação de amostras (*data augmentation*), na qual se aumenta artificialmente o número de amostras para treinamento através de transformações aleatórias (e.g. rotação, translação, espelhamento, aumento/diminuição de brilho); iii) utilização do *keras* API (Interface de Programação de Aplicações), recentemente implementado no R. O algoritmo desenvolvido recebe pedaços de imagens aéreas (janelas de 128x128 px) e as classifica como "cervo" ou "plano-de-fundo". Obtivemos desempenhos razoáveis considerando independentemente as duas redes neurais que treinamos com sucesso, próximo de 90% de cervos detectados, no entanto, apresentando um grande número de falsos positivos. Verificamos que uma classificação usando o consenso entre as duas redes pode reduzir consideravelmente o número de falsos positivos sem comprometer muito a proporção de cervos detectados.

O algoritmo aqui desenvolvido pode ser aprimorado à medida que mais expedições forem realizadas, inclusive em diferentes regiões de ocorrência de cervos.

Para o processamento dos alvos detectados pelos algoritmos, um procedimento semiautomático foi aplicado, ou seja, um observador conferiu cada alvo, confirmando se continha ou não cervo. Apesar de exigir um pouco mais de tempo do que um processo totalmente automatizado, com essa abordagem foi possível descartar os falsos positivos, reduzindo significativamente o tempo necessário na revisão das imagens e processamento dos cinco voos usados para teste. A redução total de tempo foi de 2 meses na revisão manual para 66 horas no método semiautomático. A configuração utilizada no planejamento dos voos, programando as fotos com sobreposição frontal (um mesmo registro geralmente aparece em 2-4 fotos) trouxe benefícios consideráveis de modo a produzir mais amostras para o treinamento das redes e aumentar a probabilidade do algoritmo detectar um indivíduo de cervo presente nas imagens. Esse último benefício foi particularmente impactante na detecção de cervos parcialmente escondidos, uma vez que as fotos são tiradas de ângulos diferentes.

As contagens obtidas a partir do processamento semiautomático podem ser usadas para estimativas de abundância de duas formas: em amostragens espaço temporalmente replicadas com observador simples, analisadas com modelos *N-mixture* binomiais; ou integradas com detecções manuais (feitas em apenas uma parcela dos voos) com uma abordagem de observadores múltiplos para serem incorporadas na estrutura de modelagem de abundância como um dos níveis de observação (probabilidade de percepção), analisadas com modelos *N-mixture* multinomiais.

Distribuição da abundância e monitoramento de cervos-do-pantanal com drones

O cervo-do-pantanal é um ungulado sul-americano com certa especificidade de habitat, estando bastante relacionado com áreas úmidas (Piovezan et al., 2010). Os cervos apresentam algumas características com adaptação atribuída a esses ambientes aquáticos como pernas longas com membrana interdigital e forrageio em vegetação aquática. Porém, esses ambientes podem apresentar fortes contrastes sazonais com períodos de seca que podem ser severos, como no Cerrado e no Pantanal. Esses momentos provavelmente são os mais restritivos às populações de cervo. Encontramos que durante a seca no Pantanal, a distribuição da abundância de cervos está bastante restrita às manchas de habitat de maior qualidade. Essas manchas contêm altos índices de vegetação verde e são próximas aos corpos d'água permanentes que restam nessa época (processos base-topo influenciando a abundância). Essas regiões mais favoráveis apresentaram altas densidades de cervo-do-pantanal (até 8 ind./km²). Como esperado para grandes herbívoros, a disponibilidade de forragem foi um fator determinante para a distribuição dos indivíduos, sobretudo em épocas de maiores restrições. Apesar dessas altas concentrações nas áreas mais baixas e úmidas da região de estudo, os cervos-do-pantanal também puderam ser encontrados na região mais seca da reserva em menores densidades. Nessa região, alguns locais apresentaram abundâncias intermediárias relacionadas a corpos d'água artificiais remanescentes da época das fazendas. Essas estruturas podem ser importantes para a manutenção das populações de cervo em áreas mais secas, principalmente na época mais restritiva.

Além disso, não encontramos relação da distribuição da abundância de cervos com a densidade de onças-pintadas. Apesar de não ser possível afirmar que a predação não afeta as populações de cervos, provavelmente esse mecanismo é relativamente mais fraco do que processos base-topo. Interessantemente, os locais com maior abundância de cervos-do-pantanal se sobrepõem com as áreas onde se espera haver maior pressão de predação (altas densidade de onças e próximas a corpos d'água). Como já descrito para outros ungulados em ambientes de savana (Owen-Smith, 2014; Riginos, 2015), áreas com remanescentes de vegetação verde na seca são determinantes na distribuição dos indivíduos. O benefício de acessar essas áreas de alta qualidade deve, portanto, se sobrepor os riscos de predação por onças-pintadas. É possível também que a pressão de predação não seja muito alta uma vez que os cervos não são uma das presas mais frequentes das onças, segundo dados disponíveis na literatura levantados em outras regiões do Pantanal (Cavalcanti & Gese, 2010; de Azevedo & Murray, 2007; Hayward et al., 2016; Perilli et al., 2016).

Futuras explorações, contemplando também a época da vazante, podem complementar o entendimento de como os cervos-do-pantanal são influenciados pelos processos *bottom-up* e *top-down* no Pantanal. É relatado na literatura que na época das chuvas, os cervos se dispersam nas áreas inundadas (Tomas et al., 2001), mas o mecanismo subjacente a isso ainda não foi testado. Assim, seria interessante avaliar em próximas etapas se as forças base-topo são atenuadas nessa época com uma possível maior influência relativa da predação. Esses futuros passos se beneficiarão dos métodos desenvolvidos ao longo desta tese.

Esperamos que métodos de amostragem desenvolvidos ao longo desta tese tenham uma ampla aplicação para estudos populacionais de cervos-do-pantanal. Demonstramos como é importante considerar a detecção imperfeita em levantamentos aéreos para estimativas de abundância, em especial o erro de disponibilidade que raramente é considerado. Os métodos apresentados podem ser replicados para estimar o tamanho populacional em locais em que os cervos se encontram restritos e ameaçados. Adicionalmente, o monitoramento de populações de cervo-do-pantanal pode ser conduzido de maneira eficiente e robusta. Nesse sentido, os algoritmos aqui treinados podem ser diretamente utilizados para outras populações ou aperfeiçoados a partir de novas imagens coletadas.

Ressaltamos aqui um interesse especial no monitoramento das populações de cervo em áreas afetadas pelos grandes incêndios no Pantanal, como a da RPPN Sesc Pantanal. Dessa forma, é possível entender os potenciais impactos desses eventos que se mostram cada vez mais frequentes devido as mudanças climáticas globais e manejo dos usos do solo (Leal Filho et al., 2021; Marengo et al., 2016), acompanhando as flutuações populacionais dessa espécie. Particularmente, no caso da população da RPPN Sesc Pantanal, teremos a possibilidade de acompanhar os cervos comparando duas estimativas anteriores ao grande incêndio de 2020, que afetou mais de 90% da reserva (https://youtu.be/ESIG4uicxPY), com estimativas pós-incêndio. A abordagem desenvolvida também pode embasar avaliações no sentido de prever o efeito da construção de barragens hidrelétricas que afetam ambientes de várzea onde os cervos-do-pantanal ocorrem. Finalmente, visualizamos um grande potencial de aplicação desses métodos para avaliação global do tamanho populacional de cervos-do-pantanal ao longo de toda sua área de distribuição, permitindo uma reavaliação do seu status de conservação e subsidiando ações de conservação para a espécie.

Protocolo de amostragem com drones para cervo-do-pantanal

A partir das abordagens desenvolvidas ao longo desta tese, apresentamos a seguir uma sequência de passos para uma amostragem com drones de cervo-do-pantanal, visando estimar ou monitorar o tamanho populacional da espécie. O protocolo é focado em amostragens espaço-temporalmente replicadas com drone usando câmeras do espectro visível (RGB). O protocolo acomoda, no processo de modelagem, os erros de disponibilidade e de percepção e busca evitar os erros de identificação e contagens duplas. Os passos podem ser adaptados para outras situações de amostragem de cervo-do-pantanal como, por exemplo, com o uso de câmeras termais ou para outras espécies. Disponibilizamos material com códigos para executar todos os passos nos repositórios do GitHub https://github.com/ismaelvbrack/designNmix4droneSurveys e https://github.com/ismaelvbrack/CervoNet.

1. Defina o objetivo da amostragem

Defina o objetivo da amostragem, entre estimar o tamanho populacional, entender as relações da abundância com algum(ns) aspecto(s) espacial(is) ou monitorar a população e associações com variáveis explanatórias, incluindo ações de conservação, ao longo do tempo. Os passos a seguir consideram uma expedição única com o objetivo de obter uma estimativa de tamanho populacional. No caso de monitoramento populacional, deve-se repetir esse conjunto de passos em intervalos definidos pelo objetivo do estudo.

2. Escolha o drone e sensores

Os voos podem ser executados tanto com drones de asa-fixa quanto multirrotores. Em áreas mais extensas e de acesso mais difícil, os drone de asa-fixa podem apresentar vantagens, sobretudo pela maior autonomia de voo. Para situações em que a disponibilidade de locais de aterrissagem de drones de asa-fixa pode ser limitada, os multirrotores podem ter vantagens pela sua flexibilidade. Nos dois casos é importante ter múltiplas baterias, mas isso é especialmente necessário para os multirrotores. Utilize uma câmera RGB com maior resolução possível; pode fazer diferença na largura da faixa amostrada. A distância focal da câmera não deve ser baixa a ponto de distorcer muito as bordas das imagens.

3. Planeje as missões de voo

Planeje as linhas de voo com espaçamento suficiente para evitar que o mesmo indivíduo de cervo possa ser detectado em mais de uma linha. Um espaçamento de 2km deve garantir essa independência, embora essa definição dependa do tempo decorrido entre a primeira e a última repetição naquelas linhas e das características da área e da população estudada. Uma resolução do pixel no nível de solo de aproximadamente 2cm é suficiente para identificar os cervos-do-pantanal nas imagens. Portanto, configure a altura do voo para atingir um valor próximo disso, levando em conta as características do sensor e da lente. Considere que as linhas de voo serão divididas em segmentos para formar os sítios para os quais a abundância local e sua relação com variáveis de paisagem serão estimadas. Caso haja interesse em alguma relação específica com a paisagem, a disposição das linhas pode levar isso em conta no desenho.

4. Execute os voos

Priorize horários em que os cervos estejam mais expostos (disponíveis). Por exemplo, no início da manhã e final da tarde. Concentre os voos repetidos numa mesma missão antes de iniciar uma nova, de modo a diminuir o intervalo de tempo entre o primeiro e o último voo no mesmo sítio. O intervalo entre diferentes repetições deve ser suficiente para garantir a oportunidade de um indivíduo indisponível se tornar disponível e vice-versa. Intervalos de tempo muito grandes entre visitas aumentam a probabilidade de saída e entrada de novos indivíduos, podendo prejudicar interpretações sobre a abundância local. Durante os voos, colete variáveis que podem influenciar a disponibilidade e a percepção de cervos nas imagens. Por exemplo, temperatura, condição do tempo e luminosidade.

5. Revise as imagens

A revisão das imagens coletadas durante os voos pode ser feita com um ou dois observadores. Um protocolo de revisão com observadores duplos pode trazer vantagens nas estimativas como maior acurácia e segregar os dois processos de observação (disponibilidade e percepção). Apenas uma proporção dos voos com observadores duplos já é suficiente (25-30%). É possível utilizar o algoritmo já treinado para detectar cervos em imagens aéreas como um primeiro observador, restando para um segundo observador humano apenas essa parcela do conjunto de imagens. Nesse caso, confira se cada alvo detectado pelo algoritmo corresponde ou não a um cervo, num procedimento semiautomático. Somente considere incluir na contagem os indivíduos que forem identificados com certeza como cervo. Para cada cervo detectado, anote as coordenadas centrais usando, por exemplo, o software ClikPoints (Gerum et al., 2017). No caso de sobrevoos com sobreposição frontal, é importante dar atenção especial para diferenciar os registros quando esses aparecem pela primeira vez no banco de imagens e quando se trata de registros repetidos.

6. Compile os dados

Para as análises é preciso compilar três conjuntos de dados usando os sítios como base: variáveis de sítio, variáveis de ocasião e as contagens. Os sítios devem ser definidos a partir de segmentos de voo, por exemplo, de 1 km de comprimento. As variáveis de sítio (um valor por sítio) são usadas para modelar a variação na abundância (e.g. índice de vegetação, distância a corpos d’água, proporção de alguma classe de cobertura) ou na disponibilidade (e.g. cobertura florestal). Variáveis associadas com a abundância local, mensuradas a partir de imagens de satélite ou outra forma que cubra completamente o universo amostral, permitem fazer extrapolações espaciais da abundância para toda a região de interesse. As variáveis de ocasião são usadas para modelar variações na disponibilidade (e.g. temperatura) ou percepção (e.g. luminosidade da foto) e apresentam tantos valores quantas repetições houver para cada sítio. Para compilar as contagens, é preciso reconhecer quais indivíduos foram detectados por cada observador, usando as coordenadas centrais anotadas. Assim, para cada sítio em cada ocasião, compile quantos indivíduos foram detectados pelos dois observadores; apenas pelo primeiro e apenas pelo segundo. No caso de uso de observador simples, compile apenas as contagens para cada sítio em cada ocasião.

7. Analise os dados

Ajuste as contagens em relação as variáveis usando modelos *N-mixture*. Utilize o *N-mixture* binomial para o protocolo de observador simples ou *N-mixture* para observadores duplos. O modelo binomial possui apenas dois níveis, a abundância local e a detecção, enquanto o modelo multinomial, com três níveis, tem o nível da detecção separado em disponibilidade e percepção. É possível ajustar os modelos usando uma abordagem bayesiana com JAGS através do programa R ou utilizando máxima verossimilhança com o pacote *unmarked* no R. Pode ser importante verificar se o tamanho do sítio escolhido para segmentar as linhas de voo influencia as estimativas de abundância. Para isso, utilize um modelo nulo (sem covariáveis) e rode a análise para diferentes escolhas de tamanho de segmento comparando as estimativas ponderadas pelo seu comprimento. Para estimar a abundância em toda a área de estudo, utilize as relações encontradas entre a abundância local e as covariáveis de sítio para extrapolar para as áreas de interesse. É possível aplicar uma extrapolação simples no caso de um desenho totalmente aleatório na área de estudo, mas uma extrapolação baseada em variáveis tende a ser mais robusta.

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