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Estimating carcass detection and persistence heterogeneity and roadkill numbers with open population capture-recapture models

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Talvez não haja melhor demonstração da tolice das vaidades humanas do que essa imagem distante do nosso pequeno mundo. Ela enfatiza nossa responsabilidade de tratarmos melhor uns aos outros e de preservar e valorizar o pálido ponto azul, o único lar que nós conhecemos.

Carl Sagan

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Resumo

A contagem de carcaças em rodovias é amplamente utilizada para quantificar o impacto dessas infraestruturas na fauna. Um número confiável de atropelamentos é essencial para tomadas de decisão efetivas quanto a mitigação desse impacto. Para isso, é necessário considerar não apenas a contagem simples de carcaças, mas corrigir as principais fontes de erros da amostragem de fatalidades: a detecção e persistência das carcaças. Os métodos usados consideram os erros constantes no espaço, no tempo e, às vezes, entre espécies. Mas, é esperado que eles apresentem variação, já que podem ser influenciados pelo tráfego de veículos ou condições climáticas, por exemplo. Nesse trabalho, apresentamos uma abordagem com modelos hierárquicos de população aberta, usando inferência Bayesiana e dados de captura e recaptura para estimar taxas de atropelamento e exploramos a variação na detecção e persistência das carcaças em diferentes segmentos de rodovia, períodos de amostragem e entre duas espécies: um mamífero (gambá-de-orelha-branca) e um réptil (lagarto-teiú). Procuramos pelas carcaças em um trecho de 104 km de rodovia no sul do Brasil, subdividido em três trechos, em sete campanhas amostrais com quatro dias consecutivos cada. As carcaças foram marcadas para serem reconhecidas ao longo dos dias dentro da mesma campanha, resultando em um histórico de capturas para cada carcaça. Estimamos as probabilidades de detecção e persistência das carcaças, o número de atropelamentos e taxas diárias de atropelamentos por quilômetro para cada espécie, trecho e campanha. Foram feitas 218 capturas de 94 indivíduos de gambá e 61 capturas de 41 indivíduos de teiú. Houve grande incerteza nas estimativas dos parâmetros, principalmente para o teiú, devido ao menor número de capturas, dificultando a visualização da variação da detecção e da persistência. A taxa de atropelamento que estimamos demonstrou ser o parâmetro mais confiável para avaliar e comparar atropelamentos em rodovias. O padrão estimado pelas taxas no comparativo entre as duas espécies diferiu do observado, embora tenham mais registros de gambás, as taxas de atropelamento são semelhantes entre as espécies.

Palavras-chave: detecção imperfeita; ecologia de rodovias; erros de amostragem; modelos hierárquicos, modelo de superpopulação, taxa de atropelamento

Abstract

The number of carcasses found on roads is widely used to quantify road impact on wildlife. However, only a raw count of carcasses does not represent the actual roadkill number that is essential to support mitigation effort decisions. Carcass detection and persistence are the main sources of error in roadkill estimates. Current methods used to correct carcass counts consider detection and persistence as not varying in space, time and, sometimes, among species. However, it is expected these parameters to vary. Here, we present a hierarchical approach in a Bayesian framework using an open population model and capture-recapture data to directly estimate roadkill rates and explore carcass detection and persistence variation among segments, sampling sessions and two species, a mammal (opossum) and a reptile (tegu). We surveyed carcasses on a 104 km road stretch in Southernmost Brazil splitted in three segments, during seven sampling sessions, each one with four consecutive days. Carcasses were marked and could be recaptured over the sampling days within the same sampling session, resulting in a capture history for each carcass. We estimated carcass detection and persistence probabilities, roadkill numbers and a daily roadkill rate per kilometer for species, segments, and sessions. We recorded 218 captures from 94 individuals of opossums, and 61 captures, from 41 individuals of tegus. Parameter estimates presented large uncertainty, mainly for tegus, due to the lower number of captures, thus variation in detection and persistence was not clear. The roadkill rate is the best parameter to evaluate and compare roadkill numbers. The roadkill rates diverged from the observed pattern when comparing the two species, we found a higher number of opossums carcasses, but estimated roadkill rates were similar with tegus.

Keywords: hierarchical models; imperfect detection; superpopulation model; road ecology; roadkill rates; sampling errors

Sumário

Introdução Geral

A amostragem de seres vivos por meio de contagens permeia muitas das perguntas ecológicas que buscamos responder a respeito da natureza (Kery & Schaub, 2012; MacKenzie et al., 2006; Williams et al., 2002). Esse tipo de dado é utilizado para quantificar aspectos demográficos e biogeográficos, como abundância e distribuição de espécies, e para o entendimento de questões desde dinâmica populacional, organização de comunidades, até aspectos ligados à conservação e ao manejo de espécies (ver exemplos em Kellner & Swihart, 2014). Estimativas a partir da contagem de organismos são, portanto, parte de muitos trabalhos ecológicos há bastante tempo. A amostragem por contagem de indivíduos, porém, pode não ser uma boa representação da realidade, pois são raras as situações em que o universo disponível para a amostragem representa o todo do que queremos amostrar (Anderson, 2001). Qualquer amostragem está sujeita à capacidade do método empregado em detectar indivíduos ou espécies na área amostrada, e essa capacidade também está sujeita a diversos fatores, como condições do momento da amostragem, ou características da espécie ou local amostrado, por exemplo. Mesmo que um indivíduo ou espécie esteja presente, ele pode passar despercebido e não ser detectado (Kéry & Schmidt, 2008; MacKenzie et al., 2006). A maioria das observações ecológicas são, portanto, resultantes de um processo ecológico subjacente não diretamente observado e também de um processo amostral que pode mascarar o processo ecológico (Kery & Schaub, 2012).

Os modelos hierárquicos têm se estabelecido como um método que permite modelar explicitamente o processo ecológico e o de amostragem juntos. Eles conseguem separar a variação observada nos dados que é realmente devida à variação de abundância, da que é devida à amostragem, permitindo que se possa fazer inferências confiáveis sobre o processo ecológico de interesse (Royle & Dorazio, 2006). Em um único modelo, a estrutura dos modelos hierárquicos é capaz de acomodar a heterogeneidade em múltiplos parâmetros (como a variação da probabilidade de detecção dos indivíduos ou o efeito de covariáveis na abundância) e propagar a incerteza entre os níveis hierárquicos do modelo para cada estimativa obtida (Kery & Royle, 2016; Kery & Schaub, 2012).

O interesse em estimar um número de indivíduos de determinadas espécies em um determinado período ou local, entretanto, vai além das populações vivas. Seres humanos são responsáveis por gerar diversos impactos no planeta, dentre eles a mortalidade direta de animais por meio da implantação e operação de inúmeras infraestruturas como prédios, parques eólicos e rodovias (Hill et al., 2019). A contagem de carcaças vem sendo utilizada para estimar a magnitude dessa mortalidade, seja por envenenamentos, colisões de animais com turbinas de energia eólica, com construções humanas ou com veículos em estradas e ferrovias, por exemplo (Dornas et al., 2019; Fleischli et al., 2004; Gonçalves et al., 2018; Machtans et al., 2013; Péron et al., 2013). Quantificar de maneira acurada esse impacto é necessário para entender como ele pode afetar as populações e a persistência de espécies e ajudar no planejamento de medidas de mitigação e na tomada decisões mais efetivas para a conservação das espécies (Barrientos et al., 2018; Fahrig & Rytwinski, 2009; Kéry & Schmidt, 2008).

Saber quantos indivíduos e quais espécies morrem (ou morrem mais) em determinados locais, ou períodos, em uma rodovia é essencial para tentar evitar ou reduzir as colisões de veículos com animais. Apenas a contagem de carcaças nas rodovias, sem considerar os erros relacionados à amostragem, como muitas vezes ocorre, não é o suficiente para que se possa fazer inferências ou comparações confiáveis entre rodovias ou trechos de uma rodovia, períodos ou espécies (Teixeira et al., 2013). O problema se assemelha a qualquer outro em que existe o interesse de saber o número de indivíduos de determinadas espécies que ocorrem em determinada área ou período, mas nesse caso, são indivíduos atropelados em rodovias.

As principais fontes de erro das amostragens com contagens de carcaças são a detecção imperfeita dos observadores e a remoção de carcaças da pista (Barrientos et al., 2018). Existem algumas abordagens propostas para corrigir esses erros e se obter estimativas mais acuradas de fatalidades. A maioria delas é baseada em modelos utilizados para estimar abundância em populações vivas com a premissa de população fechada (sem indivíduos entrando ou saindo da população durante o tempo do estudo) e adaptados para o contexto das estimativas de fatalidades (Bernardino et al., 2013; Korner-Nievergelt et al., 2015; Péron, 2018). Entretanto, o sistema que envolve os atropelamentos de animais em rodovias se encaixa melhor dentro de um contexto de população aberta, já que durante o tempo do estudo as carcaças não são um número fixo na estrada. Novos indivíduos podem constantemente ser atropelados e entrar na população, assim como as carcaças podem ser removidas, seja por fluxo de veículos, carniceiros ou outros fatores.

Recentemente surgiram algumas propostas para estimar a abundância de carcaças em estradas e parques eólicos por meio de modelos de população aberta derivados de modelos de captura-recaptura (Guinard et al., 2012; Péron et al., 2013). Nesses modelos se faz uma analogia conceitual dos parâmetros demográficos originalmente usados em populações de animais vivas para o contexto das fatalidades ou, no caso de rodovias, atropelamentos. Onde a população de interesse é a de animais atropelados (carcaças na rodovia), a probabilidade de captura é a probabilidade de detecção das carcaças, a probabilidade de sobrevivência é a probabilidade de persistência das carcaças na rodovia e o recrutamento é a probabilidade de entrada das carcaças na população.

Na maioria das abordagens, porém, as correções relacionadas à detecção imperfeita são consideradas homogêneas no espaço e no tempo, e em alguns casos, entre as espécies também. Isso significa considerar que a capacidade de detecção pelos observadores e a persistência das carcaças é a mesma ao longo de uma rodovia e/ou do tempo, ou para diferentes espécies. Porém, é razoável pensar que exista variação nesses parâmetros. Como ocorre em outras amostragens, a probabilidade de detecção deve variar, entre outros fatores, ao longo de ambientes, entre observadores e entre dias de amostragem (Anderson, 2001; Royle & Dorazio, 2006). Pensando nas rodovias, características da pista, como o tipo de pavimentação, e do tráfego de veículos também podem gerar essa variação (Guinard et al., 2012). O mesmo vale para a persistência das carcaças, que pode ter influência da atividade de carniceiros, condições climáticas e variações no tráfego de veículos (Beckmann & Shine, 2015; Guinard et al., 2012). Todos estes fatores podem estar sujeitos a variação espacial, temporal e entre espécies. Essa variação nos erros parece óbvia se considerarmos, por exemplo, a persistências de carcaças para espécies de tamanhos diferentes: uma espécie menor tende a ser mais facilmente removida da pista do que uma espécie maior. Alguns estudos já ressaltam a necessidade de estimar o efeito desses erros nas estimativas de fatalidades por espécies ou grupos de espécies (Teixeira et al., 2013).

Não levar em conta essa variação pode implicar numa classificação incorreta de quais estradas ou segmentos de estradas, períodos ou espécies apresentam maior número de atropelamentos. Um trecho que pelo número observado apresenta um grande acúmulo de carcaças, poderia, na verdade, ser um trecho onde as carcaças permanecem por mais tempo ou um trecho onde a capacidade dos observadores de detectarem as carcaças é maior, ou uma combinação de ambos. Essa mesma lógica pode ser aplicada para diferentes períodos ou espécies. Isso pode ter consequências na tomada de decisão em relação à localização de medidas mitigadoras e de espécies (ou grupos alvo) de mitigação, bem como na avaliação da efetividade dessas medidas ao longo do tempo (se elas realmente reduziram o número de fatalidades). Levando em consideração a heterogeneidade desses parâmetros nas estimativas de fatalidades teríamos um número de atropelamentos mais próximo à realidade e confiável para tomar decisões, por isso, nesse trabalho, queremos explorar essa heterogeneidade no espaço, no tempo e entre espécies por meio de uma abordagem hierárquica com modelos de população aberta.

Minha motivação

Talvez pareça estranho que a minha motivação não comece com dúvidas científicas ou curiosidades sobre o tema da ecologia de estradas. Mas a motivação mais clara dentro de mim está na minha infância: a Talita criança, que queria saber sobre animais, sobre ciência e que gostava de estudar. Fui a criança, às vezes estranha, que achava divertido fazer o tema de casa.

Sei que fui privilegiada por poder apenas estudar, brincar e sonhar (como todas as crianças deveriam), e ainda receber incentivo da família, de amigos, professores e até de uma vizinha bióloga, que me deu de presente uma caixa (cheia de coisas legais) para eu brincar de ser cientista.

Quando eu vi, a Talita da caixinha de cientista estava fazendo uma seleção para o mestrado sem saber muito o porquê. Parte dos porquês está justamente na caixinha e a outra, nas aulas do último semestre da graduação. Durante as aulas de Biologia da Conservação eu saia da minha zona de conforto e ficava inquieta. Sem perceber, estava de novo me divertindo com o tema de casa. Foi assim que eu descobri o Núcleo de Ecologia de Rodovias e Ferrovias (NERF) e fui apresentada a um mundo, até então, quase desconhecido para mim.

Durante os primeiros meses no NERF, um pouco perdida, fui me inteirando dos projetos e das questões que o grupo tinha interesse, principalmente, mas não só, em ecologia de rodovias. A primeira ideia de mestrado, mais próxima do que eu tinha me dedicado na graduação, não foi para a frente, principalmente pelo orçamento. Com o passar do tempo, fui conhecendo e me interessando por outras demandas dentro do NERF, e das conversas com os colegas de laboratório, surgiu a oportunidade de fazer esse trabalho. Da busca por estimativas mais acuradas e de explorar as variações nos erros relacionados às amostragens de carcaças em rodovias, junto com a minha curiosidade e vontade de ir para campo foi se desenhando o plano B da minha dissertação, que virou A, rapidamente. Espero com esse trabalho contribuir para geração de informações mais confiáveis e que possam dar suporte para decisões efetivas, principalmente no cenário de mitigação da fauna atropelada.

Estimating carcass detection and persistence heterogeneity and roadkill numbers with open population capture-recapture models*[1]

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1. Abstract

1. Carcass counting is widely used to quantify the impact of roads on wildlife. However, only a simple count can poorly represent the actual roadkill number. Carcass detection and persistence are the two main sources of error in roadkill estimates. Current methods used to correct carcass counting consider carcass detection and persistence constant in space, time and, sometimes, among species. However, it is expected for these parameters to vary in most cases. Using an open population capture-recapture model we estimated roadkill rates and explored variation in carcass detection and persistence for different road segments, periods, and species.

2. We surveyed for carcasses on a 100 km road stretch in Southern Brazil during seven

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sampling sessions, each one with four consecutive survey days. We focused on a mammal (opossum) and a reptile (tegu) species since they present different skin and body shape characteristics that can highlight differences in carcass detection and persistence. Individuals were marked and could be recaptured over the survey days within the same sampling session, resulting in a capture history for each individual.

3. We estimated carcass detection and persistence probabilities using a hierarchical open-population model using Bayesian inference. We also estimated roadkill numbers and a daily roadkill rate per kilometer.

4. We recorded 218 captures, from 94 individuals of opossums, and 61 captures, from 41 individuals of tegus. Parameter estimates presented large uncertainty, mainly for tegus, due to the lower number of captures, thus variation in detection and persistence was not clear. The roadkill rate is the best parameter to evaluate and compare roadkill numbers. The roadkill rates diverged from the observed pattern when comparing the two species, opossums presented a higher number of carcasses found, but estimated roadkill rates were similar with tegus, indicating possible implications on identification of mitigation priorities.

5. *Synthesis and applications*. Spatial, temporal, and inter-species variation in carcass detection and persistence should be considered to obtain accurate roadkill estimates and make comparisons. The approach presented here, mainly through the roadkill rates, can be used to make reliable prioritization of mitigation efforts.

Keywords

hierarchical models; imperfect detection; superpopulation model; road ecology; roadkill rates; sampling errors

2. Introduction

Animal-vehicle collisions on roads and railways are a major impact of human infrastructures on wildlife (Beckmann & Shine, 2015; Forman & Alexander, 1998). Quantifying this impact is necessary to understand how it can affect animal populations and how to minimize its negative effects. Roadkill estimates are used to compare different road network segments, periods or species, enabling impact assessment after road pavement or widening, and to plan and assess mitigation effectiveness (Borda-de-Água et al., 2014; Guinard et al., 2012).

Carcass surveys on roads are widely used to estimate roadkill numbers, however, the raw count of carcasses may poorly represent the actual number of killed animals. As in most sampling methods, data from carcass counting has false-negative errors due to imperfect detection. False-negatives in carcass counts can be due to: (1) detection probability - not all available carcasses during survey occasions will be seen by the observers; (2) persistence probability - some carcasses are removed from the road before the survey occur and therefore, are not counted; and (3) some carcasses may fall outside the searched road area (Guinard et al., 2012). Not taking these errors into account may bias the estimates and compromise their utility (Guinard et al., 2015; Teixeira et al., 2013).

There are different approaches to address the two first sources of bias (detection and persistence) and to correct animal fatalities counts based on carcass surveys, each one adapted for different data and sampling circumstances (Bernardino et al., 2013; Korner-Nievergelt et al., 2015). Most of them are based on the Lincoln-Petersen (LP) estimator, widely used to estimate the population size of living animal populations (Williams et al., 2002) and adapted to the context of carcass abundance estimates (Péron, 2018). Basically, to estimate abundance (N), the LP estimator considers the ratio of the number of individuals detected (n) to the overall detection probability (p^*): $E(N) = n/p^*$. In a capture-recapture framework, p^* is the proportion of marked individuals (from a first sampling) that are recaptured in subsequent occasions (Williams et al., 2002). For carcass abundance estimates, $p*$ is usually estimated from experiments designed to measure the proportion of carcasses detected by the observers (from a known set) and the carcass persistence probability by following the carcasses fate through time, then both are used to obtain the overall detection probability (Dornas et al., 2019; Gonçalves et al., 2018).

Although the LP based estimators aim to obtain a more accurate number of animal fatalities than just the raw counts, some limitations have been highlighted (Péron, 2018). Possibly the major limitation is that the LP based estimators assume a closed-population context (no individuals leaving or entering the population). Recently, there have been some proposals for a shift in the approach for modeling "carcass populations" using open population capture-recapture models and process-based modelling (i.e. based on explicit assumptions about how the ecological system of interest works to estimate the parameters; Cuddington et al., 2013), these approaches represent better the roadkill context, which new carcasses are continuously entering the road or being removed (Guinard et al., 2012; Péron et al., 2013; Dalthorp et al., 2018; Simonis et al., 2018). Furthermore, as many different LP based estimators are being used to obtain carcass abundance and each one is designed to specific situations, this could often imply on assumption violations of the used estimator and result in biased estimates (Péron, 2018).

The roadkill open-population models are based on the superpopulation formulation (Schwarz & Arnason, 1996), used for living populations. Péron et al. (2013) proposed this approach for fatalities in wind-power farms and the parameter of interest is the superpopulation size, which corresponds to all individuals that passed through the population, that is, the total number of carcasses that were available for detection in at least one sampling occasion. The superpopulation model is modified to use a single carcass counting occasion and trial experiments to estimate carcass detection and persistence probabilities (instead of capture-recapture data from several sampling occasions).

Both the LP estimators and the current applications with the open population approach commonly assume homogeneity on detection and persistence probabilities in space and time. However, it is expected that they vary either along the road(s) or in different periods of the year(s), as the road paving, traffic volume, weather, scavenger abundance and activity also vary (Guinard et al., 2012; Korner-Nievergelt et al., 2015). Among species, this variation is also expected, as carcasses can vary in size, tissue characteristics, and attractiveness to scavengers (Beckmann & Shine, 2015; Colino-Rabanal et al., 2011). If the approach used to correct the roadkill counts assumes that detection and persistence are homogeneous in space, time and among species, it can mask roadkill temporal and spatial patterns. It is important to note that some studies of bat and bird mortality estimation at wind-power farms already tried to accommodate some degree of variation in these errors sources (Péron et al., 2013; Korner-Nievergelt et al., 2015; Dalthorp et al., 2018; Simonis et al., 2018).

A general approach widely used to assess ecological variables of interest (e.g., abundance, distribution, survival) while accounting for imperfect detection and modelling heterogeneities are the hierarchical models (e.g., occupancy models, capture-recapture) (Kery & Royle, 2016). This approach allows us to handle carcass survey data in a hierarchical manner, considering the ecological process (generally the one that the interest relies on, e.g. roadkill rates) and the sampling process that masks the ecological process (Kery & Schaub, 2012). Hierarquical models explicitly model the data without the necessity of an external experiment, they are flexible and can incorporate many different processes, mainly under a Bayesian inference (Kery & Schaub, 2012). The road ecology and the assessment of roadkill impact may benefit from this approach by estimating straightforward roadkill rates.

Here we present a process-based approach in a Bayesian framework to directly estimate roadkill rates and explore how carcass detection and persistence can vary among species, space, and time. To do this we used capture-recapture carcass data, collected in successive days. We sampled a road splitted in three segments in different months, searching for roadkills of a mammal (opossum) and a reptile (tegu) species, marking and recapturing the carcasses. We expect that detection and persistence probabilities would be lower and more variable in space and time for the tegu compared to the opossum, based on their body shape, size and softer tissues. Although adults of both species are of similar size, tegus have a thinner body shape and individuals of a larger range of ages and sizes cross roads. We also suspect that tegu's softer skin and slender shape would make them more prone to removal by traffic and more attractive or easier to carry by scavengers. We expect that the ranking of species, segments and months with higher roadkill numbers will change if we account for carcass detection and persistence variation.

3. Materials and methods

3.1 Open-population capture-recapture models for roadkill estimation

The modeling approach applied here is based on the superpopulation (POPAN) formulation of the Jolly-Seber (JS) open-population model (Schwarz & Arnason, 1996). We used a similar approach to Guinard et al. (2012) and Péron et al. (2013), but with an explicit assessment of roadkill rates by marking and recapturing carcasses in successive days.

Open population models assume that individuals are entering and leaving the population, that is, there are mortality, recruitment and/or dispersal (Pine et al., 2003). The JS models were first developed due to the interest in estimating animal population abundance and later in parameters such as survival and recruitment rates for open populations (Schwarz & Arnason, 2017). To estimate these parameters, the model requires capture-recapture data (i.e. individual encounter histories) that provide information about detection probability, the disappearance of individuals from the studied population and also the arrival of new ones (Kery & Schaub, 2012). Capture-recapture data is presented in a matrix containing the history of encounters for each individual that was captured in at least one occasion (e.g., 0 1 0 1; this individual was not seen in the first occasion, seen in the second, not seen in the third, and seen again in the last one). For this, captured individuals need to be individually recognized in successive occasions by tagging or using individual natural marks. Then, the capture histories can be used to estimate three basic parameters: entry, survival, and detection probabilities. In the superpopulation parametrization of JS model, individuals of the population are assumed to come from the superpopulation, which corresponds to all individuals that were available for detection in the sampled population at some time during the study period (between first and last occasions).

The JS models have been used for many years in population ecology to address similar issues that we explore in road ecology (Péron, 2018). Here, we made a conceptual analogy of the original demographic parameters estimated for living populations to the roadkill/carcass context, as in Guinard et al. (2012) and Péron et al. (2013). Superpopulation size is recognized as carcass superpopulation size, which corresponds to all carcasses that were available for detection on the road on any occasion during the sampling period. Capture probability becomes carcass detection probability, the probability of a carcass available on the road during a survey to be detected. Survival probability is interpreted as carcass persistence probability, the probability that a carcass present on the road in occasion t persists until occasion $t + 1$. Entry probability (or recruitment) as carcass entry probability, the probability of a carcass from the superpopulation to enter in the population (in this case, the roadkill population) immediately before occasion *t*. The model provides as many carcass entry probability estimates as sampling occasions, the first one has no biological meaning (Kery & Schaub, 2012), since it does not correspond to a known time interval.

In order to estimate the parameters of interest, this model has some important assumptions, most of them similar to other models that use capture-recapture data (Schwarz & Arnason, 2017; Seber, 1982): (1) carcass do not lose their identification while the study occurs; (2) the identification is read correctly; (3) sampling is instantaneous, i.e. sample periods have a short duration; (4) the study area is constant; (5) both marked and unmarked individuals have the same catchability (i.e. detection probability) at each sampling occasion; (6) both marked and unmarked individuals have the same survival probability (i.e. carcass persistence) between each pair of sampling occasions.

3.2 Studied species

We evaluated the proposed open-population approach for capture-recapture carcass data using the mammal species *Didelphis albiventris* (White-eared Opossum) and the lizard *Salvator merianae* (Black-and-white Tegu). Both are common species showing high roadkill records in Brazil (Grilo et al., 2018). As they have different life histories and ecological and morphological traits, they can highlight possible variations in detection and carcass persistence. The opossum can reach around 400 mm of main body length and has a mean body weight of 1.786 g for adults (Cáceres & Monteiro-Filho, 1999), while the tegu can reach 500 mm of snout-vent length (length without the tail; Winck, Blanco, & Cechin, 2011) and has a mean body weight of 2.800 g (Vieira, 2016). Although the species have similar body sizes, the thinner body shape of the tegus, their tegument and tissues characteristics and the more variable size of active individuals (including very small ones with 160 mm of snout-vent length) may influence in lower persistence probabilities when compared to the opossums. The variable size of individuals may also result in lower detection probabilities. The opossum has nocturnal and crepuscular behavior, with concentrated activity in the first hours of the night (Oliveira-Santos et al., 2008), while the tegu has its activity highly related to the temperature and the sunlight, with preference to the hours slightly before noon (Winck et al., 2011). As the removal rates in highways are grater during the day (Ratton et al., 2014), the tegus may be a fresher and more attractive meal being roadkill during day and present lower persistence probabilities. Tegus overwinter in their shelters and present a clear seasonal pattern of activity (Vieira, 2016). Different ratios of activity for males, females and juveniles are observed in warmer months, but in general, the peak of activity is between November and December and individuals are seen active up to April in southern Brazil (Vieira, 2016; Winck et al., 2011) which also may represent more variability in the tegu detection and persistence probabilities since opossums do not present such a variation.

3.3 Study area and data collection

We conducted our roadkill surveys in southern Brazilian coast in two continuous roads: BR-101 and ERS-389. Both are two-lane roads with a speed limit at 80 km/h. Our chosen stretch has 104 km of extension and presents some variation in the traffic volume and in the surrounding landscape. Traffic volume can influence both in carcass detection and persistence, as vehicles movement can accelerate carcasses fragmentation and removal and difficult observers' visibility of the road or interfere in scavengers' activity. Landscape can also be related to scavenger presence and activity, urban areas may have less abundance of them, for example. Based on these general attributes the road was subdivided into three segments of approximately 35 km each, segment 1 is entirely located in the ERS-389 and segment 3 in the

BR-101, segment 2 is in the transition between the two roads (Figure 1.A). Segments 1 is surrounded by more urban areas and presents the highest traffic volume among segments, followed by segment 2 and 3, respectively (the data from traffic volume was retrieved from DAER/RS (2020).

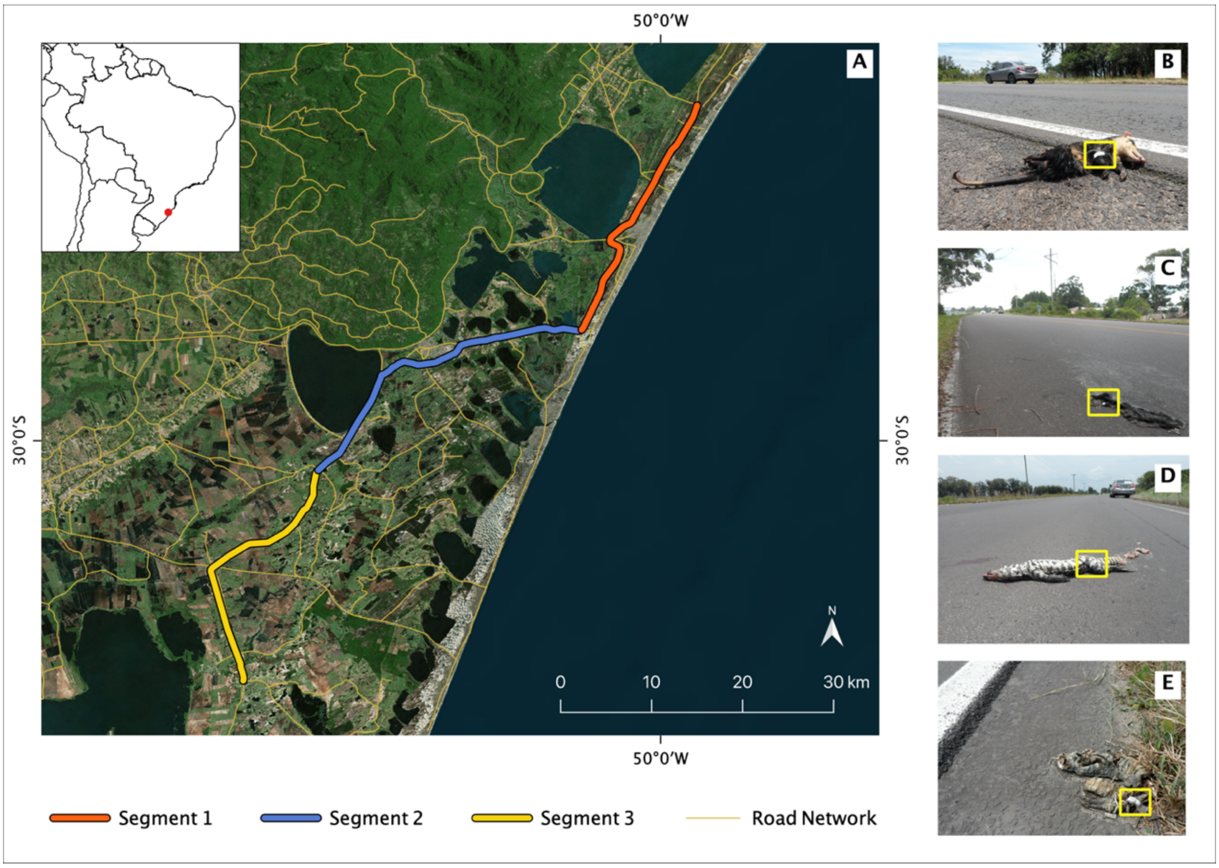

Figure 1. Study area localization with the three sampled road segments (A). Captured and marked individuals of *Didelphis albiventris*, a more recently roadkill in (B) and an older one (C). The same for *Salvator merianae* in (D and E). After the pictures, the marks were hidden as much as possible (turned around and faced to the road side).

We surveyed the roads and shoulders looking for carcasses monthly, in a total of seven sampling sessions each one with four occasions, from October 2018 to April 2019, period with variation in rain and sun incidence and vehicle traffic volume. This period was also chosen because it corresponds to a higher activity of the studied species. These roads are the main connection between large urban centers and the coast, so it is expected that traffic volume increases in the summer season (from December to February).

The road stretch was surveyed by two observers in a car at 40 to 45 km/h, each observer surveyed one lane to make sure all the road was covered. The stretch was surveyed four successive days with interspersed directions (north-south/south-north) to make it difficult to remember carcass locations. Each day corresponds to a sampling occasion hereafter. Location of found carcasses were recorded (handheld GPS coordinates), and carcasses were marked with a tag and identification number (Figure 1. B-E). Therefore, through the occasions within the same sampling session, the carcasses could be classified as a new capture (first record) or a recapture, resulting in a capture history for each individual of both species.

We built species-specific capture history matrices, with individuals in the rows and sampling occasions in the columns. The number of rows was variable, depending on the number of individuals captured for each species, segment or session. The number of columns was always four, according to the number of occasions we sampled. Each cell of these matrices was filled with a 1 or 0 (individual captured or not on a given occasion). To analyze the variation in the parameters between the two species as whole we built two capture history matrices, one for each species, containing all the individuals captured in all segments and sessions. For spatial variation, we built the species-specific capture history matrices for each segment of the road. Each matrix contains all the individuals registered in all sessions for that segment, resulting in three matrices for each species. For the temporal variation analysis, we built the species-specific capture history matrices for each sampling session. Each matrix includes all the individuals registered in all segments for that session, resulting in seven matrices of capture histories for the opossum and six for the tegu (the tegu had no captures in the last session: April).

3.4 Model fitting

We fitted the open-population model under a Bayesian framework, as suggested by Kery & Schaub (2012) for living populations, using the software JAGS (Plummer, 2003) through the package *jagsUI* (Kellner, 2019) in R (R Core Team, 2020). Detection, persistence and superpopulation were modeled as constant parameters and the entry probability was time dependent (i.e., one entry probability per occasion). We used data augmentation approach by adding all-zero capture histories of pseudo-individuals (as much individuals as necessary for estimates stabilization, most cases 101 individuals) and estimated the superpopulation size from an inclusion probability parameter (from a Bernoulli distribution) for the possible individuals of the capture history matrix (Royle et al., 2007; Russell et al., 2012). We assigned vague prior distributions for detection, persistence, inclusion (uniform distributions between 0 and 1) and entry probabilities (Dirichlet distribution). From these basic parameters estimated by the model we derived the superpopulation size and the daily roadkill rate per kilometer. The superpopulation size is the sum of all included individuals (from the latent inclusion parameter). The daily roadkill rate ($RKrate$) is obtained from the carcass entry probabilities, first converting the entry probabilities to the number of individuals that entered before each occasion (B_i), then summing the number of individuals that entered after the first occasion, and dividing to the number of occasions (n) (excluding the first) and the road extension in kilometers (RL):

$$RKrate = \sum_{i=2}^{n} B_i \frac{1}{(n-1)RL}$$

For segments and species roadkill rates, as we modeled the captures from all sessions together, we also divided the roadkill rate by the number of sessions.

For each capture history matrix, we ran the model with 3 parallel Markov Chain Monte Carlo (MCMC) chains with 100 000 steps, throwing out the first 10 000 and keeping all subsequent ones. We assessed model convergence by visually inspecting the chain plots and based on R-hat values (<1.1). From the 270 000 resultant samplings of the posterior distribution, we extracted the mean of the parameters (except for superpopulation that we extracted the median) and their credibility interval of 95%.

4. Results

We recorded 218 captures from 94 individual carcasses of the White-eared Opossum (*Didelphis albiventris*), and 61 captures from 41 individual carcasses of the Black-and-white Tegu *(Salvator merianae).* Number of individuals and captures divided by segments and sessions is in Table 1. For the whole data, 29 carcasses of opossum were captured just once, 24 had two captures, 23 had three and 18 were captured in the four occasions. For the tegu, 26 carcasses were captured just once, 11 had two captures, three had three and just one was captured in the four occasions.

Data arrangement		**Number of individuals**		**Number of captures**	
					
Species	-	94	41	218	61
Segment	1	28	5	70	7
	2	19	12	41	19
	3	47	24	107	35
Session	1	11	2	25	5
	2	12	10	27	16
	3	11	8	26	9
	4	11	11	19	15
	5	17	4	45	9
	6	11	6	21	7
	7	21	0	55	0

Table 1. Number of individuals and captures for each species separated by the total of each species, segments, and sessions.

Overall parameter estimates presented large uncertainty in most cases, mainly for the tegu (Fig. 2, 3 and 4). The exception was the superpopulation size estimates for the opossum (Fig. 2E, 3E and 4C). Although the credible intervals overlap considerably, it seems that carcass detection and persistence were higher and varied less for the opossum (mean values between 0.56 - 0.90 for detection and 0.70 - 0.99 for persistence) than for the tegu (mean values between 0.28 - 0.78 for detection and 0.54 - 0.98 for persistence) in all dimensions, the difference in carcass persistence is clearer in the direct comparison between the two species (Fig. 4B). The model was not able to estimate the parameters for the sessions of December and March for the tegu (Fig. 3B, D, F and H).

Although the superpopulation size estimates for the opossum showed the same pattern of segments or sessions with higher roadkill numbers than the observed number (from the raw count), the differences between these segments or sections changed, making some of them more similar or different in roadkill numbers. For example, in the December session the number of opossum carcasses was smaller than in November, but the estimates show that these two sessions had almost equal numbers of roadkills. Differences generally increased among segments and decreased among sessions. The differences between the two species in the observed number were also smaller in the estimates.

Contrasting with the perception from the observed numbers and the superpopulation size, comparing opossums and tegus, the roadkill rate estimates showed that both species tend to have similar roadkill numbers (Fig. 4C and D).

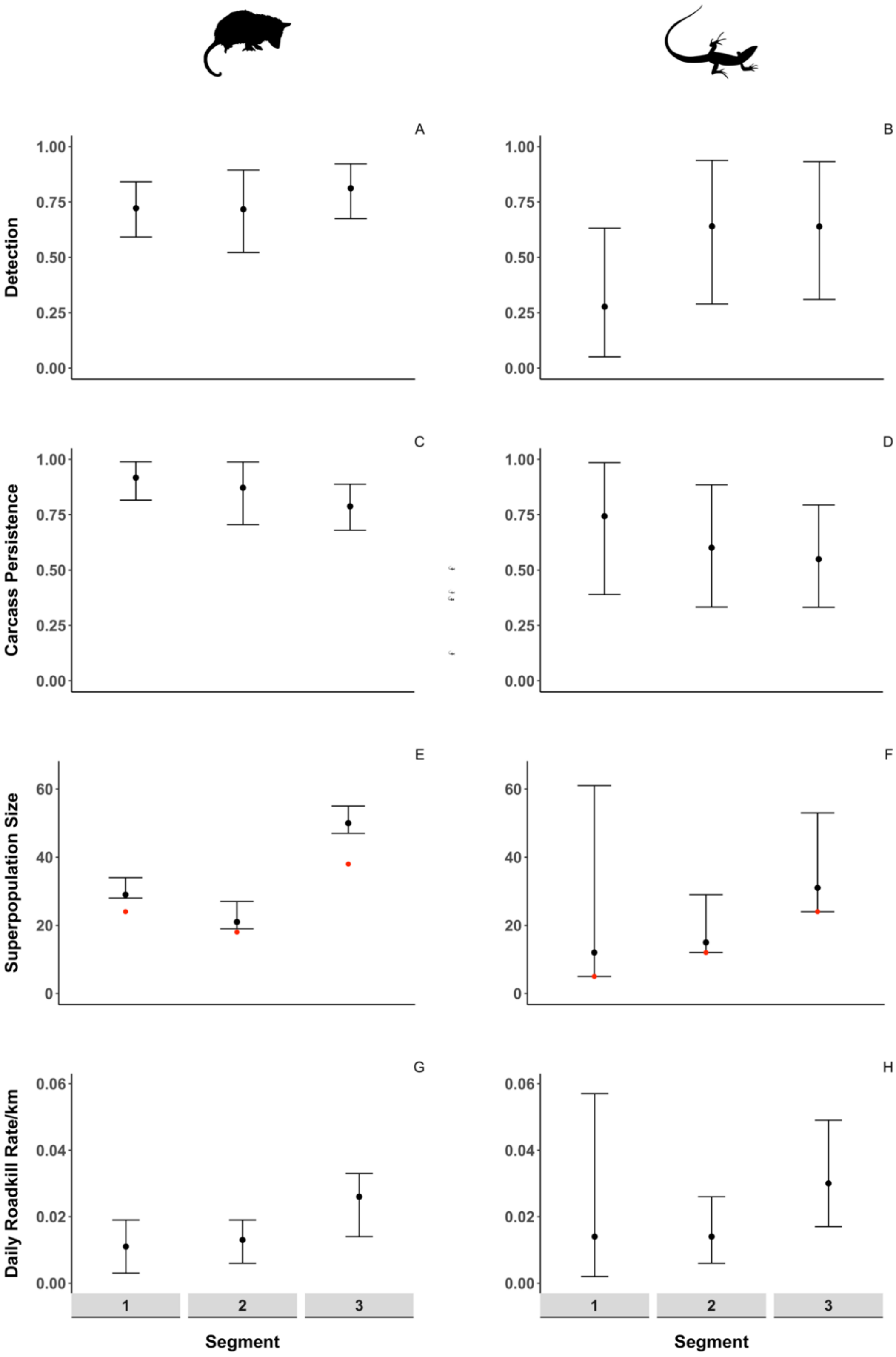

Figure 2. Spatial variation along three road segments in: Carcass detection probability (A-B); Carcass persistence probability (C-D); Superpopulation size of carcasses (E-F); Daily roadkill rate per kilometer (G-H), for a mammal

(*Didelphis albiventris*) and a lizard (*Salvator merianae*) in southernmost Brazil. The red points in E and F represent the number of carcasses observed.

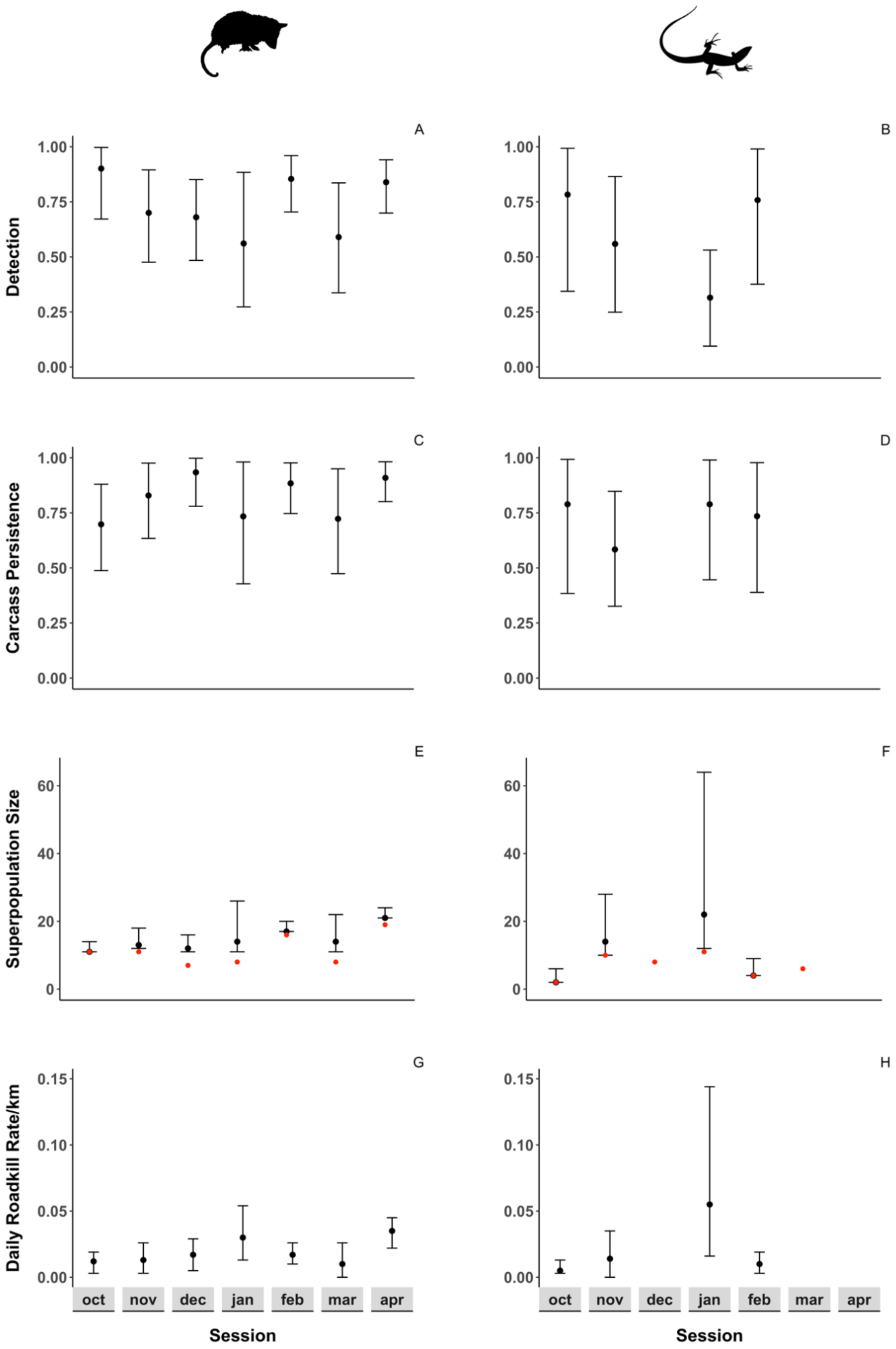

Figure 3: Temporal variation in 7 months (sessions) in: Carcass detection probability (A-B); Carcass persistence probability (C-D); Carcass superpopulation size (E-F); Daily roadkill rate per kilometer (G-H), for a mammal (*Didelphis albiventris;* left) and a lizard (*Salvator merianae*; right) in southernmost Brazil. The red points in E

and F represent the number of carcasses observed. Sessions of December and March for the tegu do not have estimates due to model failure.

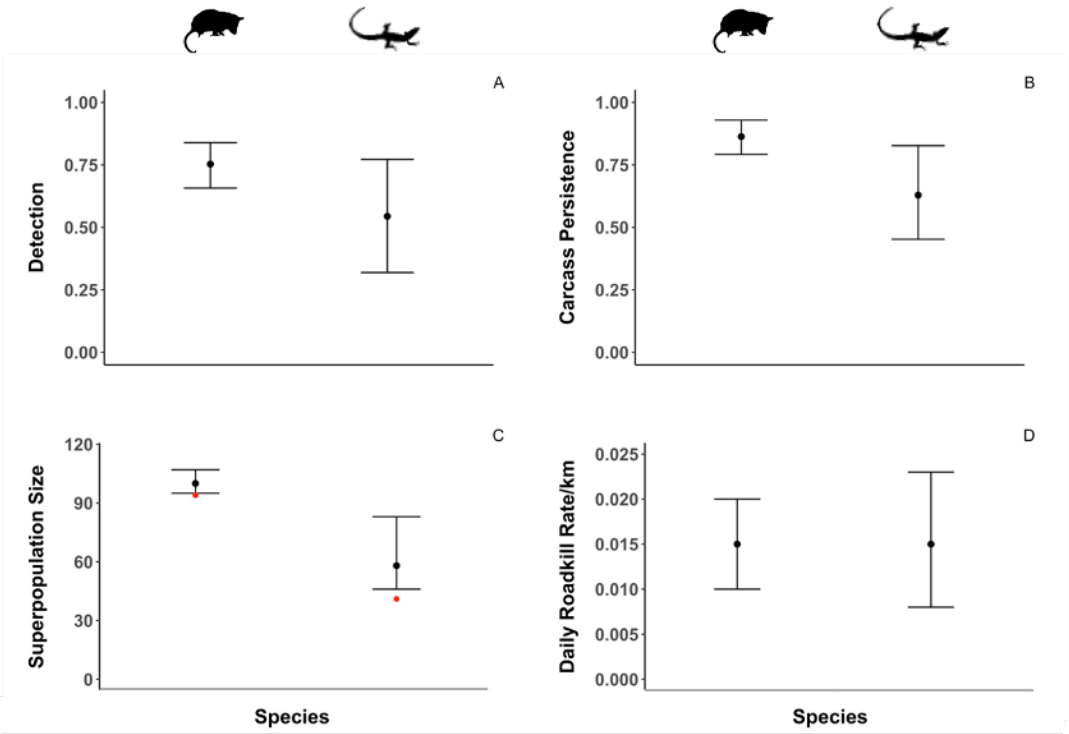

Figure 4. Variation according to species in: Carcass detection (A); Carcass persistence (B); Carcass abundance (C); Daily roadkill rate per kilometer (D), for a mammal (*Didelphis albiventris*) and a lizard (*Salvator merianae*) in Southernmost Brazil. The red points in C represent the number of carcasses observed.

5. Discussion

We used here an open population approach to explicitly model roadkill estimates while addressing the two main sources of bias in roadkill surveys: observer imperfect detection and carcass removal. Using this approach with a Bayesian framework, we can directly estimate roadkill rates (Fig. 2G-H, 3G-H and 4D), propagating the uncertainty through the hierarchical levels of the model, due to the repeated sampling occasions and the capture-recapture data that is required. This estimated roadkill rate, derived from the carcass entry probabilities, should be the main parameter of interest in road ecology, since it discounts the carcasses that were already present on the road in the first occasion (roadkill in other previous unknown time). Therefore, the roadkill rate is the best parameter to make comparisons among different situations we may have interest in, especially for mitigation prioritizing efforts. Other studies using open population models to estimate roadkill demonstrated more interest in carcass abundance, represented by the superpopulation size (Guinard et al., 2012; Péron et al., 2013) because they were not able to mark and recapture carcasses in sequential occasions and therefore, they had to estimate roadkill rates indirectly in a two-step approach. The correction to discount the old carcasses already in the study area as implemented in (Péron et al., 2013) is not needed in our approach.

The framework used here is very flexible and is conceptually adequate for being used in the roadkill context, however, our results presented high uncertainty and did not highlight, for our context, the variation in carcass detection and persistence we expected for space, time and species. Although there was no strong evidence of this variation, our results do not discard it either. In the cases that the precision was acceptable (Fig. 2E, 3E and 4C), the estimated roadkill numbers changed the magnitude of the differences seen between segments, sessions, and species. These results could indicate the possibility of changes in the ranking of higher number of roadkills in all those dimensions if variation in detection or persistence is considered. If carcass detection is higher in a certain road segment than in the others, this place may be misidentified as a segment with high concentration of roadkills and be prioritized in mitigation efforts. The same logic is applied to carcass persistence, segments where carcasses persist longer may be misidentified as segments with higher roadkill rates. The problem of misidentification of sites due to differences in detection and persistence in different road segments was already reported by Santos et al. (2015), suggesting this problem should be more deeply investigated.

The high uncertainty we observed in the estimates and the impossibility of parameters estimation in some cases (December and March for the White-and-Black Tegu; Fig. 3B, 3D, 3F and 3H) are due to the high demand of data this type of model requires, which may narrow its application for carcass counting data. To deal with the sparse data problem, one possible solution may be the addition of data collected from trial experiments, disposing extra known carcasses on the road, preferably simultaneous with the carcass surveys. Thus, experimental carcasses would be used to inflate sample sizes and inform detection and persistence parameters, resulting in more precision in carcass superpopulation size and carcass entry probabilities. Another possibility is to include information from experimental data under the Bayesian framework including carcass detection and carcass persistence from experiments as prior distributions (Lemoine, 2019). The use of covariates, such as traffic volume, weather conditions or carcass characteristics in the detection, persistence and entry probabilities can also reduce uncertainty. As the model uses the capture histories of the individuals to estimate the parameters, more than four occasions we made here resulting in longer capture histories, could also be helpful for improving parameters precision.

The narrower credible intervals for the opossum are resultant from the larger amount of data we had for this species. Besides the higher number of individuals, 69% of the opossums were recaptured, while only 36% of the tegus were. This could be a result of low detection probabilities for the tegus, but it also could mean that they are being removed from the road in a faster rate than the occasions interval chosen in our study (24 h) is being able to capture. The 24 h sampling intervals seems a more adequate choice for the opossum carcasses characteristics and may be another reason for the more precise estimates for this species. The matter of an adequate choice of sampling intervals according to the studied species was also highlighted by Péron et al. (2013) and Santos et al. (2015), emphasizing the importance of pilot studies to infer the adequate study design. Ideally the carcasses should persist for more than one sampling interval in a reasonable number. In the wind farm turbines context this number should be between 20 and 60% of the carcasses (Péron et al., 2013). The right balance between the sampling intervals and number of occasions may be fundamental to obtain more precise credible intervals. For studies evaluating more than one species, this choice is even more delicate, because the intervals and the number of occasions must represent well multiple organisms with different traits. In this case, the choice of the sampling intervals should be based on the species that may present lower carcass persistence, and the number of occasions on the one that presents higher carcass persistence (to avoid the absence of removals during the study duration).

Another possible practical limitation of the capture-recapture models in the roadkill context is exactly the fact that we need to mark the carcasses and leave them on the road for being recaptured in future sampling events. In some cases this requirement may not be achievable (Péron, 2018; Péron et al., 2013). Some roads, for example, for legal and driver safety reasons may require that carcasses are removed from the lane, mainly for larger species that represent a higher risk, besides that, carcasses on roads attract scavenger species and can cause more roadkills. In this case, it is possible to estimate the detection probabilities using a sampling protocol with multiple-observers (Péron et al., 2013).

For comparisons between species, although credible intervals are still overlapping, except for the superpopulation size, it seems that carcass persistence tends to be lower for the tegu (Fig. 4C). As explored before, the two organisms compared here have very different morphological and ecological traits that may determine this trend. Besides the higher size variation of tegu individuals crossing roads, which may influence in both carcass detection and persistence, the tegu skin seems to be more easily decomposed than the fur and skin of the opossum. Studies with other reptile species also found lower carcass persistence for this group (Antworth et al., 2005). The small size of the carcasses (in our study, mostly tegus) may have important influence in carcass persistence, either because small carcasses are easier to be carried by scavengers or to be removed by vehicles (Cabrera-Casas & Salinas, 2020). If differences in detection and persistence among species are not considered, we can misidentify the ranking of species with higher roadkill and misallocate mitigation efforts, which can have implication on species conservation. The experiments to estimate carcass detection and persistence in the roadkill studies have to use external carcasses collected in previous time to obtain the estimates (e.g. Gonçalves et al., 2018 and Winton, Taylor, Bishop, & Larsen, 2018). Although there is usually a concern about the set of carcasses used in the experiment, these carcasses are not necessarily representing all the species being evaluated and that can also be a source of bias (the detection and persistence probabilities to all species will be estimated from a set of carcasses). Variants of the model we used, such as a multi-species model could be applied to address this problem.

Carcasses can also vary in detection and persistence probabilities through time as they suffer from decomposition and fragmentation effects. This variation in carcass detection and persistence through different carcass states could also be a source of bias (for detection variation) and imprecision (for persistence variation) in roadkill estimates. In our case, we considered the state of the carcasses constant during the four occasions, but this heterogeneity can be accommodated in multi-state models, as proposed by Péron et al. (2013).

Here, we did not find a clear variation, as we expected, in our parameters, but it seems reasonable that carcass detection and persistence vary according to segments, time and mainly, species. The only way to know and account for this variation, if it exists, is by estimating it. Although the approach applied here is more “data hungry”, the lower precision is expected and might be more reliable since in the hierarchical modelling framework the uncertainty is accommodated and propagated through the hierarchical levels. Alternative sampling methods that could provide more data with less field effort, such as automated samplings (Sousa Guedes et al., 2019) could also be a future solution. The assumed homogeneity in carcass detection and persistence probabilities, generally adopted in roadkill estimates, may have important limitations in decision-making of where, when and for which species to prioritize mitigation efforts. These limitations highlight the importance to account for this heterogeneity, or at least investigate it more, to obtain more accurate roadkill estimates and therefore, be able to make better decisions.

Authors contributions

TMR, IVB and AK conceived the ideas and designed methodology; TMR collected the data; TMR and IVB analyzed the data; TMR, IVB and AK contributed for the writing of the manuscript and gave final approval for publication.

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Considerações finais

O objetivo dessa dissertação foi explorar a variação dos dois principais erros relacionados às amostragens de carcaças em rodovias (detecção e persistência das carcaças) e contribuir para uma mudança conceitual na abordagem geral das estimativas de fatalidades de fauna em rodovias e outras infraestruturas antrópicas. Não foi possível observar claramente essa variação entre os diferentes segmentos da rodovia, períodos do ano e espécies, devido à grande incerteza nas nossas estimativas. Apesar disso, é bastante razoável esperar que essa variação ocorra e os nossos resultados demonstram que ela deve ser mais investigada, já que pode ter implicações importantes no planejamento de medidas mitigadoras. A abordagem utilizada aqui, com a aplicação de modelagem hierárquica dentro de uma perspectiva Bayesiana, oferece bastante flexibilidade, permite estimar as incertezas de todas as estimativas e uma taxa de atropelamento confiável. Essa taxa se mostra um parâmetro importante, pois permite sabermos um número de atropelamentos mais próximo do real dentro de um período de tempo conhecido, facilitando comparações entre diferentes locais, períodos e espécies. Como perspectivas futuras estão o desenvolvimento de abordagens amostrais que permitam gerar maiores volumes de dados, para que as estimativas sejam mais precisas e acomodar essa variação nos erros para diferentes segmentos, períodos e espécies juntos, em um único modelo. Espero que essa dissertação contribua na busca de estimativas mais acuradas de atropelamentos de fauna em rodovias, facilitando a compreensão dos impactos dessas infraestruturas e de como podemos mitigá-los.

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