UNIVERSIDADE FEDERAL DE LAVRAS

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CRITICAL AREAS FOR ROAD MITIGATION:
COMBINING SOURCE-SINK DYNAMICS WITH ROAD-KILL MODELLING

LAVRAS – MG
2017

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Ecossistemas, para a obtenção do título de Mestre.

Drª. Clara Bentes Grilo
Orientadora

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Ficha catalográfica elaborada pelo Sistema de Geração de Ficha Catalográfica da Biblioteca Universitária da UFLA, com dados informados pelo(a) próprio(a) autor(a).

Barbosa, Priscilla .
Critical areas for road mitigation : Combining source-sink dynamics with road-kill modelling / Priscilla Barbosa. - 2017.
56 p. : il.

Orientador(a): Clara Grilo.
.
Dissertação (mestrado acadêmico) - Universidade Federal de Lavras, 2017.
Bibliografia.

1. Chrysocyon brachyurus. 2. Atropelamento. 3. Área fonte-sumidouro. I. Universidade Federal de Lavras. II. Título.

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APROVADA em 29 de maio de 2017.
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AGRADECIMENTOS

À Universidade Federal de Lavras (UFLA) e ao Programa de Pós-Graduação em Ecologia Aplicada, pela oportunidade de realização do mestrado, e à FAPEMIG, pela concessão da bolsa de estudo durante o mestrado.

À minha orientadora Clara Grilo, por me acolher e caminhar ao meu lado. Com certeza eu e este trabalho não teríamos crescido tanto sem seu apoio. Ao parceiro Nathan Schumaker, que desde o princípio se mostrou disponível e atencioso, me motivando sempre a aprender e inovar.

À minha mãe e ao meu pai, Adriana e Maurício, por me apoiarem durante minha jornada e me receberem de braços abertos em todos os momentos.

Ao “Super team”: Rafaela, Bianca, Clara, Flávio, Fernando e Tony, por serem meu maior suporte em Lavras, pelos jogos de sinuca, consultorias, desabafos e muitas cervejas noite adentro.

Às amigas Kibe e Luiza, e aos bons amigos de Cuiabá, “Bolo” e “Busca-bike”, pelo companheirismo e pela amizade além de qualquer tempo e distância.

Aos bons amigos que a UFLA e a Ecologia me trouxeram, às professoras e aos professores e ao suporte inesgotável das queridas Ellen e Domênica. Aos bons amigos da APG, especialmente Larissa e Tássia, com as quais compartilhei as dificuldades e emoções de construir uma pós-graduação articulada e de luta.

E, finalmente, aos companheiros Tiagão e Riobaldo por me acolherem de maneira tão especial.

Deixo minha gratidão!

Flávia Imada

RESUMO

A expansão da malha viária tem impulsionado a fragmentação e isolamento de muitas espécies, e é responsável por uma mortalidade adicional não natural devido a colisões com veículos. No Brasil, diversos estudos evidenciam que lobos-guará (*Chrysocyon brachyurus*) têm sido diretamente impactados por rodovias. Entretanto, pouco se sabe sobre os efeitos que infraestruturas viárias podem ter nessas populações a médio prazo e quais áreas devem ser consideradas prioritárias para a implementação de medidas de mitigação. O principal objetivo deste trabalho foi combinar a dinâmica populacional de fonte-sumidouro de lobos-guará sob efeito de rodovias com o risco de atropelamento a fim de identificar áreas críticas para implementação de medidas de mitigação. Nós desenvolvemos um modelo espacialmente explícito e baseado no indivíduo para identificar áreas de fonte e sumidouro dentro da área de distribuição da espécie. Utilizamos parâmetros demográficos da espécie, qualidade do habitat e potenciais comportamentos frente às rodovias: 1) evitação de estradas, 2) cruzamento de estradas (com sucesso) e 3) cruzamento de estradas (sem sucesso). Ademais, desenvolvemos um modelo de probabilidade de ocorrência de atropelamento para identificar segmentos de rodovia com alto risco de mortalidade. Áreas críticas para implementação de medidas de mitigação foram definidas como segmentos de rodovia com alto risco de mortalidade (>80%) localizados dentro da área de dispersão de áreas fonte. Nossos resultados mostraram declínios significativos no tamanho populacional de lobos-guará (10 a 23%) mesmo em cenários com baixas probabilidades de mortalidade, enquanto cenários sem mortalidade não alteraram o tamanho da população. As áreas fonte representaram cerca de 11% da distribuição da espécie. Cerca de 0,75% dos segmentos de rodovia apresentaram alto risco de mortalidade (>80%). Nós identificamos 135 km de segmentos de rodovia como áreas críticas para mitigação para a espécie, que correspondem a 0,05% da malha viária. Estes resultados devem servir como guia para a conservação dos lobos-guará e, se seguidos, têm o potencial de reduzir o número de atropelamentos nos trechos identificados.

Palavras-chave: *Chrysocyon brachyurus*. Lobo-guará. Atropelamento. Efeitos de rodovia. Área fonte-sumidouro. Modelo populacional espacialmente explícito.

ABSTRACT

The expansion of road networks has been a key driver of fragmentation and isolation for many wildlife species, and it is responsible for additional non-natural mortality due to collisions with vehicles. In Brazil, several studies show evidence that maned wolves (*Chrysocyon brachyurus*) have been directly impacted by roads. However, little is known about the effects of these transport infrastructures on maned wolf populations in the medium term and in which areas road mitigation measures should be applied. Our main goal was to combine source-sink maned wolf population dynamics under the effects of roads with the risk of being road-killed, in order to identify critical areas for road mitigation measures. We developed a spatially-explicit and individual-based model to identify source-sink areas within maned wolf's distribution. We used species demographic parameters, habitat quality and potential behaviors towards roads: 1) road avoidance, 2) crossing the road (successfully) and 3) crossing the road (unsuccessfully). Additionally, we developed a road-kill likelihood model to identify road segments with elevated risk of mortality. Critical areas for road mitigation were defined as road segments with high road-kill likelihood (>80%) that were located within the dispersal range from source areas. Our results show significant declines in maned wolf's population (10 to 23%) even with low mortality likelihood, whereas scenarios without mortality did not affect population size. The source areas represented 11% of the species range. About 0.75% of the road segments showed high road-kill likelihood (>80%). We identified 135 km of road segments as critical for road mitigation for the species, which corresponds to 0.05% of the road network. Our results should serve as guidelines for the maned wolf conservation, and if followed, have the potential to reduce the number of road-kills in the identified road segments.

Keywords: *Chrysocyon brachyurus.* Maned wolf. Road mortality. Road effects. Source–sink areas. Spatially-explicit population model.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO

Perda, degradação e fragmentação de habitat são tipicamente os principais fatores que impactam a conservação das espécies (PEREIRA et al., 2012). Sendo as rodovias uma das modificações antrópicas mais amplamente distribuídas na paisagem natural, elas afetam as espécies severamente (FAHRIG & RYTWINSKI, 2009). A expansão da malha viária nas últimas décadas tem impulsionado a fragmentação e isolamento de diversas populações e é responsável pela mortalidade não natural através de colisões entre fauna e veículos automotores (FAHRIG & RYTWINSKI, 2009). Atualmente, uma extensa literatura em Ecologia de Estradas mostra como carnívoros são particularmente suscetíveis a rodovias (e.g., GRILO et al., 2009; COLINO-RABANAL et al., 2011). Recentemente, um estudo identificou 17 espécies que têm sido intensamente expostas a rodovias e outras 72 que experimentam uma menor, mas preocupante, exposição (CEIA-HASSE et al., 2017). Por exemplo, a mortalidade por atropelamento pode representar até 12% da população de linces-ibéricos (*Lynx pardinus*) na Espanha (SIMÓN, 2012), com uma projeção de tempo de extinção abaixo de 100 anos (CEIA-HASSE et al., 2017). Ademais, rodovias com intenso tráfego de veículos também podem funcionar como barreiras para carnívoros (ALEXANDER et al., 2005; JAEGER et al., 2005). Por exemplo, coiotes e linces parecem ser negativamente afetados por rodovias em nível genético, uma vez que essas espécies são inibidas pelo limite artificial imposto em suas áreas de vida, o que impede o fluxo gênico entre populações (RILEY et al., 2006).

No Brasil, uma das espécies diretamente impactadas pela malha viária é o lobo guará *Chrysocyon brachyurus* (Illiger, 1815), listado como Vulnerável pelo Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio –

(PAULA et al., 2013) e como Quase Ameaçada pela União Internacional para Conservação da Natureza e Recursos Naturais – IUCN – (PAULA & DEMATTEO, 2016). Pesquisas mostram que a perda e fragmentação de seu habitat pode causar uma redução de até 56% na população remanescente de lobos-guará nos próximos 100 anos (PAULA & DESBIEZ, 2013). Quando avaliada a viabilidade da população frente às ameaças causadas por rodovias, foi observada uma redução de 16 a 96% no tamanho populacional original (PAULA & DESBIEZ, 2013). Outro estudo mostrou que taxas de atropelamento para a espécie podem atingir até 0,083 ind./km/ano (CARVALHO, 2014), o que em baixas densidades populacionais (0,036 a 0,096 ind./km², RODRIGUES, 2002; TROLLE et al., 2007) pode representar uma perda significativa de indivíduos em áreas com altas densidades de rodovias. A espécie apresenta parâmetros demográficos e ecológicos que podem dificultar a recuperação da espécie em luz da mortalidade não natural causada por rodovias em locais de baixa densidade populacional. Por exemplo, a espécie demora cerca de 24 meses para atingir a maturidade sexual (PAULA & DESBIEZ, 2013) e, normalmente, produz somente uma ninhada por ano, da qual aproximadamente 50% dos filhotes não sobrevivem (MAIA & GOUVEIA, 2002; RODRIGUES, 2002). O lobo-guará é um importante predador e dispersor de sementes do Cerrado brasileiro (BUENO & MOTTA-JÚNIOR, 2006), e o declínio de sua população pode inviabilizar a estrutura e funcionamento do ecossistema como um todo, devido à desregulação da população de presas e redução da dispersão de sementes (MOTTA-JÚNIOR et al., 2013).

A incerteza do impacto causado pela atual malha viária na persistência de espécies vulneráveis e em perigo é alarmante (CEIA-HASSE et al., 2017). Particularmente quando há planos de expansão de rodovias, como vem ocorrendo em países em desenvolvimento, como Brasil, China e Índia (LAURANCE et al., 2014). Portanto, é crucial avaliar as consequências que os efeitos de rodovia podem causar na persistência das populações, utilizando parâmetros demográficos e ecológicos das espécies e seu comportamento frente às estradas (JAEGER et al., 2005; GRILO et al., 2009). Uma abordagem para superar a limitação de dados consiste na modelagem de diferentes cenários utilizando uma gama de comportamentos potenciais apresentados pelos indivíduos (JAEGER et al., 2005). As espécies apresentam diferentes comportamentos frente às rodovias, podendo estes ser divididos em dois grandes grupos: 1) as que evitam a rodovia e 2) as que são atraídas pela rodovia (VAN DER REE et al., 2015). Estudos sugerem que essa atração pode ocorrer devido a fatores como facilidade de obtenção de recursos e dispersão, e aumento da probabilidade de encontro entre predador/presa (ZIMMERMAN et al., 2014; BENSON et al., 2015; RYTWINSKI & FAHRIG, 2015). Contudo, é importante ressaltar que espécies que são atraídas pelas estradas podem apresentar ou não a habilidade de evitar colisões (RYTWINSKI & FAHRIG 2015). Além disso, a identificação e quantificação de potenciais fontes e sumidouros dentro da dinâmica populacional da espécie associada a altas probabilidades de mortalidade em rodovias pode fornecer conhecimentos valiosos para a conservação dos lobos-guará, uma vez que isso permite a priorização de áreas onde medidas de mitigação devem ser aplicadas (PULLIAM, 1988; JACOBI & JONSSON, 2011; SCHUMAKER et al., 2014).

Dentro desse contexto, este trabalho visa identificar áreas críticas para implementação de medidas de mitigação associadas aos impactos causados por rodovias na população de lobos-guará do Brasil. Levando em consideração a escassez de dados de história de vida e comportamento da espécie em relação às estradas, e devido à extensão da área de estudo, desenvolvemos e exploramos um modelo espacialmente-explícito e baseado no indivíduo para responder à questão proposta acima. Usamos parâmetros demográficos da espécie, qualidade do habitat e potenciais comportamentos frente à rodovia: 1) evitação da estrada,

2) cruzamento da estrada (com sucesso) e 3) cruzamento da estrada (sem sucesso) a fim de identificar potenciais fontes e sumidouros dentro da área de distribuição do lobo-guará. Posteriormente, desenvolvemos um modelo de risco de mortalidade para identificar segmentos de rodovia com altas probabilidades de ocorrência de atropelamento. Finalmente, combinamos as áreas fonte e sumidouro com os segmentos de rodovias críticos para definir áreas prioritárias para implementação de medidas de mitigação para a conservação da espécie. Este estudo ilustra um inovador método científico que contribui para o aprimoramento da capacidade de caracterizar a dinâmica populacional de espécies em paisagens extensas, e de inferir as consequências de distúrbios locais na viabilidade regional das populações. Nós antecipamos que o uso espacial da dinâmica populacional associadas às probabilidades de atropelamento podem ser úteis em outros estudos de mortalidade em rodovias, dada a ocorrência global de tal mortalidade. Também acreditamos que essa abordagem possa ajudar a guiar órgãos e pessoas responsáveis pelo planejamento de rodovias quanto a medidas de mitigação.

2 CONCLUSÃO

A inovação no método utilizado para identificar áreas críticas para implementação de medidas de mitigação está relacionada ao uso da dinâmica populacional dos lobos-guará junto aos segmentos de rodovia com alto risco de mortalidade.

Nossos resultados sugerem que atropelamentos atuam como principal efeito negativo de rodovias em lobos-guará, e até probabilidades de atropelamento otimistas podem causar uma redução significante no tamanho populacional da espécie. Em luz da expansão planejada para a malha viária brasileira, esse impacto representa uma preocupação importante referente à conservação do lobo-guará. Nós também observamos que comportamentos de evitação de rodovia atuam de maneira negativa na população da espécie, indicando a necessidade de promover maior conectividade entre habitats.

Altas probabilidades de atropelamento parecem estar associadas a rodovias de mais intenso tráfego, alta conectividade de habitat e altas temperaturas. Apesar de nosso modelo de risco de mortalidade identificar uma quantidade significativa de segmentos de rodovia como críticos, nossa abordagem inovadora sugere que apenas 7% (135 km) desses segmentos devem ser considerados prioridade em termos de futuras pesquisa e mitigação.

A implementação de medidas de mitigação em áreas de distribuição extensas, como a do lobo-guará, pode ser uma tarefa desafiadora. Entretanto, a abordagem proposta no presente estudo permite definir um número reduzido de segmentos de rodovia como áreas prioritárias para conservação. Os próximos passos devem ser focados na validação do modelo, por meio de estimativas de densidade populacional e taxas de atropelamento nas áreas identificadas.

Ademais, a melhoria da conectividade do habitat junto à implementação de passagens e instalação de cercas em rodovias de tráfego intenso devem ajudar a minimizar futuros declínios populacionais do lobo-guará.

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SEGUNDA PARTE

For Biological Conservation

CRITICAL AREAS FOR ROAD MITIGATION: COMBINING SOURCE-SINK DYNAMICS WITH ROAD-KILL MODELING

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ABSTRACT

The expansion of road networks has been a key driver of the fragmentation and isolation of many wildlife species, and it is responsible for additional non-natural mortality due to collisions with vehicles. In Brazil, several studies show evidence that maned wolves (*Chrysocyon brachyurus*) are directly impacted by roads. However, little is known about the effects of transportation infrastructures on maned wolf populations in the medium term and in which areas road mitigation measures should be applied. Our main goal was to combine source-sink maned wolf population dynamics under road effects with the risk of being road-killed, in order to identify critical areas for road mitigation measures. We developed a spatially-explicit and individual-based model to identify source-sink areas within maned wolf’s distribution. We used species demographic parameters, habitat quality and potential behaviors towards roads. Additionally, we developed a road-kill likelihood model to identify road segments with elevated risk of mortality. Critical areas for road mitigation were defined as road segments with high road-kill likelihood located within the dispersal range from source areas. Our results show significant population declines (10 to 23%), even with low mortality likelihood whereas scenarios without mortality did not affect population size. The source areas represented 11% of the species range. About 0.75% of the road segments showed high road-kill likelihood (>80%). We identified 135 km of road segments as critical for road mitigation. Our results should be used as guidelines for species conservation and have the potential to help reduce road-kill rates in the identified road segments.

Keywords

Chrysocyon brachyurus; Road effects; Road mortality; Source–sink areas; Spatially-explicit population model.

1. INTRODUCTION

Habitat loss, degradation and fragmentation are typically the main factors impacting species conservation (Pereira et al., 2012). The expansion of road networks over the past few decades has been a key driver of fragmentation and isolation of many wildlife species and is responsible for additional non-natural mortality due to the collision with vehicles (Fahrig and Rytwinski, 2009; Laurance et al., 2009). Extensive literature on road-kills worldwide shows how carnivores are particularly vulnerable to roads (e.g., Taylor et al., 2002; Grilo et al., 2009; Colino-Rabanal et al., 2011). Recently, a study identified 17 carnivore species that have been experiencing intensive exposure to roads and other 72 that experience lower, but concerning, exposure (Ceia-Hasse et al., 2017).

In Brazil, one of the species directly impacted by the road network is the maned wolf *Chrysocyon brachyurus* (Illiger, 1815), listed as Vulnerable by the Brazilian Institution ICMBio (Paula et al., 2013) and as Near Threatened by the IUCN (Paula and DeMatteo, 2016). Research predicted that habitat loss and fragmentation may cause a reduction of up to 56% of the remaining maned wolf population over the next 100 years (Paula and Desbiez, 2013). Another study showed that observed road-kill rates can be as high as 0.083 ind./km/year (Carvalho, 2014), which on low population densities (0.036 to 0.096 ind./km^2, Rodrigues, 2002; Trolle et al., 2007) may represent a significant annual loss of individuals in areas with high road densities. Because maned wolves have a late sexual maturity (Paula and Desbiez, 2013), producing one litter per year, and considering that 50% of the cubs do not survive the first year (Maia and Gouveia, 2002; Rodrigues, 2002), the additional non-natural mortality may increase the difficulty of species recovery in low population densities. Maned wolves are an important predator and a key seed disperser of Brazil’s savannah and grasslands (Aragona and Setz, 2001; Bueno and Motta-Júnior, 2006). The decline of maned wolf may disrupt the structure and function of the entire ecosystem by deregulating prey population and decreasing seed dispersal (Consorte-McCrea and Santos, 2013; Motta-Júnior et al., 2013).

The uncertainty of the impact of the current road network system on vulnerable and endangered species’ ability to persist is alarming (but see Beaudry et al., 2008; Borda-de-Água et al., 2014; Ceia-Hasse et al., 2017). This is particularly important when there are plans to significantly expand the road network, as occurs in emerging economic countries such as Brazil, India, and China (Laurance et al., 2014). This knowledge gap represents a critical research area in which insights from both applied and theoretical investigations must be integrated. The development of predictive models that scale up from individuals to populations and forecasts the consequences of human activities on populations viability is crucial to examine the strength of the threats (e.g. Jaeger et al., 2005; Grilo et al., 2009). In the absence of knowledge on species behavior towards roads, modeling different scenarios capturing a range of potential behaviors can be an approach to overcome data limitations (Jaeger et al., 2005). Furthermore, the identification and quantification of potential habitat sources and sinks, combined with high road-kill likelihood can provide valuable insights for species conservation since it enables prioritize where road mitigation measures should be applied (Pulliam, 1988; Jacobi and Jonsson, 2011; Schumaker et al., 2014).

The main goal of this study was to identify critical areas for road mitigation measures for the maned wolf. Because data on maned wolf life history and behavior are scarce and the species range is large, we have developed and exploited a parsimonious spatially-explicit individual-based model to address the focal question stated above. We used species demographic parameters, habitat quality and three potential behaviors towards roads: 1) road avoidance, 2) successfully crossing the road, and 3) unsuccessfully crossing the road to identify potential source and sink areas within the maned wolf's distribution. Then, we developed a road-kill model to identify road segments with high road-kill likelihood. Finally, we combined the source-sink areas with road segments with elevated risk of mortality to define priority areas to implement mitigation measures for maned wolves. Our study illustrates new and scientifically-defensible methods that will improve researchers' ability to characterize population dynamics across large landscapes, and to infer the consequences for regional viability of local disturbances. We anticipate that making use of both spatial population dynamic and road-kill likelihood can help guide road planners for mitigation measures since it explores a range of potential effects.

2. METHODS

2.1 Study area

The study area corresponds to the current maned wolf range in Brazil (>3 million km²) which encompasses mainly the Cerrado biome (i.e., savannah and grasslands, Figure 1). Past records also exist for the maned wolf within the Atlantic Forest, the Amazon Forest, the Pantanal wetland, the Pampas and the Caatinga biomes (Paula and DeMatteo, 2016). The Cerrado biome is one of the world's biodiversity hotspots (Myers et al., 2000), and for the past few years more than 50% of the area has been transformed into croplands and pasture, which puts the maned wolf under severe threat (Klink and Machado, 2005). The maned wolf's range includes the most populated region of Brazil (i.e. Southeast region), which contains some of the country's main cities (e.g., Rio de Janeiro and São Paulo). To date it is estimated that the Brazilian Southeast region has an average road density of 0.55 km/km² with a planned expansion of almost 20,000 km, which corresponds to 4% of the regional road network (DNIT, 2015).

2.2. Data collection

2.2.1 Maned wolf source-sink areas

Species parameters

We recorded from literature the available demographic and ecological parameters: number of life stages (juvenile, sub-adult, adult), lifespan, month of recruitment, litter size, age at first birth, time interval between births, survival rates prior to the influence of road impacts (hereafter termed *background survival*) and home range size (Table 1).

Spatial data

The spatial data included land cover and road network maps. We used a Global Land Cover map (v. 2.3; 2009; Source: European Space Agency GlobCover Portal http://due.esrin.esa.int/page_globcover.php) to define maned wolf unsuitable and suitable habitats. We categorized the 23 land cover classes from the Global Land Cover map into seven categories based on maned wolf presence data (e.g., Queirolo et al., 2011; Torres et al., 2013): mosaic cropland/open vegetation, mosaic forested areas/open vegetation, forest area, open vegetation area, flooded area, water bodies and urban areas. We recruited five Brazilian canid specialists to assign weights ranging between 0-100 to each of the seven land cover classes (ranging from 0 – unsuitable areas – to 100 – suitable for completing the maned wolf life cycle and for their mobility) (hereafter termed *habitat suitability*) (see results at Supplementary material). We used a GIS road network map (Source: Open Street map https://www.geofabrik.de/data/download.html) and selected all roads that are paved with at least 2 lanes.

2.2.2 Maned wolf road-kill likelihood

Road-kill data

We compiled road-kill georeferenced data from Urubu Mobile and the Brazilian Conservation Units database provided by Centro Brasileiro de Estudos em Ecologia de Estradas (http://cbee.ufla.br/portal/). We also searched peer-reviewed papers and grey literature in the Web of Knowledge database and the Google Scholar database with the following keywords: ((“maned wolf” OR “*Chrysocyon brachyurus*”) AND (“road-kill”, “road kill”, “road mortality”)) both in English and Portuguese languages. Unpublished data and personal communications were also recorded. All the locations were assigned to the road network at raster format of 1x1km^2 cell size.

Environmental variables

We used the following groups of environmental variables to model the road-kill likelihood: bioclimatic (maximum temperature of the warmest month), land cover (proportion of cropland/open vegetation, forest area, forest/open vegetation, open vegetation area, Simpson’s Diversity Index, landscape connectivity and streams) and human pressure (population density and road type; see Supplementary material). Bioclimatic conditions were selected, since they directly affect the maned wolf’s distribution and abundance (Queirolo et al., 2011; Torres et al., 2013). The Cerrado biome, where maned wolf mainly occur, presents mean temperatures ranging from 22° to 27° C (Klink and Machado, 2005), thus we inferred that regions within this temperature range will have higher probabilities of road-kill occurrences. Additionally, studies that report maned wolf road-kill events are in their majority located in Cerrado biome (e.g., Rodrigues, 2002, Carvalho, 2014), reinforcing the choice of temperature as a variable for modeling road-kill risk. Maned wolves exhibit a strong preference for open areas (i.e., Brazilian savannah and grasslands), thus we only used open areas land class to estimate the landscape metrics Simpson’s Diversity Index (Simpson, 1949) and landscape connectivity (see Torres et al., 2016 for further details). Finally, we selected variables associated with human pressure since large mammals show high sensitivity to anthropogenic activities (Crooks, 2002; Kowalski et al., 2015). All estimates of variables were assigned to the road network at raster format of 1x1km^2 cell size.

2.3 Data analysis

2.3.1 Maned wolf source-sink areas

Model development

We used HexSim 4.0.6 (Heinrichs et al., 2010, Stronen et al., 2012, Schumaker, 2016) to develop a mechanistic, spatially-explicit, individual-based model to quantify the effects of roads on maned wolf population dynamics and size. Our HexSim model replicates the maned wolf life cycle, and is built up from a series of discrete life history events that simulate individuals getting older, reproducing, dispersing and establishing territories, and experiencing mortality, in that order, for each simulation year (Schumaker et al., 2014). Our models ran in a landscape composed by cells with a diameter of 500 meters over the maned wolf species range (>35 million cells). Our model linked the stage-specific vital rates to habitat suitability, accounted for density-dependent effects on reproductive rates, and allowed roads to exhibit variable avoidance, crossing and mortality probabilities. Our model used only females and considered three stage classes (juvenile, subadult, and adult) (Paula and Desbiez, 2013). The juvenile and subadult stages occurred in a single year. Simulations were initialized with 100k female maned wolves placed in the suitable habitats through the landscape (Schumaker et al., 2014)

(Table 1). The high initial population size was used to ensure the wolves were well-distributed throughout their range when the model began. The simulated wolves became reproductive in their third year of life (Rodden et al., 2004; Paula and Desbiez, 2013), with a single reproductive pulse simulated once per year. The simulated wolves could be either territorial or non-territorial and only the former could reproduce, with litter size depending on the rate of resources acquisition experienced by the individual. We assumed that maned wolves disperse during the second stage of life (Paula and Desbiez, 2013), thus being non-territorial individuals. However, we considered that adults who previously failed to obtain a breeding territory continued to search for one. Annual mortality (not associated with roads) included 1) the background survival rates experienced by all individuals, and 2) senescence (all individuals who reached a maximum estimated lifespan of 13 years). During the movement events, all individuals that encountered a road while moving across the landscape would (a) avoid the road, (b) cross it successfully, or (c) die from collision with vehicles. Varying probabilities of road avoidance, crossing the road, and road mortality were assigned for each scenario described below.

Definition of scenarios

We defined four groups of scenarios using different combinations of three known individual behaviors towards roads (Jaeger et al., 2005): 1) avoidance, 2) successful crossing and 3) unsuccessful attempt of crossing the road (hereafter termed *road mortality*). The first three groups included the absence of one behavior (0%) and the combination of the two other behaviors with a range of probabilities: the probability of one selected behavior increased in each simulation (i.e., ranging from 0% to 100%) whereas the other behavior decreased symmetrically (i.e., ranging from 100% to 0%), with a total sum of 100%. The values were changed in intervals of 10%, which totalized 11 scenarios for each group of scenarios.

The *No mortality* group of scenarios were defined by the absence of road mortality and a combination of avoidance (from 0% to 100%) and successful crossing (from 100% to 0%). The *No crossing* scenarios were defined by the absence of successful crossing and a combination of road mortality (from 0% to 100%) and avoidance (from 100% to 0%). The *No avoidance* scenarios were defined by absence of avoidance and a combination of road mortality (from 0% to 100%) and successful crossing (from 100% to 0%). The *All behaviors* scenarios were arranged as a combination of the three behaviors. In this group, road mortality changed in intervals of 10%, rising from 0% to 100%, and avoidance and successful crossing changed in intervals of 5%, ranging from 100% to 0% (see Supplementary material). Four replicates were run for each scenario over a period of 50 years.

Source-sink dynamics

Source-sink dynamics were a purely emergent property of our simulations, and were obtained by sampling the birth and death rates observed across a space-filling array of regular hexagonal-shaped patches of varying sizes. The patches had hexagonal shapes, except where they were truncated at the boundaries of the study area, because they were formed from concentric rings of the *atomic* hexagons. Following the approach developed by Schumaker et al. (2014), we sampled birth and death rates at multiple spatial scales simultaneously, producing five separate maps of the landscape source-sink properties for each scenario (see Supplementary material). In addition, the source-sink values for each map were standardized (each map was independently re-scaled to range from 0 to 100), and then the five re-scaled maps were summed – generating one single maps for each scenario. A final aggregated multi-scale source-sink map was generated to produce a more accurate population dynamic than one single-scale map.

2.3.2 Maned wolf road-kill likelihood

We used MaxEnt 3.3.3 software (Phillips et al., 2006) to develop a predictive model of the maned wolf road-kill and identify road segments with elevated risk of road mortality. MaxEnt machinery uses a presence-background algorithm to create a prediction of suitability by using occurrence records with background samples (Phillips et al., 2006). We estimated the correlation among variables to include only non-correlated variables ($r<0.9$) in the model. To avoid spatial correlation of the road-kill records we only used records with a minimum distance of 10 km (Boria et al., 2014) between consecutive points. We used a similar amount of records for training and for testing and ran the model with 500 replicates. The maximum iteration was set at 500 times with a convergence threshold of 0.00001 and 10,000 background points (Ferraz et al., 2012). Model performance was evaluated using the AUC and its standard deviation (Ferraz et al., 2012).

2.3.3 Critical areas for road mitigation

Because most road-kills occur in the dispersal period (unpublished data) and individuals emigrate from source areas (Pulliam, 1988), we defined critical areas for road mitigation as road segments with high road-kill likelihood (>80%) that were located within the dispersal range from sources. Thus, we selected the sources and created a buffer using the estimated Median Dispersal Distance using the observed maximum home range size for this species (see Bowman et al., 2002 for further details) to locate the road segments with high road-kill likelihood. All spatial analysis was performed using ArcGIS 10.3.1 software (ESRI 2015).

3. RESULTS

3.1 Maned wolf source-sink areas

Our results show significant population declines even with low road mortality likelihood (Figure 2). We found that the reduction ranged from 10 to 23% in population size. Interestingly, the *No mortality* scenarios did not affect the species' final population size whereas the *No crossing* scenarios also presented a significant population decline. Areas with high habitat suitability for maned wolf represented about 67% of the species distribution (2 201 887 km^2). The final map of source-sink dynamics showed high consistency regarding magnitude and spatial pattern (regardless of the scenario used) (Figure 3). The source areas were located mostly in the northeast part of the maned wolf distribution, representing 11% of the species distribution (366 462 km^2). Sink areas were located mainly on the Pantanal biome, representing less than 0.55% (17 303 km²) of the species range. Intermediate areas represented a major portion of the species distribution by occupying more than 88% of the maned wolf's range (2 836 798 km²).

3.2 Maned wolf road-kill likelihood

We obtained 229 road-kill records and split these data into two groups for model development (n=123) and for model validation (n=106). Our model exhibited high explanatory power with an AUC of 0.906±0.012. About 1939 km of roads were assigned to high road-kill likelihood (>80%) which represents 0.75% of the entire road network in the species range (Figure 4). The variables that best explained the model were highways with 4 to 6 lanes (53.4%), areas with high landscape connectivity (10.4%) and a mean temperature of 28° C (9.1%) (see Supplementary material).

3.3 Critical areas for road mitigation

Over the maned wolf's distribution, we were able to identify 135 km of road segments with high risk of mortality between source areas which represents 0.05% of the road network (Figure 4). The selected area is located in the Cerrado biome between two National Parks, Serra da Canastra and Serra do Cipó, and near Belo Horizonte, one of the main cities of Brazil.

4. DISCUSSION

The novelty of the framework used to identify critical areas for maned wolf road mitigation is the link between populations dynamic and road segments with an elevated risk of mortality. Because knowledge on interaction between the species and roads is scarce, we combined population dynamics with habitat suitability using different scenarios of behaviors towards roads and species dispersal ability.

Our results suggest that even optimistically-low road-kill probabilities can result in a severe reduction of the maned wolf population size, which, in light of the plan to expand the Brazilian road network (DNIT, 2015), represents an important conservation concern. In line with other studies, we show evidence that mortality due to collisions with vehicles is a major component among the negative effects of roads for maned wolf (Paula and Desbiez, 2013; Ceia-Hasse et al., 2017). We also observed that scenarios in which maned wolves avoided roads also exhibited a reduction in mean population size relative to baseline simulations in which roads had no effect on movement. High road-kill likelihood seemed to be associated with the higher traffic roads, habitat connectivity and average high temperatures. Our findings showed that there is a large amount of road segments with high road-kill likelihood and our approach suggests that about 7% of those roads should be a priority in terms of future research and mitigation.

Our source-sink analysis identified locations where the population can be stable due to the habitat quality and size (Schumaker et al., 2014). We found that source areas represented a low proportion of the species range and the vast majority of the landscape occupied by the species did not exhibit strong source-sink dynamics, suggesting that the important engines of population productivity occupied a small fraction of the species' range. This is a critical observation for conservation, because typically assessments of habitat suitability are not based on source-sink analysis, and our results suggested such an approach may produce sub-optimal results. Interestingly, the sources identified in our models correspond to the estimated subpopulations of maned wolf defined by canid specialists in Brazil (see Paula and Desbiez, 2013 for detailed population information). This overlapping suggests that our models had a good performance, since established populations (i.e., that shows no overall change in population size in a long time period) tend to act as source populations (Pulliam, 1988).

Our model showed that reductions on the maned wolf mean population size ranged from 10 to 23% even under low mortality probabilities (i.e., 10% of chance of being road-killed when encountering a road). The *No crossing* scenario (i.e., combination between the behaviors avoidance and mortality) presented the most critical population size reduction even with low mortality probabilities, suggesting that the avoidance behavior has a significant negative impact on maned wolves as well. Our results are in line with recent studies that demonstrate that maned wolves are negatively impacted by roads. For example, a spatially-implicit demographic model predicted that the maned wolf populations may suffer a reduction of 16% under moderate road-kill estimates (i.e., 20% of mortality on dispersing sub-adults) and might be reduced up to

96% under higher road-kill estimates (i.e., by increasing another 20% of mortality on dispersing sub-adults; Paula and Desbiez, 2013). Additionally, Ceia-Hasse et al. (2017) suggests that maned wolves might go locally extinct in areas with road density above 0.08 km/km^2, which is far below the observed average road density of Brazilian Southeast region. Additionally, the negative impact of barrier effects imposed by roads has been observed in other large mammals (Alexander et al., 2005).

Our road-kill likelihood model exhibited a high AUC, and helped us to identify a high number of critical road segments. The importance of habitat connectivity to explain road-kill risk is in line with several recent studies for some species (Grilo et al., 2011; Santos et al., 2013). It is expected that roads intersecting well-connected habitats may increase species crossing attempts (Santos et al., 2013). This fact was observed in low traffic roads for a nocturnal carnivore, which can be a result of a low risk perception (in average one vehicle every 5 minutes at night, Grilo et al., 2011). However, we also found that high traffic roads such as highways with more than four lanes were positively related with mortality risk. We argue that large home-ranges and the low availability of safe passages may lead to road crossing attempts even in high traffic roads. In fact, Martin and Fahrig (2016) hypothesized that historic landscape structure drives species dispersal characteristics, being the dispersal success in anthropic landscapes strictly related to it. Therefore, we argue that species adapted to well-connected and conserved areas may be poorly adapted to dispersal through altered matrix. For example, in face of a high traffic road, individuals may ignore the risk of being killed and attempt to cross those structures. The elevated temperatures may be associated with higher population abundance (Prevosti et al., 2004) or with movement patterns of maned wolves that seem to reach highest distances in temperatures between 21° and 28° C which correspond mainly to Cerrado biome (Emmons et al., 2012). Additionally, the availability of wolf's fruit (*Solanum lycocarpum*, Solanaceae) which may account for a large fraction of the maned wolf diet (Motta-Júnior et al., 2013) in Cerrado is shown to be directly related to warmer environments, road edges and disturbed areas (Sacco et al., 1985; Aragona and Setz, 2001; Rodrigues, 2002). This phenomenon may attract maned wolf to roadside areas and increase the risk of being hit by vehicles.

Our road models show that the road segments with high mortality likelihood occur mostly at the intermediate areas. Some studies suggested two mechanisms that affect source-sink dynamics of a population: constrained dispersal (Pulliam, 1988) and maladaptive habitat selection (Delibes et al., 2001). These mechanisms may explain why road segments with high mortality risk are located between source areas. Maned wolves may be obliged to disperse to sub-optimal habitats due to density-dependent forces, making maladaptive habitat choices by establishing home ranges at high road density location (Benson et al., 2015). Also, most of the observed road-kills corresponded to the species mating and dispersal season (Dietz, 1984; Rodden et al., 2004). High mobility periods were highly associated with high road-kill rates also for some Mediterranean carnivores, such as red foxes (*Vulpes vulpes*), Eurasian badger (*Meles meles*) and Egyptian mongoose (*Herpestes ichneumon*) (Grilo et al., 2009).

The maned wolf's extensive geographic distribution makes the implementation of mitigation measures logistically challenging. However, the novel approach proposed here allows us to define a reduced amount of road segments as priority areas for the maned wolf conservation. Our results show that 135 km of road length in Brazil should be a priority in terms of future research and mitigation. The next steps should be the validation of the model through estimates of road-kill rates and population densities in those areas, and then focus mitigation on road-kill reduction and promote habitat connectivity through fencing and safe passages across high traffic highways to help minimize future population declines (Huijser et al., 2016).

ACKNOWLEDGMENTS

This study was part of the project "Road Macroecology: analysis tools to assess impacts on biodiversity and landscape structure" funded by CNPq (Nº 401171/2014-0). P. B. was supported by FAPEMIG grant (Process PAPG-11686). We thank Michely R. Coimbra for helping with road-kill data collection, Katia M. P. M. B. Ferraz for helping with the road-kill likelihood model and Anthony P. Clevenger for early comments and reviewing this manuscript. Special thanks to all the Canid specialists

that responded to our enquires, Flávio H. G. Rodrigues, André G. Chiarello, Eleonore Setz, Eliana F. Santos and José C. Motta-Júnior.

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FIGURES

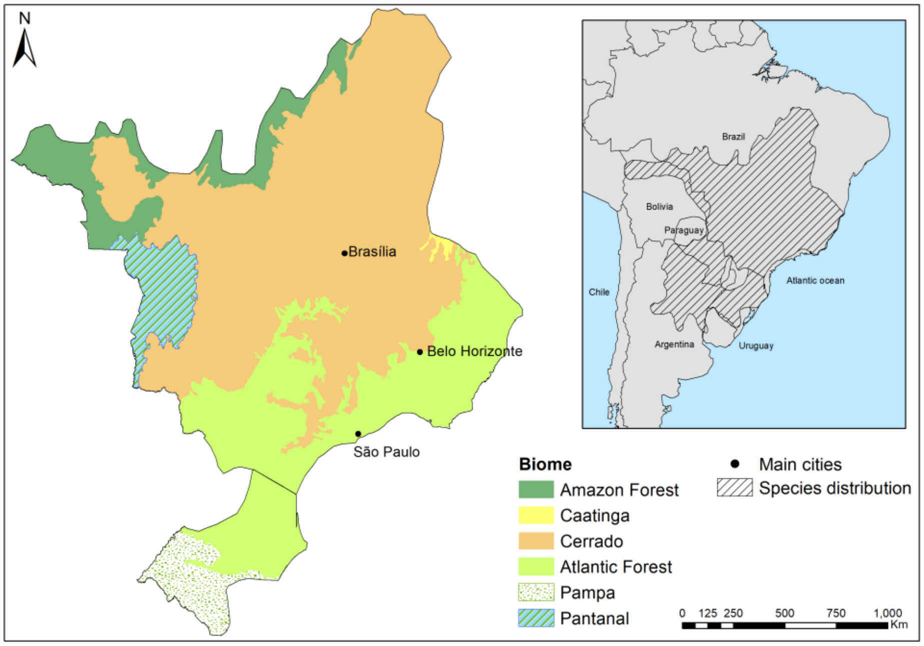


Figure 1. Maned wolf's current distribution and its location in the Brazilian biomes.

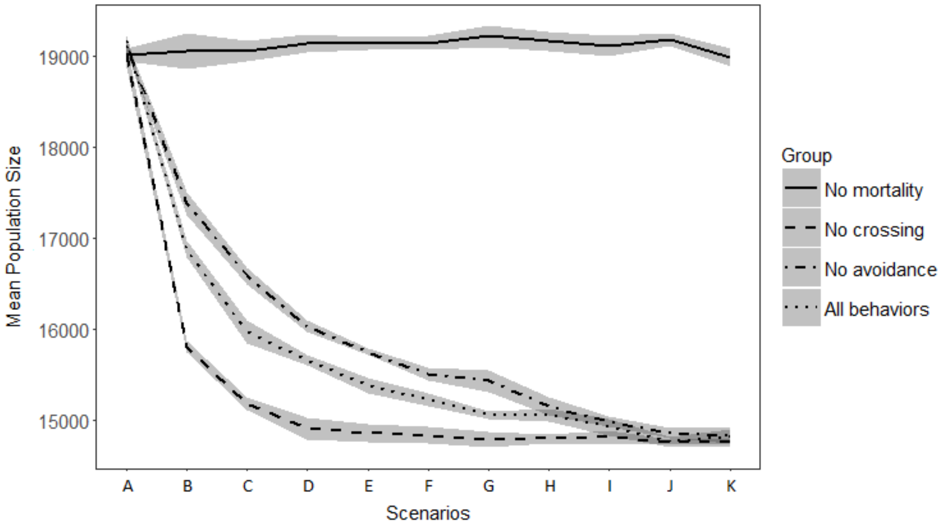


Figure 2. Maned-wolf population response to different scenarios of potential road effects. Mean population size for each group of scenarios (*No mortality*, *No crossing*, *No avoidance*, *All behaviors*). Each group is composed of 11 scenarios (x-axis). The grey ribbon represents the standard deviation.

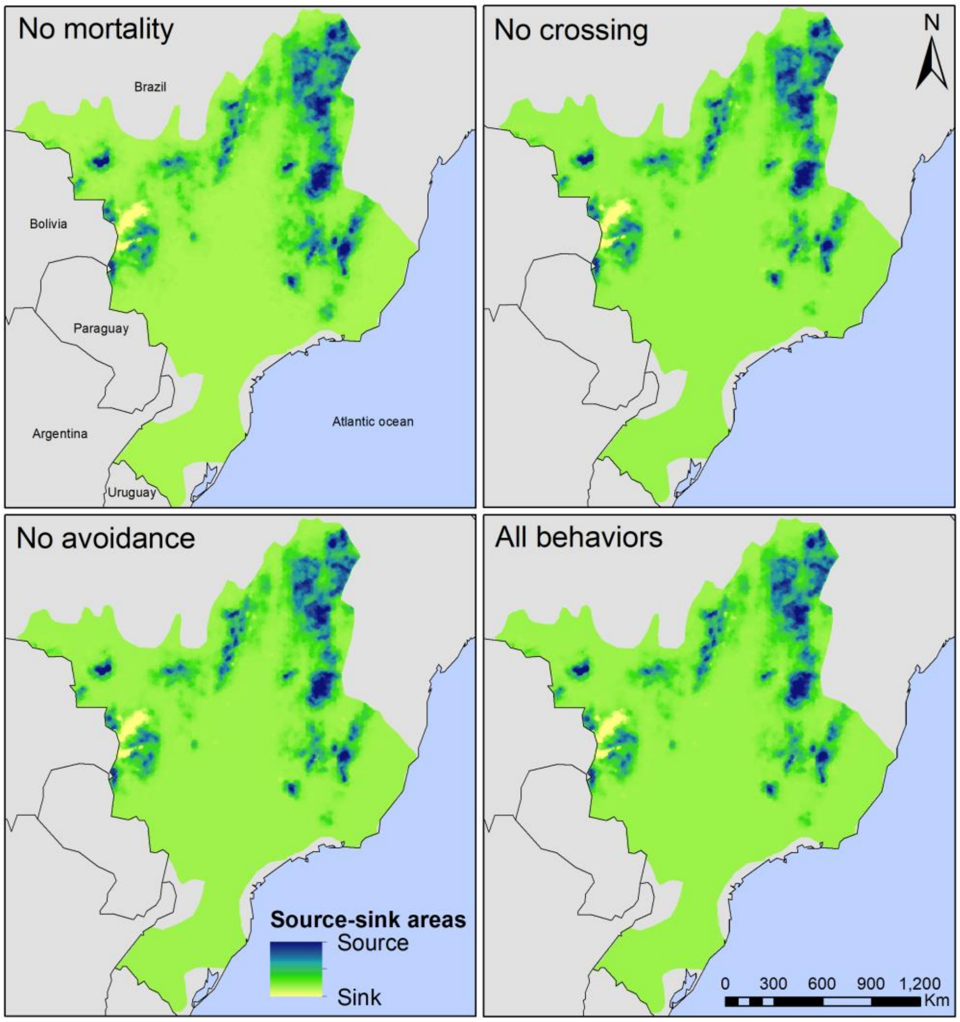


Figure 3. Maned wolf source-sink dynamics. Each map is a composition of 11 source-sink maps originated for each group of behaviors. Values ranged from -100 (sink) and +100 (source).

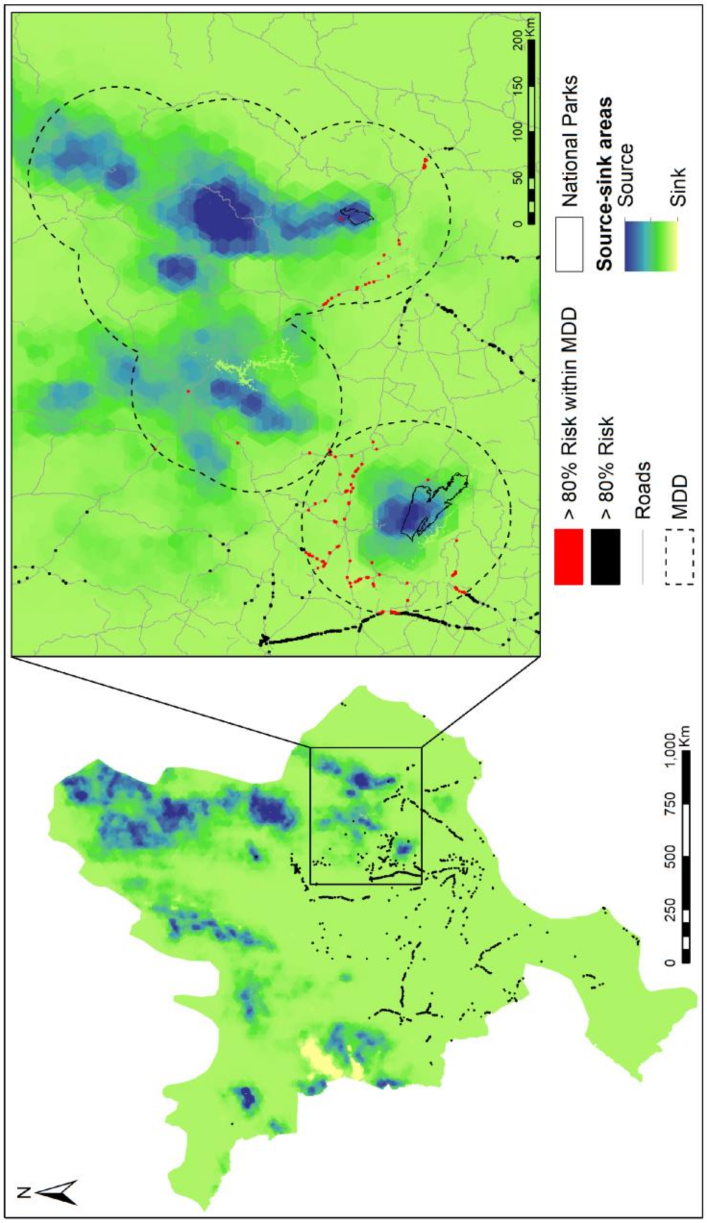


Figure 4. Critical areas for maned wolf conservation. Source-sink areas and road segments with high mortality risk (>80%). The zoomed area represents the most critical areas – road segments within maned wolf's Median Dispersal Distance (MDD, represented by dashed lines). The National Park of Serra da Canastra is located at the left and the National Park of Serra do Cipó at the right.

TABLES

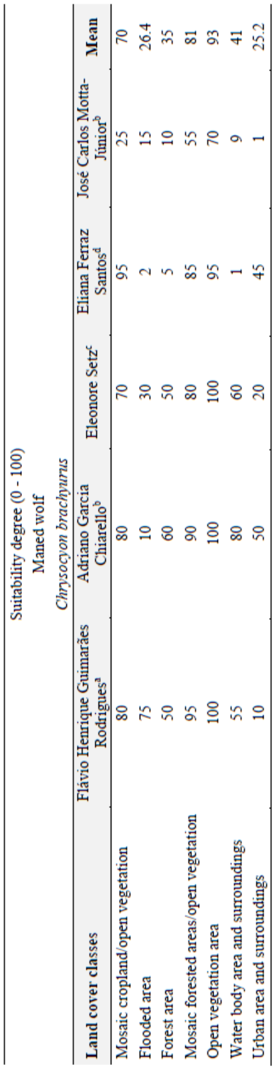
Table 1. Input parameters used in simulations for each population of maned wolves.

Demographic Parameters	**Units**	**Values**	**Reference**
Initial population size	-	100,000	Schumaker et al., 2014
Range Area			
Maximum	km²	13.63	Amboni, 2007, Azevedo, 2008, Coelho et al., 2008
Average	km²	7.55	
Home Range			
Maximum	km²	154.11	Dietz, 1984, Silveira, 1999, Rodrigues, 2002
Average	km²	45.68	
Number of stages	-	3	Paula et al., 2008
Lifespan	months	156	Rodden et al., 2004, Paula et al., 2008
Litter size			
Maximum	-	3	Dietz, 1984, Paula et al., 2008, Silveira, 1999
Mean	-	1.5	
Age at first birth	months	24	Paula et al., 2008
Interval birth	months	12	Rodden et al., 2004
Maximum background survival			
Juvenile	%	40	Paula et al., 2008
Sub-adult		76	
Adult		90	

SUPPLEMENTARY MATERIAL

Table A1

Average weight estimated from experts' opinion for land cover classes. Specialists filiation: [a] Universidade Federal de Minas Gerais, [b] Universidade de São Paulo, [c] Universidade de Campinas, [d] Canid Departament of Associação Mata Ciliar - Jundiaí/SP.



	Suitability degree (0 - 100) Maned wolf *Chrysocyon brachyurus*					
Land cover classes	Flávio Henrique Guimarães Rodrigues[a]	Adriano Garcia Chiarello[b]	Eleonore Setz[c]	Eliana Ferraz Santos[d]	José Carlos Motta-Júnior[b]	**Mean**
Mosaic cropland/open vegetation	80	80	70	95	25	70
Flooded area	75	10	30	2	15	26.4
Forest area	50	60	50	5	10	35
Mosaic forested areas/open vegetation	95	90	80	85	55	81
Open vegetation area	100	100	100	95	70	93
Water body area and surroundings	55	80	60	1	9	41
Urban area and surroundings	10	50	20	45	1	25.2

Table A2

Variables selected to evaluate road segments with high mortality risk in MaxEnt. All variables were tested for autocorrelation.

Variable	Description	Source
Bioclimatic		
Temperature	Maximum temperature of the warmest month (°C * 10)	http://www.worldclim.org/
Land Cover		
Cropland/Open Vegetation	Proportion of croplands/open vegetation mosaics	http://due.esrin.esa.int/page_globcover.php
Forest Area	Proportion of native forests areas	http://due.esrin.esa.int/page_globcover.php
Forest/Open Vegetation	Proportion of forests/open vegetation mosaics	http://due.esrin.esa.int/page_globcover.php
Open Vegetation Area	Proportion of open vegetation areas	http://due.esrin.esa.int/page_globcover.php
Simpson's Diversity Index	Relative patch diversity derived from the Land Cover map	http://due.esrin.esa.int/page_globcover.php
Landscape Connectivity	Effective mesh size derived from the Land Cover map (MEFF)	http://due.esrin.esa.int/page_globcover.php
Streams	Density of streams (km/km²)	http://hidroweb.ana.gov.br/
Human Pressure		
Population Density	Population density per municipality (inhabitants/km²)	http://www.codegeo.com.br/2013/04
Road Type	Type of road where the road-kill occurred for pixels with road-kill records + Dominant road for pixels with no road-kill occurrence	https://www.openstreetmap.org/

Table A3

Probability of occurrence for each behavior.

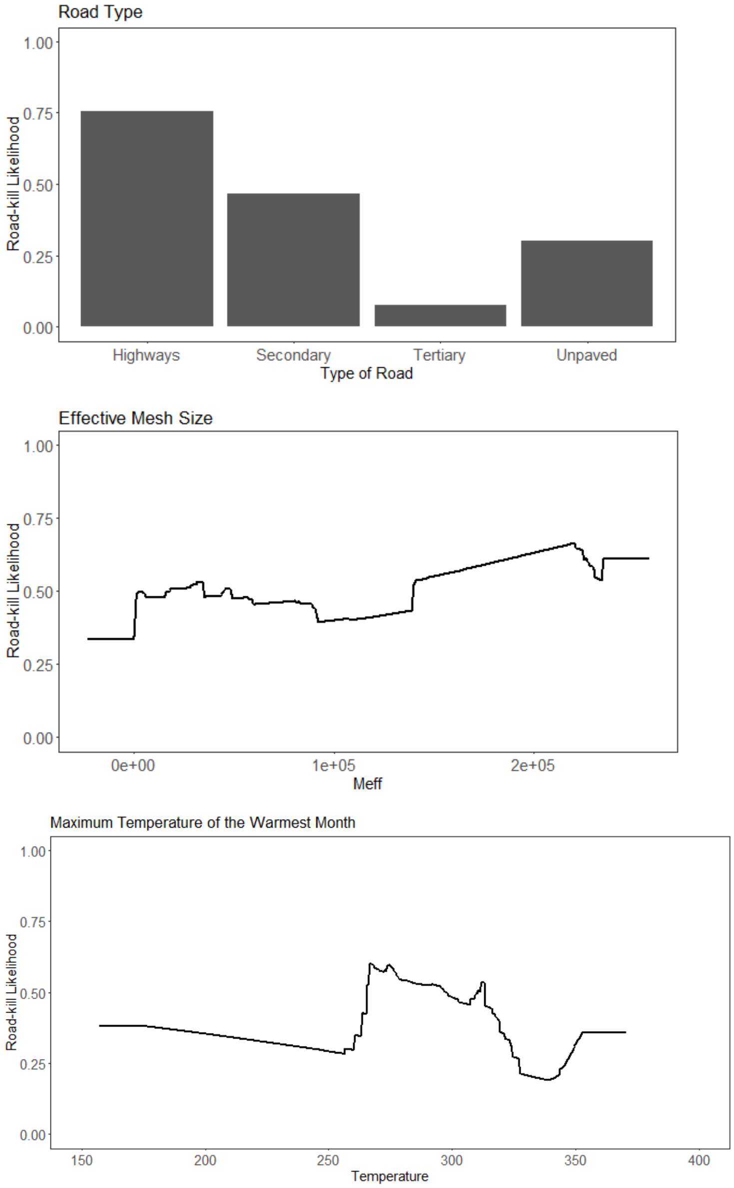
Group/Scenario	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**
No mortality											
Mortality	0	0	0	0	0	0	0	0	0	0	0
Avoidance	0	10	20	30	40	50	60	70	80	90	100
Crossing	100	90	80	70	60	50	40	30	20	10	0
No crossing											
Mortality	0	10	20	30	40	50	60	70	80	90	100
Avoidance	100	90	80	70	60	50	40	30	20	10	0
Crossing	0	0	0	0	0	0	0	0	0	0	0
No avoidance											
Mortality	0	10	20	30	40	50	60	70	80	90	100
Avoidance	0	0	0	0	0	0	0	0	0	0	0
Crossing	100	90	80	70	60	50	40	30	20	10	0
All behaviors											
Mortality	~~0~~	10	20	30	40	50	60	70	80	90	~~100~~
Avoidance	~~50~~	45	40	35	30	25	20	15	10	5	~~0~~
Crossing	~~50~~	45	40	35	30	25	20	15	10	5	~~0~~

Table A4

Patch maps with multiple spatial scales used for source-sink analysis.

Patch Area (atomic hexagons)	Patch Area (km^2)	Number of Patches
1027	222	14955
1951	422	7969
3997	865	3956
5941	1286	2698
7651	1656	2125

Figure A1



Environmental variables that show high explanatory power: 1) type of road, 2) landscape connectivity (MEFF) and 3) maximum temperature of the warmest month.

Table A5

Environmental variables with respective percent contribution.

Variable	**Percent contribution**
Road Type	53.4
Landscape connectivity	10.4
Temperature	9.1
Cropland/Open Vegetation	7
Forest Area	6.4
Open Vegetation Area	4.7
Population Density	4.6
Streams	2.1
Simpson’s Diversity Index	1.7
Forest/Open Vegetation	0.7