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RAFAELA COBUCI CERQUEIRA

FELIDS AND SPATIAL INTERACTIONS WITH ROADS: ROAD-KILL, CORRIDORS, AND SPACE USE IN BRAZIL

LAVRAS – MG

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Tese 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 em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Doutor.

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FELÍDEOS E INTERAÇÕES ESPACIAIS COM ESTRADAS: ATROPELAMENTO, CORREDORES, E USO DO ESPAÇO NO BRASIL

Tese 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 em Paisagens Fragmentadas e Agrossistemas, para a obtenção do título de Doutor.

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Aos meus pais, Francisco e Maria do Carmo.

Dedico

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“Navegante das solidões

No espaço a nos levar

Nave mãe e o nosso lar

Terra, Terra és tão delicada

Os teus homens não têm juízo

Esqueceram tão grande amor

Ofereces os teus tesouros

Mas ninguém dá o teu valor

Terra, Terra eu sou teu filho

Como as plantas e os animais

Só ao teu chão eu me entrego

Com amor, firmo tua paz”

(Estrelada: Milton Nascimento e Márcio Borges)

RESUMO

As estradas estão entre as ameaças mais importantes para a vida silvestre, principalmente porque são fontes onipresentes de mortalidade, perda e fragmentação de habitat. Quase todas as espécies de felídeos no Brasil são listadas como Vulneráveis nacionalmente, e alguns estudos relatam que são espécies particularmente vulneráveis aos efeitos negativos das estradas. Neste trabalho, utilizamos duas abordagens para avaliar como seis das dez espécies de felídeos que ocorrem no Brasil interagem espacialmente com estradas. No primeiro artigo, comparamos o resultado de dois métodos comumente usados para identificar segmentos de estradas para mitigação: modelos de corredores potenciais de movimento e modelos de probabilidade de atropelamento. Aplicamos a teoria de circuito para identificar segmentos de estrada que cruzam corredores de movimento e o algoritmo da máxima entropia para identificar segmentos de estrada com alta probabilidade de atropelamento para cinco espécies: gato-do-mato-pequeno do norte e do sul *Leopardus guttulus e L. tigrinus*, jaguatirica *L. pardalis*, jaguarundi *Herpailurus yagouaroundi* e onça parda *Puma concolor*. Descobrimos que corredores de movimento e alta probabilidade de atropelamento não ocorrem nos mesmos segmentos de estrada e sugerimos que os dois métodos devem ser usados de forma complementar ao se priorizar segmentos de estrada para mitigação. No segundo artigo, usamos a modelagem de equações estruturais para avaliar os efeitos diretos e indiretos das estradas no uso do espaço por onças-pintadas no Brasil. Os resultados mostraram que o uso do espaço por onças-pintadas não é diretamente influenciado por estradas, mas que estas influenciam o uso do espaço indiretamente por meio de seus efeitos na cobertura do solo. Estradas pavimentadas e não pavimentadas reduzem a quantidade de habitat natural e favorecem as áreas urbanas, o que por sua vez reduz a ocorrência de onças. Argumentamos que os efeitos indiretos das estradas são sutis e não devem ser subestimados, especialmente considerando as espécies ameaçadas que vivem em uma paisagem onde crescem os planos para aumentar a rede de estradas. O terceiro manuscrito é uma compilação de dados georreferenciados de atropelamentos no Brasil, no qual compartilho a autoria.

Palavras-chave: Conectividade. Atropelamento. Mitigação. Efeitos indiretos. Uso do espaço. Cobertura da paisagem. Felídeos.

ABSTRACT

Roads are among the most important threats for wildlife, mainly because they are ubiquitous sources of mortality, habitat loss and fragmentation. Almost all felid species in Brazil are listed as Vulnerable nationally, and some studies report they are particularly vulnerable to the negative effects of roads. In this study, we used two approaches to assess how six out of the ten species of felids that occur in Brazil spatially interact with roads. In the first manuscript, we compared the outputs of two methods commonly used to identify road segments for mitigation, namely, potential movement corridor models and road-kill likelihood models. We applied circuit theory to identify road segments that cross potential movement corridors and maximum entropy to identify road segments of high road-kill likelihood for five species: northern and southern tiger cats *Leopardus guttulus* and *L. tigrinus,* ocelot *L. pardalis,* jaguarundi *Herpailurus yagouaroundi,* and puma *Puma concolor*. We found that movement corridors and high road-kill likelihood do not occur in the same road segments and we suggest that the two methods should be used in a complementary way when prioritizing road segments for mitigation. In the second manuscript, we used structural equation modelling to evaluate direct and indirect effects of roads on space use by jaguars *Panthera onca* in Brazil. The results showed that space use by jaguars is not directly influenced by roads, but that roads influence space use indirectly through their effects on land-cover. Paved and unpaved roads reduce the amount of natural habitat and favour urban areas, which in reduce the occurrence of jaguars. We argue that indirect effects of roads are subtle and should not be underestimated, especially considering threatened species living in a landscape where there are continuous plans for road network expansion. The third manuscript is a compilation of geo-referenced road-kill data in Brazil, in which I share authorship.

Keywords: Connectivity. Road-kill. Mitigation. Indirect effects. Space use. Land-cover. Felids.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUCTION

Diversity of life is astonishing and it is estimated that we know only ~10% of species on Earth (MORA et al., 2011). Meanwhile, global loss of biodiversity has never been so high (WWF, 2020), and landscape change due to human activities and infrastructure development strongly influences this scenario in a negative way (FEARNSIDE, 2015; LAURANCE, 2015; KASZTA et al. 2020). It is estimated that by mid-century, new paved roads added to the existing global road network will be long enough to encircle the Earth more than 600 times (LAURANCE et al., 2014). Nearly 90% of this expansion will occur in areas of high biodiversity value, such as tropical regions (DULAC, 2013). In Brazil, the Government plans to increase the road network by 20% in the next 30 years (BAGER et al., 2015); unfortunately, these plans usually do not address environmental issues (LAURANCE, 2014; ROBERTS; SJÖLUND, 2015).

Primary negative effects of roads on wildlife are mainly associated with direct impacts such as mortality due to collisions with vehicles and changes in individual movement patterns (RYTWINSKI; FAHRIG, 2015), and indirect effects such as habitat loss and fragmentation (RANDS et al., 2010; CROOKS 2017). Road mortality can lead to severe declines in population size of many species (CEIA-HASSE et al., 2018; GRILO et al., 2020). Species that live in low densities are particularly vulnerable to risk of extinction (e.g., CEIA-HASSE et al., 2017). In addition, movements of individuals in roaded landscapes can be modified by avoidance of traffic disturbances, such as noise or light (JACOBSON et al., 2016; CHEN; KOPROWSKI, 2016). By reducing habitat amount and fragmenting natural landscapes and consequently creating edge effects (LAURANCE et al., 2002), reducing connectivity (JAEGER, 2000; JACKSON; FAHRIG, 2011) and making room for the expansion of human activities (LAURANCE; GOOSEM; LAURANCE, 2009), roads indirectly impact wildlife populations; all of these changes can modify patterns of space use and species distribution (TORRES; JAEGER; ALONSO, 2016) ultimately compromising population persistence (FAHRIG; RYTWINSKI, 2009; KASZTA et al., 2020).

Road ecologists have been engaged in studies to help guide decision-making for mitigating some of these negative effects of roads (CLEVENGER; FORD, 2010; GUNSON; TEIXEIRA, 2015). For example, studying spatial road-kill patterns as well as the variables associated with the risk of collision with vehicles, and identifying specific sites in a landscape where movement of individuals is potentially high but are crossed by roads can help identify road segments to implement effective measures (VAN DER REE et al., 2009; RYTWINSKI et al., 2016; SPANOWICZ; TEIXEIRA; JAEGER, 2020). To identify these areas, researchers have made use of modelling tools (CLEVENGER et al., 2002; ZELLER; WATTLES; DESTEFANO, 2020). These rapid and inexpensive theoretical tools are especially valuable in countries where few resources are invested in environmental issues. Interestingly, the locations predicted to have high road-kill likelihood and movement corridors crossed by roads are not always the same (KANG et al., 2016; McCLURE; AMENT, 2014). Despite road-kill data having been used to validate connectivity models (KOEN et al., 2014), it has been suggested that road-kill is not the best predictor of animal movement (LALIBERTÉ; ST-LAURENT, 2020). Clarifying this issue is important so that both segments with high biological relevance for the movement of individuals as well as high-risk segments are properly identified and mitigated (ZELLER; WATTLES; DESTEFANO, 2020) to reduce road mortality and restore habitat connectivity. Moreover, measures for road mitigation are costly, so proper definition of the most important areas is crucial (WELLER, 2015; SPANOWICZ; TEIXEIRA; JAEGER, 2020).

Understanding species-specific responses to roads also helps target mitigation measures for conservation. Behavioral responses to roads can vary widely, with some species responding positively (e.g., small mammals, RUIZ-CAPILLAS; MATA; MALO, 2013) and others negatively (e.g., wolverines *Gulo gulo luscus*, SCRAFFORD et al., 2018). Responses may be scale-dependent (e.g. cougars DICKSON; BEIER, 2002 and wolves *Canis lupus*, ZIMMERMANN et al., 2014), depend on available habitat, road characteristics, or traffic volume (e.g. barn owls *Tyto alba* and stone marten *Martes foina*, GRILO et al., 2012) and change throughout the day according to different levels of human presence (e.g., maned wolves *Chrysocyon brachyurus*, COELHO et al., 2008). These responses may be due to the presence of the roads themselves (or traffic, or noise) or, least studied, to the changes that roads promote on the surrounding landscape. Much has been said about the effects of roads on fragmentation and habitat loss (LAURANCE; GOOSEM;

LAURANCE, 2009) and about the impacts of fragmentation and habitat loss on wildlife (PÜTTKER et al., 2020), but few studies have addressed the latter as a consequence of the former.

Many studies have highlighted roads as an important anthropogenic feature that negatively impact felids in Brazil. Road-kill is continuously reported (SILVA et al., 2014) and national evaluations of the conservation status of many species include roads as a potential threat for some populations (ALMEIDA et al., 2013; OLIVEIRA et al., 2013). However, many studies on felids´ ecology only include roads as one of the variables that may influence their occurrence (ASTETE et al., 2017; MASSARA et al., 2018; HORN et al., 2020), or include felids among other studied taxa (ABRA, 2019) or even don´t include roads as a variable that might play a role in habitat selection (FERRAZ et al., 2012; CULLEN JR. et al, 2013). Only a few studies have been conducted to specifically assess the potential effects of roads on felids (CULLEN JR et al., 2016).

In this study, we used modelling tools to assess the spatial interaction of six felid species with the road network in Brazil. The species included northern and southern tiger cats *Leopardus guttulus* and *L. tigrinus*, respectively, ocelot *L. pardalis*, jaguarundi *Herpailurus yagouaroundi*, puma *Puma concolor* and jaguar *Panthera onca*. All but two are listed as “Vulnerable” on the latest national list of threatened species; northern tiger cat is considered “Endangered” while the ocelot is not on the list (BRASIL, 2014). The study of the spatial ecology of these species has grown considerably in recent years (KNOPFF et al., 2014; KASPER; SCHNEIDER; OLIVEIRA, 2016; MORATO et al., 2016; MARINHO et al., 2017; ESPINOSA et al., 2018; OLIVEIRA et al., 2020), especially due to the rising access to technologies that allow researchers to monitor them remotely (CAGNACCI et al., 2010). Consequently, new databases are becoming available (MORATO et al., 2018a; NAGY-REIS et al., 2020) allowing various analytical approaches. However, despite roads being often cited as potential threats and important determinants of the use of space by these species, few studies actually address how felids spatially interact with roads in more depth (e.g., COLCHERO et al., 2011; SETH et al., 2014; ESPINOSA; CELIS; BRANCH, 2018; SCHMIDT; LEWISON; SWARTS, 2020), especially in Brazil (CULLEN JR et al., 2016; MORATO et al., 2018b).

In the first manuscript of this thesis, we used movement-corridor and road-mortality models as means of prioritizing road segments for mitigation for tiger cats, ocelot, jaguarondi, and puma. The aim was to compare two widely used tools when choosing locations for mitigation while identifying priority areas for mitigating the effects of roads on these species (Manuscript 1, submitted to the journal *Environmental Management*). In the second chapter, we used a structural equation modeling approach to disentangle direct and indirect effects (via landscape modification) of roads on space use by jaguars (Manuscript 2, submitted to the journal *Biological Conservation*). I also present a data paper that is a compilation of geo-referenced road-kill data from published and unpublished road surveys in Brazil, in which I share authorship (Manuscript 3, published in the journal *Ecology*).

2 CONCLUSIONS

The results presented in this thesis provide important insights to create effective road mitigation plans to improve the conservation of felids in Brazil. We identified key road segments to inform mitigation planning. Within the controversial literature on whether areas of high movement coincide with areas of high road mortality, we have shown that to reduce road mortality and to restore population connectivity, different road segments should be considered. Also, for the first time, we have shown that the effects of roads on space use by jaguars can be to a large degree indirect through the reduction of the amount and quality of habitat, which represent great challenges for road planners and managers to preserve the remaining populations.

2.1 Road-kill and movement-corridor predictions are complementary tools for road mitigation for felids

Our findings showed that road segments of high movement are generally different from road segments of high road-kill likelihood, indicating that movement corridors in well-connected stretches of the landscape that are crossed by roads do not necessarily promote higher road mortality. Contrary to what previous studies suggested (GRILO et al., 2011), this means that connectivity and road mortality may be independent. This clarifies the use of both methods to define priority areas for mitigation. Road-kill data have been used to validate connectivity maps (KOEN et al., 2014; LALIBERTÉ; ST-LAURENT, 2020). However, when movement corridors and vehicle-collisions do not overlap, this means that they may represent different mechanisms of interactions of animals towards roads and therefore the methods are not suitable for validation. When different types of behavioral data are used, a lack of spatial coincidence may occur simply because each method identifies areas that are selected by individuals in different specific periods of their life cycle (ZELLER; McGARIGAL; WHITELEY, 2012; McCLURE; AMENT, 2014).

Usually, road mortality is associated with periods of high movement, such as breeding and dispersal (GRILO; BISSONETTE; SANTOS-REIS, 2009) and it is likely that most road-mortality models capture these behaviours, while movement-corridor models may capture a wide range of behavioural states (from daily movements to dispersal). Thus, in the case of a lack of coincidence, the complementary use of both approaches should be considered in decision-making.

For the felids studied here, we recommend that road segments identified by movement-corridor models should be prioritized in those areas where populations are already affected by isolation or are likely to be affected in the future, for example, where genetic variability is already compromised. Road segments identified by road-mortality models should be prioritized in areas of low population densities and where other sources of non-natural mortality may be a concern, for example, due to illegal human persecution. Despite the most important predictor of road mortality for most species being the presence of 3-6 lane roads, it is important to consider both paved and unpaved roads in the models because road mortality of felids occurs on both types of roads and also because both play an important role in fragmenting the landscape and populations (MAGIOLI et al., 2019). Any efforts to reduce or avoid additional mortality and improve connectivity are highly valuable, even on small and unpaved roads, especially in areas where populations are at risk (INSTITUTO PRO CARNÍVOROS; INSTITUTO PAMPA., 2018).

2.2 Space use by jaguars is indirectly affected by roads

We showed that space use by jaguars within their home ranges is indirectly affected by roads as roads reduce available habitat and favor the occurrence of urban areas. In contrast, a direct effect of roads was not observed. The high dependence of jaguars on natural areas (RODRÍGUEZ-SOTO et al., 2011; MORATO et al., 2014) in a modified landscape limits individuals to small and fragmented areas (PAVIOLO et al., 2016), causing serious population declines (GALETTI et al., 2013). The reduction of natural areas by ubiquitous roads as a significant cause of these declines is being demonstrated for the first time and is an important finding on the influence of roads on jaguar populations. Human-related areas have been reported as a more reliable predictor variable of habitat selection than roads by other carnivore species (ZIMMERMANN et al., 2014). In the case of jaguars, this seems to be taking place, and we showed that urban areas can be a consequence of the presence of roads. Jaguars tended to avoid urban areas, as previously described for both jaguars and other carnivore species (De ANGELO et al., 2013; GOAD et al., 2014). This tendency also constraints individuals´ space use. Male jaguars, however, were found not to be affected or even positively affected by urban areas that were favored by roads. This apparent behavioral plasticity to human-dominated landscapes seriously exposes them to a higher risk of being persecuted (MARCHINI; MACDONALD, 2018). Finally, the lack of a direct effect of roads on jaguars implies that they are highly under the risk of road mortality (SRBEK-ARAUJO; MENDES, CHIARELLO, 2015). These findings suggest that substantial efforts should be made to prevent road mortality and to control and prevent deforestation and urban sprawl from roads, and that these should be considered as a priority in all plans for the species´ conservation.

2.3 Perspectives for future research

Roads are considered important determinants of the viability of carnivore populations worldwide (CEIA-HASSE et al., 2017). Many felid populations in Brazil are threatened not only by road mortality but also by poaching, retaliatory hunting, transmission of diseases from domestic animals, decreased prey availability, and habitat loss and fragmentation (MASSARA et al., 2015; OSLOY et al., 2016; OLIVEIRA et al., 2020). Recently, the home of the world´s largest jaguar population has been affected by fires that are destroying Brazilian Pantanal, and it is not yet possible to predict the impacts of this tragedy for the species. In this scenario, we believe that any information that facilitates a better understanding of felids´ ecology should be taken into account by those responsible for decision-making and those involved with the conservation of felids. Within the subjects addressed in this thesis, and based on its findings, we identify some important gaps in knowledge that still need to be addressed.

There is a need to understand the role of different behavioral states on road mortality and space use. Specific biological characteristics may also influence spatial interactions with roads, such as age, reproductive status, species traits, and also spatial, daily and seasonal variation of some of these attributes (GRILO et al., 2014; ZIMMERMANN et al., 2014; GONZÁLEZ-SUÁREZ; FERREIRA, GRILO, 2018). Questions regarding these factors also need to be addressed. Studies that seek to understand these relationships are becoming more feasible due to the technologies of remote monitoring of individuals that are increasingly accessible (e.g., MORATO et al., 2018a). We highlight some conservation and research programs that are dedicated to obtain information on the ecology of felids in Brazil that can assist these future studies such as “Wild Cats Brazil” (www.wildcatsbrazil.com) and many others from Instituto Pró-Carnívoros (procarnivoros.org.br/); “Onçafari” (www.oncafari.org), “Onças do Yucumã” (www.curicaca.org.br/conservacao-onca), and “Projeto Felinos” (www.facebook.com/projeto.felinos).

Local scale studies are needed to better inform mitigation planning and design and to better understand how roads and the surrounding landscape influence the animals´ use of space. For example, among all the road segments of high road-kill likelihood or high movement identified here, there is a need to prioritize those that coincide with areas where felids are more vulnerable, which demands a very refined evaluation of their populations (e.g., INSTITUTO PRO CARNÍVOROS; INSTITUTO PAMPA., 2018). Information on specific habitat types near roads, prey availability and probability of human encounters have been considered as factors influencing other carnivores´ spatial relationships with roads (ZIMMERMANN et al., 2014) and should be also studied for felids. Additionally, it is important to understand local road attributes such as visibility, traffic volume and speed, road verges, topography (GUNSON; MOUNTRAKIS; QUACKENBUSH, 2011) that can influence road mortality and movement near roads. For example, it has been shown that road avoidance by carnivores increases with traffic volume (ALEXANDER; WATERS; PAQUET, 2005). For jaguars, there is still a need to clarify the lack of a direct response to the presence of roads and it is possible that this is related to traffic volume. Unfortunately, important information on road attributes are lacking in Brazil, and may require intensive field studies. For example, most of the studies that address felids´ responses to roads usually consider only primary paved roads based on the Brazilian National Department of Transport Infrastructure database (MORATO et al., 2018b). It has been widely discussed among Brazilian road ecologists how limited are the data available Government´s database in relation to the numbers and types of roads, traffic, speed limits, and other important features that are necessary for more comprehensive studies in Road Ecology.

Knowledge about individuals’ perceptions about roads could also help interpret the lack of direct response to the presence of roads by jaguars. For example, detailed analysis of individuals´ movement speed when they are in the proximity roads may indicate whether or not roads are perceived as a danger or as a degraded habitat (DICKSON; JENNESS; BEIER, 2005), even when road avoidance behavior is not taking place. Also, because roads can influence spatial use differently at different spatial scales (DICKSON; BEIER, 2002; POESSEL et al., 2014), it is necessary to assess how roads influence jaguars' home range selection (the second-order scale of habitat selection, JOHNSON, 1980). It is also necessary to evaluate areas of different road densities to test if there is a functional response by jaguars to road density, i.e., if the responses may be a function of the local abundance of these linear features (BEYER et al, 2010; BEYER et al., 2013).

Finally, although the effects of roads on landscape transformation have long been recognized (CARR; FAHRIG; POPE, 2002), in Brazil few studies have addressed this specifically (FREITAS; HAWBAKER; METZGER, 2010; BARBER et al., 2014; FEARNSIDE, 2015). Although we provided insights on the role that roads play in influencing land cover, further studies at larger scales are needed. For example, there is a need to evaluate landscape change due to road networks in different landscapes in Brazil over time (HAWBAKER et al., 2006; JAEGER et al., 2007). Comparing land-cover as well as species and biodiversity between areas of different road densities (BENNETT, 2017) could clarify the ecological effects of landscape change due to roads. Assessing how different configurations of road networks affect the landscape and wildlife populations could fill an important gap in road ecology knowledge (JAEGER; FAHRIG; EWALD, 2006; JAEGER, 2015). All of this could help anticipate future changes in landscapes facing different scenarios of planned road infrastructure to assist planners in road projects and to improve decision making.

Greater funding for road ecology research in Brazil is urgently necessary to help reduce and prevent new impacts of transportation infrastructure on the landscape and wildlife. Until then, the Brazilian Government should adopt the precautionary principle to support plans and decisions on transport infrastructure to avoid unnecessary and irreversible environmental damages (JAEGER, 2015; LAURANCE, 2018).

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SEGUNDA PARTE – ARTIGOS

ARTIGO 1 – *POTENTIAL MOVEMENT CORRIDORS AND HIGH ROAD-KILL LIKELIHOOD DO NOT SPATIALLY COINCIDE FOR FELIDS IN BRAZIL: IMPLICATIONS FOR ROAD MITIGATION*

(*MANUSCRIPT SUBMITTED TO THE JOURNAL ‘‘ENVIRONMENTAL MANAGEMENT’’*)

Environmental Management

Potential movement corridors and high road-kill likelihood do not spatially coincide for felids in Brazil: Implications for road mitigation

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ABSTRACT

The negative effects of roads on wildlife populations are a growing concern. Movement corridors and road-kill data are typically used to prioritize road segments for mitigation measures. Some research suggests that where animals move across roads following corridors coincide with locations where they are often killed by vehicles. Other research indicates that corridors and road-kill rarely occur in the same locations. We compared movement corridor and road mortality models as means of prioritizing road segments for mitigation for five species of felids in Brazil: tiger cats (*Leopardus tigrinus* and *L. guttulus* were analyzed together), ocelot *L. pardalis*, jaguarundi *Herpailurus yagouaroundi*, and puma *Puma concolor*. We used occurrence data for each species and applied circuit theory to identify potential movement corridors crossed by roads. We used road-kill records for each species and applied maximum entropy to determine where mortality was most likely to occur on roads. Our findings suggest that movement corridors and high road mortality are not spatially associated. We suggest that differences in the behavioural state of the animals in the species occurrence and road-kill data may explain these results. We recommend that the road segments for which the results from the two methods agree (~5,300 km for all studied species combined at 95th percentile) should be

high-priority candidates for mitigation together with road segments identified by at least one method in areas where felids occur in low population densities or are threatened by isolation effects.

Keywords**:** connectivity; circuit theory; road mortality; habitat suitability; wildlife

1. INTRODUCTION

Roads are a growing threat affecting many wildlife populations worldwide (Laurance et al. 2009). However, mitigation measures have often not been well planned and not properly installed (Laurance et al. 2014; Huijser et al. 2015). This is particularly critical in countries throughout the tropics, where rich biodiversity of high global conservation interest still remains, but many new road projects are being planned for the next 30 years (Alamgir et al. 2017; Ascensão et al. 2018).

Prioritizing road segments for mitigating the negative effects on wildlife should take into account areas of additional mortality due to collisions with vehicles and areas of potential habitat and movement corridors that facilitate gene flow and ultimately the genetic diversity of populations (Clevenger and Ford 2010; Zeller et al. 2018). Thus, it is recommended to consider road segments where the potential for wildlife movement and road mortality are high (e.g., Clevenger 2012; Colchero et al. 2011; Teixeira et al. 2013; Rytwinski et al. 2016; Mohammadi et al. 2018). Nevertheless, it is not clear to what degree road segments identified by the two approaches are spatially associated. Some studies suggest that areas of high movement coincide with areas of high road mortality (Girardet et al. 2015; Kang et al. 2016), while others found little overlap between corridors and high road-kill locations (McClure and Ament 2014; Boyle et al. 2017; Laliberté and St-Laurent 2020).

Felids face threats in many regions of the world and roads are a growing concern for many species (IUCN 2017). Although in Brazil there are plans for road network upgrading and expansion (Bager et al. 2015), the relationship between movement corridors and road mortality in this region has not been examined (e.g., Rabinowitz and Zeller 2010; Silva et al. 2014). Movement-corridor studies have focused on few species (e.g., puma and jaguar *Panthera onca*) and regions (e.g. Silveira et al. 2014; Castilho et al. 2015; Diniz et al. 2017), while road mortality surveys have been conducted in several regions in Brazil (Cunha et al. 2010; Hegel et al. 2012; Souza et al. 2014). To our knowledge, studies merging models of felid movement corridors and road mortality with the aim of identifying mitigation areas have not been conducted. All felid species in Brazil except the ocelot *Leopardus pardalis* are locally endangered and therefore important target species for conservation at local and regional scales (Brasil 2014). These species are facing many impacts such as habitat loss and fragmentation and cultural and retaliatory hunting (Almeida et al. 2013). Roads are important threats for many felid populations, in particular due to mortality; efforts for effective road mitigation are therefore crucial (Srbek-Araujo et al. 2015).

Our aim was to clarify the utility of movement corridors and road mortality in identifying locations for mitigation measures to reduce road-kill occurrence and restore habitat connectivity. We compared models that identify movement corridors and road mortality to predict road segments for mitigation for five felid species in Brazil. We used circuit theory to identify locations of potential movement corridors across roads and maximum entropy principles to determine road segments with probability of high mortality. We analyzed occurrence data and road-kill records of 4 species of felids: tiger cats (*Leopardus tigrinus* and *L. guttulus* were analyzed together), ocelot, jaguarundi *Herpailurus yagouaroundi* and puma.

2. MATERIAL AND METHODS

2.1 Study area

The study area encompasses the ranges of the five felid species in Brazil according to data from the Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros/ Instituto Chico Mendes de Conservação da Biodiversidade (CENAP/ICMBio, Fig. S1). The two tiger cats were analysed together (their ranges were merged) because much of the data obtained was collected prior to the classification into two distinct species (*L. tigrinus* and *L. guttulus,* Trigo et al. 2013) and there are still uncertainties about their ranges´ limits (Silva et al. unpublished data). The range of each of these species covers almost the entire Brazil territory (Fig. S1). About 65% of Brazil's territory (~5.5 million km^2) is covered by native vegetation (GlobCover Land Cover Maps V2.3 2009). The Brazilian Institute of Geography and Statistics (IBGE 2017) classifies vegetation in six major continental biomes: Amazon, Caatinga, Pantanal, Cerrado, Atlantic Forest, and Pampa (Fig. S2). Almost all of these biomes are under some degree of threat as a result of anthropogenic disturbances (Ribeiro et al. 2009). Average human population density in Brazil is 24.5 inhabitants/km^2 (IBGE 2018) and the current road network comprises more than 1.7 million km of paved and unpaved roads (CNT 2018), i.e., ca. 0.2 km/km^2.

2.2 Potential movement corridors crossed by roads

We applied circuit theory to identify potential movement corridors (de la Torre et al. 2017) using software gflow (Leonard et al. 2017). The landscape is analysed as a network of electrical nodes connected by resistors and serves as an analogue for habitats connected by movement (McRae et al. 2008). As inputs, the models use resistance surfaces to represent the degree to which the landscape facilitates or impedes individual movement and source and destination patches (called focal nodes) among which connectivity is measured. The output provides maps of movement probabilities of individuals moving through the landscape (hereafter called current density, see McRae et al. 2008).

Resistance surfaces were obtained from habitat suitability maps. We created a habitat suitability map for each species´ range in MaxEnt 3.3.3 software (Phillips and Dudík 2008), which is widely used to predict species distributions (Phillips et al. 2006). Each model used individual locations as response variables obtained from collaborating researchers who lodged occurrence records on a database of CENAP/ICMBio. Specific information about the date of these occurrence records was not available, but they were all from within the last 20 years (Morato RG, personal communication). Despite MaxEnt´s ability to account for irregularly sampled presence-only data (Phillips et al. 2006), the number of records was rarefied to reduce the geographic bias of data collection and to avoid overfitting. This method has been shown to improve the performance of species distribution models (Boria et al. 2014) and ranked better when compared to other methods of correcting sampling bias (Fourcade et al. 2014). We removed neighbouring occurrences < 10 km apart using the "Spatially rarefy occurrence data for SDMs (Species Distribution Models)" tool of SDMtoolbox (Brown 2014). This distance was chosen based on the assumption that locations separated by 10 km exhibit enough variation to be considered spatially independent (Boria et al. 2014). After correction, we used 82 locations for tiger cats, 171 for ocelot, 106 for jaguarundi, and 606 for puma (Fig. S1).

We used the following environmental data as explanatory variables that are commonly associated with felid occurrence: elevation, land cover, habitat connectivity (applying the effective mesh size only for patches of vegetation types that are considered suitable for maintaining each species' ecological needs, Text S1), streams, protected areas, pasture, and settlements/urban areas (Rabinowitz and Zeller 2010; Angelieri et al. 2016; Giordano 2016, Table 1, Text S1). We used the following land-cover classes of GlobCover Land Cover Maps (V2.3, 2009): forest (native forest with trees > 5 m), woodland (native forest with trees < 5 m), cropland, mosaic-cropland/native vegetation, and flooded areas (Table 1, Text S1). All variables were calculated along a regular grid with cells of 1 km^2. To avoid including highly correlated environmental variables, we tested for multicollinearity. Since none of the variables were highly correlated ($r \geq 0.8$, Behdarvand et al. 2014) all were included in the models (Pearson's correlation coefficient ranged from -4.3e-05 to 0.74, and all were ≤ 0.65, except for forest and puma´s habitat connectivity [$r = 0.7$] and pasture and settlements/urban areas [$r = 0.74$]).

Habitat suitability models were created with the default values for regularization multiplier, maximum number of background points, maximum iterations, and convergence threshold (Behdarvand et al. 2014). For each model, 70% of the data were used for training and 30% for testing (Silva et al. 2017). Logistic output maps with values ranging from 0 (no probability of occurrence) to 1 (100% probability of occurrence) were generated for each species. Models were evaluated by the area-under-receiver-operating characteristic curve (*AUC*), which measures the ability of model predictions to discriminate a presence location from a randomly chosen background point (Fourcade et al. 2014). Values of *AUC* greater than 0.7 indicate that a model has good performance and high predictive success (Elith et al. 2006).

We then used the inverse of habitat suitability to create resistance surfaces for each species separately (Ziółkowska et al. 2016; Bond et al. 2017). The inverse of habitat suitability was determined by applying the “Invert” tool of Geomorphometry and Gradient Metrics Toolbox v. 2.0 (Evans et al. 2014). For each pixel of the habitat suitability output map for a species, resistance value (R) was calculated based on the following formula: $R = \big((x - \max(x)\big) *$

$(-1)) + \min(x)$, where x is the value of habitat suitability for each cell. Because placing nodes within the study area can bias current density estimates due to artificial current saturation effects, we created a buffer around the border of each resistance surface (due to computer limitations for spatial analysis, the buffer was ~2 % of the species´ range width. According to Koen et al. (2014), even narrow buffers can improve current density estimates by removing bias caused by node placement). We placed 100 randomly distributed focal nodes within the buffer to conduct connectivity modelling and later removed the buffer to minimize node placement bias (Koen et al. 2014). We selected 100 nodes for each species after examining the sensitivity of current saturation with number of pairwise computations (Leonard et al. 2017).

From the resulting maps of potential movement corridors from gflow (Leonard et al. 2017), we extracted only the values of current that overlapped with the road network within each species range, which resulted in a grid with cell size of 1 km x 1 km along the road network. This resolution has been used in other studies (e.g., Grilo et al. 2015; Laliberté and St-Laurent 2020) and can account for the surrounding area beyond the road surface. All geographic analyses were performed in ArcGIS 10.3.1 (ESRI 2015).

2.3 Road mortality likelihood

We modelled road mortality likelihood for each species in a grid with cells of 1 km x 1 km along the road network using road-kill records as response variables and environmental data as explanatory variables in Maxent 3.3.3 (Phillips and Dudík 2008). All variables were calculated for each cell along the road network (~392,000 km within Brazilian territory, estimated based on a shapefile from OpenStreetMap (Geofabrik 2015; Fig. S1). We excluded roads from urban areas since these felids tend not to use urban areas (Sunquist and Sunquist 2002). The number of cells with some road section in them was ~428,000 for Brazil (see Table 2 for number of road segments for each species´ range). Road-kill occurrence data were obtained from two databases: 1. Sistema Urubu – a citizen science initiative that use a mobile based application (http://cbee.ufla.br/portal/sistema_urubu/) to record geo-referenced road-kill data and photographs (all road-kill data provided by Sistema Urubu were validated by the authors through the photographs); and 2. Grilo et al. (2018) – a compilation of geo-referenced road-kill records in Brazil. Information about collection date was not available for some records, but the majority were observed between 2000 and 2017. We used the same method as described in section 2.2 to reduce the geographical bias associated with data collection. We obtained 113 records for tiger cats, 52 for ocelot, 110 for jaguarundi, and 70 for puma (Fig. S1), which constituted independent datasets from occurrence records used in habitat suitability models.

Model settings were the same as described for habitat suitability models (section 2.2). Logistic output maps with values ranging from 0 (no probability of finding a road-kill in that road segment) to 1 (100% probability of finding a road-kill) were generated for each species. We used the same variables as for the habitat suitability models and included road type (unpaved, 2-lane paved, and 3 to 6-lane highways) and road length (Table 1, Text S1). The later variable was included as a control variable, because 1 km^2 cells did not include the same length of road.

Table 1: Description of explanatory variables used in the habitat suitability models[1] and road mortality likelihood models[2]

Variable	Description	Source
Elevation[1,2]	Average altitude (m)	SRTM database - http://www2.jpl.nasa.gov/srtm
Forest[1,2]	% of forest (native forest with trees > 5m)	
Woodland[1,2]	% of woodland (native vegetation - shrublands, grasslands, savannas and sparse vegetation - with trees < 5m)	
Cropland[1,2]	% of cropland (areas of agricultural cultivation)	http://due.esrin.esa.int/
Mosaic[1,2]	% of mosaic (areas of cropland and native vegetation blends)	
Flooded areas[1,2]	% of flooded areas (types of vegetation that are permanently or temporarily flooded)	
Habitat Connectivity[1,2]	Effective mesh size (m_{eff} – details given in Text S1)	
Streams[1,2]	Distance to the nearest stream (m)	http://hidroweb.ana.gov.br
Protected Areas[1,2]	Distance to the nearest Conservation Unit (m)	http://mapas.mma.gov.br
Pasture[1,2]	Distance to the nearest pasture area (m)	https://pastagem.org
Settlements/urban[1,2]	Distance to the nearest settlement or urban area (m)	
Road type[2]	Type of road (unpaved, 2-lane paved, and 3 to 6-lane highways)	http://www.geofabrik.de/
Road length[2]	Length of roads within the 1 km^2 cell in km (all 3 road types combined)	

2.4 Comparison of movement corridors and road mortality models

We compared potential movement corridors and road mortality likelihood models assuming that road segments with high values of current density represent movement corridors crossed by roads (Laliberté and St-Laurent 2020; Zeller et al. 2020) and we used four complementary analyses. First, for each species separately, we compared the spatial locations of values above the 95^{th}, 90^{th}, and 80^{th} percentiles of current and road mortality likelihood. We chose these three thresholds to consider three scenarios for road mitigation ranging from a less conservative strategy, in which only 5% of road segments with the highest values of current/road mortality are considered for mitigation, to a more conservative one, in which 20% of the highest values of current/road mortality are considered. For each method separately, we assigned road segments with values above the defined percentile of current/road mortality likelihood a value of 1 and the remaining road network a value of zero. We then used the unweighted Cohen's Kappa coefficient (*k*, Cohen 1960; Boyle et al. 2017) to assess how often results from the potential movement corridor models spatially agreed with those from the road mortality likelihood models, i.e., when both methods had assigned a value of 1 (or 0) to certain road segments (see Text S2 for more details on how *k* was calculated). The maximum value of the coefficient is 1 representing 100% agreement. Second, for each species separately, we explored generalized additive models (GAMs) in order to better understand if current values had any effect (linear or otherwise) on the relative change in road mortality likelihood. To parameterize the models, we used all the values of current and road mortality likelihood extracted from each cell of 1 km^2 along the road network. Models were fitted with a Gaussian distribution and we used a cubic regression spline smoother and generalized cross-validation (GCV) to estimate the optimal amount of smoothing (Zuur et al. 2009). Adjusted r^2, deviance explained and GCV scores were calculated. Third, to explore the possible role of potential movement corridors in road mortality, we created road mortality models in MaxEnt again adding current along the road network as a predictive variable. Fourth, to test whether current density is higher in road-kill locations than in locations without road-kill (as would be expected if corridors predicted road mortality) we used a *t*-test to compare current density at road segments with road-kill records with current density at random points without road-kill. To calculate *k*, run the GAMs, and perform the *t*-tests, we used packages “irr”, “mgcv” and “stats”, respectively, in R. 3.5.0 (R Core Team 2015).

3. RESULTS

3.1 Movement corridors

All models of habitat suitability had high support based on *AUC* (*AUC* > 0.85; Table S1). The variables that best explained habitat suitability were: low habitat connectivity for tiger cats (with 22.7% contribution to the model), proximity to protected areas for ocelots and pumas (24.9% and 27.5%, respectively), and proximity to settlements and urban areas for jaguarundi (31.3%, Table S1, Fig. S3).

The total road lengths of segments above the 95th percentile of current were ~16,400 km inside tiger cats´ range, ~16,150 km for ocelot, ~15,500 km for jaguarundi, and ~17,000 km for puma. These were mainly distributed in Amazonia (~46%) and Atlantic Forest (41%) for tiger cats, Amazonia (~49%) and Atlantic Forest (~40%) for ocelot, Amazonia (~50%) and Atlantic Forest (~34%) for jaguarundi, and in Atlantic Forest (~79%) and Cerrado (~9%) for puma (Fig. 1). Corresponding information for segments above the 90th and 80th percentiles is presented in text S3 and figure S4.

3.2 Road mortality

All road mortality models had high support based on *AUC* values (*AUC* ≥ 0.85; Table S1). Wider roads (3 to 6 lanes) produced the highest relative contribution to explaining road-kill occurrence for tiger cats (29.7%), ocelot (46.8%), jaguarundi (50.4%), and puma (62.2%, Table S1, Fig. S5). The second most important variable was related to landscape. Low habitat connectivity contributed with 12% for the ocelot model, low percentage of cropland explained 9.3% for the jaguarundi model, and high habitat connectivity contributed with 6.5% for puma model. For tiger cats, proximity to settlements and urban areas was the third most important variable in explaining road-kill (11%).

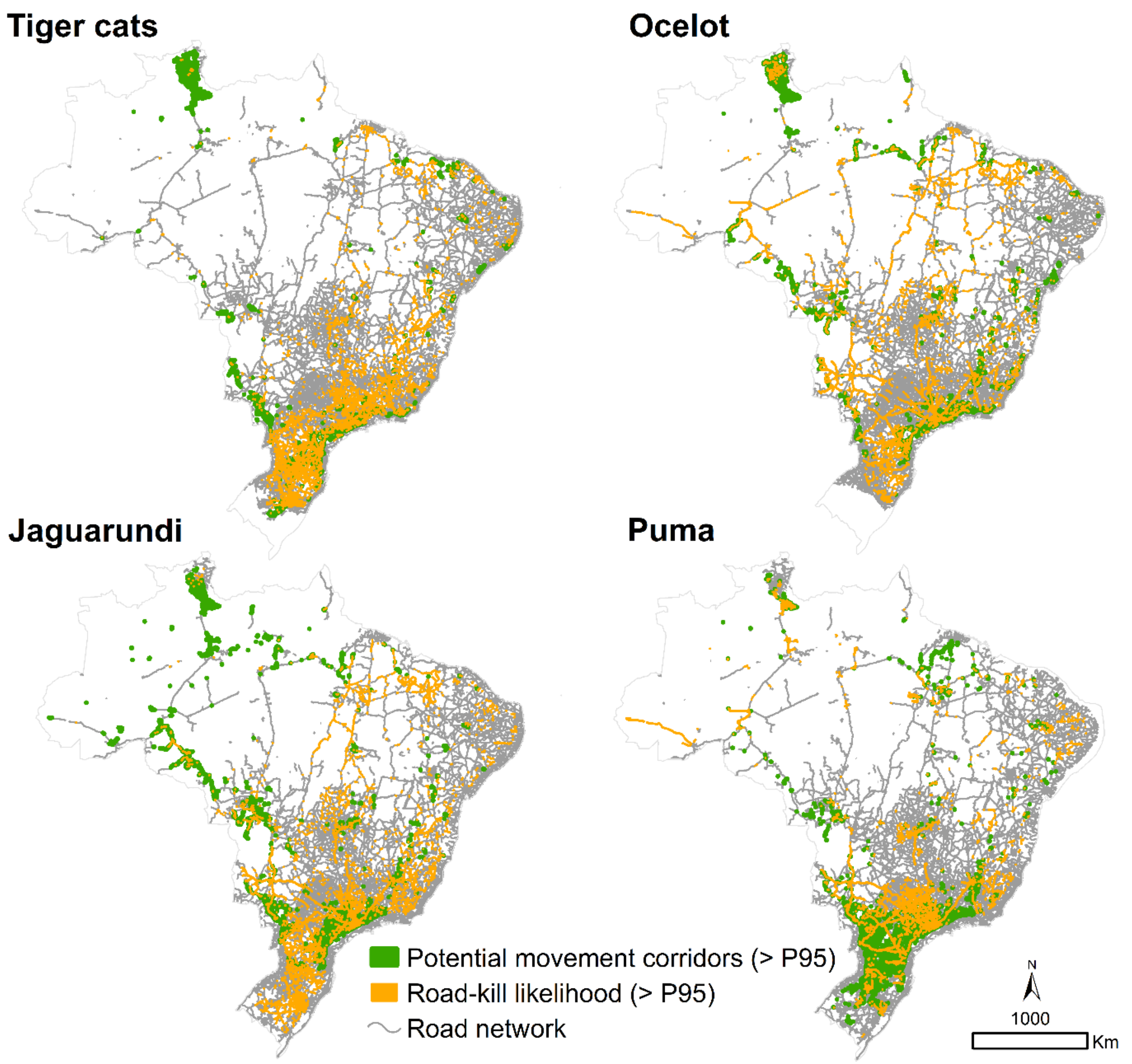

Fig. 1 Road segments with values > 95th percentile (P95) for potential movement corridors crossed by roads (measured as current) and road mortality likelihood

The total lengths of road segments above the percentile 95th of road mortality likelihood were ~24,700 km inside tiger cats´ range, ~19,400 km for ocelot, ~20,700 km for jaguarundi, and ~20,900 km for puma. These were mainly distributed in Atlantic Forest (~76%) and Cerrado (~16%) for tiger cats, Atlantic Forest (~42%) and Cerrado (~34%) for ocelot, Atlantic Forest

(~52%) and Cerrado (~30%) for jaguarundi, and in Atlantic Forest (~50%) and Cerrado (~32%) for puma (Fig. 1). Corresponding information for segments above the 90th and 80th percentiles is presented in text S4 and Fig. S4.

3.3 Comparison movement corridors and road mortality

Cohen's Kappa coefficients indicated low levels of spatial agreement between the two methods for all species and for the three scenarios (Table 2). Total road lengths for which the two methods agreed (> 95th percentile) were ~2,250 km for tiger cats, ~1,600 km for ocelot, ~1,100 km for jaguarundi, and ~2,000 km for puma. For all species together, these road segments represent a total of ~ 5,300 km. In contrast, the sum length of all road segments for all species, for which at least one method indicated the need for mitigation comprised ~81,700 km for all species combined (> 95th percentile). The GAMs showed non-linear relationships between current and road mortality likelihood for all species (Fig. 2; Table S2). A positive relationship between road mortality likelihood and current was found only for tiger cats. We found only a small contribution of current to explain road mortality (2% for tiger cats, 0.4% for ocelot, 16% for jaguarundi, and 7.2 % for puma, Table S3). Also, current was not significantly different in road segments with road-kill and without road-kill (tiger cats: t = -0.721, p = 0.471; ocelot: t = -1.536, p = 0.128, and puma: t = 0.470, p = 0.639) except for jaguarundi for which we found a higher current density in road segments without road-kill (t = 2.785, $p < 0.05$).

Table 2: Cohen's Kappa coefficients (*k*) used to compare how often potential movement corridors and road mortality likelihood models spatially agreed. T_s = total number of road segments along each species range; S_{1both} = number of road segments assigned a value of 1 by both methods; S_{0both} = number of road segments assigned a value of 0 by both methods (see Text S2). * = *p* value < 0.005

		> P95			> P90			> P80		
Species	***Ts***	***S1both***	***S0both***	***k***	***S1both***	***S0both***	***k***	***S1both***	***S0both***	***k***
Tiger cats	366450	1683	331488	0.0441*	5399	298556	0.0526*	16478	236345	0.031*
Ocelot	350829	1449	317194	0.0343*	5249	285911	0.0551*	18583	229081	0.0811*
Jaguarundi	343849	902	310365	2.59E-03	3251	278331	-6.06E-03*	12537	218847	-2.21E-02*
Puma	333024	1627	301349	0.0502*	5282	271700	0.0651*	16905	216717	0.0673*

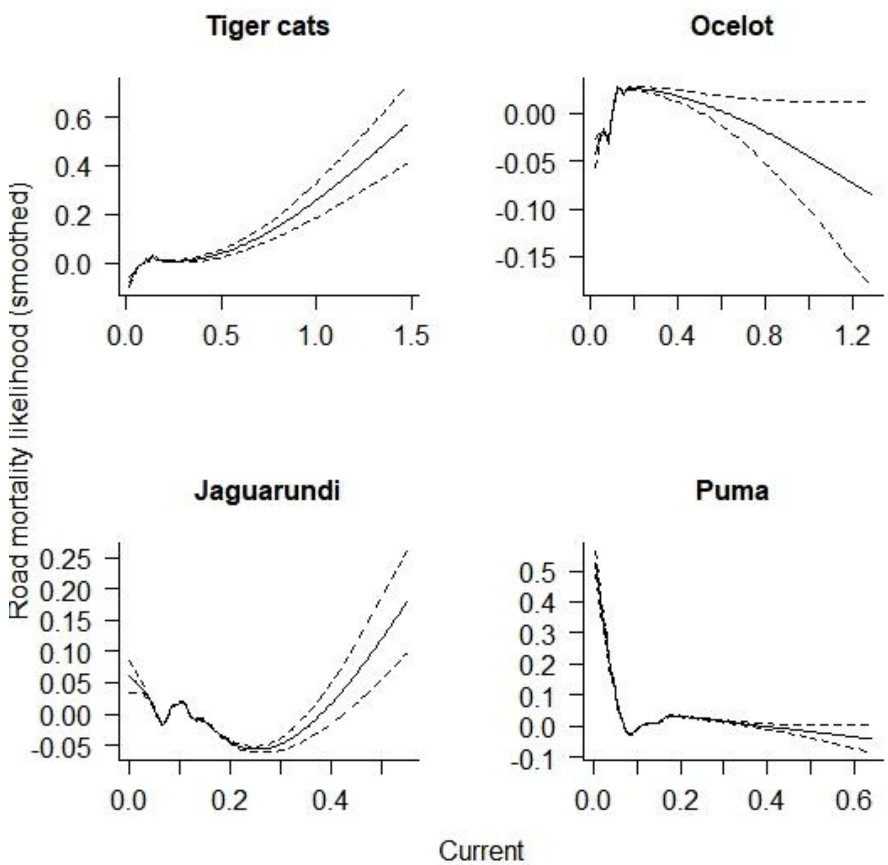

Fig. 2 Relationship between current and road mortality likelihood as shown by GAMs. Y axis shows the contribution of the cubic regression spline smoother (the function that links Y to X in the model) to the fitted values. The smoother is centred around zero. Dashed lines represent 95% confidence intervals

4. DISCUSSION

This is the first study comparing predicted movement corridors and road mortality to identify road sections for mitigation for felids in Brazil. All analyses lead to the same conclusion: there is no spatial association between our models of movement corridors and high road-kill locations.

The habitat suitability models we used to develop resistance surfaces for the five species concurred with the habitat preferences documented in the literature. While the occurrence of ocelots and pumas was best explained by proximity to protected areas, tiger cats and jaguarundis were primarily associated with suboptimal habitats, i.e., less conserved areas with low habitat connectivity and in proximity to settlements and urban areas (Giordano 2015). This can be expected since pumas and ocelots are associated to protected areas (Castilho et al. 2015; Massara et al. 2015) and are competitive dominants on the smaller cats (Oliveira et al. 2010), which therefore tend to occupy the areas on the margin that are more degraded and impacted by human activity and disturbance (Françoso et al. 2015). Also, the lower current densities in road segments with observed road-kill for jaguarundi suggest that road mortality for this species may also be associated with marginal habitats.

We found that road type (roads with 3 to 6 lanes) best explained the occurrence of road-kill for all species while landscape variables contributed weakly to road mortality models. Other research showed a stronger association between road-kill and landscape attributes (Gunson et al. 2011; Bueno et al. 2013), although road type also explained carnivore road mortality elsewhere (Grilo et al. 2009). We acknowledge a limitation in our models due to not including traffic volume; information on traffic volume was not available for the road network in Brazil. We suggest new local road mortality models can be performed accounting for traffic volume where available.

4.1 Movement corridors vs. road mortality

Movement corridor models are commonly based on resistance surfaces that represent the degree in which the landscape facilitates or impedes movement (Chetkiewicz and Boyce 2009; Abouelezz et al. 2018). Understanding how individuals move in the landscape can help predict what landscape conditions will constitute a corridor. However, individual behaviour patterns vary along life cycle: daily movements can consist of searching for food and shelter, whereas individuals in the breeding period may greatly increase movement rates and distances travelled (Powell and Zielinski 1994; Reed 2002). Thus, the behavioural state of the animals covered by species occurrence data may affect the type of habitat selected and ultimately the location of movement corridors (Zeller et al. 2012; Zeller et al. 2014; Abrahms et al. 2016).

Our study used occurrence records from various independent sources to parameterize resistance surfaces for movement corridor models. Information on type of behaviour was not provided and therefore we were not able to determine if data corresponded to breeding or non-breeding movements, which may explain the lack of spatial association between our models of movement corridors and road mortality.

Some research has found relationships between movement corridors and areas of high road-mortality when using data from the breeding period for developing resistance surfaces. For example, occurrence data collected during the breeding season of stone marten *Martes foina* and tawny owl *Strix aluco* were used to build movement models to assess the role of connectivity to explain road-kill by Grilo et al. (2011) and Santos et al. (2013). In contrast, other studies that did not rely on resistance surfaces developed using data of breeding periods were unable to find a positive relationship between movement corridors and road mortality (McClure and Ament 2014; Boyle et al. 2017; Laliberté and St-Laurent 2020). Since some studies have shown that road mortality tends to be high in periods of breeding (Clevenger et al. 2003; Grilo et al 2009; Barthelmess and Brooks 2010), we hypothesize that the spatial association among movement corridors and road-kill occurrence can be expected when data for the same behavioural state are used in the two predictive models.

4.2 Implications for research and road management

To gain a better understanding of the role different behavioural states may play in identification of movement corridors and high road-kill incidence we suggest conducting the same analysis with a range of mammal species that differ in biological and ecological traits during breeding and non-breeding periods. This could also be tested with detailed movement data provided by GPS collars or other tracking technologies. Models can then incorporate life history stages that produce different movement patterns, such as regular daily movements to meet biological needs, in addition to breeding movements that affect population persistence and species distribution. We urge researchers in Brazil to explore these questions with local-scale felid data, in addition to researchers elsewhere using global databases on species movements (Kranstauber et al. 2015). These studies will shed light on the role of behavioural state on modelling movement corridors and road-kill locations.

Until then, the complementary use of both methods may be appropriate. For the felid species we studied, at least the road segments for which the results of the two methods agreed (~5,300 km for all species combined at 95th percentile) should be high-priority candidates for mitigation. These segments provide valuable information to enhance habitat connectivity and reduce mortality on roads. Unfortunately, it is likely not realistic to mitigate all road segments identified by at least one method (~81,700 km for all felids at 95th percentile). Therefore, two key strategies may help prioritize areas to reduce road impacts on the five felid species in Brazil (van der Grift and Pouwels 2006): (1) Movement corridors bisected by road segments in areas where felids are threatened by isolation effects should be considered high risk and mitigation planned accordingly (Prugh et al. 2008; Zanin et al. 2015; Vilela et al. 2020); and (2) High road-kill segments coinciding with areas of low population densities should be considered high risk and mitigation planned accordingly to protect the viability of populations (Barbosa et al. 2020).

Despite the scarcity of information about these species´ ecology and populations in Brazil (e.g., Oliveira et al. 2020), recent studies have estimated population densities of these species (Oliveira et al. 2018), which can provide important information to support decisions about mitigation. Our work identified the Atlantic Forest as having numerous road segments with potential movement corridors and high road-kill locations. The Atlantic Forest is one of the most threatened biomes in Brazil (Ribeiro et al. 2009) where roads are important drivers of deforestation and fragmentation (Freitas et al. 2010). The fragmentation effects of roads in the Atlantic Forest may be impacting felid conservation and therefore require special attention for road mitigation.

To reduce road mortality and improve population connectivity specific mitigation measures designed for felids need to consider the ecology and behaviour of felids, i.e., many require vegetative cover for travel. Measures such as culverts (especially for smaller species), underpasses, and fences have been proven effective for felids in other parts of Latin America and elsewhere (Tewes and Hughes 2001; Abra 2012; Mohammadi et al. 2018; González-Gallina et al. 2018). The amount of cover near entrances and leading to the crossing structures is important for most felids (Clevenger and Waltho 2000, 2005); however, most research has taken place in North America. There is a need for more monitoring of felid species' use of crossing structures in Latin America to better understand how design and landscape attributes affect passage rates (González-Gallina et al. 2018; Pinto et al. 2020).

Our approach can help identify key road segments and critical areas for mitigation to plan local scale, site-specific assessments to better inform mitigation planning and design. Local scale assessments can help identify existing below-grade passage structures (culverts, bridges) that (1) can be retrofitted for wildlife passage (Clevenger and Huijser 2011; van der Ree et al. 2015) or (2) that are part of transportation projects in the planning phase, as mitigation measures are less costly if part of a larger transportation project, e.g., road expansion or improvements (McGuire and Morrall 2000).

We also urge greater investments in road ecology research be made in Brazil to increase the body of scientific knowledge that is critical for informed decision making in all stages of road projects (Roberts and Sjölund 2015; Rytwinski et al. 2015). Thereby, it will be possible not only to mitigate impacts, but also to prevent new impacts from poorly conducted Environmental Impact Assessments (Laurance 2015; Teixeira et al. 2016) and identify transportation infrastructure projects that are high risk to threaten biodiversity conservation and landscape connectivity (Laurance 2018; Habel et al. 2019).

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Environmental Management

Supplementary Material

Potential movement corridors and high road-kill likelihood do not spatially coincide for felids in Brazil: Implications for road mitigation

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1. Supplementary Figures

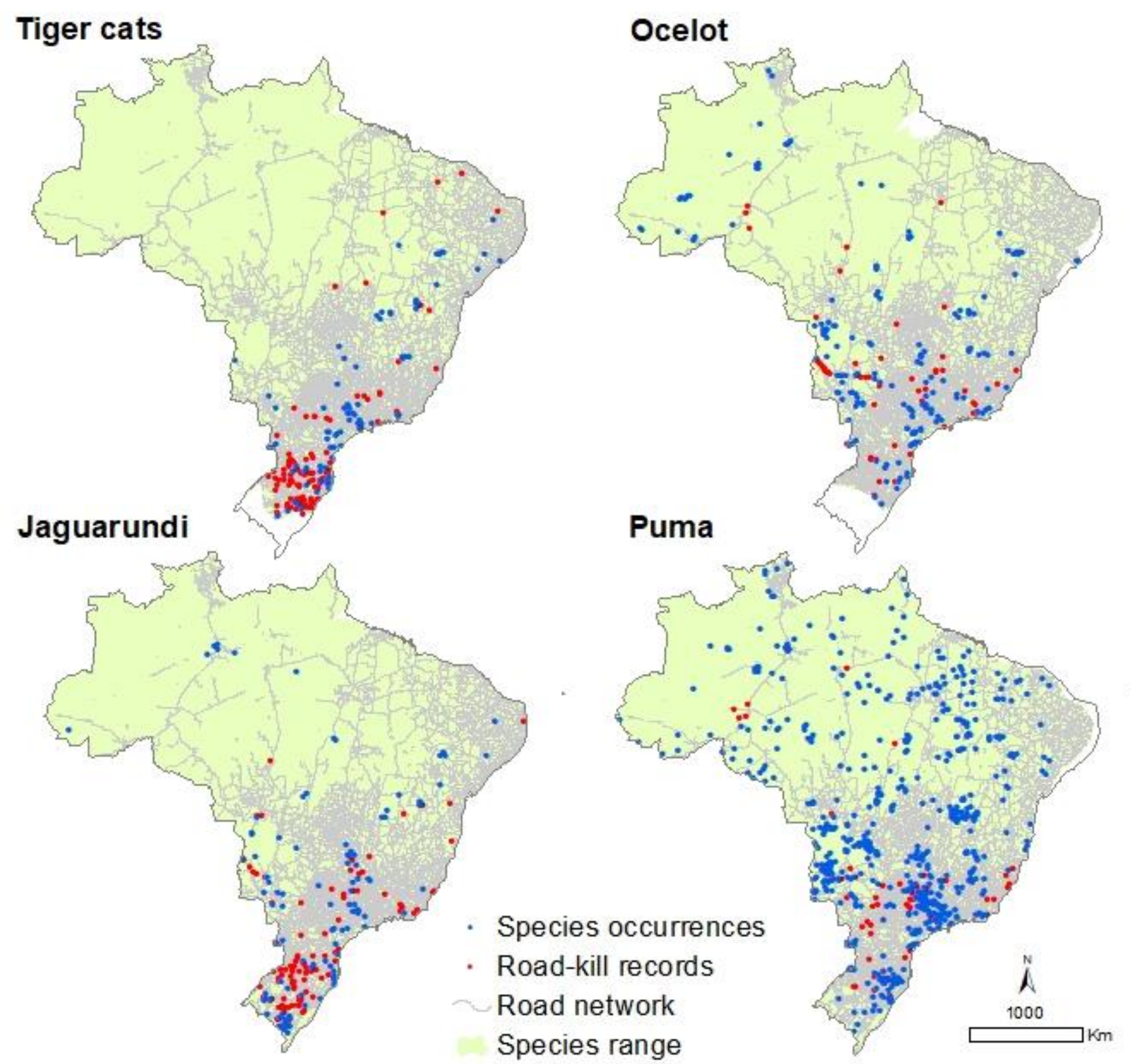


Fig. S1: Occurrence records used for habitat suitability models, road-kill records used for road mortality likelihood models, species range and road network inside species ranges.

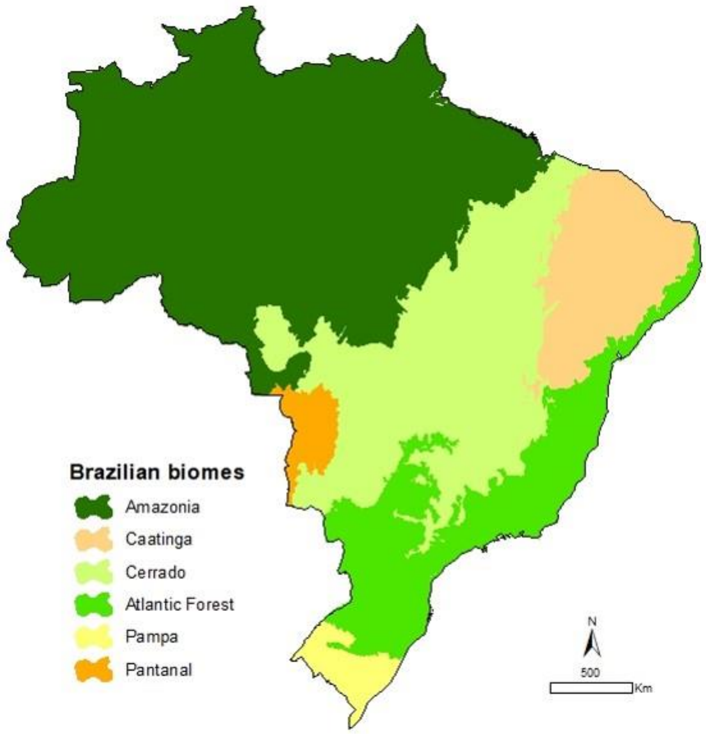


Fig. S2: Brazilian biomes according to Brazilian Institute of Geography and Statistics (IBGE 2017).

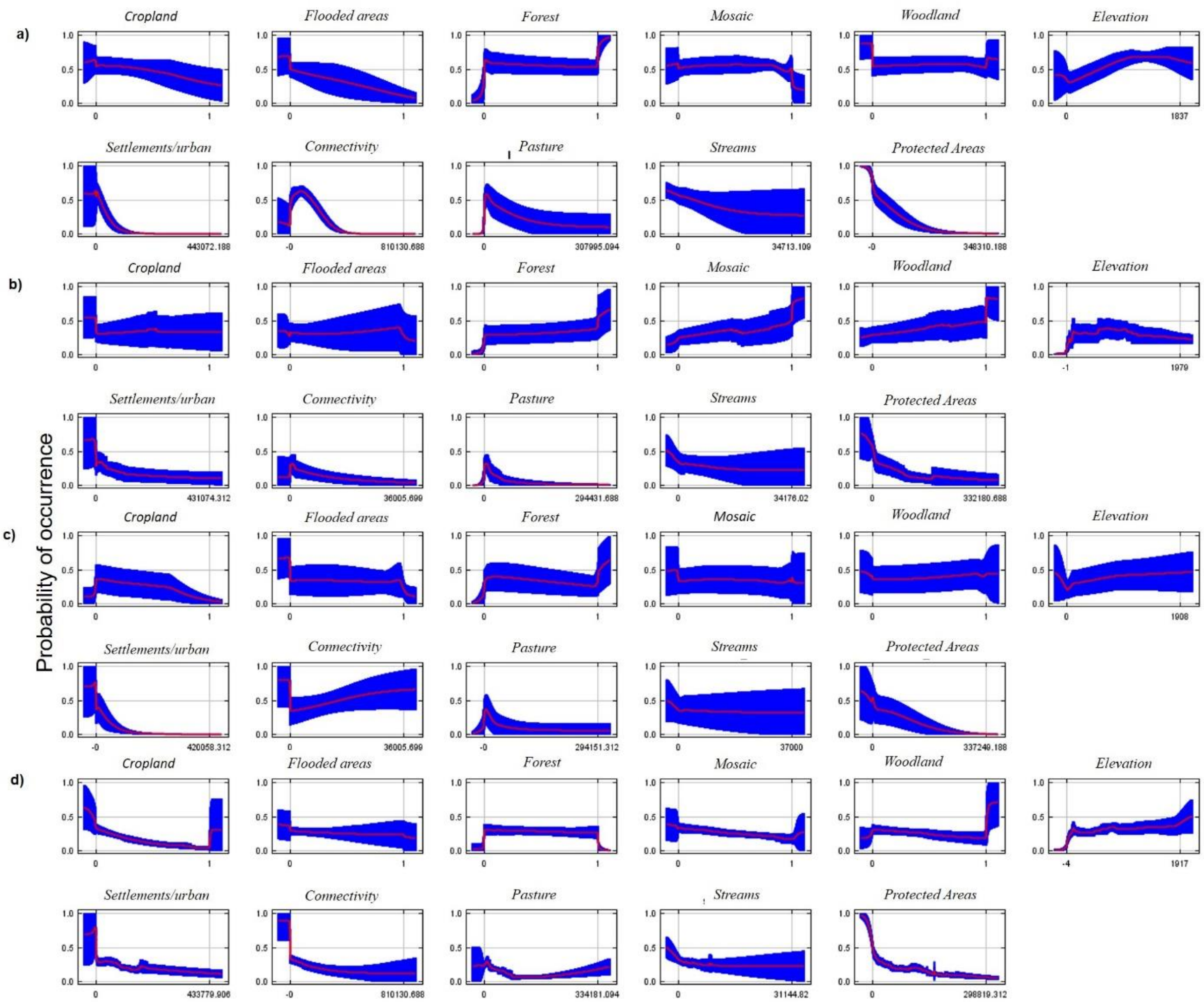
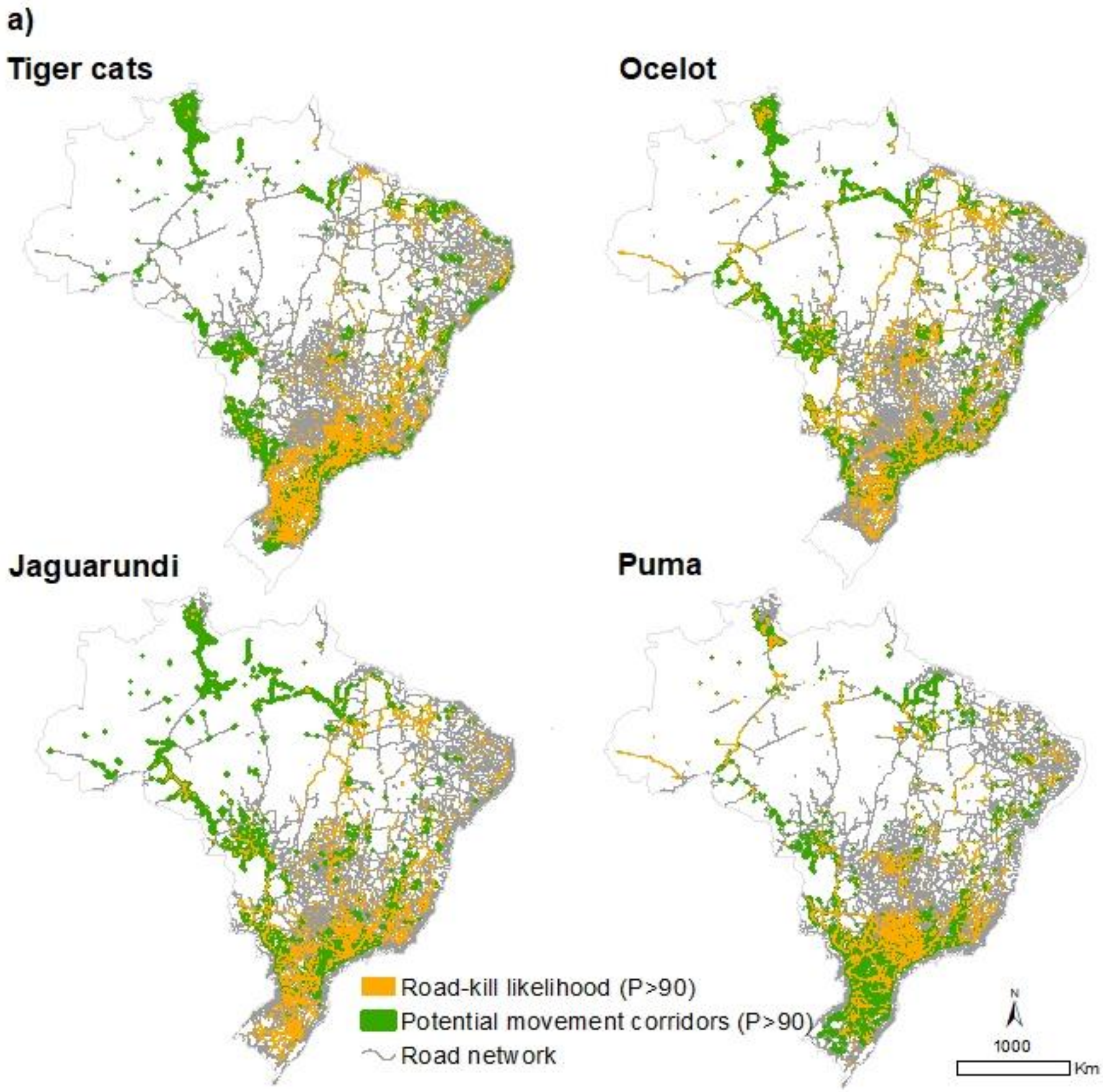


Fig. S3: Marginal response curves of Maxent habitat suitability models for each explanatory variable for a. tiger cats, b. ocelot, c. jaguarundi and d. puma. The mean response of the models with 10 replicate runs is shown in red and standard deviation in blue.


a)
Tiger cats
Ocelot
Jaguarundi
Puma
Road-kill likelihood (P>90)
Potential movement corridors (P>90)
Road network
N
1000
Km

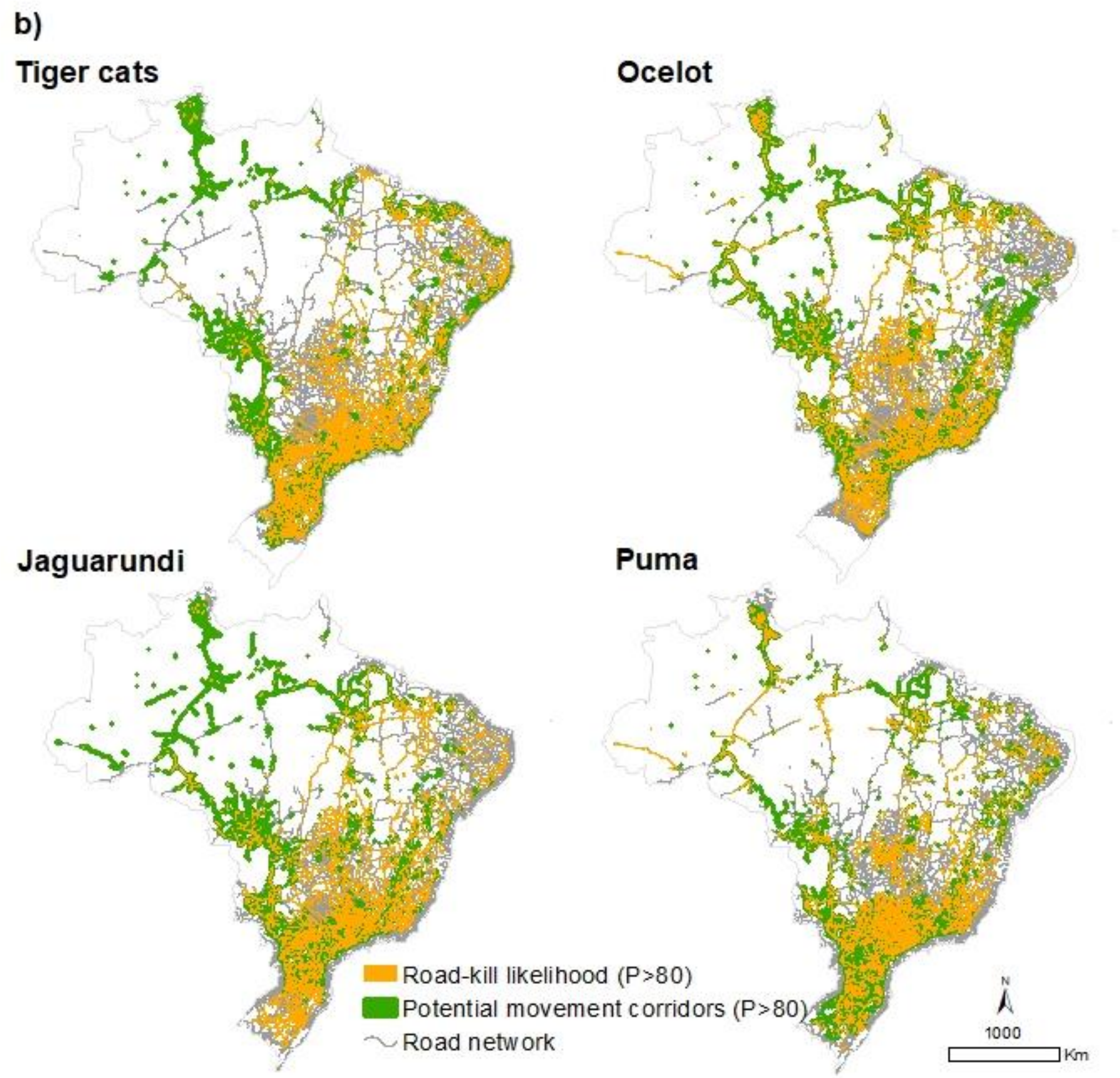


Fig. S4: Road segments with values a. > 90th percentile (P90) and b. > 80th percentile (P80) for potential movement corridors crossed by roads (measured as current) and road mortality likelihood.

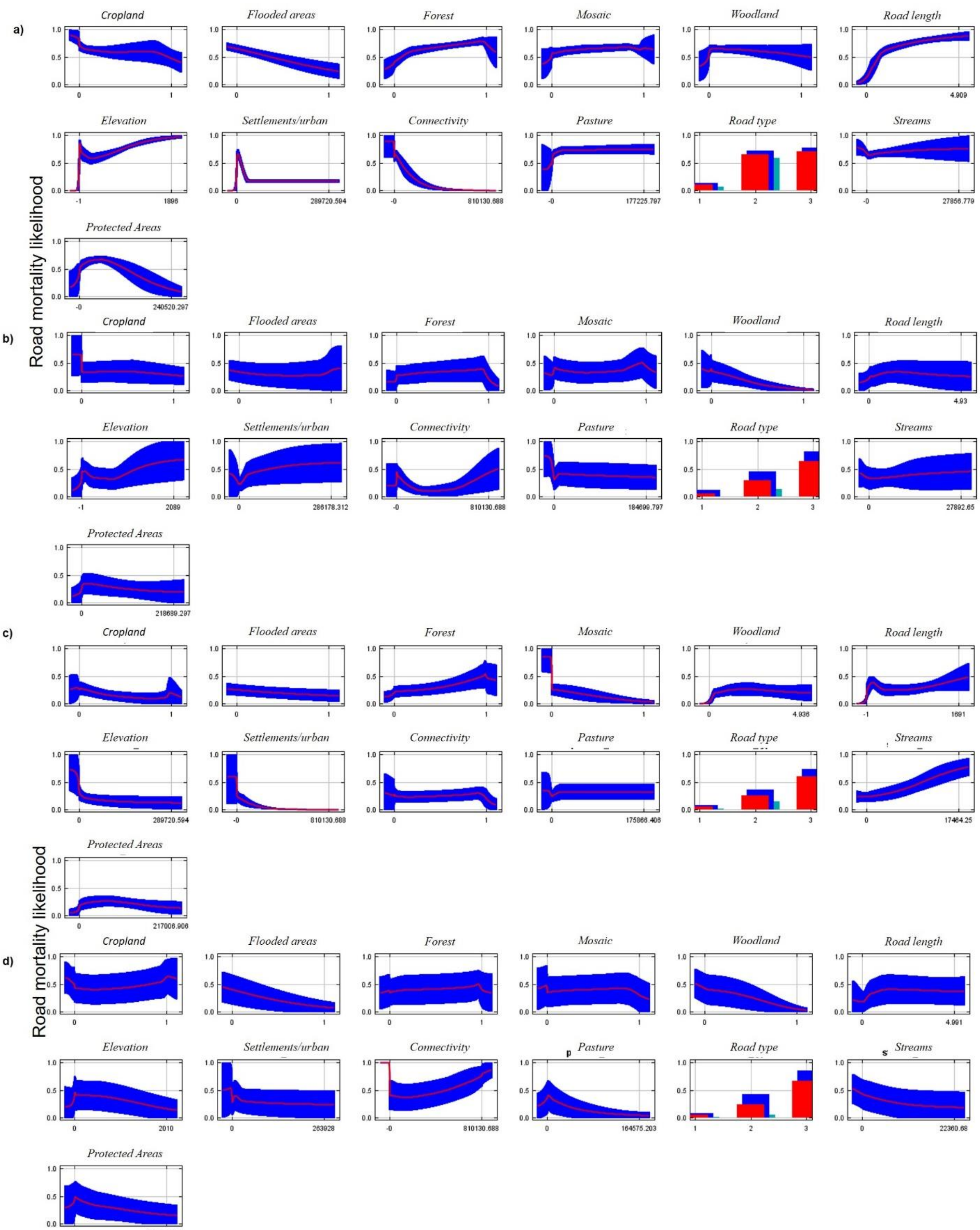

a)
b)
c)
d)
Road mortality likelihood
Road mortality likelihood
Cropland
Flooded areas
Forest
Mosaic
Woodland
Road length
Elevation
Settlements/urban
Connectivity
Pasture
Road type
Streams
Protected Areas

Fig. S5: Marginal response curves of Maxent road mortality models for each explanatory variable for tiger cats, ocelot, jaguarundi and puma. The mean response of the models with 10 replicate runs is shown in red and standard deviation in blue.

2. Supplementary texts

Text S1: Additional details on environmental data used as explanatory variables for modelling potential movement corridors and road mortality likelihood

We calculated the values of all explanatory variables for each 1 km^2 cell. Average altitude was derived from a digital elevation database (SRTM database). We calculated the percentage of each defined land cover class. Landscape connectivity was estimated through the Effective Mesh Size (m_{eff}) (Jaeger 2000), a metric that is based on the probability of two random points in an area to be connected and not separated by barriers, using the formula according to the cross-boundary connections procedure:

$$m_{\mathrm{eff}}(\mathrm{cell}\ j) = \frac{1}{A_{\mathrm{t}j}} \sum_{i=1}^{n} A_{ij} \cdot A_{\mathrm{t}ij},$$

where n is the total number of patches in a cell, A_{tj} is the total area of the cell j (1 km^2), A_{ij} is the area of patch i inside the cell j, and $A_{\mathrm{t}ij}$ is the total area of patch i including the parts that extend beyond the boundary of cell j (Moser et al. 2007). Despite these species´ ability to use a wide variety of habitats, including human-dominated landscapes (Knopff et al. 2014; Giordano et al. 2016), for each species we only included patches of vegetation types that are considered suitable habitat for maintaining each species' ecological needs. For jaguarundi and ocelot, we considered forest, woodland, and flooded areas (Nowell and Jackson 1996, Abreu et al. 2008, Giordano 2016). For puma and tiger cats we considered forest and woodland (Nowell and Jackson 1996). We calculated Euclidian distance to the closest stream using a vector map from ANA (2010). We also calculated Euclidian Distance to the nearest protected area (Federal, State and Municipal

Conservation Units), to the nearest pasture, and to the nearest settlement or city. Road type was obtained through the reclassification into three categories from OpenStreetMap (Geofabrik 2015): unpaved roads, 2-lane paved roads, and 3- to 6-lane highways. For cells with road-kill events we considered the type of road where the road-kill occurred (there were no duplicate road-kill events per cell because we excluded neighbour locations, see *Methods* section for details) and for cells without road-kill events we considered the road type that was predominant (i.e, with the highest length). Road length was the extension, calculated in km, of all three road types added up within each cell.

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Text S2: Additional details on how Cohen's Kappa coefficients (*k*) were calculated

For each method separately, we assigned road segments with values above the 95th percentile of current or the 95th percentile of road mortality likelihood a value of 1 and the remaining road network a value of zero. Cohen's Kappa coefficient (*k*, Cohen 1960, Boyle et al. 2017) was then calculated using the kappa2 function of "irr" package in R. 3.2.3 (R Core Team 2015), which uses the formula: $k = (po - pe)/(1 - pe)$, where *po* is the proportion of units in which the two methods spatially agreed for road segments (i.e., both assigned a 1 or both assigned a 0), and *pe* is the observed proportion of units for which agreement between the two methods was expected by chance. The proportion of units in which the two methods agreed was calculated as $po = (S_{1\mathrm{both}} + S_{0\mathrm{both}})/\, Ts$, where S_{1both} is the number of road segments assigned a value of 1 by both methods; S_{0both} is the number of road segments assigned a value of 0 by both methods, and T_s is the total number of road segments along each species range (see Table 2). The observed proportion of units for which agreement between the two methods was expected by chance was calculated as $pe = (PS11 * PS12) + (PS01 * PS02)$, where $PS11$ is the probability that method 1 assigns 1 to a road segment, $PS12$ is the probability that method 2 assigns 1 to a road segment, $PS01$ is the probability that method 1 assigns 0 to a road segment and $PS02$ is the probability that method 2 assigns 0 to a road segment. When *po* equals *pe*, *k* = 0; greater than chance agreement (*po* > *pe*) results in positive values of *k* and less than chance agreement (*po* < *pe*) leads to negative values. The same was performed for values above the 90th and 80th percentile.

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Text S3: Additional information of results of movement corridors (section 3.1)

The total road lengths of segments above the 90th percentile of current were ~33,050 km inside tiger cats´ range, ~32,600 km for ocelot, ~30,700 km for jaguarundi, and ~32,720 km for puma. These were mainly distributed in Atlantic Forest (~46%) and Amazonia (32%) for tiger cats, Atlantic Forest (~41%) and Amazonia (~40%) for ocelot, Amazonia (~47%) and Atlantic Forest (~32%) for jaguarundi, and in Atlantic Forest (~73%) and Cerrado (~12%) for puma.

The total road lengths of segments above the 80th percentile of current were ~66,670 km inside tiger cats´ range, ~64,400 km for ocelot, ~61,390 km for jaguarundi, and ~63,500 km for puma. These were mainly distributed in Atlantic Forest (~44%) and Amazonia (27%) for tiger cats, Atlantic Forest (40%) and Amazonia (~35%) for ocelot, Amazonia (~38%) and

Atlantic Forest (~32%) for jaguarundi, and in Atlantic Forest (~63%) and Cerrado (~16%) for puma.

Text S4: Additional information of results of road mortality (section 3.2)

The total road lengths of segments above the 90th percentile of road mortality were ~46,800 km inside tiger cats´ range, ~36,860 km for ocelot, ~38,930 km for jaguarundi, and ~38,530 km for puma. These were mainly distributed in Atlantic Forest (~67%) and Cerrado (22%) for tiger cats, Atlantic Forest (~40%) and Cerrado (36%) for ocelot, Atlantic Forest (~49%) and Cerrado (30%) for jaguarundi, and in Atlantic Forest (~46%) and Cerrado (~32%) for puma.

The total road lengths of segments above the 80th percentile of road mortality were ~87,300 km inside tiger cats´ range, ~70,100 km for ocelot, ~73,240 km for jaguarundi, and ~72,300 km for puma. These were mainly distributed in Atlantic Forest (~57%) and Cerrado (29%) for tiger cats, Atlantic Forest (~41%) and Cerrado (36%) for ocelot, Atlantic Forest (~45%) and Cerrado (35%) for jaguarundi, and in Atlantic Forest (~43%) and Cerrado (~34%) for puma.

3. Supplementary Tables

Table S1: *AUC* values and relative contributions (%) of environmental variables of habitat suitability (*HS*) and road mortality likelihood (*RM*) models for each felid species.

Species	**Tiger cats**		**Ocelot**		**Jaguarundi**		**Puma**	
Models	***HS***	***RM***	***HS***	***RM***	***HS***	***RM***	***HS***	***RM***
AUC	0.95	0.91	0.89	0.93	0.88	0.89	0.83	0.91
Elevation	21.7	10.4	16.3	5.7	10	4.2	12	1.4
Forest	7.3	9.5	3.6	9.9	7.6	5.4	3.9	2.7
Woodland	0.5	1.6	3	5.6	3.8	8.8	2.1	5.9
Cropland	1	6.2	5.7	1.8	4.3	9.3	2.5	2
Mosaic	1.5	1	4.6	4.4	3	1.7	1.7	1.3
Flooded areas	1	0.2	5.3	1	2.2	0.1	0.4	0.4
Connectivity	22.7	5.3	5.6	12	7.3	7.9	24.2	6.5
Streams	0.5	0.6	1.7	0.8	1.2	0.6	2	1.1
Protected areas	18.1	3.1	24.9	2.2	12.6	2.5	27.5	6.5
Pasture	7.7	8.9	14.7	2.7	16.7	1.4	12.1	1.5

Settlements/urban	18.1	11	14.6	5.1	31.3	2.1	11.5	2.8
Road type	-	29.7	-	46.8	-	50.4	-	62.2
Road length	-	12.4	-	2	-	5.4	-	5.7

Table S2: GAMs output parameters regarding the relationship between current and road mortality likelihood for all species. GCV scores (similar to cross-validation) provide an estimate of the mean square error and can be used to indicate the level of smoothing required to minimise prediction error (smaller values indicate a better model fit).

	Tiger cats	**Ocelot**	**Jaguarundi**	**Puma**
***p*-value**	<2e-16	<2e-16	<2e-16	<2e-16
Degrees of freedom	8.98	8.98	8.98	8.98
Adjusted R^2	0.005	0.03	0.008	0.01
Deviance explained (%)	0.52	3.04	0.85	1.59
GCV score	0.03	0.02	0.03	0.02

Table S3: *AUC* values and relative contributions (%) of environmental variables of road mortality likelihood (*RM*) models for each felid species, including current as a variable.

Species	**Tiger cats**	**Ocelot**	**Jaguarundi**	**Puma**
AUC	0.93	0.93	0.91	0.93
Elevation	7.5	9.3	4.1	1.7
% of forest	8.3	6.4	4.3	1.8
% of wood	1.4	3.9	8.1	3.6
% of cropland	5.8	3.2	6.6	2.4
% of mosaic	2.5	2.3	6.2	2
% of flooded areas	0	2.7	0	0.1
Connectivity	5.1	7.9	5.2	9
Streams	0.4	0.6	1.8	0.9
Protected areas	2.7	2.5	1.7	2.7
Pasture	13	1.1	2	3.6
Settlements/urban	9.1	5.4	1.4	2.7
Road type	26.7	50	35.5	57.9
Road length	15.5	4.3	6.9	4.4
Current	2	0.4	16	7.2

ARTIGO 2 – *DIRECT AND INDIRECT EFFECTS OF ROADS ON SPACE USE BY JAGUARS IN BRAZIL*
(*MANUSCRIPT SUBMITTED TO THE JOURNAL "BIOLOGICAL CONSERVATION"*)

TITLE PAGE

Biological Conservation

Direct and indirect effects of roads on space use by jaguars in Brazil

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Declaration of competing interest

The authors declare they have no known competing interests that could have influenced this study.

MANUSCRIPT

Direct and indirect effects of roads on space use by jaguars in Brazil

Abstract

Roads pose an imminent threat to wildlife, mainly directly through mortality and changes in individual behavior, but also indirectly through modification of the amount and configuration of wildlife habitat. However, few studies have addressed how these mechanisms interact to determine species response to roads. We used structural equation modeling to assess direct and indirect effects (via landscape modification) of roads on space use by jaguars in Brazil, using radio-tracking data available from the literature. We fit path models that directly link jaguars' space use to roads and to land cover, and indirectly link jaguars' space use to roads through the same land cover categories. Our findings show that space use by jaguars was not directly affected by roads, but strong indirect effects occurred through reductions in natural areas on which jaguars depend, and through urban sprawl. Males´ space use, however, was not negative influenced by urban areas. Since jaguars seem to ignore roads, mitigation should be directed to road fencing and promoting safe crossings. We argue that planners and managers should take into account the deforestation and the unbridled urban expansion from roads to ensure jaguar conservation in Brazil.

Key-words: *Panthera onca***,** road effects, habitat loss, urbanization, space use, structural equation modeling

1. Introduction

Guided primarily by the argument of socio-economic development, investments in road expansion worldwide have never been so high as today (Meijer et al. 2018, Hughes et al 2020). In Brazil, the government is planning to add nearly 129,000 km to the existing 1.7 million kilometers of roads in the next 20 years (DNIT 2013; Teixeira 2016). Many of the planned roads will be built in areas of high biodiversity value such as the biomes Amazon, Cerrado and Atlantic Forest (Reid and de Souza 2005; Barber et al. 2014).

Roads are among the most important impacts on wildlife populations and species distribution (Fahrig and Rytwinski 2009; Bowman et al. 2010). Their effects can be direct as they cause mortality through collision with vehicles, e.g., by attraction to suitable roadside vegetation for refuge or predation (Laurance et al. 2009; Ruiz-Capillas et al. 2013), and changes in spatial behavior, e.g., by avoidance of traffic noise and light (Grilo et al. 2012; Jacobson et al. 2016). Road effects on wildlife can also be indirect by promoting changes in the landscape as they remove natural vegetation and bisect large contiguous areas (Li et al. 2010; Walker et al. 2013). Roads are known to facilitate the urban sprawl, deforestation, intensive farming, and illegal human activities such as poaching (Laurance et al. 2009, Barber et al. 2014). Habitat loss due to landscape changes caused by human activities negatively affects many species' occurrence and abundance and species richness (Fahrig 2003; Signorelli et al. 2016; Püttker et al. 2020).

Road ecology research has long focused on the impacts of infrastructure on wildlife behavior, occurrence, abundance, and persistence (Fahrig and Rytwinski 2009; Zimmermann et al. 2014). Such studies are typically conducted to evaluate how roads and traffic affect wildlife (e.g. Jaeger et al. 2005; Grilo et al. 2012) or to analyze how roads change landscape composition and the spatial configuration of wildlife habitat (e.g., Jaeger et al. 2006) without considering how these two mechanisms interact when the wildlife populations respond to roads.

Apex predators such as the jaguar (*Panthera onca*) are particularly vulnerable to the negative effects of roads due to low population densities, large spatial requirements, and low reproductive rates (Rytwinski and Fahrig 2011, 2012). The jaguar is the largest felid in the Americas (Nowell and Jackson 1996) and has been extirpated from more than 50% of its historical range (from southwestern United States to Central Argentina, de la Torre et al. 2017). As a result, it is now ranked 15th among large mammal species with the greatest range contractions due to anthropogenic effects globally (Morrison et al. 2007). Several studies have assessed the behavior of jaguars in response to roads and land cover (Zeilhofer et al. 2014; Pallares et al. 2015; Espinosa et al. 2018). They showed that jaguars move preferentially in undisturbed natural areas far from roads and other human occupations such as agricultural lands and areas of high human population density (Conde et al. 2010; Colchero et al. 2011; De Angelo et al. 2013). However, no study has analyzed if the effects of roads are direct or indirect through the modification of jaguars' habitat.

The main goal of this study is to disentangle the direct and indirect effects of roads on jaguars' space use at the scale of home range throughout their range in Brazil. We used structural equation modelling, an approach that combines multiple predictor and response variables in a single causal network (Grace 2006). We fit path models (Shipley 2009) that link directly jaguars' space use to roads and to four land cover categories, namely, forest (natural dense vegetation and secondary forest), natural open areas (savanna formations and grasslands, hereafter, open areas), farming (pasture and/or agriculture) and urban areas, and also link indirectly jaguars' space use to roads through the same land cover categories. We specifically tested four hypotheses: 1) Jaguars prefer areas far from roads primarily because of the direct effect of roads (Figure 1a); 2) Jaguars prefer areas far from roads because roads are associated with a reduction in the amount of forest and open areas that favor their occurrence, i.e., the indirect effects of roads via natural areas are predominant (Figure 1b); 3) Jaguars prefer areas far from roads because roads promote the expansion of farming and urbanized areas that impair the occurrence of jaguars, i.e., the indirect effect of roads via human-dominated areas is predominant (Figure 1c); 4) Space use by jaguars is primarily determined by land cover rather than roads, i.e., the direct effects of land cover are predominant (Figure 1d). This study intends to contribute to a more comprehensive and integrated understanding of species' responses towards roads to promote effective measures for jaguar conservation in roaded landscapes.

2. Methods

2.1 Jaguar data and study area

We used a large dataset of jaguar locations tracked by GPS technology in Brazil from Morato et al. (2018b). The data are from 82 individuals monitored by eleven studies encompassing different terrestrial biomes in Brazil (Figure A1 in supplementary material). The jaguar locations are distributed in 15 areas (Figure A1 in supplementary material). We delimited each area using kernel density of points to derive 95% utilization distribution. To estimate de utilization distribution we selected one random location per individual from every 24 hour period to control for differences among studies regarding the sampling frequency (Table A1 in supplementary material). Because we were interested in analysing the influence of roads on jaguars and on the landscape, we selected only the areas that were intersected by both paved and unpaved roads (Figure A1 in supplementary material).

To estimate the space use by jaguars, for each individual we calculated relative frequency of locations (number of locations of one individual divided by the total number of sampling days of that individual) in a grid with cell size of 1 km x 1 km. For cells with more than one individual, we estimated their average frequency. Lastly, we selected "zero cells" (cells not used by jaguars) to represent one third of the number of cells with information on relative frequency of jaguar locations.

2.2 Environmental data

We obtained the road network (paved and unpaved roads) from OpenStreetMap (Geofabrik 2019 - http://www.geofabrik.de) and land cover variables from MapBiomas (collection 2, Projeto MapBiomas 2019 http://mapbiomas.org). We relied on the map of 2015 of MapBiomas because most of the jaguar data were from between 2008-2015 (Table A1 in supplementary material). We aggregated and reclassified land cover into four categories that were reported to influence jaguar occurrence (Morato et al. 2018a): forest (natural dense vegetation and secondary forest), open areas (savanna formations and grasslands), farming (pasture and/or agriculture) and urban areas. For each 1 km x 1 km cell, we estimated the variables as follows: distance between the centroid of the cell and the nearest road (paved and unpaved separately, located within or outside the cell); distance between the centroid of the cell and the nearest urban area (located within or outside the cell); proportion of forest, open areas, and farming within the cell. All variables were calculated using ArcGIS 10.3 (ESRI 2015).

2.3 Data Analysis

We inspected for a threshold distance above which paved and unpaved roads may not have any influence on jaguars and analysed direct and indirect effects of roads only for cells within the distance threshold determined. To find this threshold we explored generalized additive models (GAMs) using the package mgcv in R (RStudio Team 2016).

We estimated direct and indirect (via land cover) effects of roads on jaguars' space use using piecewise Structural Equation Modelling (SEM, Lefcheck 2016). SEM is a probabilistic approach that allows for using multiple predictor and response variables to assess simultaneous influences and responses in a single causal network (Grace 2006). SEM is usually represented with path diagrams. In piecewise SEM, a path diagram is translated to a set of linear (structural) and individual equations (Shipley 2009, Lefcheck 2016).

We assessed whether paved and unpaved roads affect jaguar´s space use directly or indirectly through land covers. The space use by jaguars was the main variable to be explained and the five other variables (four land cover variables and paved roads or unpaved roads) were linked in causal relationships (Shipley 2009, Figure 1; these and other hypothesized links are presented in Table A2 in supplementary material, as well as the possible mechanisms explaining the links). Specifically, we used simultaneous autoregressive (SAR) models (Cressie 1993; Haining 2003) to account for spatial autocorrelation of jaguar data and calculated Generalized R-square values (see details in Text A1). We applied the SEM by type of road, for males and females together (global model), and by sex, resulting in six models: global - paved roads, global - unpaved roads, males - paved roads, males - unpaved roads, females - paved roads, and females - unpaved roads.

We did not perform any model selection process because we wanted to assess the relationships between roads, land cover variables (natural and human-dominated), and jaguars' space use. All variables were scaled (x-mean(x))/sd(x)) prior to the analysis to make coefficients comparable. An initial Spearman's rank correlation was performed on the dataset to check for multicollinearity, and all of the variables were included in the model.

Output model coefficients (path coefficients) allow for a comparison of the relative importance of direct and indirect causal links. The indirect effect of roads on jaguars' space use was obtained by multiplying the patch coefficient linking roads to the land cover variables and the path coefficient linking the land cover variables to jaguars' space use (Grace 2006). We considered as significant relationships those with p-values < 0.1 (Amrhein et al. 2019). The models were carried through the package piecewiseSEM (v.2.0.2, Lefcheck, 2016) implemented for R statistical software (RStudio Team 2016).

3. Results

We observed that the frequency of jaguars tended to be higher as the distance to paved roads increased until a value of 5 km, after which it started to decrease (Figure 2). The relationship between the frequency of jaguars and distance to unpaved roads was not very clear. We then assumed that 5 km correspond to a road-effect zone for jaguars (Benítez-López et al. 2010; Torres et al. 2016b) both for paved and unpaved roads and the analyses were performed only for the cells located within 5 km of the roads.

The value of frequency of jaguars for cells with jaguar locations varied between 0.002 and 0.21 for the global - paved roads model and for the global - unpaved roads model, 0.002 and 0.21 for males - paved roads model and males - unpaved roads model, 0.002 and 0.19 for females - paved roads model and females - unpaved roads model (see Figure A2 in supplementary material for information on the distribution of each variable).

Path analyses for the global, males' and females' models revealed that neither paved nor unpaved roads had significant direct effects on jaguars' space use (Figure 3, Table A3 and Table A4 in supplementary material). However, both paved and unpaved roads had indirect effects on jaguars´ space use through their negative association with forest and open areas and their positive association with urban areas. The indirect effects of paved roads via forest on jaguars in the global model was also observed for both males and females, while the indirect negative effect of paved roads via urban areas at the global model was replicated only for females (Figure 3). The indirect negative effects of unpaved roads via open areas was also observed on males, but not on females; the indirect effect of unpaved roads via urban areas was also found on females. The indirect effect of unpaved roads on males via urban areas was positive, i.e., the frequency of male jaguars was higher in cells near urban areas associated with unpaved roads (Figure 3).

Land cover had significant direct effects on jaguars in the global model as well as on males and females. As expected, forests and open areas favoured jaguars´ space use (except on females - unpaved roads model, where open areas had no effect). Urban areas in turn affected space use by jaguars. Unexpectedly, farming had a positive effect on jaguars´ space use for all models and urban areas had either no effect (paved-roads model) or a positive effect (unpaved-roads model) on the frequency of males. All the direct effects of land cover variables on jaguars´ space use were higher than the indirect effects of roads (Figure 3).

4. Discussion

Our findings show that the negative effects of roads on jaguars' space use occur indirectly, through the effects of roads on land cover. We observed that paved roads are associated with a low proportion of forest, which in turn negatively affect jaguars. Similarly, unpaved roads were associated with low proportion of open areas, which reduce jaguars´ use of space. The indirect effects of roads were also observed through the association with human-dominated areas.

The indirect effect of roads on jaguars' space use via forest and open areas shows that the commonly reported high dependence of jaguars on natural areas (Rodríguez-Soto et al. 2011; Morato et al. 2014) is negatively influenced by the presence of roads, which despite being intuitive, has not been discussed in the literature. Because of jaguars´ large spatial needs, reduction and fragmentation of available habitat by roads can modify the species' spatial patterns of movement (Ripple et al. 2014).

Avoidance of anthropic areas by jaguars has already been described (Rabinowitz and Zeller 2010; De Angelo et al. 2013) and we showed that this can be partly caused by roads. Roads facilitate access to remote areas (Barber et al. 2014) which favors the establishment of human settlements (Laurance et al. 2009). In turn, the growing demand of urban areas increase the need for new transport infrastructure, triggering an endless self-reinforcing cycle of human interference (Jaeger 2002; Torres et al. 2016a). Not surprisingly, males seem to be unaffected by urban areas, which is in line with an earlier study that showed that male jaguars tend to be more adventurous than females as they moved close to areas with high human population densities (Colchero et al. 2011). The tolerance of males to anthropic areas is usually attributed to the large sizes of male´s home ranges that include ranges of many females, and to large distances travelled per day (Sollmann et al. 2011; Morato et al. 2016). This adds to the fact that increasing urbanization is leaving few options for jaguars so they are forced to adapt. However, conversion of habitat tends to increase the spatial requirements of apex predators, rising conflict with humans (Ripple et al. 2014; Marchini and Macdonald 2018). A recent study that tracked a male jaguar in the vicinity of a city in Mexico reported that the core areas of the jaguar's home range included a landfill where the jaguar opportunistically predated on dogs, raccoons, and other animals that visited the area (González-Gallina et al. 2017). More recently, a male jaguar became famous in Brazil after traveling through different places within a city, including a church, a hotel's parking lot, industrial neighborhood streets, and the backyard of a residence to feed on chickens, and intervention by environmental agencies was necessary to relocate the individual (Associação Onçafari 2019).

The effects of roads on space use by felids have been reported in various species, including jaguars (Dickson et at. 2005; Colchero et al. 2011; Thatte et al. 2018). However, the response to roads appears to be scale-dependent. For example, cougars (*Puma concolor*) and bobcats (*Lynx rufus*) in southern California selected against roaded areas in home range selection, but they did not avoid roads in movements within home ranges (Dickson and Beier 2002; Poessel et al. 2014). Since we analyzed the areas immediately surrounding jaguar's occurrences, it is not possible to make inferences about home range selection; thus, our inferences are limited to jaguars´ response to roads and land cover within their territories, corresponding to the third-order selection of resources (Johnson 1980). At this scale, our results for jaguars are similar to those for cougars and bobcats (Dickson and Beier 2002; Poessel et al. 2014). Morato et al. (2018a) studied jaguars in most of the sites we analyzed here, and also found that roads had no effect on resource selection of jaguars at the scales of home range and foraging, i.e., third and fourth-order resource selection, respectively (Johnson 1980). This is not surprising since road mortality of jaguars is commonly reported (Silva et al. 2014; Srbek-Araujo et al. 2015) and some carnivores can use roads as travel corridors (Kerley et al. 2002; Zimmermann et al. 2014). In contrast, Colchero et al. (2011) modeled the movement of jaguars and found that the jaguars avoided moving close to roads within their home ranges in the Mayan Forests of Mexico and Guatemala. None of these studies, however, discussed whether the behavior of the species studied was related to the road disturbance or due to the habitat in the surroundings. We took the analysis a step further and showed that the effects of roads can be rather subtle.

We have disentangled direct and indirect effects of roads on jaguars, which can be a powerful tool to appropriately prioritize preventive and adaptive management actions for conservation (Teixeira et al. 2020), but there are some limitations that need to be considered. First, we assumed that roads are the main drivers of land cover changes, which is theoretically sound (Laurance et al. 2009), but other landscape features may play a role as well, such as mines, dams and other human constructions (Laurance 2019). Likewise, other factors may also influence jaguars´ space use, such as prey availability (Espinosa et al. 2018) and movement of conspecifics (Kanda et al. 2019). Second, information about traffic volume could also help clarify the direct effects of roads (Jacobson et al. 2016); the lack of detailed and systematic traffic data is one of the main limitations in many road ecology studies. Finally, the positive association of farming to jaguars´ space use may be related to the nature of our data layer; farming included both agriculture and pasture areas where livestock occur and it has been reported that livestock may attract jaguars (Zarco-González et al. 2013; but see Kanda et al. 2019). More specific analysis will be necessary to better understand these relationships.

The growing plans to expand the road network in Brazil (Bager et al. 2015) urgently require an evaluation of all the potential environmental impacts to properly balance development and conservation (Kaszta et al. 2020). The results presented here are useful to guide prevention and mitigation actions for jaguars. Our findings indicate a lack of road avoidance behavior at the level of home range, which makes road mortality an important concern for jaguar conservation considering existing and planned future roads (Cullen Jr. et al. 2016). Since additional mortality may become a critical threat to a species with low reproduction rates, in particular when combined with other sources of non-natural mortality (Ceia-Hasse et al. 2017; Grilo et al. 2020), it is an important recommendation to identify areas of high road-kill rates and areas of movement corridors crossed by roads to implement effective measures to avoid road mortality and provide safe crossings (Clevenger and Waltho et al. 2005; González-Gallina et al. 2018; Spanowicz et al. 2020). Also, our study highlighted that substantial efforts should be made to control and prevent deforestation (Laurance et al. 2014) and urban sprawl (Torres et al. 2016a) due to roads; for example, by funding studies that simulate the impacts of planned roads on the landscapes still inhabited by jaguars (Carter et al. 2020). Unfortunately, jaguar populations most at risk to disappear in Brazil are those in areas that have the highest road densities (Galetti et al. 2013; Paviolo et al. 2016), which have promoted deforestation and urban expansion (Freitas et al., 2010) and where road mortality has been reported as an imminent threat (Srbek-Araujo et al. 2015). Given the high vulnerability of many jaguar populations in Brazil and other frequent threats they face throughout their range (Marchini and Macdonald 2018), efforts by scientists, road managers, and government environmental agencies need to be joined to be able to minimize the negative effects of roads before they exceed jaguars´ ability to maintain their populations and ecosystemic relationships.

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Figures

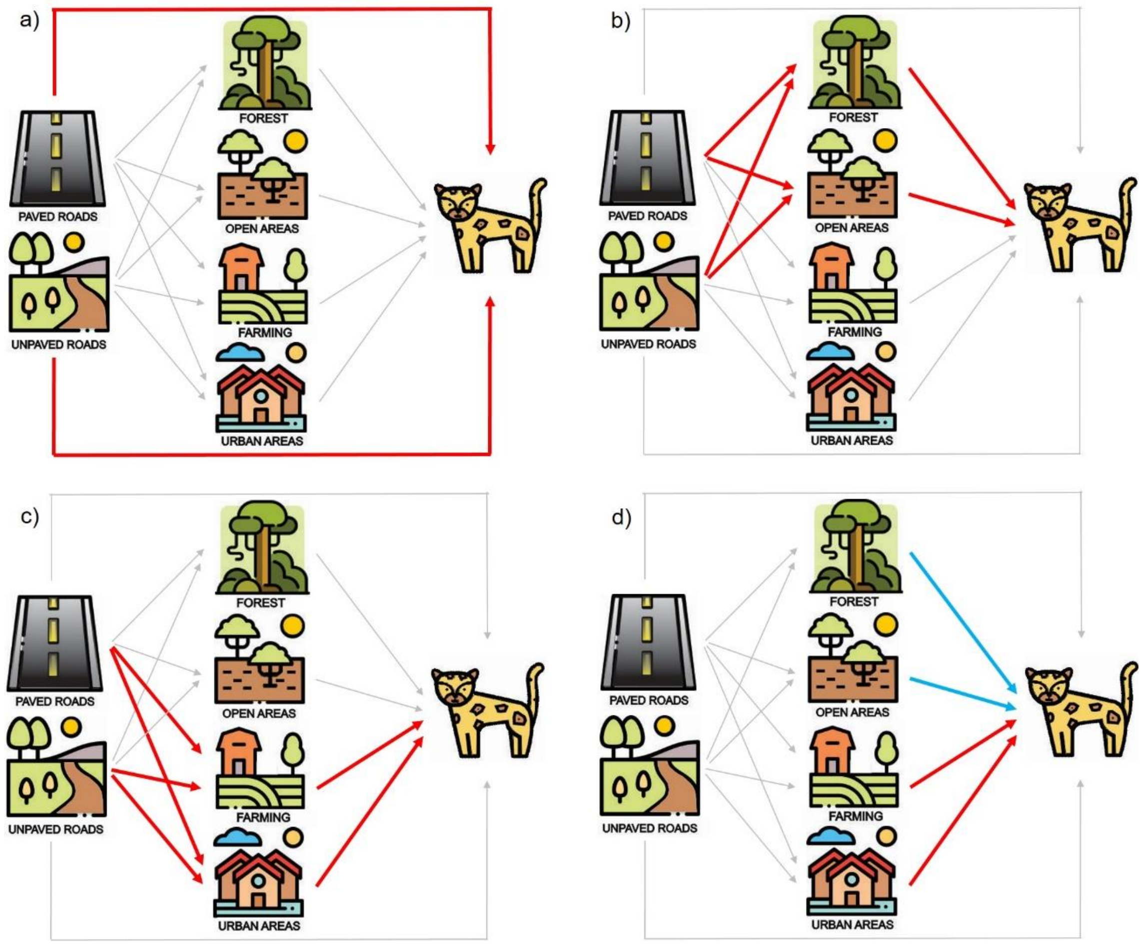

Fig. 1: Conceptual framework to assess the direct and indirect effects of roads on jaguars' space use according to four hypotheses: a) Space use by jaguars is predominantly affected directly by roads; b) Space use by jaguars is strongly affected indirectly by roads via the effects of roads on natural areas (i.e., roads promote a reduction in forest and open areas and consequently have a negative effect on jaguars' use of habitat); c) Space use by jaguars is primarily affected indirectly by roads via the effects of roads on human-dominated areas (i.e., roads promote an increase on the farming and urban areas and consequently have a negative effect on jaguars' use of habitat); d) Space use by jaguars is mostly affected directly by land cover independently of roads (i.e., forest and open areas influence the jaguars space use while farming and urban areas affect them negatively). Colored arrows denote expected positive (blue) or negative (red) effects of variables on jaguar´s space use. Direct effects of variables on jaguar´s space use are depicted by solid arrows, and indirect effect of roads on jaguar´s

space use are depicted by dashed arrows. To avoid duplicate figures, the conceptual model is presented with paved and unpaved roads together, but separate models were generated for each.

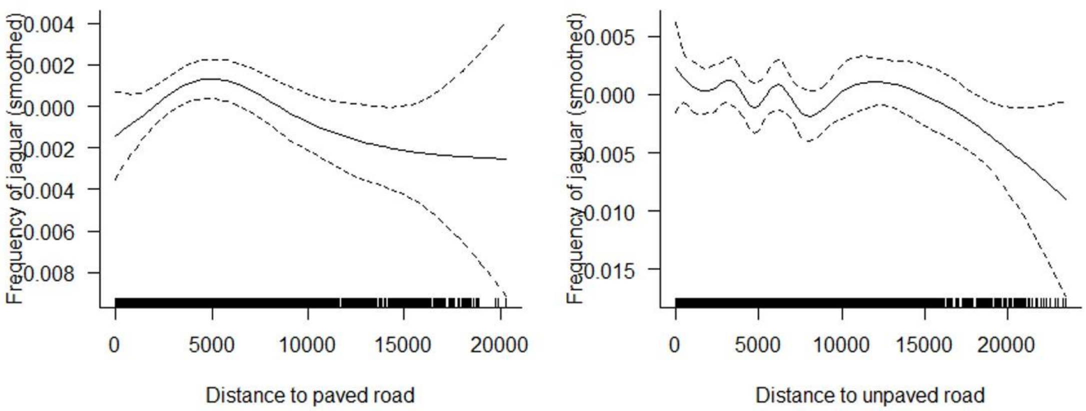

Fig. 2: Smoothed curves showing the relationships between jaguar´s spatial habitat use (measured as frequency of jaguar locations: number of locations per day) and distance (m) to paved and unpaved roads. The smoother is centred around zero. Dashed lines represent 95% confidence intervals.

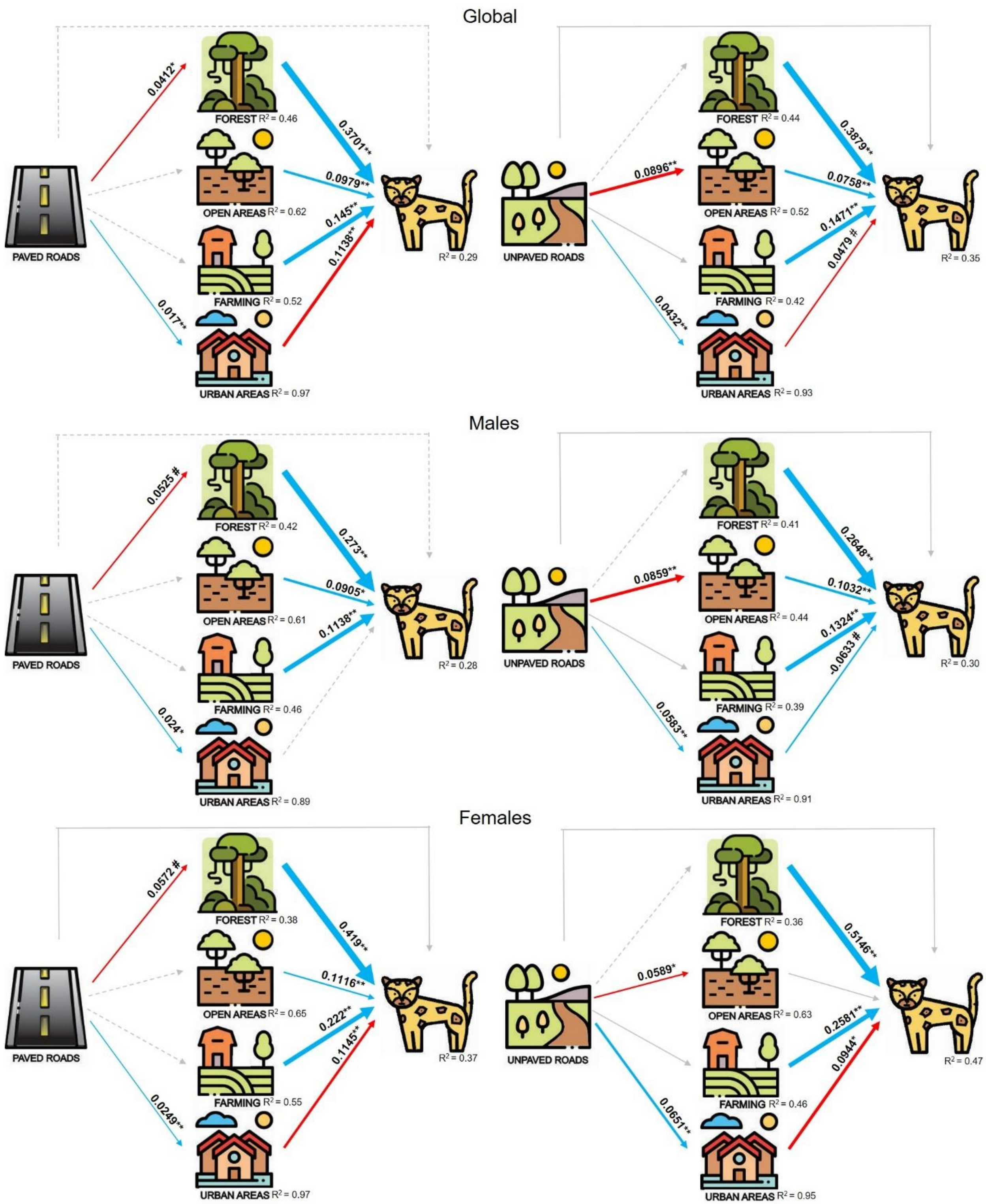

Fig. 3: Path diagrams representing the effects of roads and land cover on jaguar space use for the global case, for males, and females. Arrows represent unidirectional relationships among variables. Colored arrows indicate positive (blue) and negative (red) significant effects and

gray arrows denote non-significant positive (solid) or negative (dashed) paths. The numbers associated with the arrows provide the standardized coefficients and the width of the arrows refers to the size of the coefficients of significant effects. Numbers below the response variables are pseudo-R-squared values. Note that for those variables measured as distances (roads and urban areas), a negative effect occurred when the coefficient is positive, and vice-versa, except for the effect of roads on urban areas which are both measured as distances (see Table A2 in supplementary material for details). # marginally significant effect with p–value < 0.1, * p–value < 0.05, and **p–value < 0.01.

SUPLLEMENTARY MATERIAL

Direct and indirect effects of roads on space use by jaguars in Brazil

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Supplementary figures

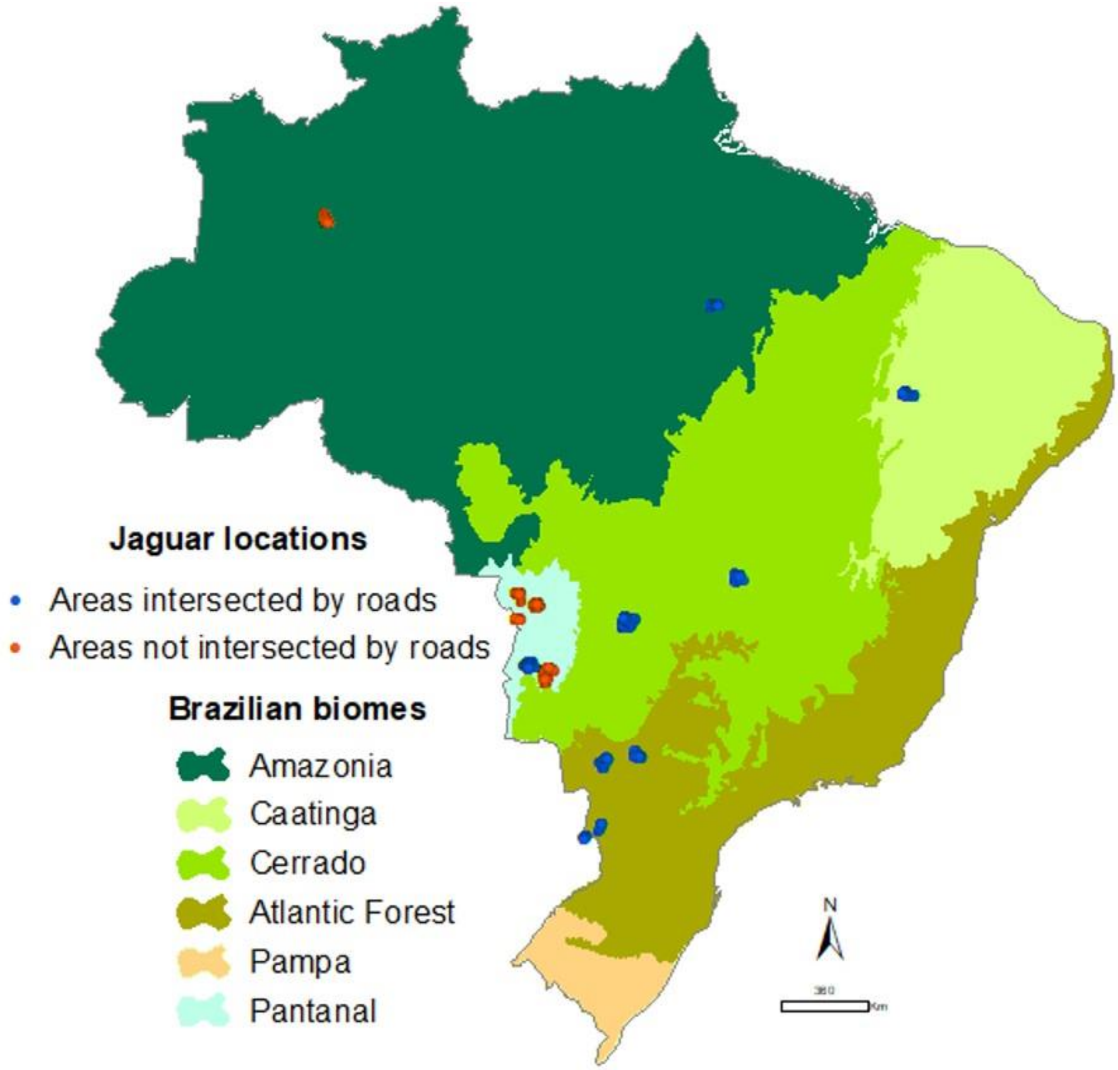
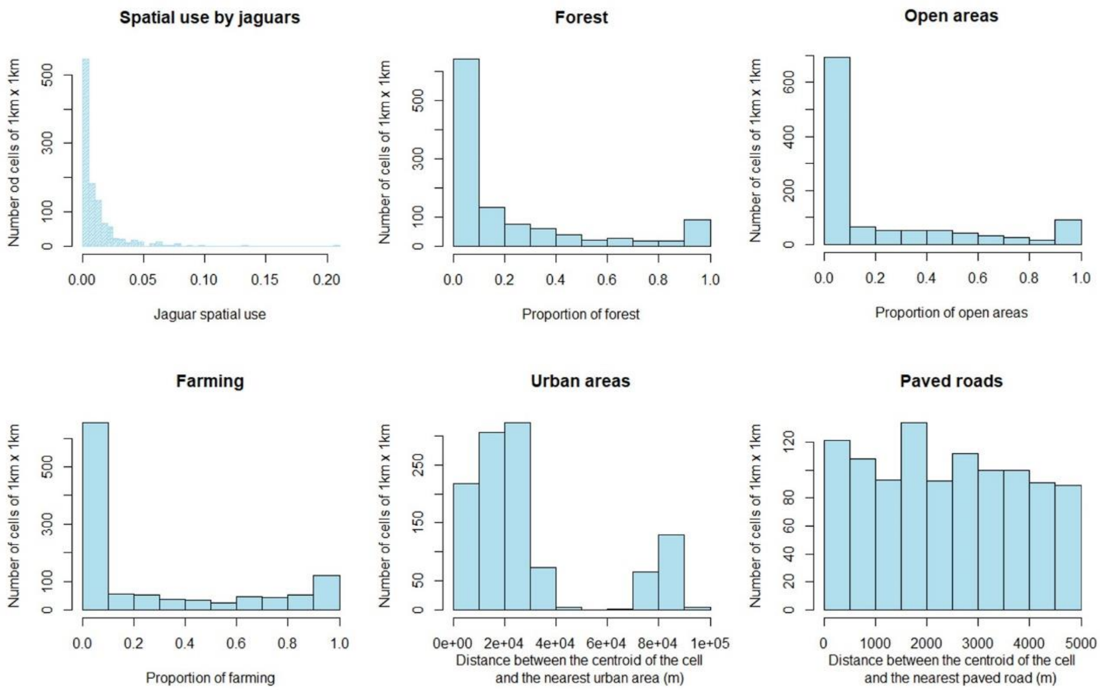
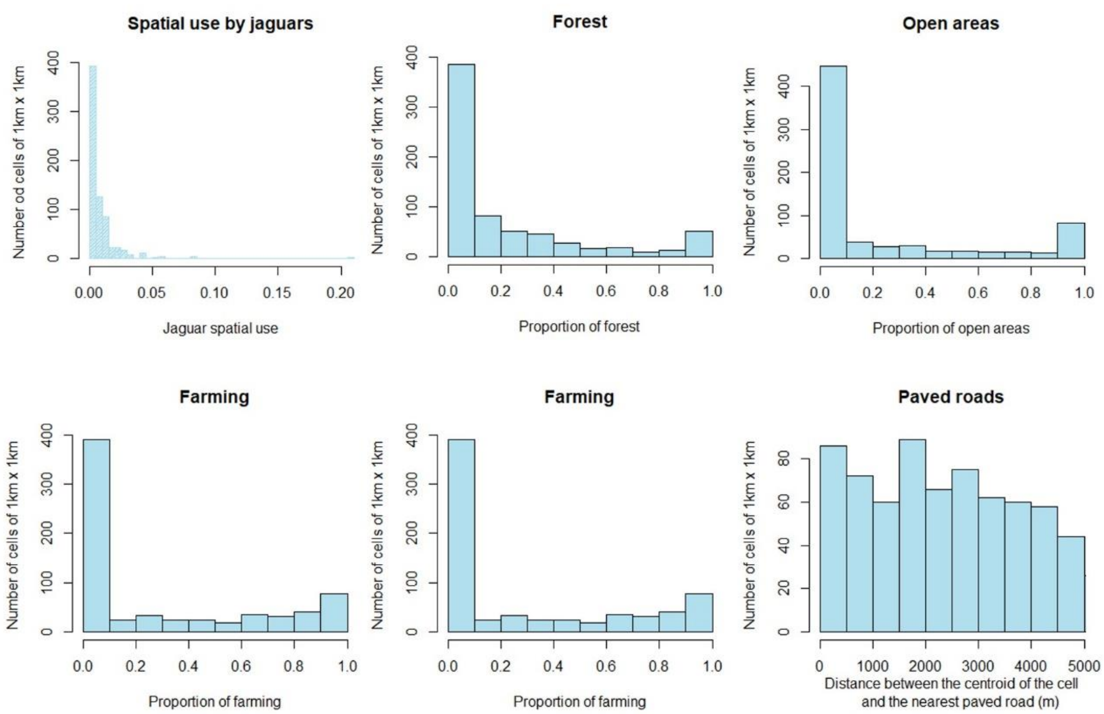


Figure A1: Jaguars locations distributed in 15 areas in different biomes in Brazil. Two areas are located in the Amazon, two in the Cerrado Biome, one in the Caatinga, five in the Pantanal, one in the transition of Cerrado-Pantanal, and four in the Atlanic Forest.

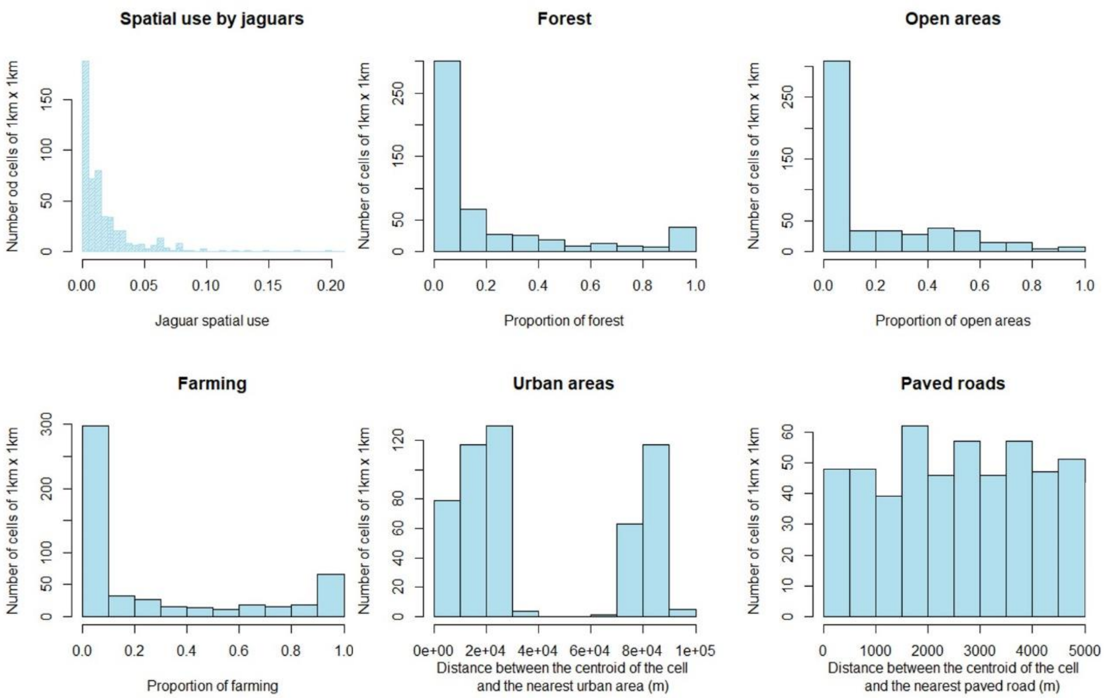
Global model: paved roads



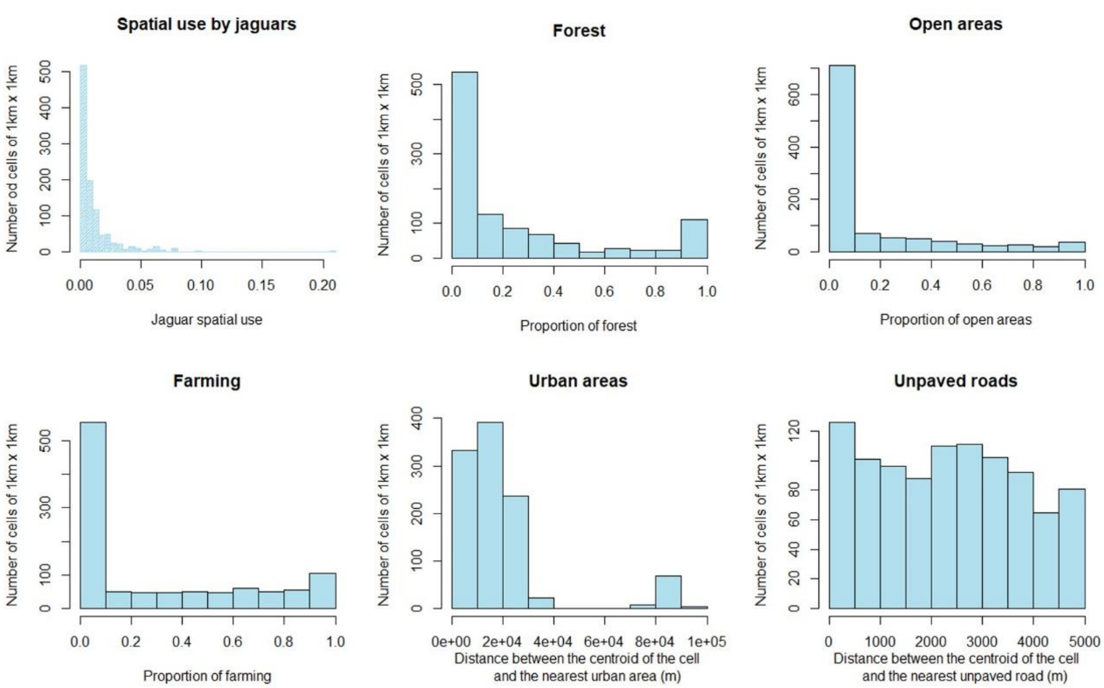
Males: paved roads



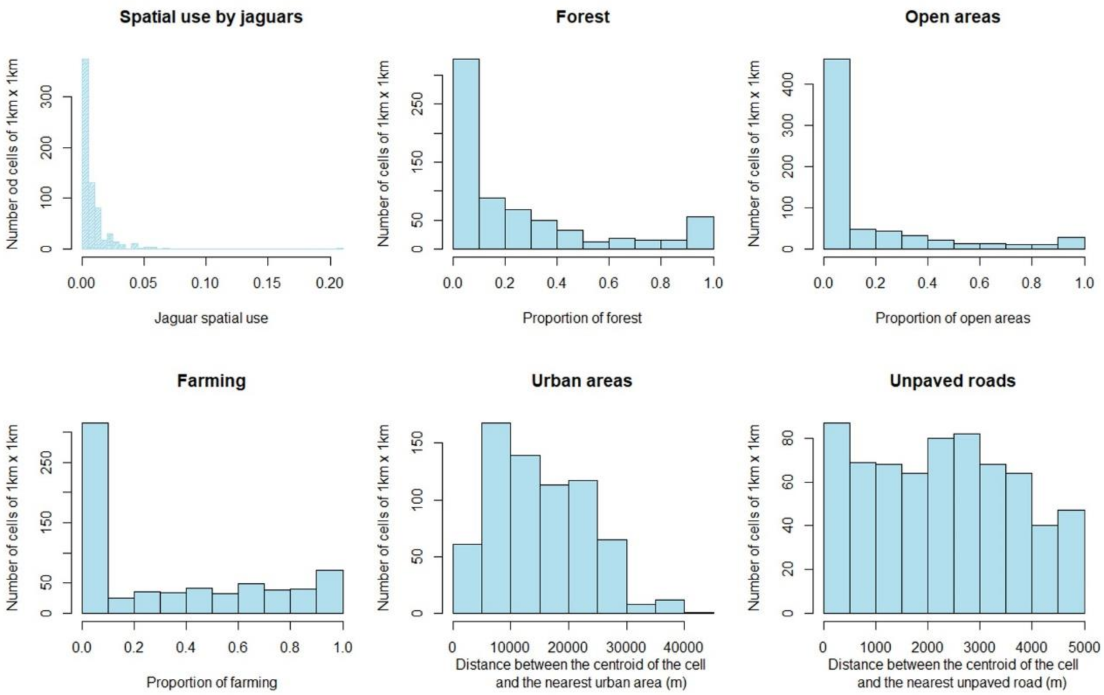
Females: paved roads



Global model: unpaved roads



Males: unpaved roads



Females: unpaved roads

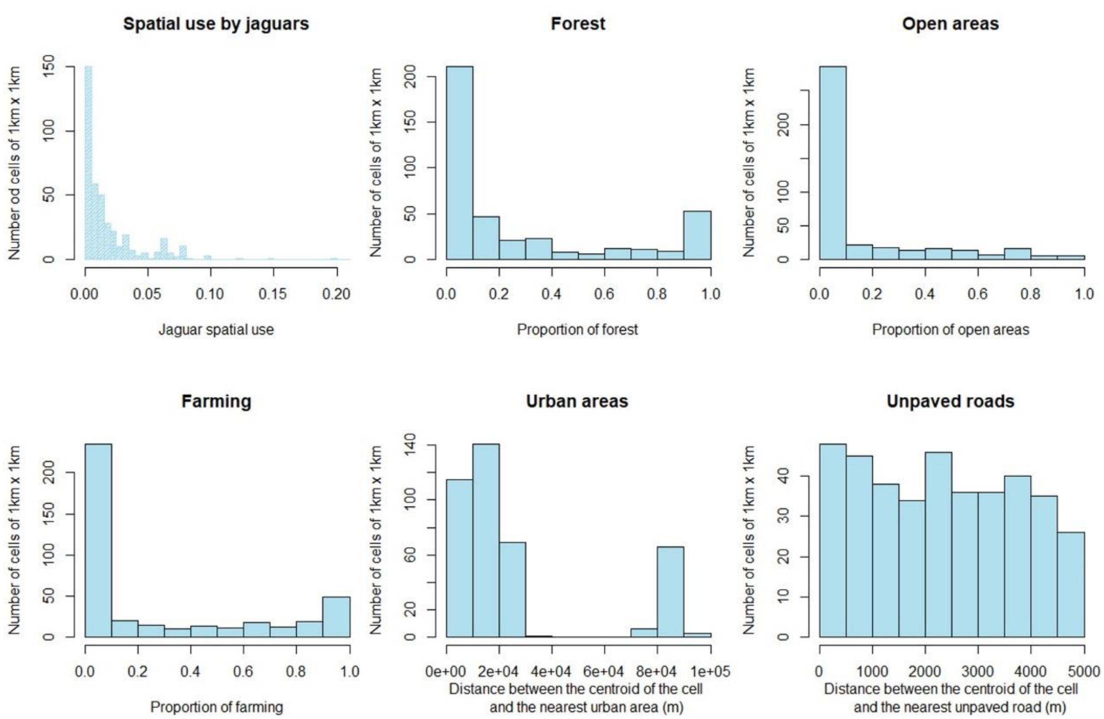


Figure A2: Histograms for the models of paved and unpaved roads for the global model, for males and females: Jaguars' space use (number of jaguar locations per day); percentages of forest, open areas, and farming; distance to the nearest urban area, paved road and unpaved road.

Supplementary tables

Table A1: Individual jaguar locations from the 15 areas, name of the project in which the animals were recorded (Morato et al. 2018b), sex, year of recording, ID of the area to which the location belongs and description of the area (if it is intersected by paved and unpaved roads or not). *(File attached separately as TableA1.xlsx)*

Table A2: Hypothesized associations between roads (distance), land cover variables, and jaguar frequency, and possible mechanisms explaining these associations.

Causal variable	**Affected variable**	**Expected relationship***	**Expected effect***	**Hypothesized mechanism**	**Equation**
Distance to roads (paved or unpaved)	Forest	Positive	Negative	The larger the distance to roads, the higher the proportion of natural areas (forest and open areas). Roads are key in deforestation processes because they facilitate reductions in the amount of natural areas by vegetation clearance due to road construction and use (Fearnside et al. 2006).	forest ~ paved roads forest ~ unpaved roads
Distance to roads (paved or unpaved)	Open areas	Positive	Negative		open ~ paved roads open ~ unpaved roads
Distance to roads (paved or unpaved)	Farming	Negative	Positive	The shorter the distance to roads, the higher the proportion of farming. Roads facilitate rural livelihoods (Laurance et al. 2014).	farming ~ paved roads farming ~ unpaved roads
Distance to roads (paved or unpaved)	Distance to urban areas	Positive	Positive	The shorter the distance to roads, the shorter the distance to urban areas. The presence of roads facilitates urbanization (Laurance et al. 2009).	urban ~ paved roads urban ~ unpaved roads
Distance to roads (paved or unpaved)	Jaguar spatial use	Positive	Negative	The larger the distance to roads, the higher the spatial use by jaguars. Road avoidance behavior has been reported for jaguars by some studies, suggesting that they tend to occur far from roads (Conde et al. 2010, Colchero et al. 2010).	frequency of jaguars ~ paved roads + forest + open + farming + urban frequency of jaguars ~unpaved roads + forest + open + farming + urban
Forest	Jaguar spatial use	Positive	Positive	The higher the proportion of natural areas (forest and open areas), the higher the spatial use by jaguars. Jaguars are highly dependent on native forest (De Angelo et al. 2011), and forest and open areas are considered important habitats (Zeilhofer et al. 2014). Their occurrence is	
Open areas	Jaguar spatial use	Positive	Positive		

				negatively affected by habitat loss (Hatten et al. 2005; Morrison et al. 2007).	
Farming	Jaguar spatial use	Negative	Negative	The higher the proportion of farming, the lower the spatial use by jaguars. Human land use and presence, such as in agriculture land, pastures, and farms, have negative effects on jaguar presence (De Angelo et al. 2011).	
Distance to urban areas	Jaguar spatial use	Positive	Negative	The larger the distance to urban areas, the higher spatial use by jaguars. Jaguars´ presence is negatively affected by human presence and human population density (De Angelo et al. 2011).	

* ‘Expected relationship’ is related to the relationship between the variables taking into account the units of measurement of the variables, and ‘expected effect’ is related to the effect of the causal variables on the affected variable. For example, the expected relationship between (distance to) roads and proportion of forest is positive because the unit of measurement of road is distance and the unit of measurement of forest is percentage (see Section 2.2 of Methods), and we expect that the higher the distance to roads, the higher the proportion forest, which corresponds to a negative effect of roads on forest.

Table A3: Statistical results of path analyses for the models for paved roads for global model, for males, and females. Standardized effects of explanatory variables on forest, open areas, farming, urban areas, and frequency of jaguars. (◌ *p*–value < 0.1, * *p*–value < 0.05, and ***p*–value < 0.01).

		Global		Males		Females	
Response	**Explanatory**	**Estimate ± SD**	***p*-value**	**Estimate ± SD**	***p*-value**	**Estimate ± SD**	***p*-value**
Forest	Distance to paved roads	0.0412 ± 0.0204	0.0435*	0.0525 ± 0.027	0.0514◌	0.0572 ± 0.0329	0.0815◌
Open areas	Distanace to paved roads	0.0155 ± 0.0167	0.3525	0.0007 ± 0.0214	0.9744	0.0185 ± 0.0235	0.431
Farming	Distance to paved roads	0.0169 ± 0.0189	0.3724	0.0039 ± 0.0256	0.8793	0.027 ± 0.0269	0.3164
Urban areas	Distance to paved roads	0.017 ± 0.0042	0.0001**	0.024 ± 0.0109	0.0282*	0.0249 ± 0.0066	0.0002**
Frequency of jaguars	Distance to paved roads	0.0103 ± 0.0248	0.6785	0.0048 ± 0.0315	0.879	-0.0003 ± 0.0345	0.9939
	Forest	0.3701 ± 0.0288	0**	0.273 ± 0.0353	0**	0.419 ± 0.0408	0**
	Open areas	0.0979 ± 0.0271	0.0003**	0.0905 ± 0.0353	0.0104*	0.1116 ± 0.0393	0.0045**
	Farming	0.145 ± 0.0272	0**	0.1138 ± 0.0338	0.0008**	0.222 ± 0.0396	0**
	Distance to urban areas	0.1138 ± 0.0273	0**	0.0337 ± 0.0344	0.3275	0.1145 ± 0.0431	0.0079**

Table A4: Statistical results of path analyses for the models for unpaved roads for the global model, for males, and females. Standardized effects of explanatory variables on forest, open areas, farming, urban areas, and frequency of jaguars. (◌ *p*–value < 0.1, * *p*–value < 0.05, and ***p*–value < 0.01).

		Global		Males		Females	
Response	**Explanatory**	**Estimate ± SD**	***p*-value**	**Estimate ± SD**	***p*-value**	**Estimate ± SD**	***p*-value**
Forest	Distance to unpaved roads	0.0189 ± 0.0213	0.3759	0.0197 ± 0.0275	0.4745	0.0152 ± 0.0376	0.6867
Open areas	Distance to unpaved roads	0.0896 ± 0.0202	0**	0.0859 ± 0.0272	0.0016**	0.0589 ± 0.0279	0.0344*
Farming	Distance to unpaved roads	-0.0082 ± 0.0219	0.7097	0.0217 ± 0.0279	0.4363	-0.0006 ± 0.0342	0.9864
Urban areas	Distance to unpaved roads	0.0432 ± 0.0071	0**	0.0583 ± 0.0101	0**	0.0651 ± 0.0101	0**
Frequency of jaguars	Distance to unpaved roads	-0.0417 ± 0.0254	0.1008	-0.0155 ± 0.0325	0.6339	-0.0517 ± 0.0383	0.1769
	Forest	0.3879 ± 0.028	0**	0.2648 ± 0.0344	0**	0.5146 ± 0.0436	0**
	Open areas	0.0758 ± 0.0266	0.0044**	0.1032 ± 0.0336	0.0021**	0.0494 ± 0.0419	0.2378
	Farming	0.1471 ± 0.0256	0**	0.1324 ± 0.0335	0.0001**	0.2581 ± 0.0404	0**
	Distance to urban areas	0.0479 ± 0.0263	0.0684◌	-0.0633 ± 0.0353	0.0727◌	0.0944 ± 0.0454	0.0375*

Supplementary text

Text A1: Details on simultaneous autoregressive (SAR) models and R-squares used in the piecewise SEM analysis

SAR models augment the standard linear regression model with an additional term that incorporates the spatial autocorrelation structure of a given data set. This additional term is implemented with a 'spatial weights matrix' where the neighbourhood of each location and the weight of each neighbour need to be defined (Anselin & Bera, 1998; Fortin & Dale, 2005). We have applied the SAR lagged model that assumes that the autoregressive process occurs only in the response variable ('inherent spatial autocorrelation'), and thus includes a term (ρW) for the spatial autocorrelation in the response variable Y, but also the standard term for the explanatory variables and errors ($X\beta + e$) as used in an ordinary least squares regression. The SAR lag takes the following expression:

$$Y = \rho WY \ + X\beta + e$$

Where ρ is the autoregression coefficient, W is the spatial weights matrix, β is a vector representing the slopes associated with the explanatory variables in the original predictor matrix X, and e represents the (spatially) independent errors (Kissling & Carl, 2008).

Many methods have been used to evaluate model fit in non-linear regressions, including 'pseudo-R^2' measures of explained variance (Nagelkerke, 1991; Cox & Snell, 1989). In our case the model is fitted by maximum likelihood, so likelihood-based measures are more appropriate. Also, the model is non-linear in the spatial coefficient. For that reason we have used Generalised R-squared, also known as the Nagelkerke or Craig and Uhler R^2 (Nagelkerke, 1991), which is an extension of the R^2 measure that can be applied to general regression models. It compares the likelihood of the fitted model (L_M) to the likelihood of the intercept-only (constant) model (L_0) and it is scaled to have a maximum of 1:

$$GeneralisedR\text{-}squared = 1 - \left(\frac{L_0}{L_M}\right)^{\left(\frac{2}{n}\right)}$$

A value of 1 indicates a perfect model; a value of 0 indicates that a model is no better than a constant. The measure simplifies to the traditional *R*-square for continuous normal responses in the standard least squares setting.

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ARTIGO 3 – *BRAZIL ROAD-KILL – A DATASET OF WILDLIFE TERRESTRIAL VERTEBRATE ROAD-KILLS*

(*MANUSCRIPT PUBLISHED IN THE JOURNAL "ECOLOGY"*)

Data Papers

Ecology, 99(11), 2018, pp. 2625

BRAZIL ROAD-KILL: a data set of wildlife terrestrial vertebrate road-kills

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Abstract. Mortality from collision with vehicles is the most visible impact of road traffic on wildlife. Mortality due to roads (hereafter road-kill) can affect the dynamic of populations of many species and can, therefore, increase the risk of local decline or extinction. This is especially true in Brazil, where plans for road network upgrading and expansion overlaps biodiversity hotspot areas, which are of high importance for global conservation. Researchers, conservationists and road planners face the challenge to define a national strategy for road mitigation and wildlife conservation. The main goal of this dataset is a compilation of geo-referenced road-kill data from published and unpublished road surveys. This is the first Data Paper in the BRAZIL series (see ATLANTIC, NEOTROPICAL, and BRAZIL collections of Data Papers published in *Ecology*), which aims make public road-kill data for species in the Brazilian Regions. The dataset encompasses road-kill records from 45 personal communications and 26 studies published in peer-reviewed journals, theses and reports. The road-kill dataset comprises 21,512 records, 83% of which are identified to the species level (n = 450 species). The dataset includes records of 31 amphibian species, 90 reptile species, 229 bird species, and 99 mammal species. One species is classified as Endangered, eight as Vulnerable and twelve as Near Threatened. The species with the highest number of records are: *Didelphis albiventris* (n = 1,549), *Volatinia jacarina* (n = 1,238), *Cerdocyon thous* (n = 1,135), *Helicops infrataeniatus* (n = 802), and *Rhinella icterica* (n = 692). Most of the records came from southern Brazil. However, observations of the road-kill incidence for non-Least Concern species are more spread across the country. This dataset can be used to identify which *taxa* seems to be vulnerable to traffic, analyze temporal and spatial patterns of road-kill at local, regional and national scales and also used to understand the effects of road-kill on population persistence. It may also contribute to studies that aims to understand the influence of landscape and environmental influences on road-kills, improve our knowledge on road-related strategies on biodiversity conservation and be used as complementary information on large-scale and macroecological studies. No copyright or proprietary restrictions are associated with the use of this data set other than citation of this Data Paper.

Key words: 1988–2017; amphibians; birds; Brazil; mammals; reptiles; road effects; road mortality; road survey; species occurrence; wildlife-vehicle collisions.

The complete data set is available as Supporting Information at: http://onlinelibrary.wiley.com/doi/10.1002/ecy.2464/suppinfo.

Data Availability

Associated data is also available https://doi.org/10.5281/zenodo.1420508.

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