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 locations 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 *Leopardus guttulus* were analyzed together), ocelot (*Leopardus 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 behavioral state of the individuals 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 (~5300 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

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

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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 2020). 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 five species of felids: tiger cats (*Leopardus tigrinus* and *Leopardus*

guttulus were analyzed together), ocelot, jaguarundi (*Herpailurus yagouaroundi*), and puma.

Material and Methods

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 analyzed together (their ranges were merged) because much of the data obtained were 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). We chose to make use of available data that have been compiled across the species ranges and to analyze how felids spatially interact with roads in Brazil, in order to provide a first overview of the potential impact of roads on felids and the need for mitigation. 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 2018) 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 2014), i.e., ca. 0.2 km/km^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 analyzed as a network of electrical nodes connected by resistors and serves as an analog 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

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

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

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 neighboring 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] and 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] and 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]).

Table 2 Cohen's Kappa coefficients (k) used to compare how often potential movement corridors and road mortality likelihood models spatially agreed

Species	T_s	>P95			>P90			>P80		
		S_{1both}	S_{0both}	k	S_{1both}	S_{0both}	k	S_{1both}	S_{0both}	k
Tiger cats	366,450	1683	331,488	0.04*	5399	298,556	0.05*	16,478	236,345	0.03*
Ocelot	350,829	1449	317,194	0.03*	5249	285,911	0.05*	18,583	229,081	0.08*
Jaguarundi	343,849	902	310,365	2.59e−03	3251	278,331	−6.06e−03*	12,537	218,847	−2.21e−02*
Puma	333,024	1627	301,349	0.05*	5282	271,700	0.06*	16,905	216,717	0.07*

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

Values of AUC > 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: $R = ((x - \max(x)) \times (-1)) + \min(x)$, 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 modeling 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 × 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).

Road Mortality Likelihood

We modeled road mortality likelihood for each species in a grid with cells of 1 × 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), which has been used to predict road mortality for felids (Garrote et al. 2018; Schmidt et al. 2020). 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 uses 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 "Potential movement corridors crossed by roads" 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 (in "Potential movement corridors crossed by roads"). 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, two-lane paved, and three to six-lane highways) and road length (Table 1 and Text S1). The later variable was included as a control variable, because 1 km^2 cells did not include the same length of road.

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 95th, 90th, and 80th 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 0. 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 2018).

Results

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 and 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 Fig. S4.

Road Mortality

All road mortality models had high support based on AUC values (AUC ≥ 0.85; Table S1). Wider roads (three to six 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 and 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%).

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.

Comparison of Movement Corridors and Road Mortality

Cohen's kappa coefficients indicated low levels of spatial agreement between the two methods for all species and for
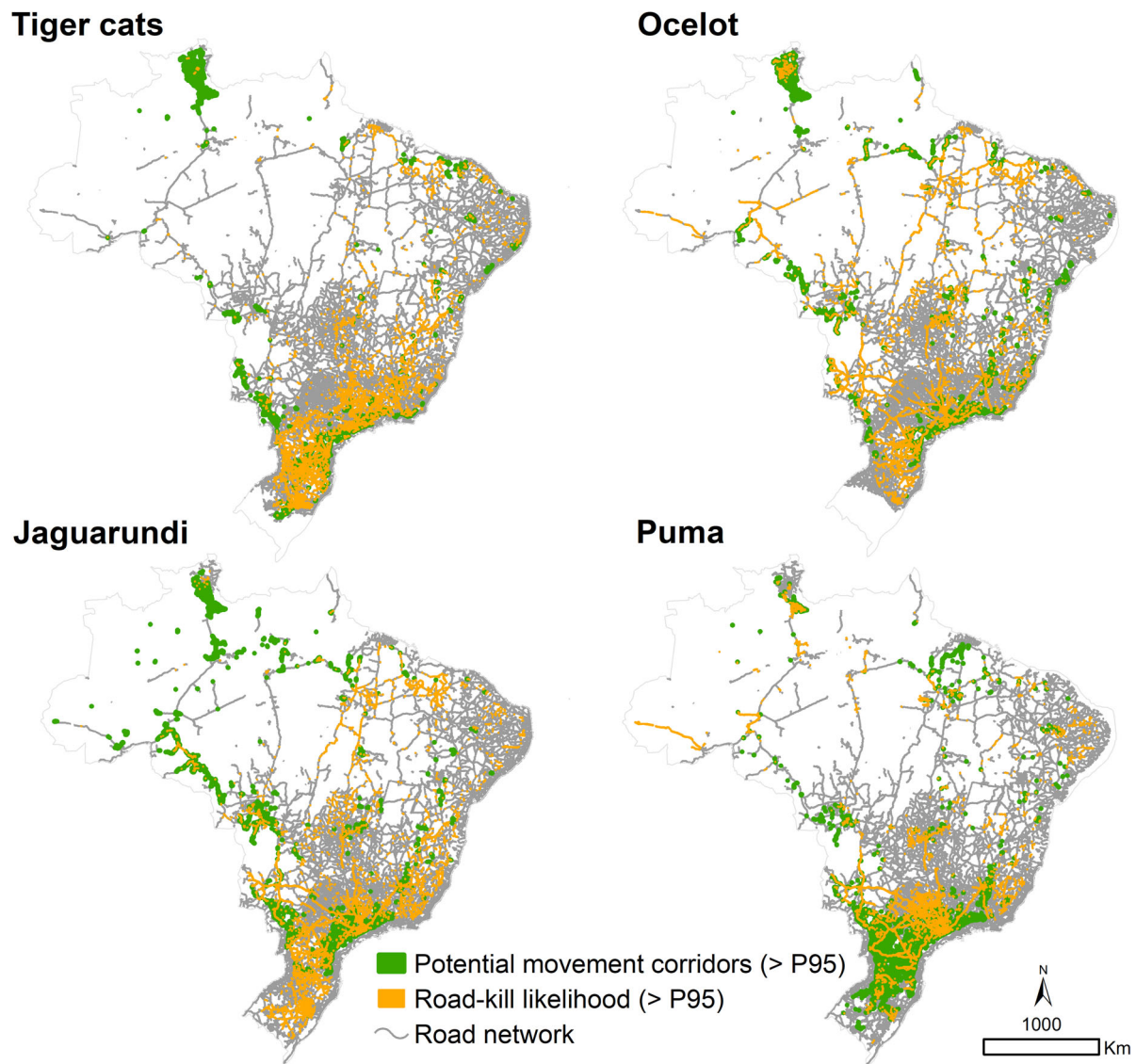
Tiger cats

Ocelot

Jaguarundi

Puma

Legend:
- 🟩 Potential movement corridors (> P95)
- 🟧 Road-kill likelihood (> P95)
- 〰 Road network

N

1000 Km

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

the three scenarios (Table 2). Total road lengths for which the two methods agreed (>95th percentile) were ~2250 km for tiger cats, ~1600 km for ocelot, ~1100 km for jaguarundi, and ~2000 km for puma. For all species together, these road segments represent a total of ~5300 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 nonlinear relationships between current and road mortality likelihood for all species (Fig. 2 and 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 ($t = 2.785$, $p < 0.05$, but see McShane et al. 2019).

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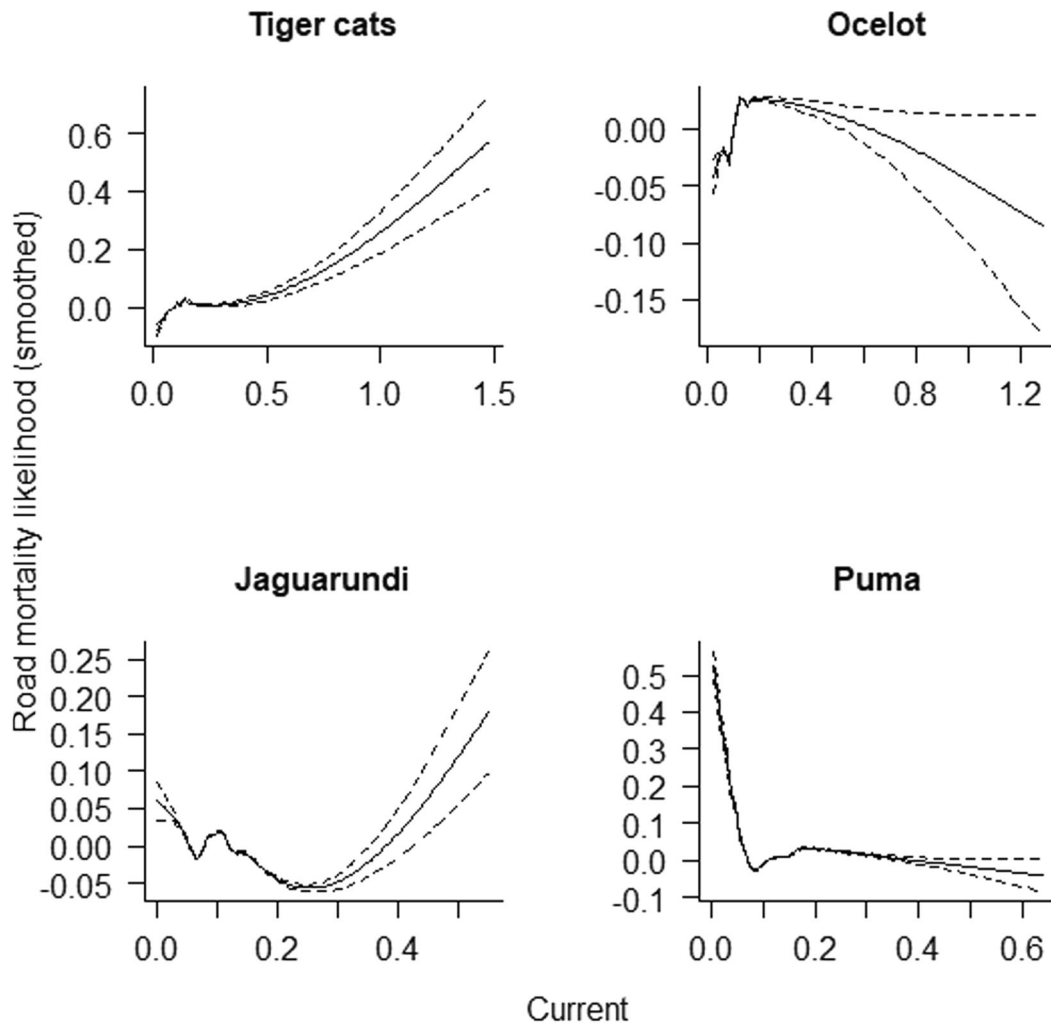
Fig. 2 Relationship between current and road mortality likelihood as shown by GAMs. *Y*-axis shows the contribution of the cubic regression spline smoother (the function that links *Y* to *X* in the model) to the fitted values. The smoother is centered around zero. Dashed lines represent 95% confidence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

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 2016). This can be expected since pumas and ocelots are associated with protected areas (Castilho et al. 2015; Massara et al. 2015) and outcompete and are dominants to 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 three to six lanes) best explained the occurrence of road-kill. Since information on traffic volumes was not available for the road network in Brazil, we assumed that the type of road can be a proxy of traffic intensity, and our results suggest that traffic can be an important predictor of felid road-kill. Unexpectedly, landscape variables contributed weakly to road mortality models for all species, which is not in line with other research that showed a stronger association between road-kill and landscape attributes (Gunson et al. 2011; Bueno et al. 2013).

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 behavior 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 traveled (Powell and Zielinski 1994; REED 2002). Thus, the behavioral state of the individuals covered by species occurrence data may affect the type of habitat selected and ultimately the location of movement corridors (Zeller et al. 2012, 2014; Abrahms et al. 2016).

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 (Grilo et al. 2011; 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 peak during 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 behavioral state are used in the two predictive models. Our study used occurrence records to parameterize resistance surfaces for movement corridor models. Information on type of behavior was not provided, and therefore, we were not able to determine if data corresponded to breeding or nonbreeding movements. However, given their independent sources, it is unlikely that they correspond only to the breeding period, which may explain the lack of spatial association between our models of movement corridors and road mortality. The lack of spatial agreement can also be explained by the association of road mortality with type of road, while movement corridors are associated with landscape features.

Implications for Road Management and Research

According to our findings, 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 (~5300 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 decision 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) and 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 by government agencies responsible for road mitigation.

To reduce road mortality and improve population connectivity, specific mitigation measures designed for felids need to consider the ecology and behavior 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 on measures for felids 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. 2019).

To gain a better understanding of the role different behavioral 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 nonbreeding 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. 2011). These studies will shed light on the role of behavioral state on modeling movement corridors and road-kill locations. We also suggest that estimates of average daily traffic are essential to understand the role of traffic on felids mortality and therefore provide guidance for more effective actions to minimize mortality.

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 and 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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Compliance with Ethical Standards

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