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RESEARCH ARTICLE

Landscape connectivity for an endangered carnivore: habitat conservation and road mitigation for ocelots in the US

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Abstract

Context Maintaining landscape connectivity for wildlife has become a conservation priority in response to increasing land development and road networks. Roads affect many wildlife populations worldwide, with the distribution and density of roads having negative impacts on gene flow and landscape connectivity.

Objectives We aimed to identify areas along roadways that promote movement in a fragmented landscape. Our objective was to gain a deeper understanding of drivers of connectivity in a patchwork landscape of human uses.

Methods We applied a spatial absorbing Markov chain (SAMC) framework to test hypotheses about landscape connectivity for a federally endangered carnivore, the ocelot (*Leopardus pardalis*). We modeled landscape connectivity for ocelots based on spatio-temporal trends in habitat use, which we derived using telemetry dataset collected 1982–2017. We compared three increasingly restrictive resistance surfaces to predict trends in landscape connectivity.

Results Ocelot avoidance of high-traffic roads (> 5000 cars/day) largely influenced patterns of predicted connectivity. We simulated connectivity between habitat patches and identified highly connected areas of conservation concern due to proximity to high-traffic roads. Connectivity was greatly influenced by ocelot habitat use rather than resistance scenarios. Further, we found no evidence of connectivity between populations of ocelots, indicating isolation within a fragmented landscape.

Conclusion Our spatially-explicit results describing landscape connectivity with respect to roads provides critical information needed for strategic placement of wildlife crossing structures. Wildlife crossing structures for resident ocelots should be placed in areas of relatively high conductance near roads with well-connected habitat on both sides of the road. We describe an approach that leverages long-term habitat use data

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for examining connectivity and improving landscape permeability.

Keywords Landscape connectivity · Ocelot · Road ecology · Spatial absorbing Markov chains · Texas

Introduction

Biodiversity is threatened globally by anthropogenic influences with a pervasive and ubiquitous threat from loss of landscape connectivity. Landscape connectivity is key for supporting biological processes, including animal movement and gene flow (Cramer and Bissonette 2005; Cushman et al. 2006; Merrick and Koprowski 2017). Reduced landscape connectivity can lead to the isolation of populations (Lindenmayer and Fischer 2006; Wade et al. 2015), which can compound issues of gene flow for small populations and add to already high extinction risks (Fahrig 2003; Keller and Largiader 2003). Landscapes are becoming increasingly impermeable because of habitat loss, fragmentation, and degradation (Theobald et al. 2012; Chen and Koprowski 2016a). Retaining landscape connectivity has therefore become a conservation priority in response to increasing threats from land development and road networks (Cramer and Bissonette 2005; Reed et al. 2017). Increased human activity threatens wildlife populations by influencing animal movement, survival, and reproductive success (Fahrig 2003; Chen and Koprowski 2016a).

Road networks are a major driver of the loss of landscape connectivity worldwide, with the distribution and density being linked to restricting gene flow and isolation of subpopulations (Forman and Alexander 1998; Trombulak and Frissel 2000; Laurance et al. 2009; Chen and Koprowski 2016a). Wildlife populations can be affected directly (e.g., vehicle collisions) or indirectly from roads (e.g., behavioral avoidance, Forman and Alexander 1998; Malo et al. 2004; Chen and Koprowski 2016a). Roads can serve as fatal barriers, threatening population persistence (Trombulak and Frissell 2000; Strasburg 2006; Chen and Koprowski 2016b). Further, road construction often leads to collateral habitat loss and fragmentation (Trombulak and Frissell 2000; Chen and Koprowski 2016a). Therefore, understanding animal-habitat relationships across vast landscapes, and the effects of roads on connectivity, is critical for the conservation of ecological communities, including wide-ranging species. Road permeability is not homogeneous however, roads may be traversable for some species while acting as complete barriers for others (Assis et al. 2019). The impact of roads on connectivity for many species of conservation concern is still relatively unknown.

As wide-ranging species, carnivores are highly sensitive to road networks and their extirpation from areas isolated by landscape fragmentation could be particularly problematic given their important roles in ecosystem function and high priority for conservation (Woodroffe and Ginsberg 2000; Estes et al. 2011; Poessel et al. 2014; Baigas et al. 2017). Permeability of road networks for carnivores is key for wildlife conservation in areas where habitat loss and fragmentation are already substantial (Frakes et al. 2015; Baigas et al. 2017).

There has been increased interest in considering landscape connectivity for habitat management and road network planning (e.g., Rudnick et al. 2012; Wade et al. 2015; Lookingbill et al. 2022). Inclusion of mitigation measures in transportation programs and project plans can help restore permeability to road networks across landscapes (Cramer and Bissonette 2005; Loro et al. 2015). Mitigation efforts can include warning signs, animal detection systems, modified road design, fences, bridges and underpasses, and measures to reduce traffic volume/speed (van der Grift et al. 2013). Wildlife crossing structures can effectively mitigate the negative impacts of roads on species (Smith et al. 2015) and have been successful for improving connectivity for species across the globe (e.g., Mata et al. 2005; Grilo et al. 2008; Soanes et al. 2017). However, some mitigation measures are poorly planned or are not placed in suitable habitat for target species (Laurence et al. 2014; Blackburn et al. 2022). Often mitigation measures are placed based on vehicle collision hotspots, rather than movement corridors. There is still much debate over if these metrics are comparable, as well as which is most appropriate when deciding on conservation goals for a mitigation measure (e.g., Kang et al. 2016; Laliberté & St-Laurent 2020; Cerqueira et al. 2021). Further, high construction costs limit mitigation measures that can be implemented; it is therefore important to optimize the placement of crossing structures in road networks in a strategic fashion

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based on long-term conservation goals for target species (Downs et al. 2014; Tarabon et al. 2020).

We examined landscape connectivity of an endangered carnivore in a fragmented landscape that is a mosaic of land uses. Urbanization, agricultural development, and road networks have resulted in isolated and fragmented habitat for this species (Harveson et al. 2004; Jackson et al. 2005; Lombardi et al. 2020a; Veals et al. 2022), as is the case for many wildlife species globally (Forman and Alexander 1998; Clevenger 2012). We used the ocelot (*Leopardus pardalis*) in the United States (US) as a case study for predicting landscape connectivity based on habitat selection. The ocelot is a felid with remnant populations confined to South Texas in an area that has been identified as one of the most rapidly developing urban centers in the US (Leslie 2016). South Texas is a mosaic of private working ranchlands, agricultural fields, and urban areas (Lombardi et al. 2020a). This area hosts the only known breeding populations in the US (Tewes and Everett 1986; Janečka et al. 2011), with a majority of high-quality habitat occurring on private lands (Veals et al. 2022). Ocelots are considered forest cover specialists across their geographic range (Cruz et al. 2019; Wang et al. 2020; Lombardi et al. 2021); ocelots in South Texas demonstrate consistent use and selection of woody cover and show strong negative responses to roads (Blackburn et al. 2020; Veals et al. 2022). Ocelots have demonstrated consistent habitat-relationships over the last several decades despite habitat loss and fragmentation (Lombardi et al. 2020a; Veals et al. 2022), making this species an ideal model for examining trends in landscape connectivity. Ocelots are facing a growing pressure to survive in an increasingly fragmented landscape, exacerbated by the development and extension of road networks. Understanding landscape connectivity for a species like the ocelot, and how populations are threatened by the loss of such connectivity, is necessary to inform conservation and mitigation strategies.

We identified areas along roads and the surrounding landscape that appear to promote ocelot movement. We generally expected areas of high habitat suitability, as measured through habitat selection, to lead to high landscape connectivity for ocelots. This expectation was based on ocelot habitat selection at the landscape scale (2nd order selection, Johnson 1980; Veals et al. 2022), as well as four decades of research on ocelot behavior (Tewes and Everett 1986; Laack 1991; Leonard et al. 2020; Lombardi et al. 2020b) and natural history (Janečka et al. 2011; Janečka et al. 2016; Blackburn et al. 2021). Vehicle collisions are the greatest known source of mortality for ocelots in Texas (Haines et al. 2005; Blackburn et al. 2021). Crossing structures designed for ocelot use have been implemented throughout South Texas since the 1990s, however, they are rarely used by ocelots (Blackburn et al. 2022). Many of these structures were based on roadkill locations and placed in unsuitable habitat (Blackburn et al. 2022). We assessed vehicle collisions, major roadways, and current wildlife crossing structures across the modeled connectivity surface to inform potential locations for future wildlife crossing structures as well as assess variation in performance across resistance values. We provide recommendations for habitat conservation and mitigation measures focused on improving movement across the landscape based on habitat use and landscape resistance.

Methods

Study system

We defined the study area as areas with documented ocelot populations and the surrounding landscape (Janečka et al. 2011; Veals et al. 2022) in South Texas (8 km buffer around population core areas, Fig. 1). This area spans differing land-use practices and vegetation communities. In the US, ocelots exist in only two known isolated breeding populations in South Texas (Haines et al. 2006; Janečka et al. 2011; Janečka et al. 2016). One ocelot population resides on and around Laguna Atascosa National Wildlife Refuge (hereafter refuge) within the Lower Rio Grande Valley (Tewes and Everett 1986; Janečka et al. 2016). The refuge consists of salt flats, marshes, chaparral, and thornshrub-grasslands (Lonard and Judd 1985). The other population occupies private ranchlands approximately 30 km north of the refuge (Tewes and Everett 1986; Janečka et al. 2016; Lombardi et al. 2020b). These ranchlands have a similar vegetation community to the refuge as well as native woodlands dominated by honey mesquite (*Prosopis glandulosa*) and live oak (*Quercus virginiana*) with varying levels of understory thornshrub cover (Leonard et al. 2020). The refuge is situated near developed areas

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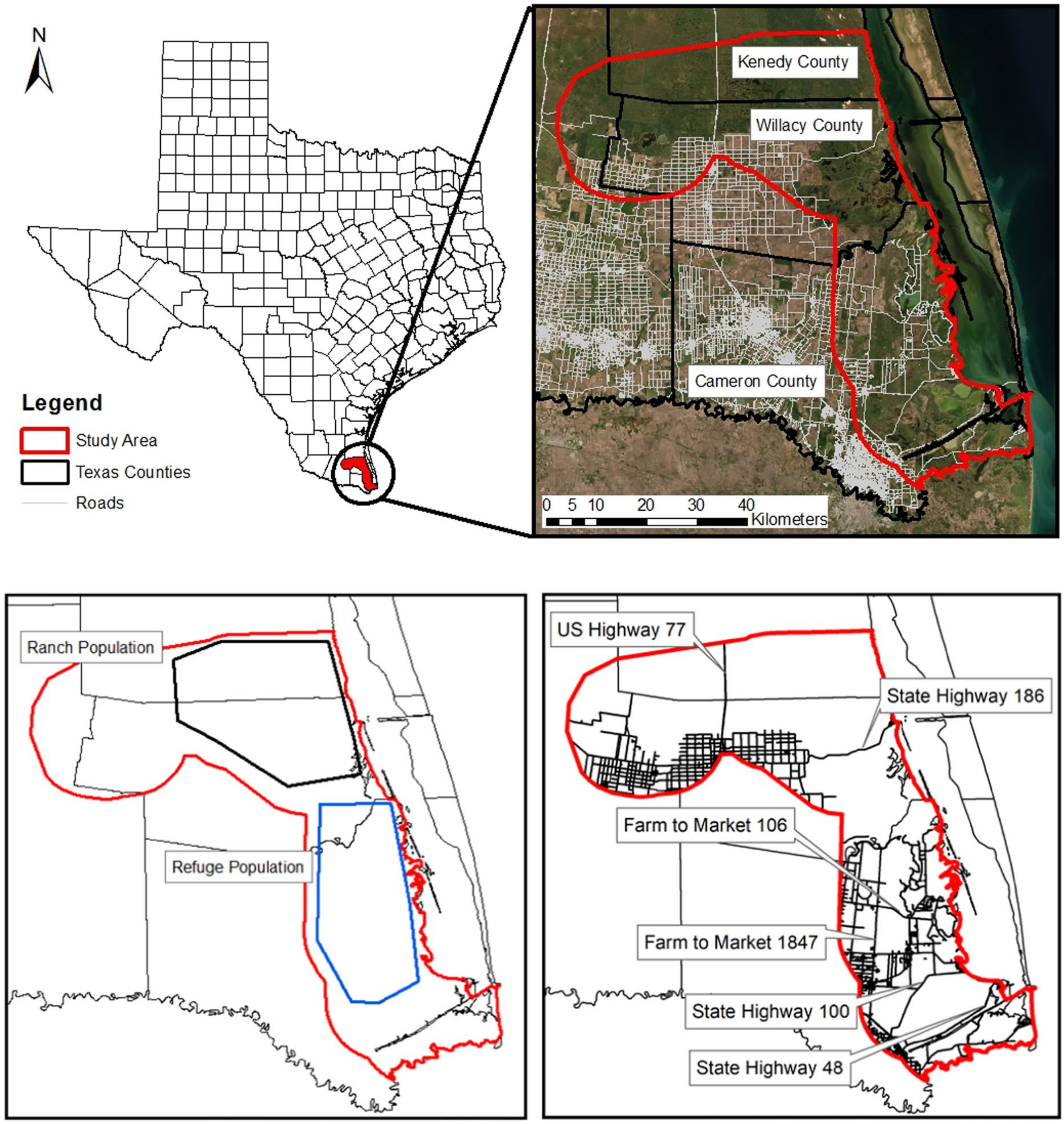

Fig. 1 Study area extent based on an 8 km buffer around known ocelot populations from the dataset from 1982 to 2017, including portions of Kenedy, Willacy, and Cameron counties in South Texas, US. Several key medium- and high-traffic volume roads are indicated by name within the study area for reference

containing a network of highways with an average of 600–11,000 vehicles/day (TXDOT 2019). In contrast, the private ranches are contiguous rangelands with few paved roads bordered by two highways with comparable traffic volumes (1000–10,000 vehicles/day) to the refuge (TXDOT 2019). Genetic analyses have documented little to no genetic interchange between these populations for many generations (Janečka et al. 2011; Janečka et al. 2016). These two populations are separated by ~30 km characterized by high- and low-traffic roads, agricultural fields, wind farms, coastal

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rangeland and prairie, estuarine wetlands, and small patches of thornshrub.

Ocelots use dense vegetation and select for areas with high proportions of woody cover across their geographic range (Horne et al. 2009; Cruz et al. 2019; Wang et al. 2020; Lombardi et al. 2021; Veals et al. 2022). Availability of woody cover in the Lower Rio Grande Valley decreased by 5% of total landcover in the area between 1982 and 2017 (Veals et al. 2022) and became more fragmented, resulting in small, isolated patches of woody cover (Lombardi et al. 2020a). Despite the decline in woody cover, ocelots consistently selected for areas with high proportions of woody cover over the last several decades (Veals et al. 2022). Temporally consistent, high-quality habitat for ocelots exists farther from high-traffic volume roads at the landscape scale (2nd order selection, Johnson 1980; Veals et al. 2022). Ocelots avoided roads at higher orders of selection but did not avoid roads as expected within their home ranges (3rd order selection, Johnson 1980; Veals et al. 2022) which is likely a mechanism for vehicle-induced mortality. Vehicle collisions represent 35–40% of mortality, the highest source of direct mortality for ocelots in this region (Haines et al. 2005; Blackburn et al. 2021). Expansion of road networks will likely lead to a continued increase in transportation-related ocelot mortality and decrease in accessible quality habitat (Haines et al. 2005; Blackburn et al. 2021).

Probability of use

We used probability of use data at the landscape scale for ocelots from Veals et al. (2022). Briefly, Veals et al. (2022) used land-cover and spatial data from radio tracked ocelots over 35 years (1982–2017) to estimate habitat use based on resource selection functions (RSF, Manly et al. 2002) at the second order (home range placement on the landscape, Johnson 1980) with habitat and road variables. Remotely sensed imagery was classified into cover types and annual average daily traffic metrics were used to classify roads. Using a two-staged approach, RSF coefficients were estimated at the individual level and then averaged for each sex and time period. Then, relative probability of use for ocelots was predicted across the study area at 30 m^2 resolution using averaged RSF coefficients for each sex. Resource variables included the proportion of woody cover, proportion of non-woody cover (i.e. herbaceous vegetation), heterogeneity of woody cover, and the log-distance to low-, medium-, and high-traffic paved roads (Supplemental Materials, Veals et al. 2022). Ocelots consistently selected for areas with greater proportions of woody cover and areas farther from high-traffic roads (Veals et al. 2022).

We used Veals et al. (2022) contemporary (i.e., 2015) probability of use layers for male and female ocelots across the same study area. However, due to computation demands of the connectivity analyses, we aggregated the probability of use layers to 90×90 m resolution (Fig. 2a). We determined the median probability of use value using a radius of 3 cells to aggregate raster cells. Our aggregated probability of use layers for male and female ocelots were used to parameterize landscape resistance across the study area.

Focal nodes

We used location data for adult ocelots collected between 1982 and 2017 across South Texas (Veals et al. 2022) as source and destination patches (i.e., focal nodes) in our connectivity analyses. Any 90×90 m raster cell containing ≥ 1 ocelot location was designated as a focal node (Supplemental Materials). We separated male and female ocelot locations to compare connectivity between the sexes. Focal nodes are modeled as either origin or destination points using spatially absorbing Markov chains (SAMC). We chose the pairwise approach to model all combinations of focal nodes in our analyses, such that movement was simulated bi-directionally.

Modeling resistance

We applied a relatively new framework to predict movement and connectivity across landscapes that incorporates the concept of matrix resistance and using Markov chains (e.g., Moorter et al. 2021; Wang 2021; Fletcher et al. 2022). Understanding matrix resistance—how challenging the landscape matrix is for movement (Ricketts 2001)—can be critical for predicting and mapping landscape connectivity (Taylor et al. 1993; Beier et al. 2011). We applied a SAMC framework that separates the impacts of landscape resistance on movement behavior and mortality (Fletcher et al. 2019). This framework can make predictions of movement across complex landscapes and improves upon commonly used least-cost analysis and

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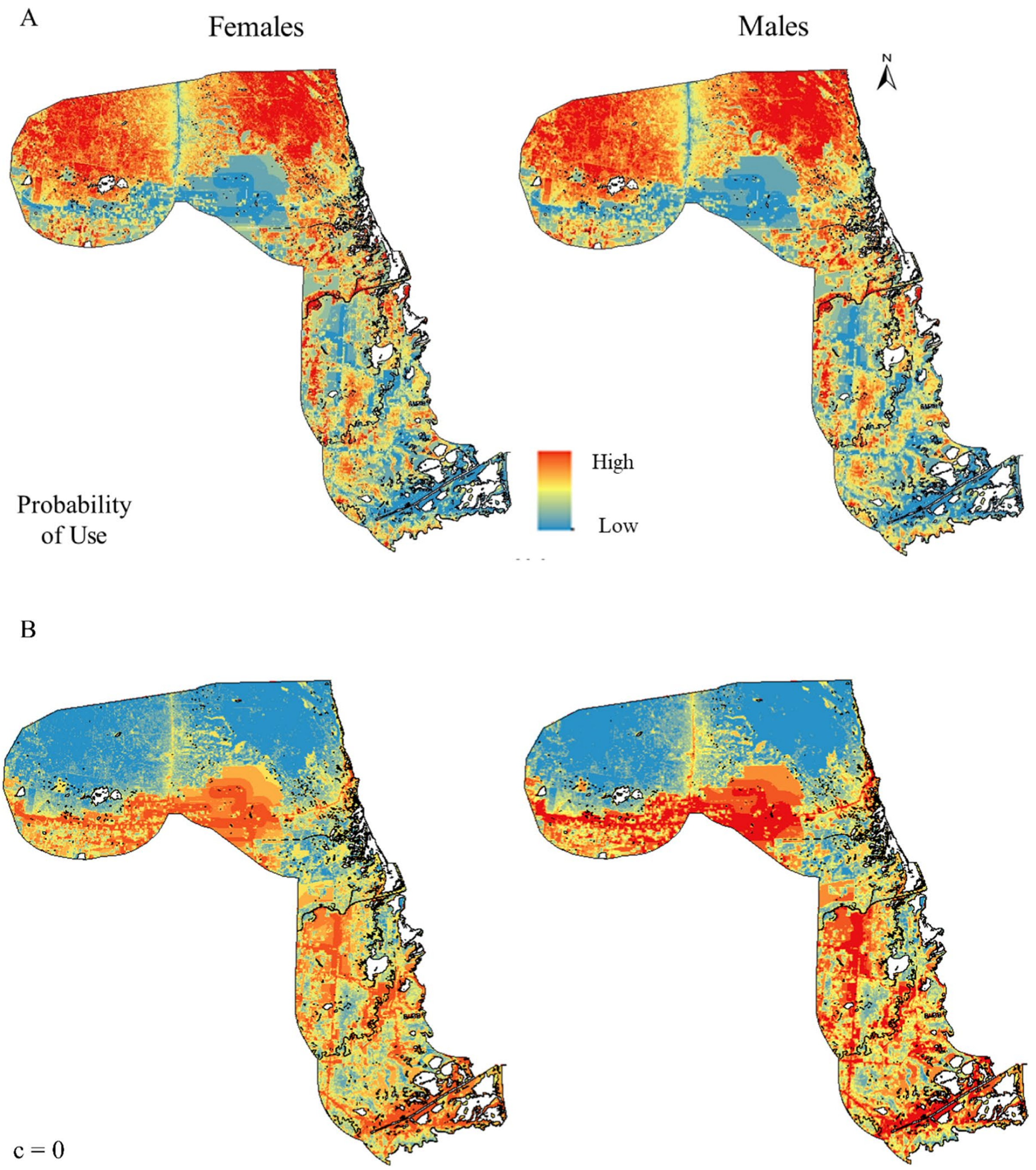

Fig. 2 Probability of use and landscape resistance surfaces for adult ocelots in South Texas, US with females (left) and males (right). The probability of use surfaces (**A**) are based on resource selection functions for habitat and road variables, where high values represent areas with greater selection by ocelots. Resistance surfaces to account for variation in ocelot perception of landscape resistance include approximately linear ($c=0$; **B**), intermediate ($c=0.25$; **C**), and non-linear ($c=0.5$; **D**) transformation of the probability of use surface, where high values represent areas of high resistance to movement

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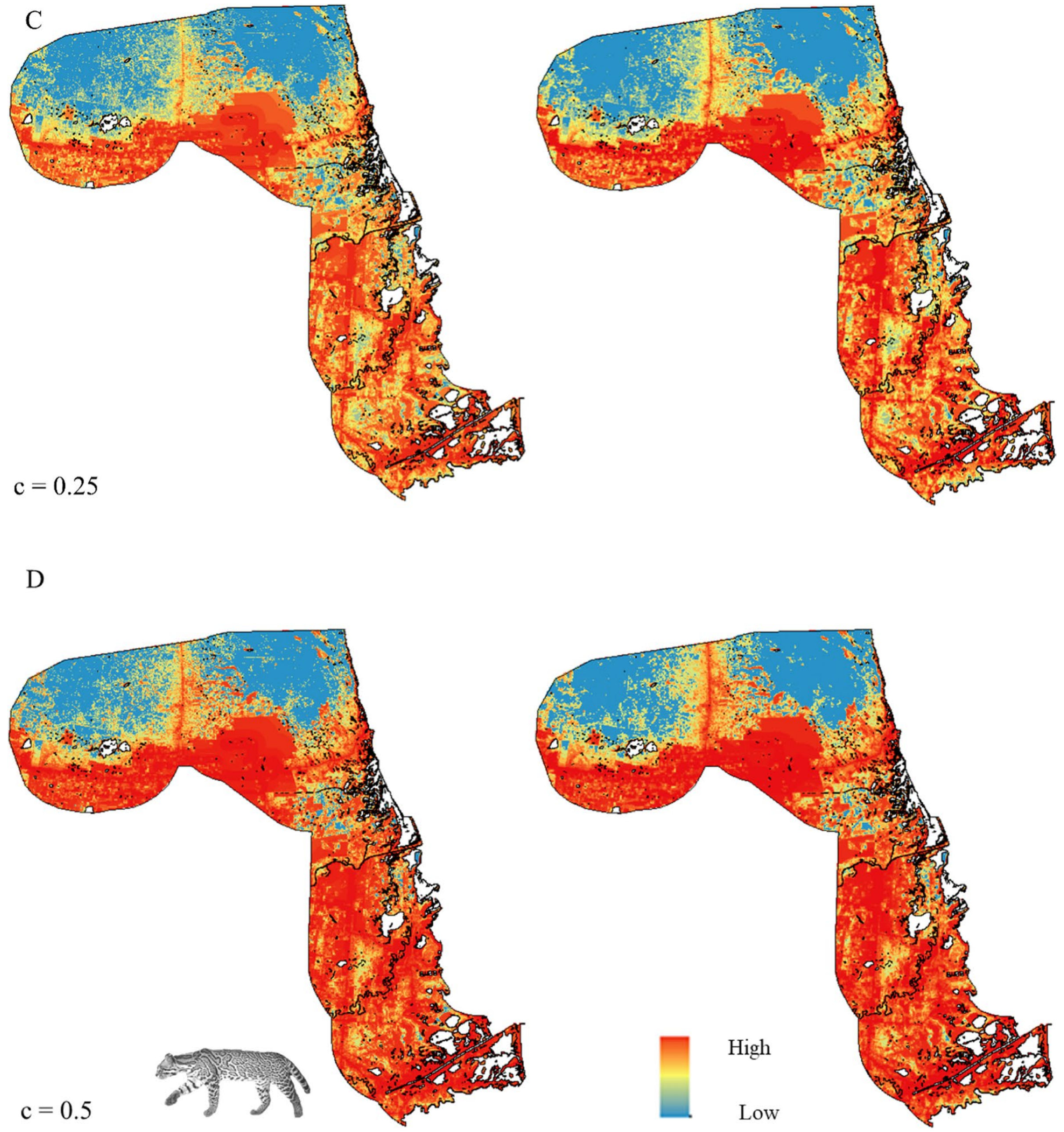

Fig. 2 (continued)

circuit theory in several ways. The SAMC framework extends random walk theory with absorbing Markov chains, which explicitly acknowledge the potential for absorption such as mortality (Ross 2010; Fletcher et al. 2019).

The SAMC is a general and expandable framework for connectivity modelling that builds upon random walk theory (Fletcher et al. 2019). It is closely related to circuit theory (McRae et al. 2008), which can be considered a special case of SAMC (Fletcher et al. 2019; Marx et al. 2020). However, SAMC does not have the same limitations as circuit theory when applied to a large and highly fragmented landscape. Most connectivity models function in a patch-to-patch

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fashion, which limits their use for assessing connectivity over large, highly fragmented landscapes. In highly fragmented systems, there may be so many habitat patches of interest that assessing connectivity among all possible combinations is prohibitive (Pelletier et al. 2014). When more sites are considered habitat patches, SAMC is not computationally slowed by iterative calculations, unlike randomized shortest paths with circuit theory (Panzacchi et al. 2016; Marx et al. 2020). Further, the mathematical framework provides a probabilistic approach that has been optimized to find computationally practical solutions in landscapes comprised of $>2\times10^6$ raster cells (Marx et al. 2020).

In the simplest form, the SAMC requires two maps: a resistance map relevant to movement and a mortality risk map. We were not able to leverage the advantage SAMC provides by decoupling mortality risk from landscape resistance (Fletcher et al. 2019). This was due to inconsistent and opportunistic monitoring of ocelot mortality throughout South Texas (Schmitt et al. 2020; Blackburn et al. 2021). Therefore, we assumed constant mortality risk across the landscape. However, we were able to leverage the advantage of SAMC for predicting connectivity in a system with a large number of habitat patches for assessment across a large raster grid (Supplemental Materials, Marx et al. 2020). South Texas consists of highly fragmented woody cover for ocelots (Lombardi et al. 2020a; 2020b; Veals et al. 2022), therefore we modeled landscape connectivity based on a resource selection-derived resistance surface by applying a SAMC framework.

Animals may perceive and respond to landscape features differently (Stamps 2006; Merrick and Koprowski 2017). We developed three landscape resistance scenarios that varied the relationship between probability of use and landscape resistance to represent individual heterogeneity in perception of functional landscape permeability. We used three different negative exponential curves to transform probability of use values into resistance values (Merrick and Koprowski 2017; Carroll et al. 2020). We calculated one linear and two non-linear resistance or friction surfaces (*f*) using Eq. 1 (Trainor et al. 2013; Keeley et al. 2017), where h is the inverse probability of use value of each pixel obtained from the above resource selection functions, and c is a rescaling parameter determining the shape of the curve relating probability of use and resistance to movement.

$$f = 100 - 99\frac{1 - exp\,(-ch)}{1 - exp(-c)}$$

For the scaling parameter (c), we used values of 0, 0.25, and 0.5, where $c=0$ is a linear function ($f=1-h$) and is the least prohibitive resistance surface, $c=0.5$ approaches a negative exponential ($f=h^{-1}$) and is the most prohibitive resistance surface, and $c=0.25$ produces an intermediate, non-linear resistance surface (Fig. 1). In our system, $c=0$ results in a resistance layer where each one-unit increase in habitat quality equated to a one-unit decrease in resistance. Alternatively, $c=0.5$ results in high resistance when habitat quality is very low. Resistance surfaces varied from values of 0.084–0.363 where cells with a higher value represent the highest resistance to movement (range 0–1).

Connectivity analysis

We were interested in understanding and mapping landscape connectivity across South Texas in relation to roads for male and female ocelots. We applied a SAMC framework following the approach illustrated by Fletcher et al. (2019) and Marx et al. (2020). We built models for both sexes and three resistance surfaces, which yielded 6 models (3 resistance surfaces × 2 sexes).

We ran models using package *samc* in R v 4.1.0 (R Core Team 2019) using the *dispersal* function (Marx et al. 2020) to predict the probability of an ocelot visiting a particular location based on the underlying resistance surface and focal nodes. We ran our models in pairwise mode to account for bi-directional movement between focal nodes (Fletcher et al. 2019; Marx et al. 2020). Additionally, we allowed movement to occur in eight directions from the starting cell.

To validate our predictive connectivity surfaces and compare our different resistance layers, we assessed connectivity values at observed ocelot locations and compared those to random locations. We used observed ocelot locations that were withheld when creating the probability of use layer (Supplemental Materials; Veals et al. 2022), which was the main driver of resistance in our case. We used a Kruskal–Wallis Test to compare ocelot locations to

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random locations. We compared our three resistance surfaces per sex by examining the mean predicted connectivity value surrounding observed locations at 90×90 m. Our goal was to determine if any connectivity surface predicted higher connectivity at observed ocelot locations not used in parameterizing the models, and thus performed better, compared to other surfaces for each sex. Validating also demonstrated if our models were accurately predicting connectivity at observed ocelot locations compared to the background landscape.

Connectivity across roads and mortalities

To assess potential areas for wildlife crossing structures, we examined connectivity predictions across medium- and high-traffic volume roads. Medium traffic volume was classified as between 1000 and 5000 annual average daily traffic (AADT), where 1000 AADT corresponds to <1 car/min, and high traffic volume was >5000 AADT (Supplemental Materials, TXDOT 2019; Veals et al. 2022). These classifications of traffic volume were relative to our study area but compare to similar classification schemes regarding AADT (Jacobson et al. 2016). Paved roads varied in traffic volume, number of lanes, and presence of roadside barriers (i.e., guard rails, mediums), therefore we classified paved roads within the study area based on 33% quantiles of the observed distribution of AADT for the study area (TXDOT 2019; Veals et al. 2022). We extracted predicted connectivity values across medium- and high-traffic roads within the study area from each 90×90 m raster cell from our six models (3 resistance surfaces × 2 sexes). We classified the distribution of connectivity along roads into five quantiles for displaying relative connectivity values from this extraction. Areas with relatively higher connectivity across roads would be more suitable locations for potential crossing structures aimed at improving landscape connectivity and presumed movement of ocelots.

We examined the distribution of estimated connectivity values from our six models in the areas surrounding ocelot road mortalities and completed wildlife crossing structures targeted for ocelots in the study area. We used an independent data set of ocelot road mortality locations ($n=26$) from 1984 to 2017 (Blackburn et al. 2020) and wildlife crossing structures ($n=15$) built for ocelots completed as of 2020 (Blackburn et al. 2022). We used focal statistics to determine the average connectivity value in the neighboring raster cells surrounding road mortalities and crossing structures (radius = 270 m) for each connectivity model. Many of the completed wildlife crossing structures built for ocelots have been placed based on previous road mortalities, typically in areas of non-woody cover that lack the vegetation structure ocelots in South Texas use (Blackburn et al. 2020; Lombardi et al. 2021; Blackburn et al. 2022; Veals et al. 2022). Given the diverging approaches for crossing structures to be placed based on mortality hotspots vs. movement corridors (e.g., Kang et al. 2016; Laliberté & St-Laurent 2020; Cerqueira et al. 2021), we wanted to evaluate if mortality locations as well as current crossing structures were in areas predicted to have high landscape connectivity for ocelots.

Results

Our assessment of functional landscape connectivity using SAMC across three resistance scenarios for ocelots identified areas of highest connectivity for male and female ocelots (Fig. 3). We found minor differences in our resistance surfaces, with the linear resistance surface ($c=0$) predicting the most connectivity across the landscape. The linear resistance surface transformed all probability of use values from the RSFs ≥ 0.90 to resistance values near 0. Our connectivity model predictions ranged from 0 to 1, with 1 representing higher connectivity estimates (Fig. 3). We did not find significant differences between male and female ocelot connectivity across the study area regardless of resistance scenarios. In areas estimated with relatively higher predicted connectivity (≥ 0.50), there was 93.3% overlap between female models and 97.9% overlap between male models.

Predicted connectivity was concentrated around focal nodes and was relatively restricted elsewhere in the study area, regardless of resistance surface. Simulated connectivity between focal nodes identified highly connected areas (Fig. 3). We were not able to identify specific pathways where ocelots were predicted to move across roads (i.e., pinch points); this may have been a function the pairwise approach to model all combinations of focal nodes in our analyses, such that movement was simulated bi-directionally. We observed significant differences between

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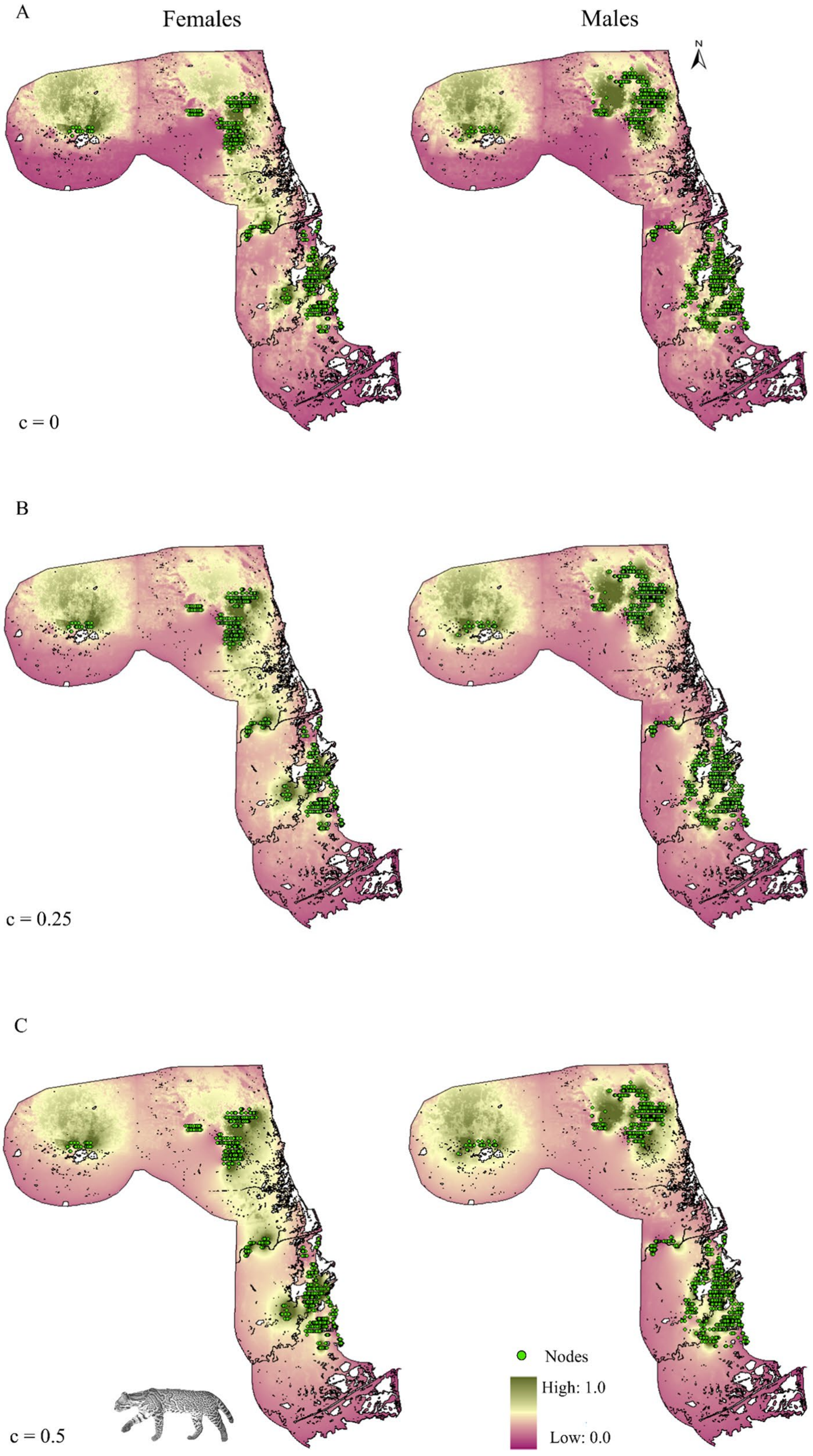

Fig. 3 Connectivity estimates based on the pairwise dispersal model using spatially absorbing Markov chains as a function of 3 increasingly prohibitive resistance functions: linear ($c=0$; **A**), intermediate ($c=0.25$; **B**), and non-linear ($c=0.50$; **C**) for female (left) and male (right) ocelots in South Texas, US. Connectivity measures indicate the probability of a random-walking animal using a given cell. Green circles represent habitat patches (focal nodes) for our models for each sex

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resistance surfaces for both females and males ($P<0.001$, $\alpha=0.05$), with higher predicted connectivity at ocelot locations when $c=0$. This indicated that the linear resistance surface was the most supported based on withheld ocelot locations. Further, predicted connectivity values were higher at withheld ocelot locations compared to random location for both sexes ($P<0.001$, $\alpha=0.05$), indicating our connectivity models discriminated between ocelot use and the background landscape.

We identified areas near roads that are of conservation concern for ocelots of both sexes for all models (Fig. 4). Connectivity across roads was low (0.0–0.3) relative to other portions of the study area, specifically core ocelot habitat. Areas of highest relative connectivity across roads was on State Highway 186 that cuts from east to west, separating the refuge from the northern ranchlands (Fig. 4). Further, we observed that connectivity was limited by several highways across the study site (Fig. 3). Much of the area surrounding the refuge was predicted to have high-connectivity up to road edges (Fig. 3). Specifically, two highways with medium to high traffic volumes overlapped relatively higher connectivity areas near the refuge (Fig. 4). We found no evidence of connectivity between the two populations of ocelots in Texas (Figs. 3 and 4). Across all six models, connectivity was low surrounding mortalities and crossing structures (average >0.1 connectivity) relative to core ocelot habitat. While there was substantial variability in the distribution of connectivity around mortalities and crossing structures (Fig. 5), mortalities were consistently in areas of relatively high connectivity relative to the overall study area and roads.

Discussion

We modeled landscape connectivity for an endangered carnivore based on 35 years of habitat selection and movement data (Veals et al. 2022). Our spatially explicit results identified well-connected areas for habitat conservation and disjoint patches separated by roads. We identified key areas for wildlife crossing structures that could improve landscape permeability based on ecological drivers for ocelot-habitat relationships. We simulated connectivity between habitat patches and identified relatively high connected areas of conservation concern. We examined connectivity at known vehicle collision sites and along medium- and high-traffic roads to inform potential locations for wildlife crossing structures. We provide recommendations for habitat conservation and mitigation measures focused on improving movement across the landscape based on long-term trends in habitat use and landscape resistance.

We predicted functional landscape connectivity using SAMC across three resistance surfaces for male and female ocelots. Connectivity was greatest around focal nodes but was relatively limited elsewhere in the study area. High landscape permeability around focal nodes corresponded to areas with established breeding populations of ocelots and large patches of habitat (i.e., northern ranchlands and refuge). However, we did not observe evidence for connectivity between the two ocelot populations in South Texas (Fig. 3). In a highly fragmented landscape like South Texas and under a modeling approach where we simulated bi-directional movement between focal nodes, the SAMC framework might not be able to identify potential pinch points. Regardless, our findings support previous work on ocelot connectivity in the area (Lehnen et al. 2021) as well as genetic analyses showing little to no genetic interchange between these populations (Janečka et al. 2011; Janečka et al. 2016).

We found no clear existing, continuous movement corridor between the two ocelot populations in South Texas, similar to a previous study (Lehnen et al. 2021). The two populations of ocelots in South Texas have been isolated from each other for multiple generations (Janečka et al. 2011; Janečka et al. 2016). The populations are separated by ~30 km of a highly fragmented landscape (Lombardi et al. 2020a, 2020b; Veals et al. 2022). The core population areas (i.e., northern ranchlands and refuge) appeared relatively well connected and there was strong evidence of limited connectivity between the two populations (Lehnen et al. 2021). Lehnen et al. (2021) connectivity models identified marginal and narrow bands of habitat as the most likely corridors available to dispersing ocelots. Similar to our results, their models also predicted connectivity leading west and south of the refuge; however, they also concluded that this may lead ocelots to sink habitats as only small, fragmented habitat patches of woody cover remain in those areas (Lehnen et al. 2021). Their results indicate the importance of how focal nodes and habitat patches are defined for connectivity predictions (Lehnen et al.

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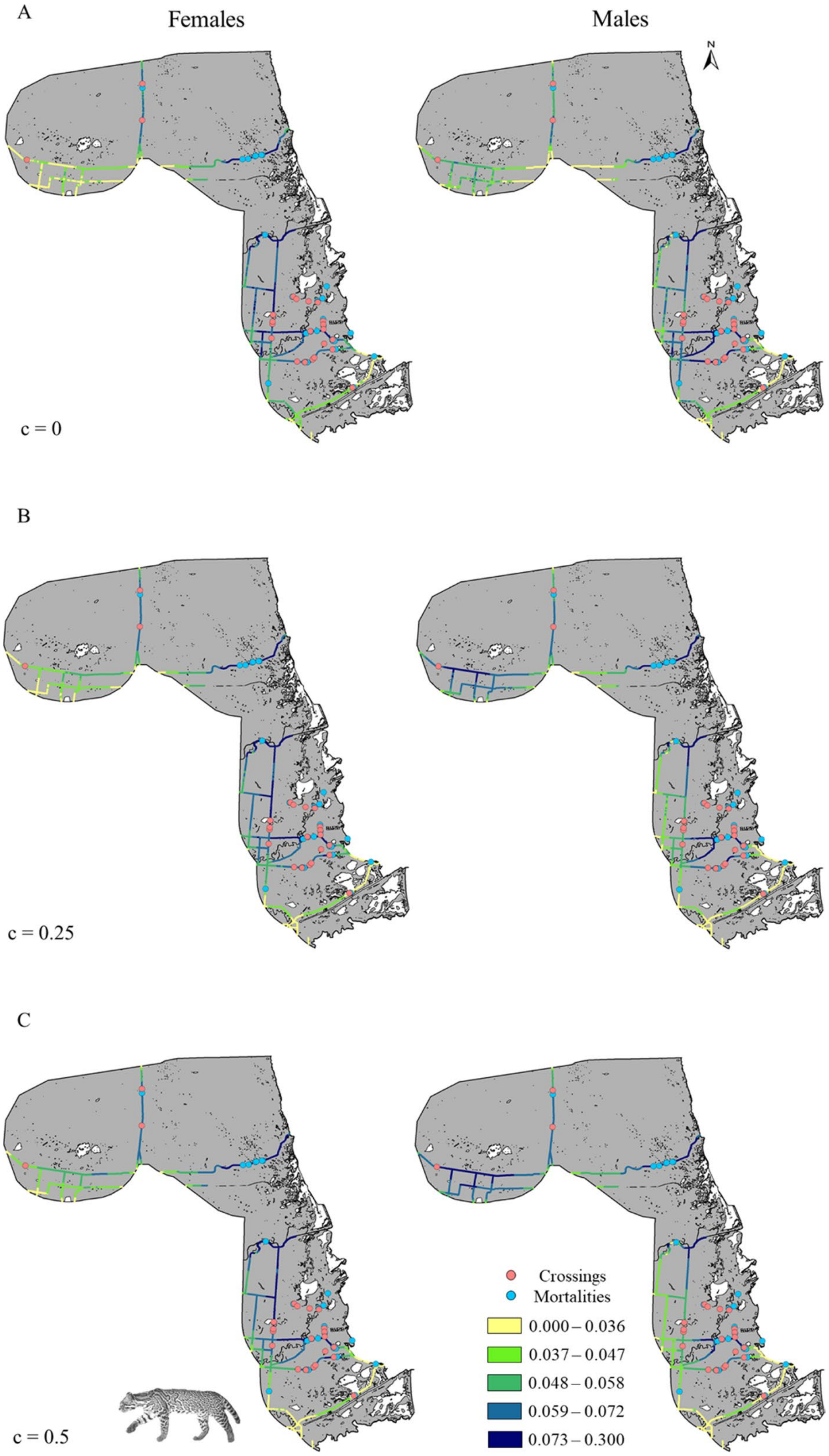

Fig. 4 Connectivity estimates across high- and medium-traffic volume roads based on the 3 increasingly prohibitive resistance functions: linear (*c* = 0; **A**), intermediate (*c* = 0.25; **B**), and non-linear (*c* = 0.50; **C**) for female (left) and male (right) ocelots in South Texas, US. Connectivity ranged from 0–1 for our models and we categorized connectivity based on five quantiles for the distribution of values along roads. Therefore, connectivity across roads was relatively higher in cool colors (blue and purple) than warmer colors (green and yellow). Blue circles represent known ocelot road mortality locations and pink circles represent completed wildlife crossing structures targeted for ocelots within the study area

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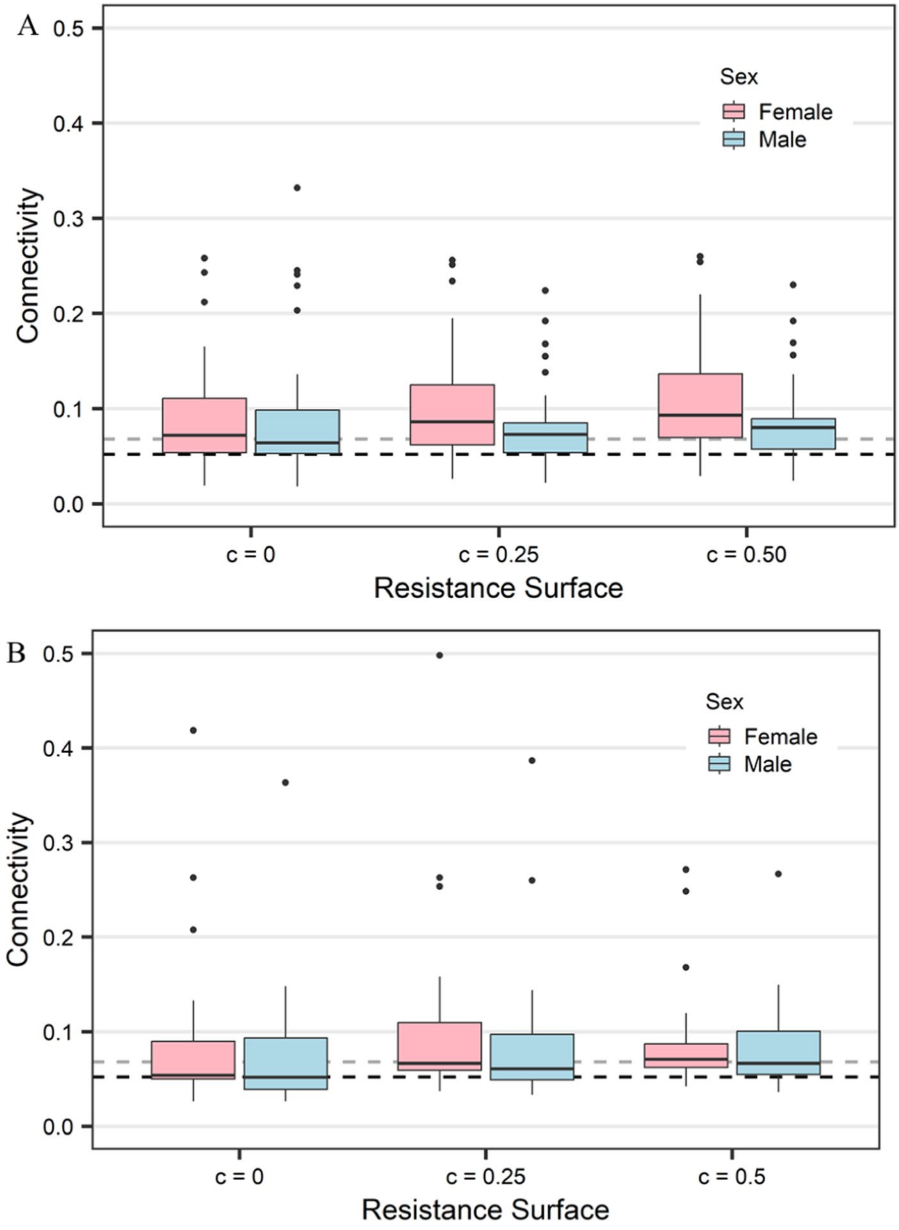

Fig. 5 We examined the distribution of estimated connectivity values from our six models (3 resistance surfaces × 2 sexes) surrounding ocelot road mortality locations (**A**) and wildlife crossing structures (**B**). We used an independent data set of ocelot road mortality locations ($n = 26$) from 1984–2017 and wildlife crossing structures ($n = 15$) built for ocelots completed by 2020 within the study area. The dashed gray line represents the average connectivity across our six models at the study area extent. The dashed black line represents the average connectivity across our six models around roads at 90 × 90 m resolution. Our models were based on increasingly prohibitive resistance functions: linear ($c = 0$), intermediate ($c = 0.25$), and non-linear ($c = 0.50$). Connectivity values for our models ranged from 0–1

2021). Our analyses were based on a multi-decadal dataset on ocelots ($n = 78$) with our focal node definition being indicative of ocelot space use. While our methods differed from Lehnen et al. (2021), we found evidence for similar patterns in ocelot connectivity.

Characterization of landscape resistance is a crucial step in connectivity analyses as results are sensitive to the underlying surface (Zeller et al. 2014; Wade et al. 2015; Merrick and Koprowski 2017). Despite the importance of this step, we found minor differences in our resistance surfaces for male and female ocelots, with high overlap across models in predicted high connectivity areas. Our linear resistance surface ($c = 0$) predicted the most connectivity across the landscape. Increasingly prohibitive resistance surfaces ($c = 0.25$ and $c = 0.50$) may simulate landscape permeability perceived by ocelots that are less prone to dispersing (i.e., residents). Given that our models were parameterized using data from resident ocelots, this is likely why our linear surface was

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the best fit. Our models show areas of high-connectivity around intact woody cover in areas with known breeding populations of ocelots (Haines et al. 2006; Janečka et al. 2011; Janečka et al. 2016). Within these areas, connectivity was relatively consistent across models. Comparing the resistance scenarios revealed the impact roads have on ocelot connectivity through the increasing resistance of areas closer to high-traffic roads. Resistance scenarios varied the relationship between probability of use and landscape resistance to represent heterogeneity in perception of functional landscape permeability. However, we did not observe significant differences across our resistance surfaces in predicted high-connectivity areas for male and female ocelots.

We found no significant differences in functional connectivity for male and female ocelots, which did not support our hypothesis for male-biased landscape permeability (e.g., Janečka et al. 2007; Poessel et al. 2014; Kantek et al. 2021). We built our connectivity models from resource selection functions applied to habitat use data from resident adult ocelots, which indicate that male ocelots were less likely to avoid roads than females when selecting their home ranges (Veals et al. 2022). Most vehicle collisions in the area are young males (Haines et al. 2005; Blackburn et al. 2022) and most transient individuals that dispersed across the landscape were males (Haines et al. 2005; Blackburn et al. 2021). However, we did not have a large enough sample size to include transient individuals (n = 3) into our parameterization of probability of use by ocelots. Focusing on resident ocelots could explain why we did not observe differences between the sexes for connectivity. Our models predict landscape connectivity for resident ocelots, which could introduce potential bias to areas of high conductance as there are limits to basing movement predictions on non-transient individuals (e.g., Jackson et al. 2016; Diniz et al. 2020). Inter-individual variability in dispersal behavior can impact estimates of functional landscape connectivity (Palmer et al. 2014; Osipova et al. 2019). Another medium-sized felid and habitat specialist, the Iberian lynx (*Lynx pardinus*), used suboptimal habitat and took more risks such as crossing roads while dispersing (Gastón et al. 2016). While other carnivores have demonstrated individual variability in their response to roads (e.g., Ascensão et al. 2014; Carvalho et al. 2018), resident ocelots did not demonstrate functional responses to roads within their home ranges (Veals et al. 2022). By parameterizing our resistance surface based on 2nd order habitat selection (Veals et al. 2022), our model incorporates home range establishment based on multiple decades of ocelot behavioral data.

We aimed to identify and recommend areas for wildlife crossing structures that may reduce ocelot mortality and increase landscape permeability. It can take time for wildlife to acclimate to newly placed wildlife crossing structures (Clevenger et al. 2009; Seidler et al. 2018). While transient individuals often engage in more risky behavior (e.g. Gastón et al. 2016), it is unclear the extent to which a transient ocelot would use a novel feature such as a wildlife crossing structure. Future research should focus on monitoring dispersing and transient ocelots to better understand landscape connectivity and risky behavior regarding roads. There are still many knowledge gaps for ocelot behavior around current wildlife crossing structures based on physical features of the structure, road type, and traffic volume, especially at night. Further work is needed to understand ocelot movement ecology between resident and transient individuals and the impacts of human infrastructure on these behaviors.

A resident female ocelot was documented crossing a high-traffic road (State Highway 186, Fig. 1) several times in 2019, 2021, and 2022 as part of her regular home range (Lombardi et al. *in review*). This female crossed in areas of relatively high connectivity compared to roads on average in the study site (Fig. 4). This emphasizes the importance of incorporating resident ocelot data in the modeling of connectivity across roads in South Texas. Resident animals may be more willing to use novel wildlife crossing structures given time to habituate. Resident ocelots were found to use areas near roads, regardless of traffic volume, in proportion to availability within their home range (Veals et al. 2022). Additionally, probability of mortality from vehicle collisions increased for ocelots with greater density of low-traffic roads within their home range (Blackburn et al. 2021). While transient ocelots have a higher mortality risk (Haines et al. 2005; Blackburn et al. 2021), modeling connectivity for resident ocelots is likely more applicable for long-term mitigation efforts, habitat conservation, and population persistence than transient individuals.

Connectivity across medium- and high-traffic roads was lower compared to the rest of the study

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area, especially core ocelot habitat. However, we were able to identify areas of relatively higher connectivity across these roads based on our six models. We observed several high-traffic roads in the study area functioned as barriers to ocelot movement across the landscape given that these roads separate high-connectivity areas and are immediately surrounded by lower connectivity (Fig. 3). These areas of relatively higher connectivity across roads, especially roads that separate well connected habitat patches in the northern ranchlands and the refuge, would be the best areas to focus mitigation efforts (Schmidt et al. 2020). Wildlife crossing structures placed in these areas could potentially increase landscape connectivity for ocelots in South Texas (Fig. 4).

Mitigation efforts for the negative effects of roads on wildlife should consider areas of high vehicle collision rates, potential habitat, and movement corridors (Clevenger and Ford 2010; Zeller et al. 2018; Cerqueira et al. 2021). Thus, road segments where wildlife movement and road mortality are both high should be considered priorities (e.g., Clevenger 2012; Rytwinski et al. 2016; Mohammadi et al. 2018). However, it is not clear to what degree mortality and movement paths across road segments correspond. Some studies suggest areas of high movement coincide with areas of high road mortality (Girardet et al. 2015; Kang et al. 2016), whereas others found little overlap between corridors and concentrated roadkill locations (Boyle et al. 2017; Laliberté and St-Laurent 2020; Cerqueira et al. 2021). Similar to other taxa, we found road mortalities in the study area occurred in areas of lower connectivity. Relative to roads ~ 75% of road mortalities fell within areas with < 0.1 predicted connectivity (Fig. 5). Predicted connectivity was relatively lower at road mortality locations and along roads in general compared to core habitat areas in the study area.

Connectivity in close proximity to roads was relatively lower than areas with more suitable habitat. Building crossing structures in mortality hotspots may reduce ocelot-vehicle collisions, especially for resident ocelots, however, we found evidence that these areas do not coincide with potential movement corridors. On average, connectivity was predicted to be quite low across our study areas, except in key habitat patches. Road mortalities occurred in low connectivity areas compared to core habitat, but ocelots were trying to cross roads in areas of higher connectivity relative to roads and the study area in general (Fig. 5). Ocelot road mortalities were occurring along higher connectivity areas relative to the restrictive surrounding landscape.

Many previous wildlife crossing structures built for ocelots were not well-planned or placed in suitable habitat for ocelots (Blackburn et al. 2022). Fifteen crossing structures have been placed on highways for ocelots in the study area as of 2020 (Kline et al. 2019; Tewes et al. 2021); these were placed based on previous roadkill sites in an effort to reduce road mortalities. Current crossing structures, like road mortalities, occurred in areas of lower connectivity relative to core ocelot habitat (Fig. 5). While some crossing structures, such as those placed on State Highway 100 and Farm to Market 106 occurred in areas with higher connectivity compared to roads (Fig. 3), most current crossing structures were improperly placed according to our six models (Fig. 5) such as those on Farm to Market 1847 and State Highway 48 (Fig. 3).

Our models predicted several areas of importance for resident ocelots. Wildlife crossing structures for resident ocelots should be placed in areas of relatively high conductance near roads with well-connected habitat on both sides of the road (Figs. 3 and 4; Blackburn et al. 2022). The eastern stretch of State Highway 186 was predicted to have relatively high connectivity across all six of our models, compared to roads in general (Fig. 4). This highway bisects the two known ocelot populations with high quality habitat occurring on both sides of the road (Figs. 2 and 3). Further, four documented road mortalities occurred on this stretch of State Highway 186 (Blackburn et al. 2021, 2022) and this same high-traffic road was crossed successfully by a resident female ocelot multiple times (Lombardi et al. *in review*). This stretch of highway may prove to be a unique location where movement corridors and roadkill hotspots overlap. Crossing structures for ocelots have the potential to reduce road mortalities as well as improve connectivity across the landscape and barriers if placed near current core ocelot habitat. Future wildlife crossing structures for ocelots placed on State Highway 186 could present the unique opportunity to test connectivity predictions and mortality hotspots, as well as prove incredibly useful for ocelot conservation.

Information on the impact roads have on ocelot landscape connectivity and movement can be integrated into transportation projects with strategic

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placement of crossing structures. Our analyses indicate ocelots occur in a highly fragmented landscape within the US. We found no evidence to suggest there is movement between the two known breeding populations in Texas. Further, high-traffic roads and habitat availability played important roles in predicting functional connectivity for ocelots. We identified high connectivity areas which are often separated by a single highway. Crossing structures that would enhance connectivity among these areas should be prioritized. We recommend mitigation measures focused on improving landscape permeability for the ocelot in South Texas.

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Data availability The dataset analyzed in this current study are from previously published work (Lombardi et al. *in review*; Sergeyev et al. *in review*; Veals et al. 2022).

Declarations

Conflict of interest All authors declare that we have no competing interest that are directly or indirectly related to the work submitted for publication.

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