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RESEARCH ARTICLE

Landscape patterns of ocelot–vehicle collision sites

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Abstract
Context Road networks can negatively impact wildlife populations through habitat fragmentation, decreased landscape connectivity, and wildlife-vehicle collisions, thereby influencing the spatial ecology and population dynamics of imperiled species. The ocelot (*Leopardus pardalis*) is a federally endangered wild felid in South Texas, with a high mortality rate linked to vehicle collisions.
Objectives Using a multi-scale approach, we quantified and examined landscape spatial structure at ocelot roadkill locations, and between roadkill locations of male and female ocelots.
Methods We quantified the spatial distribution of land cover types at 26 ocelot–vehicle collision sites in South Texas that occurred from 1984–2017. We compared landscape metrics of woody, herbaceous, and bare ground cover types across multiple spatial scales at roadkill locations to those from random road locations, and between male and female ocelots.
Results Roadkill sites consisted of 13–20% more woody cover than random locations. Woody patches at roadkill sites were 7.1–11% larger (2.4 ha) closer to roads and spaced 10–16 m closer together farther away from roads compared to random locations. Percent woody cover was the best indicator of ocelot–vehicle collision sites; there were no differences in woody cover between male and female road mortality locations.
Conclusion These findings suggest that ocelots are likely struck by vehicles while crossing between habitat patches. Roads that bisect areas of woody cover have negative impacts on ocelots by increasing habitat fragmentation and vulnerability to vehicle collisions. Crossing structures should be placed in areas with ≥ 30% woody cover and 3.5 ha woody patches.

Keywords Landscape ecology · Multi-scale spatial analyses · Ocelot · Wildlife-vehicle collisions · Wildlife crossing structures

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Introduction

Roads can negatively impact survival and movements of wildlife, including reptiles and amphibians (Marsh et al. 2005; Shephard et al. 2008), birds (Laurance et al. 2005), and mammals (Oxley et al. 1974; Groot Bruinderink and Hazebroek 1996). Negative impacts

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may be direct, due to vehicle collisions and physical barriers to movement, or indirect, when roads act as functional barriers reducing gene flow and reproductive success (Harris and Scheck 1991; Forman and Alexander 1998; Smith and Dodd 2003; Riley 2006; Litvaitis et al. 2015). Roads are often the principal threat to successful dispersal of wildlife within urban areas (Forman and Alexander 1998), and vehicle collisions have become an increasing source of wildlife mortality as transportation infrastructure increases because of urban sprawl (Forman et al. 2003). Road mortality has been shown to impact population demographics of species of conservation concern (e.g., Kerley et al. 2002; Cypher et al. 2009), and population sizes of threatened or endangered species, including the Florida panther (*Puma concolor coryi*) and Key deer (*Odocoileus virginianus clavium*) (Evink et al. 1996; Land and Lotz 1996). Landscape structure and habitat suitability are leading predictors of vehicle collision locations for mammals, passerines, and herpetofauna worldwide (Carvalho and Mira 2011; Roger et al. 2012; Medinas et al. 2013). Understanding the relationship between landscape structure and wildlife-vehicle collisions is critical for the conservation of populations that are negatively affected by roadways.

Spatial structure of land cover types can dictate animal space use, movement, and abundance (Thornton et al. 2011; Baigas et al. 2017; Marchand et al. 2017). For example, an evaluation of landscape spatial structure is useful in the assessment of habitat fragmentation for wild felids (Jackson et al. 2005; Zemanova et al. 2017). However, the relationship between landscape structure and road mortality patterns remains largely unknown for many species, particularly those threatened or endangered. Studies suggest wildlife-vehicle collisions are often spatially aggregated (Main and Allen 2002) and occur along roadways near natural vegetation cover (Romin and Bissonette 1996; Clevenger et al. 2003). Further, many ecological patterns are influenced by elements acting at multiple spatial scales (Wieins 1989; Bauder et al. 2018). The spatial scale at which a landscape feature has the strongest effect on species response (e.g., movement, abundance) is termed the "scale of effect," and although the "scale of effect" varies with the response variable, it does not always vary in a predictable manner (Jackson and Fahrig 2012; Moraga et al. 2019). Without previous multi-scale studies to base analyses of the effects of landscape structure on wildlife behavior, it is recommended to estimate the "scale of effect" empirically using a multi-scale study design (Moraga et al. 2019). Understanding landscape patterns and scale associated with wildlife-vehicle collisions can inform mitigation strategies for sensitive species within a fragmented landscape.

The ocelot (*Leopardus pardalis*) is a medium-sized neotropical felid that is widely distributed from South America through Mexico, with only remnant populations in the United States (U.S.) in the southern portion of Texas (Caso et al. 2008). Though ocelots are of least concern throughout much of their geographic range, Texas represents their northern distribution limit where they are listed as state and federally endangered (USFWS 1982; TPWD 2018). Fewer than 80 ocelots remain in the U.S. (Tewes 2019), divided between 2 isolated breeding populations in the eastern Coastal Sand Plain and the Lower Rio Grande Valley of Texas (Janečka et al. 2011, 2016).

Ocelots in this region are habitat specialists with spatial patterns strongly linked to dense thornshrub (Harveson et al. 2004). Ocelots select for areas with $\geq 75\%$ thornshrub canopy cover with a strong preference for habitat with $> 95\%$ canopy cover (Horne et al. 2009). This dense thornshrub cover type used by ocelots is uncommon throughout the southernmost 13 counties of Texas, as an estimated $< 1\%$ of this area presently contains suitable ocelot habitat (Tewes and Everett 1986). Native woodland in the Lower Rio Grande Valley declined 91% between the 1930s–1980s due to the expansion of agriculture and urban development and human population growth (Tremblay et al. 2005; Lombardi et al. 2020a). The challenge for ocelots to survive in an increasingly fragmented landscape is further exacerbated by the development and expansion of road networks, as vehicle collisions represent the highest source of direct mortality for ocelots in this region (Haines et al. 2005).

Few studies have examined the spatial structure of land cover of South Texas that may influence ocelot movement and dispersal (Harveson et al. 2004; Jackson et al. 2005). Schmidt et al. (2020) conducted a broad scale analysis to identify predictors of ocelot road mortality in South Texas. However, the identification of spatial patterns in the landscape associated with ocelot–vehicle collisions at the appropriate scale can help precisely determine critical locations where ocelots may be vulnerable to vehicle mortality. This information can then be integrated into mitigation strategies. The goal of this study was to understand the scale of effect of landscape structure associated with ocelot–vehicle collisions and aid conservation planners in the development of mitigation strategies. Our main objectives were: (i) to quantify the spatial distribution of land cover types at ocelot–vehicle collision locations, (ii) to determine the scale at which spatial patterns of land cover at ocelot–vehicle collision locations differ from landscape spatial structure across our study area, and (iii) to compare spatial structure of landscape features at vehicle collision sites between male and female ocelots.

Methods

Study area

Our study area is located in the 3 southernmost coastal counties of Texas: Cameron, Kenedy, and Willacy. Ocelots reside in 2 isolated breeding populations within these counties (Tewes and Everett 1986; Janečka et al. 2016). The southernmost ocelot population, the "Refuge Population", occurs in and around the Laguna Atascosa National Wildlife Refuge (26.2289° N, 97.3467° W), a federally protected area in Cameron County. The northernmost population, the "Ranch Population", occurs on private lands primarily in Kenedy and Willacy counties (Tewes 2017; Lombardi et al. 2020b). Cameron and Willacy counties lie within the Lower Rio Grande Valley, which has been substantially modified by urban development and agriculture over the past century (Leslie 2016). Urban expansion in this region has increased anthropogenic infrastructure, including housing developments, shopping centers, and road networks (Tiefenbacher 2001; Lombardi et al. 2020a).

Our study area represents a transition zone between temperate and tropical conditions, with humid subtropical and semiarid climates resulting in hot summers and mild winters (Leslie 2016). Rainfall fluctuates seasonally and among years with an annual average of 660 mm (Norwine and John 2007). This region is in the Tamaulipan Biotic Province, constituting of hardwood and dense thornshrub forest. Dominant woody vegetation includes Texas ebony (*Ebenopsis ebano*), honey mesquite (*Prosopis glandulosa*), spiny hackberry (*Celtis pallida*), live oak (*Quercus virginianus*), lime prickly ash (*Zanthoxylum fagara*), huisache (*Acacia farnesiana*), and Texas lantana (*Lantana horrida*; Harveson et al. 2004; Leslie 2016).

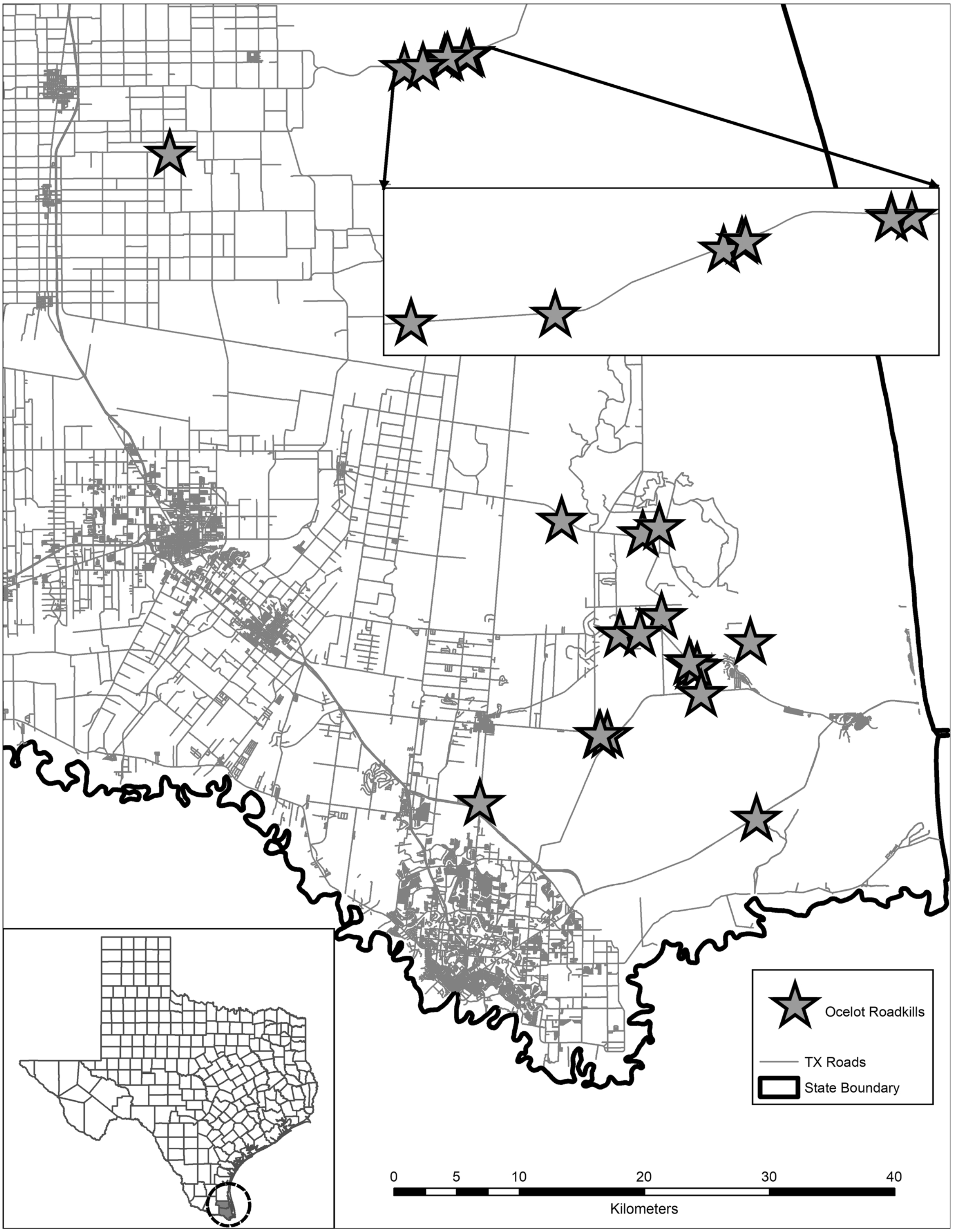
Data collection

There were 50 recorded (U.S. Fish and Wildlife Service; Texas Department of Transportation) ocelot–vehicle collisions in the Lower Rio Grande Valley during 1982–2017. Of those records, 32 had documented geographic coordinates. The spatial accuracy of 2 road mortality locations did not fall on a road and were removed from analysis. Four ocelot–vehicle collisions were within completely urbanized areas; initial data analysis indicated these were aberrations compared to other mortality locations, thus were not included in the analyses. The final data set consisted of 26 known road mortality locations: 18 males, 7 females, and 1 unknown (Fig. 1). The ocelot–vehicle collisions were collected through incidental sightings over the 35-year time frame of this study. As such, we acknowledge the potential bias in our nonsystematic sampling design. We defined our area of interest by generating a 10 km buffer around the aggregated road mortality locations to include a broad possible area these ocelots could have used. Within our area of interest, there is a total of 3381 km of roads.

Landscape analysis

We used 30 m LANDSAT satellite imagery that overlapped with the timeframe of known ocelot–vehicle collisions to evaluate spatial structure of land-cover features in the study area. We acquired 15 LANDSAT images taken within 2 years of each collision through the U.S. Geological Survey Global Visualization Viewer (https://glovis.usgs.gov/). Images consisted of 10 LANDSAT 5 Thematic Mapper scenes (1986–2010) and 5 LANDSAT 8 Operational Land Imager scenes (2014–2017; Table 1).

We created land use cover maps using an unsupervised image classification (Xie et al. 2008; Lombardi et al. 2020a) in ERDAS IMAGINE 2018 (Hexagon Geospatial, Norcross, GA). We grouped each image into 4 cover classes: woody vegetation cover, herbaceous vegetation cover (i.e., non-woody), bare ground, and water. To properly address and classify urban areas, we fused layers of digitized urban areas from


Ocelot Roadkills
TX Roads
State Boundary
0
5
10
20
30
40
Kilometers

◀**Fig. 1** Locations of 26 ocelot–vehicle collision locations during 1984 to 2017 in Cameron and Willacy counties of South Texas, USA. The cluster of road-kills to the north come from the Ranch population of ocelots, the group to the south come from the Refuge population

1987, 1992, 2000, 2008, and 2016 based on spatial data from the U.S. Census Urban Area from the Texas Natural Resource Information System (TNRIS, Austin, TX). Cropland varied by year and season and often had similar spectral signatures to woody cover, which led to inaccurate images. Therefore, we manually digitized crop fields for each image and fused these layers to our classified imagery in addition to the digitized urban layers. Final imagery included 6 cover classes: woody, herbaceous, bare ground, water, cropland, and urban. We conducted accuracy assessments on each image by generating 200 random points across each satellite image, assigning each random point to 1 of the 6 classes, and compared the observed cover class to the expected cover class from the classified image. We used a threshold of $\geq$ 85% accuracy for image classifications (Jensen 2016; Pulighe et al. 2016).

We quantified landscape characteristics within multiple spatial extents surrounding ocelot road mortality locations to estimate the potential scale of effect. To evaluate land cover variation by spatial scale, we measured landscape variables within each of 11 nested extents surrounding road mortality locations from 150–1650 m in radii at 150 m increments. The largest spatial extent (1650 m) encompassed the maximum average daily movement length of radio-marked ocelots (M. Tewes, Texas A&M University-Kingsville, unpub. data). Increments of 150 m were used to create fine-scale spatial increments while incorporating enough pixels in each new spatial extent to accurately quantify land cover patterns. To evaluate differences of land cover patterns at mortality sites from those across the landscape, we established 1 paired random road location for each road mortality location. From each mortality location, we doubled the largest spatial scale value (1650 m) and increased this by a randomly generated factor between 0 and 1 to estimate the distance to the random road location (Perotto-Baldivieso et al. 2011). This technique ensured there were no buffer overlaps between mortality and random locations. The random road locations were placed on the same road as the corresponding ocelot–vehicle collisions as best as possible, and were analyzed with the same 11 spatial extents for comparison (Fig. 2).

Table 1 Years of LANDSAT satellite imagery data acquisition used to quantify spatial scale of landscape features on ocelot–vehicle collisions in South Texas, USA during 1984 to 2017, and the number of vehicle collisions within each year

LANDSAT imagery year	Number of ocelot–vehicle collisions
1986	3
1988	4
1990	3
1994	2
1995	1
1999	2
2000	1
2001	2
2004	1
2010	1
2014	2
2015	2
2016	1
2017	1

For each road mortality and random location, we clipped each extent to the corresponding classified imagery and quantified landscape structure for woody, herbaceous, and bare ground cover types. We calculated 7 class-level landscape metrics (Table 2) previously used to evaluate habitat features of endangered felids (Jackson et al. 2005; Zemanova et al. 2017): percent land cover (PLAND, %), patch density (PD, patches/ha), largest patch index (LPI, %), edge density (ED, m/ha), mean patch area (MPA, ha), mean nearest neighbor (ENN, m), and aggregation index (AI, %). These metrics described the amount and spatial distribution of land cover features within each scale and describe the fragmentation across the landscape encountered by ocelots (Jackson et al. 2005). All landscape metrics were calculated using FRAGSTATS 4.2 (McGarigal et al. 2012).

Statistical analysis

We used 2 approaches to compare landscape metrics between vehicle collision sites and paired random locations. First, we tested the hypothesis that neither

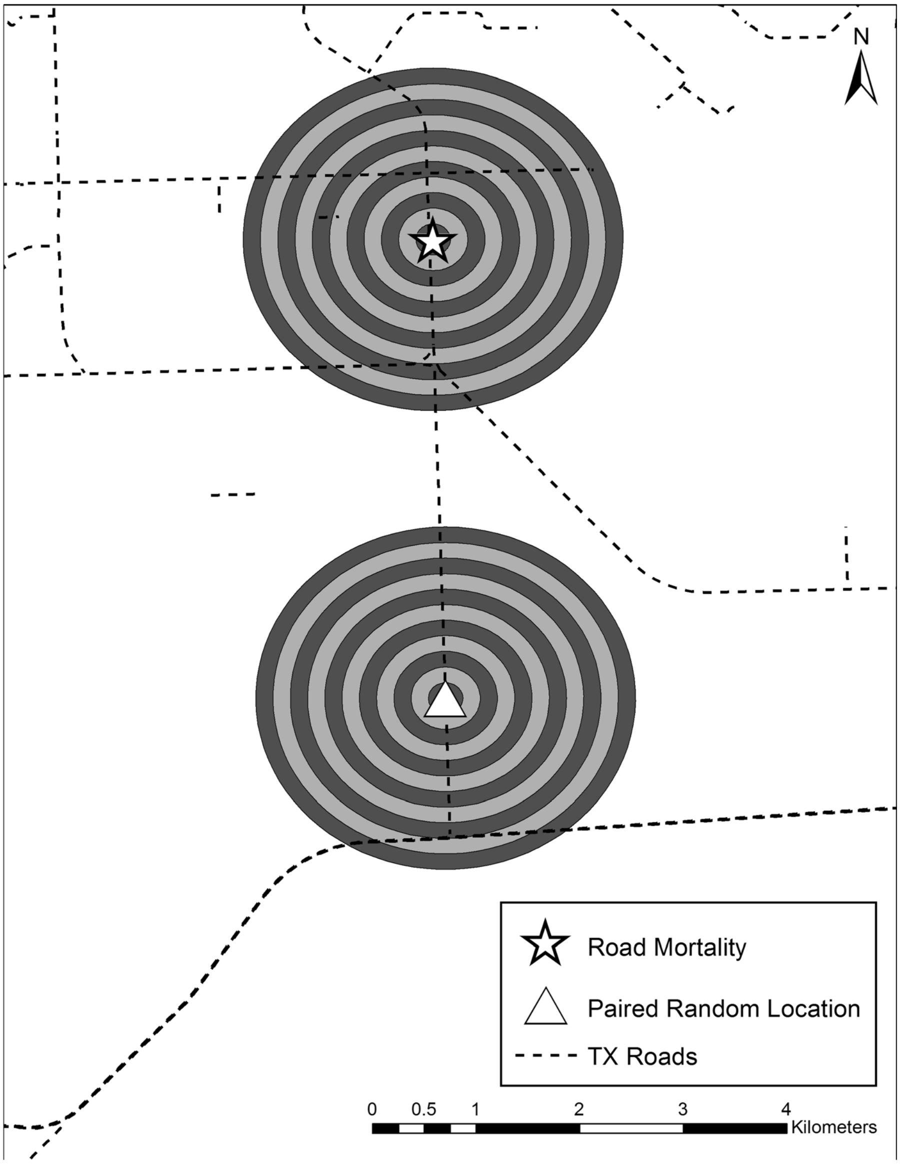


Fig. 2 Example of multi-buffer system used to analyze landscape structure surrounding ocelot–vehicle collision locations in South Texas, USA during 1984 to 2017. Each road mortality and random road location consists of 11 buffers increasing in size by a radius of 150 m

vehicle collision sites nor random locations were likely to have larger values of a given metric using a sign test (Conover 1999). This approach considers only whether a given metric is larger at 1 site or the other but does not consider the magnitude of the difference. Second, our landscape metrics were highly skewed in their distributions, thus we compared medians of each of the 7 landscape metrics at all spatial extents at road mortality locations to random road locations using a Wilcoxon signed-rank test (Conover 1999). Although this is formally a test of median equality, given the skewed distributions, differences between locations may occur at other quantiles. Differences can be assessed with effect size and p-values. Therefore, we calculated effect size for the Wilcoxon signed-rank test following Field (2009), where small, moderate, and large effect sizes are

Table 2 Definitions of class-level landscape metrics used in analysis of landscape spatial structure of 26 ocelot–vehicle collision sites that occurred between 1984 and 2017 in South Texas, USA

Landscape metric	Definition
PLAND	Percent land cover (%)
PD	Patch density (patches/ha)
LPI	Largest patch index (%)
ED	Edge density (m/ha)
MPA	Mean patch area (ha)
ENN	Euclidean nearest neighbor (m)
AI	Aggregation index (%)

indicated by values of 0.1, 0.3, and 0.5, respectively (Cohen 1988, 1992).

We also compared differences in landscape structure around male and female ocelot–vehicle collision locations. We analyzed PLAND, ENN, LPI, and MPA for woody vegetation, herbaceous vegetation, and bare ground. Because initial data analysis indicated these metrics were skewed, we compared distributions of each metric at each extent between male and female locations with Kolmogorov–Smirnov tests (Conroy 2012). Kolmogorov–Smirnov tests are sensitive to differences between distributions (e.g., related to variances) that other tests (e.g., a Mann–Whitney test) may not detect (Conroy 2012). We report the maximum difference between the empirical distribution functions (D_{max}) as a measure of effect size, which ranges from 0 to 1.

The Wilcoxon signed-rank test, with 7 landscape metrics, 11 spatial extents, and 3 cover types for comparisons between mortality and random sites involved 231 hypothesis tests. The Kolmogorov–Smirnov test, with 4 landscape metrics, 11 spatial extents and 3 cover types between male and female mortality sites involved an additional 132 tests of hypotheses for each test statistic. The Kolmogorov–Smirnov test does not have an omnibus test (analogous to an overall *F*-test in the analysis of variance) that controls for comparison-wise error rates. Thus, we also applied Bonferroni's adjustment to *p*-values (Miller 1981) for each set of comparisons among the 11 spatial extents. All statistical analyses were performed using SAS version 9.4 (SAS Institute, Cary, NC, USA).

Results

Woody vegetation cover values for PLAND, LPI, ED, and MPA were more likely to be greater at ocelot–vehicle collision sites than at random road locations (sign test: $p \leq 0.01$; Table 3), whereas ENN values were marginally more likely to be larger for random locations (sign test: $p < 0.07$). Values of PD and AI were similar between location type (sign test: $p < 0.55$). Median percent woody cover varied from 30–38% at ocelot–vehicle collision sites. The Wilcoxon test indicated median woody PLAND was 13–20% greater at ocelot–vehicle collision sites compared to random road locations at all extents (effect size 0.28–0.40, $p \leq 0.05$; Fig. 3) except 150 m. Median LPI was 7.1–11% greater only at the 450 and 600 m extents, respectively (Wilcoxon test: effect size 0.23–0.32, $p < 0.05$). Median MPA was 3.5 ha at vehicle collision sites at the 450 m spatial extent, which was 2.4 ha larger than at random sites (Wilcoxon test: effect size 0.32, $p \leq 0.02$) and 1.2–1.4 ha larger at 750–1050 m (Wilcoxon test: effect size < 0.19, $p \leq 0.10$). Nearest neighbor median values were 10.2–16 m shorter at collision sites for

Table 3 Results of the sign tests from woody, herbaceous, and bare ground comparisons of 26 ocelot–vehicle collision sites that occurred from 1984 to 2017 in South Texas, USA and 26 random locations

Metric	Woody[a] Sign test $p <$	Herbaceous Sign test $p <$	Bare Sign test $p <$
PLAND	0.001	0.001	1.00
PD	1.00	1.00	0.001
LPI[b]	0.01	0.001	1.00
ED	0.01	0.001	0.07
MPA	0.001	0.23	0.01
ENN	0.07	1.00	0.55
AI[c]	0.55	0.001	1.00

P-values are relative to ocelot–vehicle collision sites

[a]Results from the Wilcoxon tests for woody cover are in Fig. 3

[b]From the Wilcoxon tests, bare ground LPI was significantly greater at 600 m and lower at 1650 m at ocelot–vehicle collision sites than random locations

[c]From the Wilcoxon tests, bare ground AI was significantly lower at 1650 m at ocelot–vehicle collision sites than random locations

the 1200–1500 m extents (Wilcoxon test: effect size 0.23–0.32; $p < 0.04$). Median AI values were 3.8–6% greater at ocelot–vehicle collision sites only for the 450 m and 600 m extents (Wilcoxon test: effect size 0.26–0.28, $p < 0.07$). There were no statistical differences in median PD (Wilcoxon test: effect size < 0.16, $p > 0.26$) or ED although median values ranged from 20–35 m/ha greater at vehicle collision sites than at random sites (Wilcoxon test: effect size < 0.15, $p > 0.26$). Using Bonferroni-adjusted p-values for Wilcoxon signed ranks tests, PLAND was higher at vehicle collision locations only for 600 and 750 m spatial extents only.

The PLAND, LPI, ED, and AI metrics for herbaceous cover were more likely to be greater at vehicle collision sites than at random sites (sign test: $p \leq 0.001$; Table 3). For these metrics, however, magnitudes of differences were small: effects sizes were < 0.11, < 0.09, < 0.09 and < 0.20, respectively, and p-values were not significant. Smaller

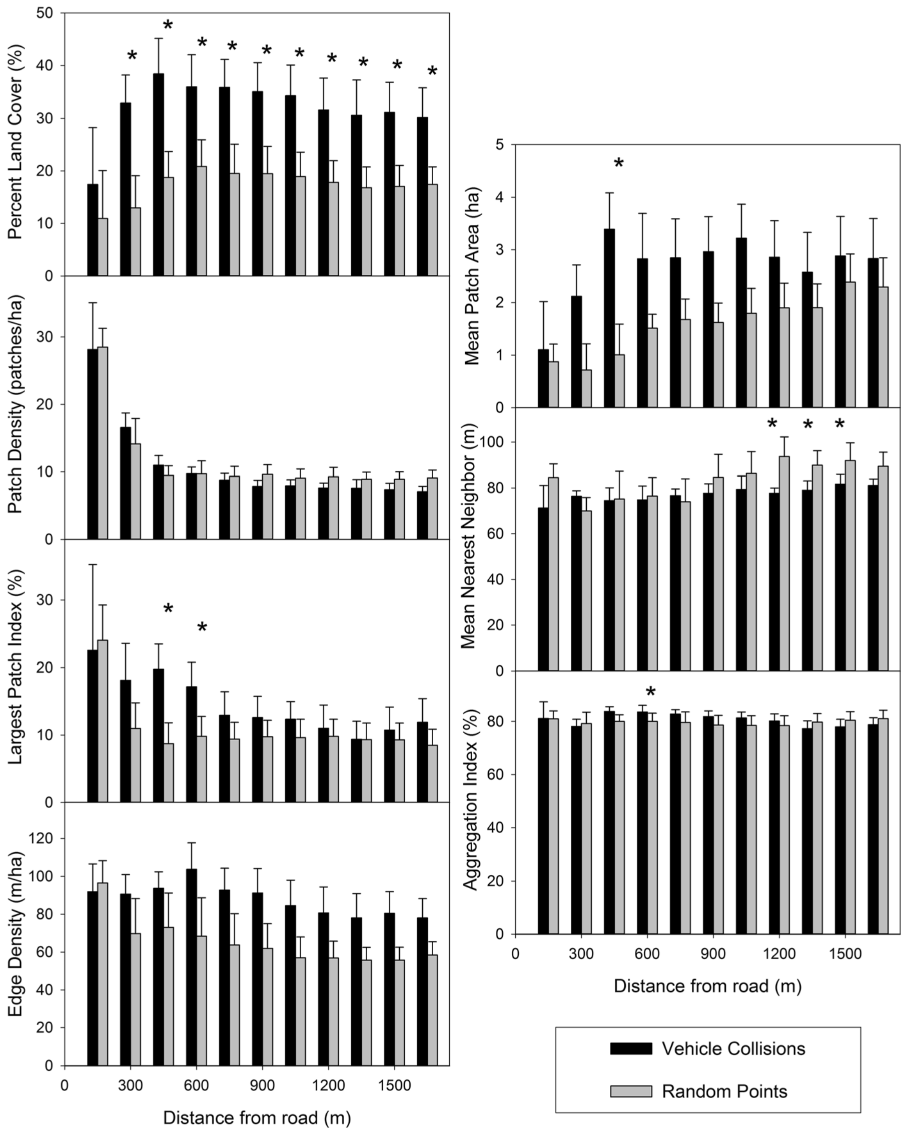


Fig. 3 Median values of woody vegetation structure between 26 ocelot–vehicle collision sites that occurred in South Texas, USA during 1984 to 2017 and their paired random road locations. Metrics of landscape structure were compared at 150 m intervals. Standard error bars were estimated by bootstrapping. Asterisks indicate significant differences based on Wilcoxon signed-rank tests

effect sizes were observed for the other metrics, which were no more likely to be greater at either location type. The above effects were not significant following Bonferroni adjustment.

For bare ground cover, PLAND, LPI, MPA, and AI were greater at random road locations than at vehicle collision locations (sign test: $p < 0.07$; Table 3), whereas PD and ED were greater at vehicle collision sites (sign test: $p < 0.07$). Nearest neighbor did not differ between location types (sign test: $p > 0.23$). Median values of PLAND, ED, MPA, and ENN were not different between location types (Wilcoxon tests: effect sizes < 0.23, $p < 0.12$). Median values of PD were only marginally different at the 150 m extent, associated with a large arithmetic difference of 14 more patches/ha at vehicle collision sites (Wilcoxon test: effect size 0.25, $p \leq 0.12$). Median LPI values were 1% larger for vehicle collision locations at the 600 m extent, whereas values for random locations were 12.1% larger at the 1650 m extent (Wilcoxon test: effect size 0.27 and 0.26, respectively, $p \leq 0.05$). Median AI was 7.3% greater at random locations at the 1650 m extent (Wilcoxon test: effect size 0.27, $p \leq 0.05$). The above effects were not significant following Bonferroni adjustment.

The Kolmogorov–Smirnov (KS) tests indicated woody cover PLAND and ENN were similar at female and male mortality locations (sign test: $p = 1.00$; Table 4). Values of LPI were marginally greater at female mortality sites than male (sign test: $p \leq 0.07$), and values of MPA were greater at female locations at all spatial extents (sign test: $p \leq 0.001$). Median woody PLAND was 15.8% greater at female mortality sites at 450 m (KS test: $D_{max} = 0.56$, $p \leq 0.05$; Fig. 4). Greater differences were observed at spatial extents > 450 m, but these were also associated with smaller effect sizes and larger p-values (KS test: $D_{max} < 0.50$, $p > 0.11$). We detected no significant differences in median LPI values between sexes at any spatial extent (KS test: $D_{max} < 0.42$, $p > 0.28$). Median values of ENN were 12.3 and 20.2 m larger for male mortality sites at 900 m and 1050 m, respectively ($D_{max} > 0.56$, $p \leq 0.05$). Although median ENN was 28 m greater for females at 300 m, the difference was associated with a smaller effect size and larger p-value ($D_{max} = 0.40$, $p = 0.63$). There was no difference in median values of MPA (KS test: $D_{max} \leq 0.50$, $p > 0.13$). The above effects were not significant following Bonferroni adjustment.

Table 4 Results of the sign tests from woody, herbaceous, and bare ground comparisons of 18 male ocelot–vehicle collision sites and 7 female ocelot–vehicle collision sites that occurred from 1984 to 2017 in South Texas, USA

Metric	Woody[a] Sign test $p <$	Herbaceous[b] Sign test $p <$	Bare[c] Sign test $p <$
PLAND	1.00	0.01	1.00
LPI	0.07	0.01	1.00
MPA	0.001	0.01	1.00
ENN	1.00	1.00	0.07

P-values are relative to female ocelot–vehicle collision sites

[a]Results from the Kolmogorov–Smirnov tests are in Fig. 4

[b]Results from the Kolmogorov–Smirnov tests are in Fig. 5

[c]Results from the Kolmogorov–Smirnov tests are in Fig. 6

For herbaceous cover, PLAND, LPI, and MPA were more likely to be greater at female road mortality sites than male (sign test: $p \leq 0.01$; Table 4). However, there were no differences in median values between male and female mortality locations for PLAND (KS test: $D_{max} < 0.46$, $p > 0.16$; Fig. 5), LPI (KS test: $D_{max} < 0.52$, $p > 0.09$), and MPA (KS test: $D_{max} > 0.46$, $p > 0.17$). Values of ENN were marginally greater at male mortality sites than male (sign test: $p \leq 0.07$), and median ENN was 4.8–6.7 m larger at male road mortality sites from 1200–1650 m (KS test: $D_{max} < 0.61$, $p < 0.03$). The above effects were not significant following Bonferroni adjustment.

The PLAND, LPI, and MPA metrics for bare ground cover were more likely to be greater at male mortality locations (sign test: $p \leq 0.01$; Table 4), while ENN was more likely to be greater at female mortality locations (sign test: p, 0.07). Median PLAND values were 8.6% greater at male mortality sites at 1650 m ($D_{max} = 0.56$, $p \leq 0.05$; Fig. 6). Additionally, PLAND was 13.3% smaller and 12.4% larger at 150 and 1350 m, respectively, for male mortality locations, which were associated with smaller effect sizes and larger p-values (KS test: $D_{max} > 0.5$, $p > 0.11$). Median LPI values were 5.3% larger at male mortality sites at 600 m (KS test: $D_{max} = 0.56$, $p \leq 0.05$). Larger differences in LPI (9%) were found at 150 and 450 m but were associated with smaller effect sizes and larger p-values (KS test: $D_{max} < 0.47$, $p > 0.35$). Median values of ENN were

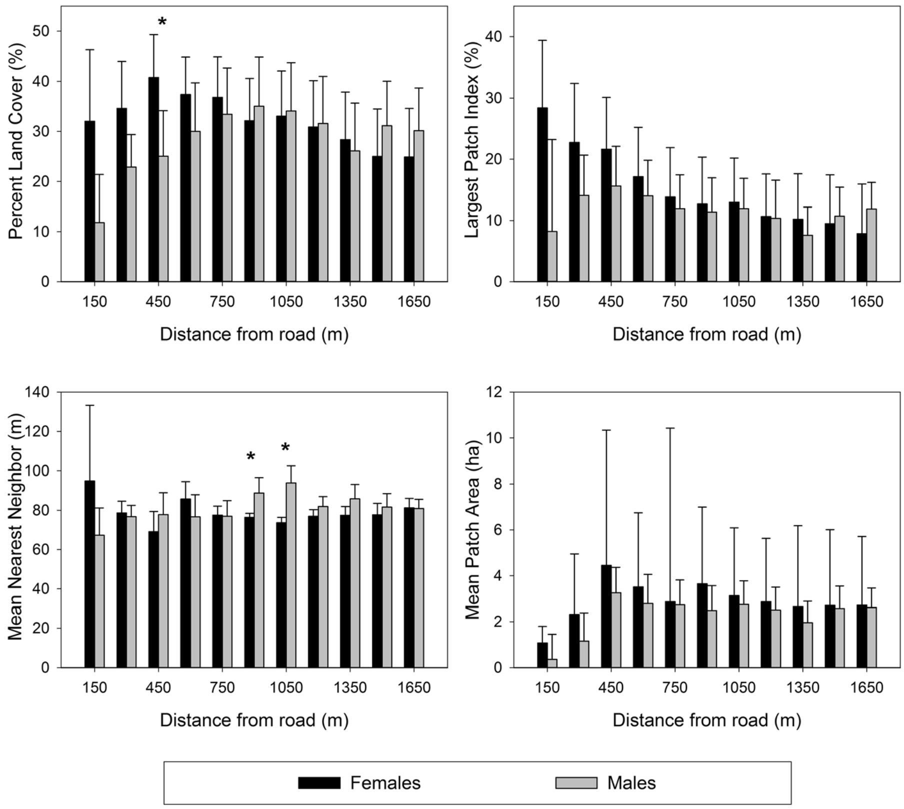


Fig. 4 Median values of woody vegetation structure between vehicle collision sites of male and female ocelots that occurred in South Texas, USA during 1984 to 2017. Metrics of landscape structure were compared at 150 m intervals. Standard error bars were estimated by bootstrapping. Asterisks indicate significant differences based on Kolmogorov–Smirnov tests

22–35 m greater at female mortality sites than male mortality sites at 1200–1500 m (KS test: $D_{max} > 0.56$, $p \leq 0.05$), and 35 m greater at 1650 m ($D_{max} = 0.52$, $p < 0.08$). There were no statistical differences in median MPA values at any spatial extent (KS test: $D_{max} < 0.47, p > 0.15$). Using Bonferroni-adjusted *p*-values, ENN values of bare ground were higher ($p = 0.008$) at female mortality locations only at the 1350 m extent.

Discussion

Ocelot–vehicle collisions were most likely to occur where roads bisect large and closely connected patches of woody vegetation. Vehicle collisions had a greater percentage of woody vegetation at all but the shortest distance from the road compared to random locations, which is consistent with habitat types ocelots are known to select (Harveson et al. 2004; Horne et al. 2009). Our results show that 10 of 18 significant results involved percent land cover of woody vegetation at spatial extents > 150 m, indicating that 55% of our statistically different measurements between ocelot–vehicle collisions and random locations occurred from the percent woody cover analysis, with collision sites having up to 20% more woody cover. Thus, percent of woody cover is likely the most informative and influential metric in terms of ocelot–vehicle collision locations, both in terms of large woody patches near roads, and woody patches closely congregated away from roads. In a similar study, ocelots in South Texas were found to be vulnerable to vehicle collisions in areas that intersect intact scrub habitat (Schmidt et al. 2020). Additionally, our observations are consistent with previous studies, which indicate that vehicle collisions of other endangered felids typically occur near habitat and use areas of those species (Maehr et al. 1991; Ferreras et al. 1992; Cain et al. 2003).

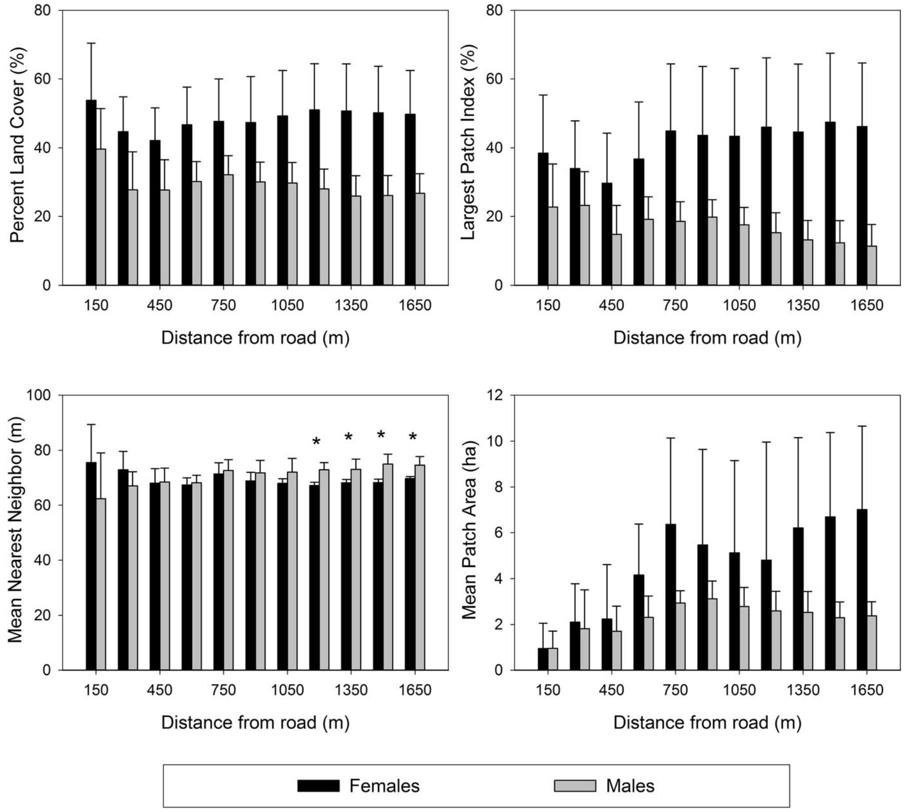


Fig. 5 Median values of herbaceous vegetation structure between vehicle collision sites of male and female ocelots that occurred in South Texas, USA during 1984 to 2017. Metrics of landscape structure were compared at 150 m intervals. Standard error bars were estimated by bootstrapping. Asterisks indicate significant differences based on Kolmogorov–Smirnov tests

There were few differences in the spatial structure of woody cover between vehicle collision sites of male and female ocelots. Results indicate that female road mortality locations had slightly greater percentages, larger patches, and shorter distances between patches of herbaceous cover at distances > 1 km from the road. Conversely, male road mortality locations had slightly greater percentages, larger patches, and shorter distances between patches of bare ground at similar distances from the road. Like most felids, male ocelots tend to have larger home ranges than females, which can include more heterogenous landscapes and increase the probability of encountering a road (Sunquist and Sunquist 2002; Hunter 2015). The observation that over twice as many ocelot–vehicle collisions involved males could reflect subadult and young adult males dispersing over risky landscapes with greater road densities in search of new territories (Kramer-Shadt et al. 2004; Haines et al. 2005; Hunter 2015). Dispersing male ocelots traverse through greater heterogeneous landscapes that include more bare ground (Haines et al. 2005) whereas females likely remain in more vegetated areas near their natal ranges. Ocelot use of unfamiliar areas may increase the possibility of vehicle collision (Haines et al. 2005).

Development of roads in areas that have a high proportion of woody cover can have negative impacts on ocelots in 2 ways: fragmentation of important habitat and increased ocelot vulnerability to vehicle collisions. Habitat fragmentation can have profound negative impacts on connectivity, geographic ranges, and abundance of rare carnivores (Crooks 2002; Ordenana et al. 2010; Crooks et al. 2011). In a simulated experiment, landscape connectivity of various mammal species in France was highest where the quantity of habitat was largest, and large and carnivorous mammals had high connectivity in a highwayless scenario (Mimet et al. 2016). Given their low dispersal rates, ocelots in fragmented habitat patches may be more susceptible to local extinction than

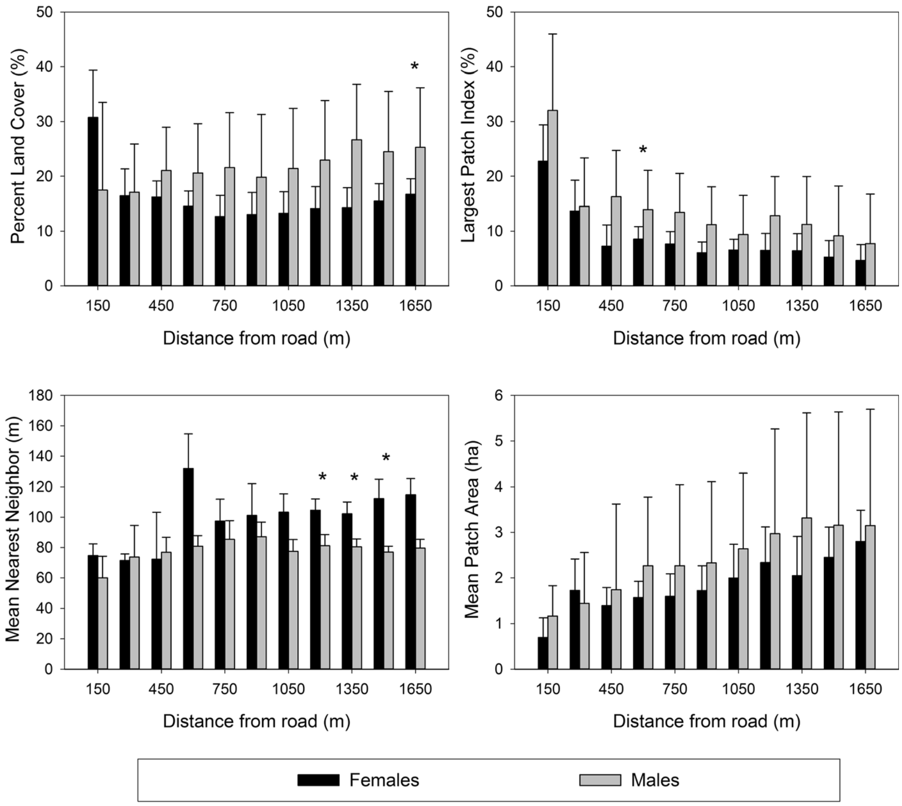


Fig. 6 Median values of bare ground vegetation structure between vehicle collision sites of male and female ocelots that occurred in South Texas, USA during 1984 to 2017. Metrics of landscape structure were compared at 150 m intervals. Standard error bars were estimated by bootstrapping. Asterisks indicate significant differences based on Kolmogorov–Smirnov tests

ocelots in continuous patches (Haines et al. 2006). The tenuous nature of small, isolated populations is supported by genetic analysis of the remnant Texas ocelot populations. The Refuge Population is severely impacted by habitat fragmentation and has lost much genetic diversity. In contrast, the Ranch Population, where ocelots can disperse through more intact rangelands, has retained genetic diversity (Janečka et al. 2011, 2014; Korn 2013).

Population viability models concluded that reducing road mortality was the most effective strategy to reduce the likelihood of local extinction for South Texas ocelots (Haines et al. 2006). The establishment of wildlife crossing structures (e.g., culverts), in addition to reducing road mortality of ocelots, could promote successful dispersal by providing safer linkages between fragmented habitat patches. Though it has been advised that implementing such structures in areas consisting of intact scrub habitat could reduce road mortality of ocelots in this area (Schmidt et al. 2020), our analysis provides additional information on the amount and spatial structure of woody vegetation to identify optimal locations for new crossing structures. Use of wildlife crossing structures has been effective at reducing road mortality and increasing connectivity in other felid populations such as cougars, including the endangered Florida panther (Foster and Humphrey 1995; Land and Lotz 1996; Gloyne and Clevenger 2001). Although wildlife crossing structures can play a key role in the mitigation of wildlife-vehicle collisions, structures must be placed in optimal locations based on the biology of the target species (Clevenger et al. 2002; van der Ree et al. 2015; Zeller et al. 2020). Ideally, wildlife crossing structures will link to habitat that will allow for dispersal and restore connectivity among habitat patches (Clevenger and Huijser 2011).

Measuring the effects of landscape structure within the appropriate spatial extent is important to correctly identify the effects the landscape has on a particular species or behavior (Moraga et al. 2019). This is because landscape features may influence a species response or behavior at varying spatial scales, termed the "scale of effect" (Jackson and Fahrig 2012). The limited information provided by single scale analyses can be strengthened by multi-scale analyses that allow more detailed understanding of fine-scale patterns in selection and behavior, which may make conservation planning more effective. Landscape-based analyses that incorporate multiple scales and landscape metrics provide a useful framework to evaluate space use by wildlife and select sites for wildlife crossing structures (Weins 1989; Snow et al. 2014). The multi-scale method used in this study provided critical information on landscape similarities at ocelot roadkill locations which will be beneficial in mitigation measures such as crossing structures. This method allows the integration of wildlife behavior, habitat selection, and movement patterns at finer scales often missed by single-scale analyses (Martin and Fahrig 2012).

Vehicle collisions likely occur as ocelots attempt to cross between woody habitat patches. Therefore, crossing structures designed for ocelots should be placed where roads bisect areas of 30–38% woody cover, with woody patches of about 3.5 ha in size, preferably in areas with woody cover on both sides of the road. Additionally, crossing structures should avoid open areas such as grasslands, coastal prairies, and agricultural fields. Crossing structure locations should facilitate safe passage to a viable destination and avoid leading to habitat sinks or population sinks. Our study demonstrates how coupling animal movement ecology with landscape analyses can efficiently guide the placement of road crossing structures designed to facilitate safe movement of ocelots in South Texas. We encourage conservation planners to prioritize properly sited crossing structures in the near future, as reduction of road mortality and restoration connectivity are critical to the persistence of ocelots in the US.

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