Global Ecology and Conservation 27 (2021) e01582

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original Research Article

Cats, cars, and crossings: The consequences of road networks for the conservation of an endangered felid

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ARTICLE INFO

Article history:
Received 16 November 2020
Received in revised form 28 March 2021
Accepted 4 April 2021

Keywords:
Anthropogenic encroachment
Cox proportional hazards
Demographics
Endangered species
Kaplan-Meier
Ocelot
Wildlife-vehicle collisions

ABSTRACT

Encroaching urban development is a leading cause of habitat loss, replacing natural areas with anthropogenic infrastructure and road networks. Roadways can influence the spatial ecology and survival of mammalian carnivores, particularly felids, thereby threatening long-term persistence and conservation of sensitive populations. Ocelots (*Leopardus pardalis*) are a federally endangered felid in the United States with breeding populations restricted to the Lower Rio Grande Valley of South Texas, an area of extensive anthropogenic expansion. We evaluated the influence of road networks on ocelot survival using a long-term telemetry dataset (1982–2001, $n = 59$) and draw comparisons with a spatially referenced historical dataset of ocelot-vehicle collisions in the same area (1982–2020, $n = 54$). Vehicle collisions accounted for 40% of radio-collared ocelot fatalities. Annual survival rates were 0.90 (95% CI = 0.84–0.95) for resident ocelots and 0.66 (95% CI = 0.45–0.97) for transient ocelots. We evaluated biological and road-related factors that may influence ocelot survival using Cox proportional hazards regression. The top model included density of unpaved, low-volume, and high-volume roads within home ranges and resident-transient status. Mortality risk increased 16% with every 0.07 km/km^2 increase of high-volume roads within annual home range, decreased 45% with every 1.12 km/km^2 increase of unpaved roads, and decreased 276% for residents compared to transients. Further, probability of mortality specifically from vehicle collision increased with greater density of low-volume roads within ocelot home ranges. Within the historical dataset of ocelot-vehicle collisions, 46% occurred on low-volume roads while 39% occurred on high-volume roads. Our results highlight the necessity for mitigation strategies on low-volume roads which cause the most ocelot-vehicle collisions. In addition, continued attention towards high-volume roads is necessary to ocelot conservation. Understanding how road attributes affect the survival of species sensitive to urbanization and habitat fragmentation can aid in their conservation.

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https://doi.org/10.1016/j.gecco.2021.e01582
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1. Introduction

Anthropogenic development has become a threat to biodiversity in the United States (U.S.) through urban expansion and the spread of energy development (Czech et al., 2000; Trainor et al., 2016). Although the global urban population is growing 1% annually, major cities are expanding in area twice as fast as their populations (Forman et al., 2003; UN, 2011). Urban sprawl can directly influence the environment through land conversion and destruction of natural habitats (Cieslewicz, 2002; Dupras et al., 2016; Gounaridis et al., 2020). Some aspects of urban expansion, such as housing development, can be a major threat for protected areas that provide refugia for species threatened by habitat loss (Volker et al., 2010). Not only is urban development a leading cause of habitat loss, it may also induce conservation concern through species endangerment and a high rate of local extinction including a large proportion of native species (Czech et al., 2000; Marzluff, 2001).

Urbanization replaces natural areas with human infrastructure, including road networks (McDonnell et al., 1993). Currently, over 6.5 million kilometers of road networks occur in the U.S. (Central Intelligence Agency, 2013). Although the length of the U.S. road system has less than doubled in the last century, most growth has come from road widening, accounting for 80% of road expansion, thus allowing for a greater volume of vehicles on the landscape (Forman et al., 2003). During the 1960s and 1970s, 74,500 km of interstate highway were constructed in the U.S., and an estimated 67% of current U.S. roadways are paved (Forman et al., 2003; Central Intelligence Agency, 2013). Paved roadways generally have greater environmental impacts and negative effects towards wildlife populations compared to unpaved roads (Laurance et al., 2009). As human dependence on roadways increases, so does widespread environmental damage, leading to direct effects towards the conservation of wildlife populations (van der Ree et al., 2011).

Direct effects resulting from road networks include habitat fragmentation by reducing available vegetation, barriers to movement for some species thus reducing landscape permeability, and increased mortality from vehicle collisions (Forman et al., 2002; Riley et al., 2006, 2014). Further, the ecological effects of roadways are typically indirectly extended to adjacent areas beyond the road itself, termed the “road-effect zone”, which can include noise and light pollution, habitat modifications, hydrological effects, and exotic plant spread (Forman and Deblinger, 2000; Forman et al., 2003; van der Ree et al., 2015b). Thus, some studies have focused on the potential demographic effects road networks have on threatened and endangered species (e.g., Ferreras et al., 1992; Kerley et al., 2002; Bjurlin et al., 2005). For example, Schwab and Zandbergen (2011) found that roads impact male and female Florida panthers differently, segregating the movement of the two sexes. Understanding the influences road networks have on species survival, reproduction, and overall population performance can be effective for mitigating the effects of anthropogenic factors on vulnerable populations and direct conservation measures toward population recovery (Boulanger and Stenhouse, 2014). The influence of roads on landscape permeability and movement between subpopulations for a vulnerable population should be considered in the management and conservation of ecological corridors (Schwab and Zandbergen, 2011).

Wildlife road crossing structures as mitigation measures can minimize the rate of vehicle collisions and road mortality, improve survival rates, and promote or increase movement across landscapes by allowing individuals to successfully cross roads (van der Ree et al., 2009; Clevenger and Huijser, 2011; Rytwinski et al., 2016). Wildlife crossing structures are the most effective method to mitigate the barrier effect of roads on wildlife (Smith et al., 2015). Although the primary goal of crossing structures is to restore connectivity, there are typically more distinct goals dependent on the target species (Smith et al., 2015). Due to funding limitations, it is costly to implement multiple crossing structures in a given area. Incorporating fencing into crossing structure development can be more cost effective (van der Ree et al., 2015a). Additionally, wildlife crossing structures can be more effective when animals are guided towards them with the use of fencing (McCollister and Van Manen, 2010; van der Ree et al., 2015a; Rytwinski et al., 2016) Therefore understanding the resource needs and movement habits of the target species should guide the locations of future crossing structures (Downs and Horner, 2012; Loraamm and Downs, 2016). Insight into how wildlife populations sensitive to habitat fragmentation respond to road networks can be effective in minimizing vehicle collisions and increase connectivity among populations with the use of wildlife crossing structures.

Vehicle collisions can be an important source of mortality for mammalian carnivores, which are particularly susceptible to the negative effects of road network expansion. Species most vulnerable typically have larger home ranges, lower population densities, lower reproductive rates, and exhibit territorial behavior (Grilo et al., 2015). Many carnivores have large home ranges, disperse long distances, and thus may traverse through areas with suboptimal habitat increasing the probability of encountering a road (Grilo et al., 2015; Rytwinski and Fahrig, 2015). Specifically, vehicle collisions are a major source of annual fatalities among felid species (Ferreras et al., 1992; Taylor et al., 2002). Roadkill rates have significantly affected population sizes of imperiled cat species such as the Florida panther (*Puma concolor coryi*, Evink et al., 1996; Schwab and Zandbergen, 2011). In addition, greater road density within home ranges strongly increased the risk of mortality for Eurasian lynx (*Lynx lynx*) in Norway (Basille et al., 2013). In Spain, roadkill rates of Iberian lynx (*Lynx pardinus*) were strongly linked to habitat fragmentation caused by linear infrastructure and increased edge effect (Garrote et al., 2018). Road networks can also influence home range placement and boundaries of bobcats (*Lynx rufus*) by acting as physical barriers (Riley, 2006; Poessel et al., 2014). Therefore, anthropogenic encroachment and road expansion can be a threat to the long-term survival of imperiled species, particularly for those with low densities and low fecundity such as felids (Clevenger and Huijser, 2011).

Ocelots (*Leopardus pardalis*) are a neotropical wild cat widely distributed and abundant throughout Central and South America but are federally endangered within the U.S. since 1982 and are restricted in geographic range to the southern portion of Texas (USFWS, 1982; Caso et al., 2008). Fewer than 80 individuals are divided between two remnant breeding populations in South Texas with no genetic exchange (Janečka et al., 2008). Ocelots in Texas are habitat specialists that typically select for areas with dense thornshrub communities (e.g., > 95% canopy cover and 85% horizontal cover; Shindle and Tewes, 1998; Harveson et al., 2004; Horne et al., 2009). Currently, < 1% of South Texas supports optimal ocelot habitat, as land conversion by humans has significantly altered the landscape (Tewes and Everett, 1986; Leslie, 2016). As development of urban and transportation infrastructure within this region expands, habitat for ocelots continues to diminish (Lombardi et al., 2020a). One of the remnant breeding populations of ocelots resides in the Lower Rio Grande Valley (LRGV) of South Texas (Janečka et al. 2008), one of the fastest-growing metropolitan areas in the U.S. resulting from development of agriculture, urban areas, and transportation infrastructure (Leslie, 2016; Lombardi et al., 2020a). Towards the end of the 20th century, human population growth within the LRGV resulted in the expansion of residential, commercial, and subsequent road development, which further affected remnant native vegetation communities (Tiefenbacher, 2001). The increase in human population size will likely increase the number of roads and vehicles on the natural landscape, leading to conservation challenges for the ocelot (Leslie, 2016; Lombardi et al., 2020a).

Development and expansion of road networks in the LRGV are added stressors for the vulnerable ocelot population in this increasingly fragmented landscape. Although vehicle collisions represent the greatest source of mortality for ocelots in this region (Haines et al., 2005), it remains unclear what aspect of road networks influences annual survival, and the magnitude of this influence. We examined a 20-year telemetry dataset to understand the attributes of road networks that influence ocelot mortality risk. Our objectives were to (1) evaluate biological factors and road attributes that may influence ocelot mortality risk, and (2) analyze similarities among road-killed ocelots to predict roadkill occurrence. We hypothesized that (1) a greater density of higher-traffic volume roads will negatively influence survival, and (2) road-killed ocelots will have a higher density of roads within annual home ranges compared to ocelots that died of other causes. Results of this study will improve wildlife conservation efforts by demonstrating the link between landscape attributes and an important vital rate, survival, using a habitat specialist in a highly fragmented landscape. This will also highlight the need for effective mitigation measures, such as crossing structures and fencing, to be implemented in appropriate locations.

2. Materials and methods

2.1. Study area

We conducted our study on the southernmost ocelot population which resides on the Laguna Atascosa National Wildlife Refuge (LANWR), a 390-km^2 federally protected area within the LRGV in Cameron County (hereafter Refuge Population; Lombardi et al., 2020b). The northernmost population of ocelots resides on private ranchlands in Willacy and Kenedy counties (hereafter Ranch Population). The LRGV is in the Tamaulipan Biotic Province and represents a transition zone between temperate and tropical environments, 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 constitutes dense thornshrub communities consisting of woody vegetation such as Texas ebony (*Ebenopsis ebano*), honey mesquite (*Prosopis glandulosa*), spiny hackberry (*Celtis pallida*), live oak (*Quercus virginiana*), lime prickly ash (*Zanthoxylum fagara*), huisache (*Acacia farnesiana*), and Texas lantana (*Lantana horrida*; Harveson et al., 2004; Leslie, 2016). The proportion of road networks within and surrounding LANWR consist of three primary road types: unpaved roads (50%), low-volume roads (34%), and high-volume roads (16%).

2.2. Data collection

We used previously collected location data from adult ocelots from the Refuge Population on LANWR from 1982 to 2001 (Tewes, 1986; Shindle and Tewes, 2000; Laack et al., 2005; Horne et al., 2009). Individuals were fitted with very high frequency radio collars with mortality sensors (Advanced Telemetry Systems, Isanti, Minnesota; Telonics, Mesa, Arizona, USA). Over the 20-year period, ocelots were typically located 2–3 times each week from ground stations and aerial telemetry, and ocelot fatalities were recovered to determine cause of mortality. From 1982–2001, 59 individual ocelots (32 males, 27 females) were monitored, with 26 fatalities documented (12 males, 14 females). Further, we used a historic dataset of spatially referenced ocelot road mortalities provided by U.S. Fish and Wildlife Service that occurred from 1982 to 2020 throughout South Texas as a means of comparison to the results of our study. The historic dataset was compiled largely from incidental roadkill observations reported from the general public, game wardens, and ocelots actively being monitored. From this dataset there were 54 ocelot-vehicle collisions from 1982 to 2020, including those that were actively being monitored (n = 11), previously monitored (n = 3), and unmonitored completely (n = 40).

2.2.1. Ocelot space use and drought status

We calculated annual home ranges for each individual with ≥ 5 locations using 95% minimum convex polygons (MCPs). We created MCPs because this method generally provides a realistic representation of the area used by ocelots given limited number of locations each year, and to avoid overestimation and increased variance with kernel density estimators (Fieberg, 2007; Downs and Horner, 2008).

Further, Haines et al. (2005) found that survival of transient ocelots was significantly lower than resident ocelots, particularly during drought conditions. Thus, we also included movement status (i.e., resident or transient) and hydrological drought in our analyses to account for a priori knowledge in variability while testing hypotheses about the influences of road networks on ocelot mortality risk (Tewes and Hornocker, 2007). Resident ocelots were classified as individuals that used a single restricted area for three months or more, and transients were classified as individuals that moved from natal or breeding ranges and roamed until establishing a new range, albeit most ocelots moved less than 10 km with few moving longer distances and none leaving the study area (Haines et al., 2005). Drought was classified based on the mean 12-month Palmer Modified Drought Severity Index (PMDI). The mean PMDI was − 2.42 and − 2.48 within the LRGV from January 1989 to April 1991, and January 2000 to December 2002, respectively, whereas outside of these time frames the mean PMDI was 0.55 and 0.11 (Haines et al., 2005; http://www.ncdc.noaa.gov). Individuals during those low PMDI years were classified as drought samples.

2.2.2. Temporal variables

Data availability can be particularly difficult to obtain when monitoring rare or elusive species because of low sample size (Thompson, 2004). Thus, temporal trends at an annual scale may be difficult to detect which may be resolved with the use of larger binned temporal categories. For our modeling, we analyzed temporal trends both annually and within 5-year intervals over the 20-year period. Our 5-year binned categories were 1982–1986, 1987–1991, 1992–1996, and 1997–2001.

2.2.3. Road classifications

Multiple factors may influence ocelot mortality risk, with road attributes likely being the most influential (Appendix A). We examined the effects of density and distance to varying road types on ocelot mortality risk. We first classified roads within LANWR and the adjacent areas into two categories: paved and unpaved (i.e., soil and gravel roads; Fig. 1). Previous analyses indicated that ocelots from this population crossed soil and gravel roads at similar rates, thus we grouped them into one category (Anderson, Texas A&M University-Kingsville, *unpublished data*). We further classified paved roads based on annual average daily traffic (AADT) data provided by the Texas Department of Transportation (2018) as: low-volume (AADT $<$ 1000) or high-volume (AADT $>$ 1000). Traffic volume data was not collected prior to 1999, therefore through much of our study (1982–1998) we did not have traffic volume estimates. However, when reviewing trends in traffic volume from 1999 to 2019 and extrapolated backwards to pre-1999, roads classified as high-volume still would have had substantially greater traffic volume than roads classified as low-volume, relatively. Additionally, when analyzing satellite imagery from the time frame of this study, there did not appear to be a considerable amount of change in the road structure or number of roads on the landscape that ocelots would have encountered. For these reasons, we kept the road classifications as categorical rather than using exact AADT values and cautiously assigned roads to our limited suite of categories to not extrapolate beyond the coarse AADT data available. We calculated road density (km/km^2) within each annual home range per ocelot. Additionally, we calculated the distance from the center of each individual's annual home range to the nearest road of each category. Distance to road variables were log-transformed to consider skewness and the nature of the road effect zone (Eigenbrod et al., 2009; Shanley and Pyare, 2011). We scaled and centered all variables and estimated Pearson's correlation coefficient; no variables were included in the same model if high correlation ($|r| > 0.70$) was detected. See Appendix A in the Supplementary Materials for variable definitions. Additionally, we calculated the proportion of vehicle collisions that occurred on each road type for monitored ocelots and from the historic dataset.

2.3. Influence of road network variables on mortality risk

We conducted survival analyses on radio-marked ocelots to estimate annual survival rates using the Kaplan-Meier method (Kaplan and Meier, 1958) modified by Pollock et al. (1989) using the "survival" package in R version 3.6.1 (Therneau, 2020; R Core Development Team, 2019). We estimated annual survival rates between resident and transient ocelots to account for a priori knowledge in survival differences between ocelots (Haines et al., 2005). Additionally, we analyzed factors that may influence mortality risk using Cox proportional hazards regression (Cox, 1972; Fan and Li, 2002). We modeled effects on mortality risk by including biotic (sex, home range size, and movement status), abiotic (drought), and road-related (road density within home ranges of varying traffic volume and log-transformed distance to all road types) covariates. We tested biologically relevant combinations of the predictor variables including fixed effects and interactions. The distance to road and density of roads in home range variables were correlated, thus, they were not used in the same models. Therefore, we compared the performance of survival models containing one of these two road metrics to determine which predictor would be used thereafter with our suite of variables that potentially explain ocelot survival. We assessed the performance of these sets of predictors in explaining ocelot mortality risk with a model selection framework using Akaike Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson, 2002).

Many individuals were tracked multiple times over several calendar years, which resulted in more than one entry in the encounter occasion dataset for these individuals. Thus, to account for the lack of independent observations we clustered by individual to obtain robust standard errors for parameter estimates (i.e., cluster setting fixed to unique individual identifier; Therneau and Grambsch, 2000; Benson et al., 2018). For example, if an individual was monitored for 3 years, that particular ocelot would enter and exit the survival modeling encounter occasion on 3 separate occasions, while clustering takes into account that it is the same unique individual. For model selection, we compared the relative fit of models using AIC_c (Burnham and Anderson, 2002). Additionally, we used Akaike weights to evaluate strength among models. Top models were selected based on differences of < 2 ΔAIC_c scores (Burnham and Anderson, 2002). Each model was tested to meet the assumption of proportional hazards using the "cox.zph" function in R (Grambsch and Therneau, 1994; R Core Development Team, 2019). For

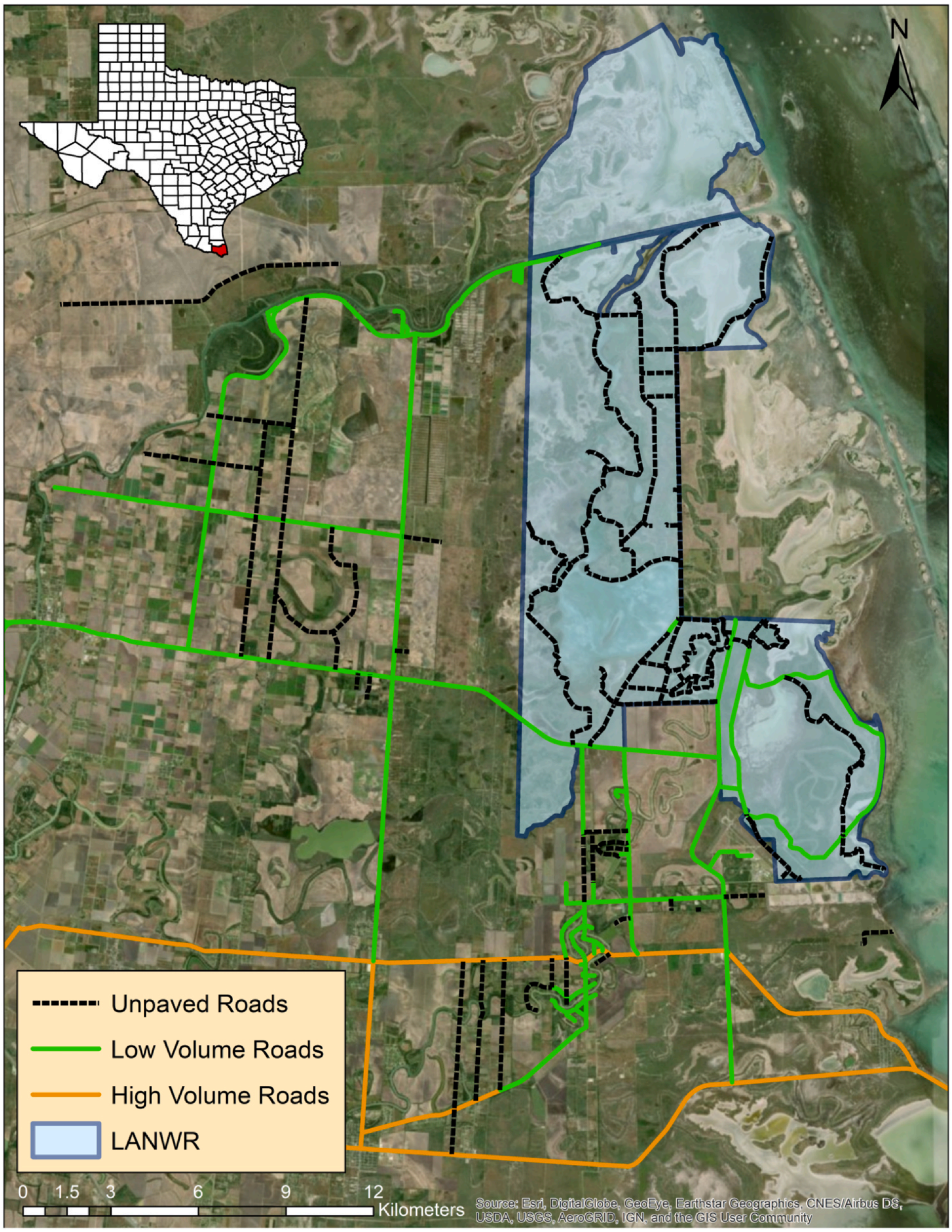

Fig. 1. Map of road types surrounding the Laguna Atascosa National Wildlife Refuge (blue polygon) in Cameron County, Texas, U.S.A. Dashed black lines represent unpaved roads (e.g., soil, gravel), green lines represent low-volume roads (< 1000 cars/day), and orange lines represent high-volume roads (> 1000 cars/day). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the top model we present hazard ratios (i.e., exponentiated beta coefficients), robust standard errors, and 95% confidence intervals.

2.4. Ocelot roadkill analysis

To expand upon our survival analysis, we examined variables influencing the probability of vehicle collision in ocelots. Specifically, we used data from ocelot fatalities during the study and evaluated differences between ocelots that died from roadkill versus mortality from other causes. We assessed the effects of our variables on ocelot fatalities caused specifically by vehicle collisions with generalized logistic models in R (R Core Development Team, 2019). We did this using the variables identified as indicative of ocelot mortality risk based on the top model from the Cox proportional hazards modeling. Model performance was assessed by calculating the area under the curve with a Receiver Operating Characteristic (ROC) curve analysis.

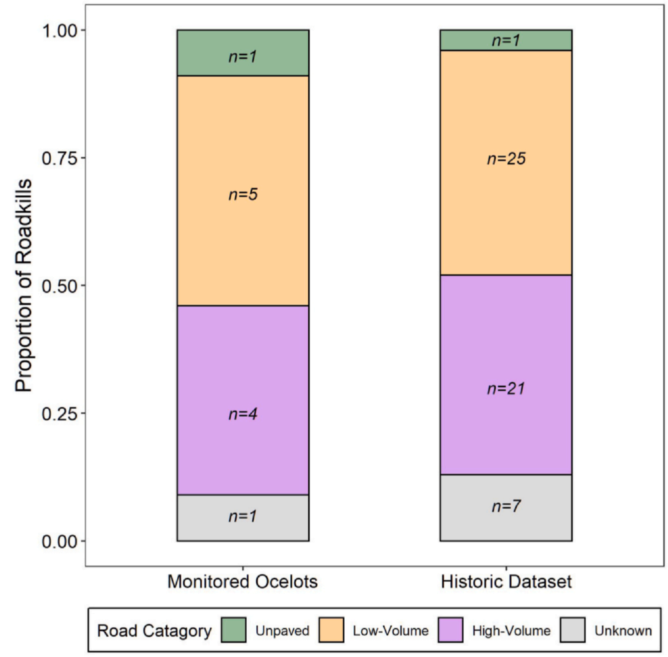

Fig. 2. Proportion of road-killed ocelots observed on unpaved (green), low-volume roads (orange), high-volume roads (purple), and unknown road types (gray). Monitored ocelots consisted of 59 individuals radio-collared and monitored on the Laguna Atascosa National Wildlife Refuge in South Texas, U.S.A. from 1982 to 2001. Of the 59 monitored ocelots, 11 fatalities were caused by vehicle collisions. The historic dataset consisted of 54 observed road-killed ocelots in South Texas from 1982 to 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

Collared ocelots averaged 52 locations per individual per year (SD = 67.5). Though variation was high, ocelots tended to occupy areas closer to and with greater densities of unpaved roads compared to low- and high-volume paved roads (Appendix B). Vehicle collisions accounted for 11 (40%) of the mortalities (7 males, 4 females; Fig. 2). Although ocelots in this study consisted of 89% residents and 11% transients, the transients represented 45% of the vehicle collisions and only 27% of other causes of mortality. Our study site was comprised of 50% unpaved roads, 34% low-volume roads, and 16% high-volume roads. Of the ocelot-vehicle collisions included in the historic dataset, 46% occurred on low-volume roads and 39% on high-volume roads with only 1 of 54 ocelot-vehicle collisions occurring on an unpaved road (Fig. 2).

3.1. Influence of road network variables on mortality risk

Our Kaplan-Meier survival analysis indicated that the annual survival rate for resident ocelots was 0.90 (95% CI = 0.84–0.95), while the annual survival rate for transient ocelots was 0.66 (95% CI = 0.45–0.97; Appendix C). We first compared models with only distance to road variables to models with only density of road variables and found that density measures were more indicative of mortality risk ($\Delta AIC_c = 5.65$, $w = 0.06$ versus $\Delta AIC_c = 0.00$, $w = 0.94$, respectively). Therefore, subsequent model building focused on the density of roads within home ranges as variables of road influence toward mortality risk. Our top model included density of unpaved roads, low-volume roads, and high-volume roads within annual home ranges, and transient status (Table 1). A competing model included the aforementioned variables with the addition of sex. However, sex did not influence ocelot mortality risk (hazard ratio = 0.43, 95% CI = 0.15–1.24, $p = 0.12$) or improve model weight, therefore it was considered an uninformative parameter in the model, thus we only considered the top model. The top model indicated that for every one standard deviation increase of density of high-volume roads (0.07 km/km^2) within annual home range, the risk of mortality

Table 1
Top 5 models from model selection of Cox proportional hazards analysis of ocelot survival based on 59 ocelots monitored from 1982 to 2001 on the Laguna Atascosa National Wildlife Refuge in South Texas, USA.

Model	logLik	AICc	ΔAICc	Weight	Concordance
Density Unpaved + Density Low + Density High + Transient	-93.32	197.14	0	0.23	0.73
Density Unpaved + Density Low + Density High + Sex + Transient	-91.63	197.27	0.13	0.21	0.74
HR Size + Transient	-97.35	199.37	2.23	0.07	0.72
Density Unpaved + Density Low + Density High + Year + Transient	-92.78	199.55	2.41	0.07	0.73
Density Unpaved + Density Low + Density High	-96.22	199.86	2.72	0.06	0.67

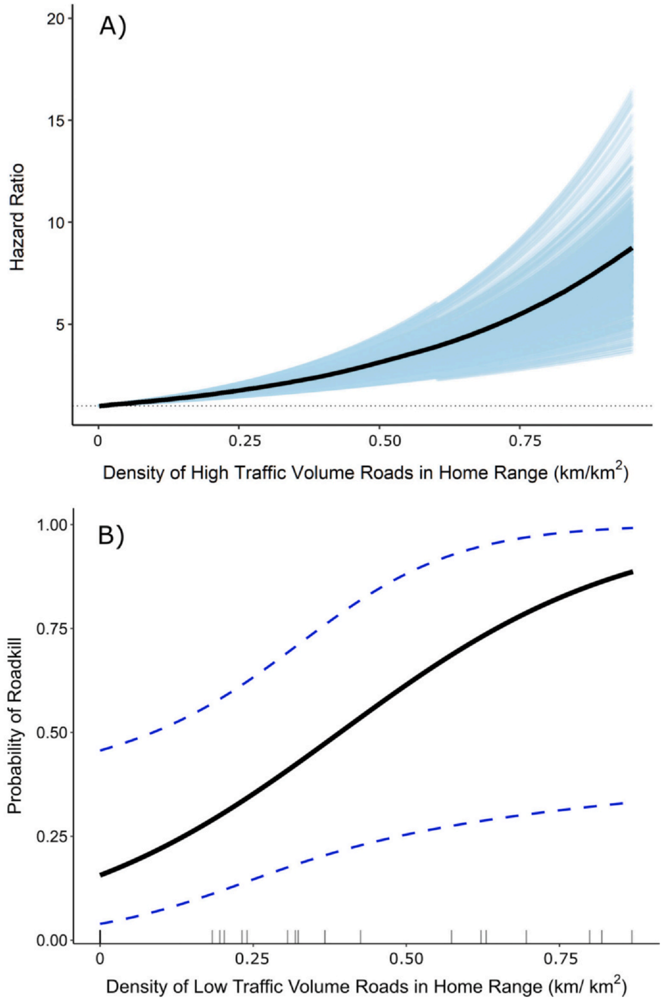

Fig. 3. The effect of increasing density of roads within home range of ocelots on A) the risk of mortality (i.e., hazard ratio) from high-volume roads and B) the probability of roadkill from low-volume roads based on 59 ocelots monitored from 1982 to 2001 in South Texas, U.S.A. **Panel A)** The effect of high-volume roads on hazard ratio were derived from 500 simulations where values of covariates from our top Cox proportional hazards model were randomly extracted from the observed distribution of values (R package "simPH"). Light blue lines represent each simulated iteration and the solid black line represents population mean effect of high-volume roads on ocelot hazard ratios. **Panel B)** Top performing predictor of the probability of mortality from vehicle collision was low-volume roads. The solid black line indicates predicated probabilities and dotted blue lines indicate the 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increased by 16% (Fig. 3A). Alternatively, for every one standard deviation increase of the density of unpaved roads (1.12 km/km^2) within an annual home range, the risk of mortality decreased by 45% (Table 2). Ocelots that exhibited transient behavior had an increased risk of mortality by 276%. Density of low-volume roads and mean distance to any type of road did not influence

Table 2
Standardized estimates of scaled and centered covariates, robust standard errors (SE), hazard ratios, and 95% confidence intervals for the top model from the Cox proportional hazards regression predicting risk to ocelots based on 59 ocelots from 1982 to 2001 on the Laguna Atascosa National Wildlife Refuge in South Texas, U.S.A.

Covariate	Coefficient	Hazard Ratio	Robust SE	Lower 95%	Upper 95%	*p*-value
Density Unpaved[a]	-0.59	0.55	0.33	0.29	1.06	0.07
Density Low[b]	-0.39	0.67	0.27	0.39	1.15	0.15
Density High[c]	0.15	1.16	0.04	1.08	1.25	< 0.001
Transient[d]	1.32	3.76	0.49	1.44	9.82	0.007

[a] Density of unpaved (soil or gravel) roads within annual home range (km/km^2)
[b] Density of paved roads with < 1000 annual average daily traffic within annual home range (km/km^2)
[c] Density of paved roads with > 1000 annual average daily traffic within annual home range (km/km^2)
[d] Movement status of an ocelot in a given year (Transient or Resident)

overall ocelot mortality risk. Additionally, we found weak support for sex and did not find support for drought influencing ocelot mortality risk and we detected no significant interactions among our variables.

3.2. Ocelot roadkill analysis

Of the 26 ocelot fatalities, only three ocelots had high-volume roads within their home ranges, leading the density of high-volume roads variable to cause non-convergence for the generalized logistic regression model, and thus was removed. Our model therefore included the density of unpaved and low-volume roads within home range, and movement status (e.g., resident or transient). Our model indicated that the density of unpaved roads ($\beta = -0.07$, 95% CI = − 1.3 to 0.99) within home range, as well as movement status ($\beta = 0.12$, 95% CI = −2.02 to 2.13), did not predict vehicle collision. However, the density of low-volume roads within home range positively influenced the probability of vehicle collision ($\beta = 1.27$, 95% CI = 0.22–2.66; Fig. 3B). Area under the curve (AUC) from our ROC analysis indicated sufficient predictability from our model (AUC=0.84).

4. Discussion

The presence of road networks draws conservation concerns for an endangered carnivore in a quickly changing landscape. Our survival modeling indicates that a greater density of high-volume roads within ocelot home ranges was associated with an elevated risk of mortality, supporting our hypothesis that a greater density of higher-traffic volume roads within home ranges negatively influences ocelot survival. High-volume roads have been linked with lower survival for other species affected by anthropogenic encroachment (Jones, 2000; McCall et al., 2010). Few ocelots during our study occupied areas with high-volume roads, which could indicate avoidance of this road type. However, high-volume roads still pose a threat to ocelot persistence and conservation as they can act as a barrier to movement across the landscape, similar to bobcats and coyotes (*Canis latrans*) in southern California (Riley et al., 2006). Further, ocelots with a greater density of low-volume roads within their home ranges had a higher probability of mortality from a vehicle collision than alternative causes, moderately supporting our hypothesis that road-killed ocelots will have a greater density of roads in their home ranges. We did not find support that a greater density of other road types would influence the probability of roadkill. Low-volume roads are more common on the landscape surrounding LANWR compared to high-volume roads, thus ocelots are more likely to encounter this road type and be hit by a vehicle. The historic ocelot roadkill dataset also complements our findings, where more vehicle collisions occurred on low-volume roads than high-volume. Risk of vehicle collisions does not always increase linearly with traffic volume. For species like the ocelot, that can recognize the threat of vehicles and will avoid roads when possible, road mortality increases initially until reaching an asymptote (Jacobson et al., 2016). Although more ocelot-vehicle collisions are occurring on low-volume roads, high volume roads still pose a risk to ocelot mortality.

Surprisingly, the density of unpaved roads within annual home ranges was positively related to ocelot survival. Nearly 90% of ocelots had unpaved roads within their home ranges. Presumably, the areas with a greater density of unpaved roads also have the necessary resources for ocelot occupancy. Unpaved roads on LANWR are located near or within ocelot habitat (e.g., dense thornshrub) and may not degrade the quality of such habitat. Indeed, roads in protected areas tend to be designed to blend into the landscape (Grilo et al., 2015), similar to the private rangelands in South Texas which can act as protected areas for ocelot habitat. The rangelands that support the Ranch Population of ocelots retain the largest remaining patches of woody cover (e.g., thornshrub and live oak) in the LRGV (Lombardi et al., 2020a). Ranches in South Texas usually contain few roads, most of which are typically unpaved, leaving room for ocelot habitat to remain undisturbed. Carnivores sensitive to the effects of fragmentation caused by road networks typically require large undisturbed natural areas to support viable populations (Grilo et al., 2015). Therefore, large tracts of natural woodland with few roads may allow ocelots to thrive and potentially expand their range.

The effects of roads can be more prominent given the conservation status of a species or population due to the inability to recover properly (Rytwinski and Fahrig, 2015). The ocelot is a territorial carnivore with low fecundity (Laack et al., 2005) and its conservation status makes it particularly vulnerable to the effects of road networks, as supported by our study. Similar results have been found in the threatened Channel Island gray fox (*Urocyon littoralis*), which had lower survival rates when living near roads compared to living away from roads (Snow et al., 2011). Additionally, vehicle collisions account for a substantial proportion of annual mortality for other endangered felids such as Florida panthers (Taylor et al., 2002) and Iberian lynx (Ferreras et al., 1992), similar to our results. It is critical to understand the ways in which road networks can influence the survival of an endangered species for long-term conservation and management.

Endangered species conservation is critical as human encroachment alters natural landscapes leading to habitat degradation. As anthropogenic features such as roads and urban areas increase across the landscape, habitat and other important requirements for endangered species continue to fragment and diminish. Habitat fragmentation can have profound negative effects on the connectivity and abundance of rare carnivores (Crooks, 2002; Crooks et al., 2011). Further, roads can have detrimental influences on vulnerable wildlife populations by altering landscape connectivity, enhancing genetic isolation, and causing direct mortality, thereby threatening the long-term survival of these populations (Clevenger and Huijser, 2011; Rytwinski and Fahrig, 2015). Understanding how human influences affect the survival of species sensitive to urbanization and subsequent habitat fragmentation can aid in conservation planning and mitigation strategies to benefit species of conservation concern.

Our results highlight the effects that both low-volume and high-volume paved roads have on ocelot survival and population measures. Unpaved roads did not have a negative effect towards overall ocelot survival or increase the probability of mortality via vehicle collision, despite making up 50% of the entire road network in our study area. Therefore, observed ocelot road mortality was greater in proportion on both low- and high-volume roads than what occurs on the landscape. Mitigation strategies through the construction of wildlife crossing structures has been focused greatly on high-volume roads. Our study shows that perhaps low-volume roads need to be considered when allocating resources towards the conservation of ocelots in the United States. Current wildlife crossing structures in South Texas have received little use from ocelots (USFWS, 2020), indicating improvements must be made to benefit the species. Thus, there is a need for future studies examining the placement of these structures on a larger landscape scale, their features such as the inclusion of fencing and landscape attributes, and incorporating ocelot movement in order to improve their success rate. Conservation planning towards mitigating ocelot road crossing development must include all spatiotemporal factors in order to benefit the species. Further, it is crucial to incorporate the combination of direct influences toward vital rates of this endangered carnivore presented here and future discussions or research involving road network influences on ocelots.

Wildlife crossing structures can mitigate the negative effects of roads by reducing vehicle collisions and facilitating movement (Clevenger and Huijser, 2011). Roads are significantly influencing ocelot mortality and spatial ecology, which highlights the necessity of mitigation measures towards conservation. Indeed, continued allocation of conservation efforts must remain towards high-volume road networks, however, our research suggests attention towards low-volume roads may also be important. Wildlife crossing structures on low-volume roads may have an additive effect towards ocelot survival when used in conjunction with previously implemented crossing structures on high-volume roads. Knowledge of where wildlife crossing structures promote ocelot movement with demographic benefits remains critical. Crossing structures that guide ocelots into areas that have a high density of paved roads, regardless of traffic volume, will ultimately increase ocelot mortality risk. Not only should crossing structures minimize wildlife-vehicle collisions, they should also link to sufficient habitat that will allow individuals to acquire necessary resources (Clevenger and Huijser, 2011), allowing for ecological corridors to form. For the ocelot this would include protected and private lands. This is especially important for transient ocelots, which had a significantly lower annual survival and greater risk of mortality than resident ocelots, including from vehicle collisions. Being a transient implies traversing through new and unfamiliar areas, with an increased likelihood of encountering a road, thus an increased chance of vehicle collision. Our results show that road networks significantly influence the survival of the endangered ocelot in the U.S., thereby necessitating strategies to mitigate vehicle collisions and improve landscape connectivity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Research funding was provided by the Texas Department of Transportation, Environmental Affairs Division. We acknowledge the U.S. Fish and Wildlife Service for providing ocelot mortality data. We also acknowledge Linda Laack and John Horne who collected ocelot location data over the course of this study period. We thank M. Cherry, E. Tanner, and 4 anonymous reviewers whose comments improved this manuscript greatly. This is manuscript #20-123 for the Caesar Kleberg Wildlife Research Institute.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01582.

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