



Influence of traffic volume on mammal beta diversity within the road effect zone

Thomas J. Yamashita^{a,*}, David B. Wester^a, Zachary M. Wardle^{a,3}, Daniel G. Scognamillo^a, Landon R. Schofield^b, Michael E. Tewes^a, John H. Young Jr.^c, Jason V. Lombardi^{a,4}

^a Caesar Kleberg Wildlife Research Institute, Texas A&M University – Kingsville, Kingsville, TX 78363, USA

^b East Foundation, San Antonio, TX 78216, USA

^c Environmental Affairs Division, Texas Department of Transportation, Austin, TX 78701, USA

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ABSTRACT

Disturbance from vehicle noise and human activity extends into nearby habitat, creating a road effect zone characterized by changes in wildlife community structure and species behavior. This can affect conservation efforts along roads, such as wildlife crossing construction. To ensure that conservation efforts are effective, it is important to understand how mammals use road areas. We aimed to assess how traffic volume and distance to highway influenced mammal beta diversity within the road effect zone. We placed camera traps along a low-traffic and high-traffic highway in Texas, USA, between May 2022 to April 2023. We placed camera traps using a randomized block design with transects set perpendicular to the roadway. Starting 50 m from the road, seven camera traps were set at 200 m intervals in each of seven transects. We assessed how traffic volume and distance from road affected mammal beta diversity. We detected nearly all known mammal species larger than rodents (24 species) in the study area, including all known carnivores (10 species). We detected fewer species around the high-volume road, which contributed to a significant difference in beta diversity between the low and high-volume roads. Additionally, community composition tended to be more variable around the high-volume road than the low-volume road. Our study provides insights into the impacts of vehicle traffic on mammal use of road effect zones. Traffic volume is an important indicator of mammal community composition around roads, and road mitigation structures for wildlife will need to account for and mitigate potential effects of traffic volume.

1. Introduction

Globally, human activity and development threaten wildlife communities, contributing to declines in biodiversity (Wilson, 1985; Ripple et al., 2014; Ripple et al., 2015). Development, including road construction, can cause wildlife mortality, habitat fragmentation and loss, altered behavior and can introduce pollution, and spread invasive species (van der Ree et al., 2015; Ch. 1). These impacts lead to population declines, reduced connectivity between sub-populations, altered community structure, and changes in behavior (Forman et al., 2003; Ch. 5). While road impacts are more significant in urbanized areas, rural areas

also experience strong effects from humans, particularly related to road development (McKinney, 2002). Additionally, these impacts often extend beyond the road right-of-way into surrounding natural areas, sometimes affecting animals for kilometers beyond the road surface (Forman and Deblinger, 2000).

The area surrounding a road into which road and traffic impacts extend is called the road effect zone (REZ; Forman and Deblinger, 2000). The size of the REZ varies based on road and traffic characteristics, surrounding land cover, climatic conditions, and species characteristics, but has been estimated to be about 5000 m for mammals (Benitez-Lopez et al., 2010). Understanding how animals use the REZ is critical to

* Corresponding author at: 1125 W. Ave. B, Kingsville, TX 78363, USA.

E-mail address: tjyamashta@gmail.com (T.J. Yamashita).

¹ Present address: Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA.

² Present address: Rocky Mountain Research Station, United States Forest Service, Fort Collins, CO 80526, USA.

³ Present address: Division of Habitat and Species Conservation, Florida Fish and Wildlife Conservation Commission, Naples, FL 34114, USA.

⁴ Present address: Wildlife Health Laboratory, California Department of Fish and Wildlife, Rancho Cordova, CA 95670, USA.

mitigating road impacts on wildlife. Road mitigation for wildlife typically focuses on the direct effects of roads (Taylor and Goldingay, 2010) and includes wildlife crossing structure construction and fencing installation, but the success of these efforts is likely to be impacted by the species diversity in the REZ, especially when wildlife conservation is the goal of the mitigation (van der Grift et al., 2013).

Most commonly, road impacts on wildlife are assessed through observational comparisons between abundances in disturbed and undisturbed areas (Eigenbrod et al., 2009; Benítez-López et al., 2010; Andrasi et al., 2021). However, there is greater emphasis in the road ecology literature to improve study designs and improve inferences about road impacts on wildlife (Roedenbeck et al., 2007). Well-designed observational studies and field experiments likely provide a more powerful approach to the effects of the REZ on mammals than fully observational studies (Roedenbeck et al., 2007). Camera traps are a useful tool for assessing the REZ for mammals because camera traps can assess site-specific species diversity at temporal scales that point surveys or live-trapping cannot (Caravaggi et al., 2017; Steenweg et al., 2017).

Understanding individual species responses to roads are informative when addressing species-specific conservation issues. However, the multi-species benefits of wildlife road mitigation initiatives are generally of interest to agencies and the public (Clevenger, 2005). Therefore, a community-level approach is ideal for assessing broader road-related conservation objectives. It is critical that camera trap studies detect target species with sufficient frequency to have the statistical power to evaluate road impacts; however, rare and threatened species, which are often detected at low frequencies, are the normal focus of conservation efforts.

Beta diversity quantifies the difference in community composition between local species assemblages and can result from species turnover, species loss, or changes in relative abundance (Whittaker, 1960, 1972; Socolar et al., 2016). A major driver of changes in beta diversity is disturbance (Mori et al., 2018). While natural disturbances can increase species richness by providing additional habitats for species, anthropogenic disturbances, including those from roads, tend to decrease species richness and functional diversity (Swart et al., 2019; Li et al., 2022). However, a change in beta diversity does not always indicate a positive ecological change. For example, beta diversity may change due to increases in invasive and non-native species, so it is important to examine the ecological processes driving identified changes in beta diversity (Mori et al., 2018). Additionally, disturbance-sensitive species are typically rarer in more urbanized areas (areas with greater anthropogenic disturbance) and are most likely to disappear first as anthropogenic disturbance increases (McKinney, 2008; Ordoñana et al., 2010), so examining changes in species composition along a gradient in the REZ may provide a useful measure of how hard-to-detect, rare, and threatened species may alter their space use near roads. Therefore, understanding community-level dynamics, including beta diversity, around roads may provide useful information for the development of effective road mitigation structures for rare and threatened species. A community-level approach may provide critical information about how rare species use the REZ, even when they are not detected in adequate numbers to permit species-specific analyses.

We set up camera traps at different distances from two roads to examine how traffic volume and distance-to-road impacted the variation in beta diversity of medium to large mammals living around roads. Medium to large mammals represent an ideal group for assessing beta diversity around roads because they are relatively easy to detect using camera traps (Shamon et al., 2024), typically negatively affected by roads (Benítez-López et al., 2010), and are those typically considered for road mitigation efforts for wildlife (Taylor and Goldingay, 2010). We aimed to identify a threshold distance from the road at which communities living around a high and low traffic volume road became similar. We examined beta diversity and detections of individual species to assess differences in community composition and relative number of detections for a diverse group of mammals living around roads. By

comparing beta diversity to individual species analyses, we predicted that beta diversity would be more variable but generally contain fewer but more disturbance-tolerant species around the high-volume road compared to the low-volume road. Additionally, we expected that community compositions around both roads would become more similar with distance from each road.

2. Methods

2.1. Study area

Our study area was located in Willacy and Kenedy counties, Texas, USA. This region is near the McAllen-Edinburg-Reynosa and Brownsville-Harlingen-Matamoros binational metropolitan areas and is experiencing significant human population growth, increasing urbanization, and road network expansion (Lombardi et al., 2020b). Despite this development, large tracts of private ranchland maintain habitat connectivity across the landscape. These private lands provide extensive habitat for wildlife, including endangered species such as the ocelot (*Leopardus pardalis*). Ocelots are highly threatened by roads and vehicles (Haines et al., 2005; Blackburn et al., 2021), and wildlife crossings and other road mitigation structures are being constructed in the region to reduce road impacts on ocelots and other mammals (Blackburn et al., 2022). Our study focused on two ranches located near two major roads: Hacienda Yturria Ranch (HY) along United States Highway (US) 77 and the East Foundation's El Sauz Ranch (ES) along State Highway (SH) 186 (Fig. 1). These two ranches are highly connected with no major roads or development separating them.

Both ranches are high-fenced (2.4-m high wire mesh fencing) along the highway and used for cattle production, but HY operates a major commercial hunting operation, whereas hunting is much more limited on ES. Hunting on ES is primarily for the management of non-native nilgai (*Boselaphus tragocamelus*) and feral hog (*Sus scrofa*). The vegetation communities are similar, dominated by coastal gulf prairie, honey mesquite (*Prosopis glandulosa*), and thornscrub, a diverse community of low-mid story (3–5 m) thorny shrubs and trees in varying densities and patch sizes (Jahrsdoerfer and Leslie, 1988; Shindle and Tewes, 1998; Elliott et al., 2014). The area is hot and humid throughout the year with average temperatures ranging from 10 °C in January to 36 °C in July (Palecki et al., 2020), and it receives variable rainfall and episodic droughts, ranging from 313 to 529 mm per year (Cooper and Wagner, 2013).

Whereas the ranches had similar management and land use practices, US 77 and SH 186 have different characteristics. The average annual daily traffic on US 77 was 11,500 vehicles per day in 2022, compared to 669 vehicles per day on SH 186 (Texas Department of Transportation, 2022). Additionally, US 77 is a four-lane road with a median barrier, while SH 186 has two lanes with no barrier between lanes. Both roads are regularly mowed and receive regular road maintenance.

2.2. Study design

Along each of the roads, we established seven randomly placed transects, located perpendicular to the roadway. Transects were set at least 500 m apart to increase the likelihood that the transects would act independently. Along each transect, we established seven camera sites, beginning 50 m from the road to ensure that they avoided the road right-of-way where maintenance activities could damage camera traps and fencing could impact mammal site use. The seven sites were spaced 200 m apart, such that they ranged from 50 to 1250 m from the road. This interval was chosen to examine fine-scale variation in the mammal community within the REZ. To reduce flooding risk, it was necessary to move two sites from their location along the transect (50 m and 100 m) to the nearest location at the same distance from the roadway.

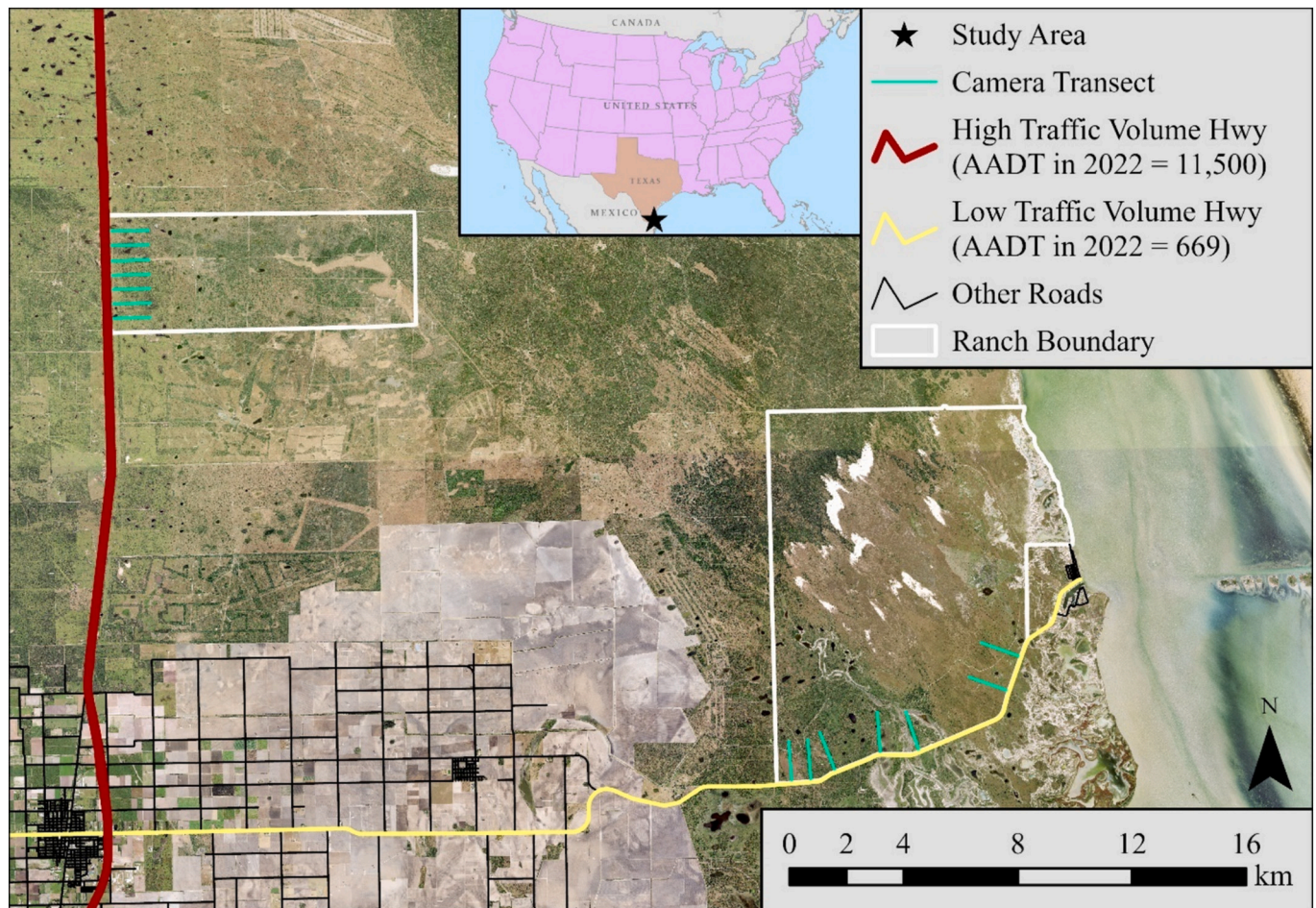


Fig. 1. Study area map showing the properties where the study took place, locations of the two roads, and the transects where camera traps were established. AADT represents the annual average daily traffic for each road in 2022 (Texas Department of Transportation, 2022).

2.3. Camera setup and processing

At each site, we placed one Reconyx HyperFire 2 camera trap (Reconyx Inc., WI, USA) facing a random direction on a U-post 30–50 cm above the ground. Some camera traps faced game trails or water features, which may have impacted detection rates on those camera traps, but we did not specifically place camera traps facing directions where we expected detection to be greatest. Camera traps were programmed to record three photographs per trigger event with no delay between triggers. We checked camera traps every two months to exchange memory cards and clear vegetation. Camera traps were active from May 2022 to April 2023.

We downloaded and renamed photographs to the date-time the photograph was taken. Protocols for organizing and sorting photographs were based on Sanderson and Harris (2013). We used the Microsoft MegaDetector v5.0a camera trap detection model to aid in the identification of false captures (Beery et al., 2019) and the program Timelapse 2 to identify species and number of individuals (Greenberg et al., 2019; Fennell et al., 2022). Using MegaDetector to identify ghost images requires selection of a threshold confidence level for false captures (called empty images by MegaDetector), animals, people, and vehicles. Using preliminary data and an extensive camera trap dataset collected for concurrent studies (Scognamiglio et al., 2023; Yamashita et al., 2025), thresholds of 0.60 for empty images and 0.55 for animals, people, and vehicles were 95–98 % accurate at identifying ghosts and balanced the removal of ghosts with the false negative rate. Next, we sorted non-ghost photographs to the lowest taxonomic level and determined the number of individuals in each photograph (Harris et al., 2010). Animals that

could not be identified to species were classified as “unknown” or the lowest classification possible (e.g., “unknown mammal” or “unknown ungulate”).

In our study, we were not able to identify every species to individual, so detections of the same species on different camera traps, especially along a single transect, may have been due to repeated detections by a single individual. While specific home range information is not available for most species in our study area, the home range sizes for nearly all species in our study (eastern cottontail [*Sylvilagus floridanus*; hereafter cottontail] being the main exception) was likely larger than the spacing of our camera traps along a transect (200 m). Repeated detections of an individual at a site are likely an indicator of microsite use (Johnson, 1980), so differences in number of detections at different distances from a road may be due to a road effect on site use.

For statistical analyses, we excluded rodents due to their low reliability of detection on camera traps (Kays et al., 2022). Cattle were also excluded because cattle are actively managed on both properties and are not free-ranging. We calculated the number of independent detections within each month. We defined independent events using a 30 min period (Tanwar et al., 2021; Davis et al., 2022) between consecutive photographs of a species, for permutational multivariate analysis of variance (PERMANOVA). Therefore, the experimental unit was a month at a given distance in a transect on a road ($n = 1176$).

Some camera traps had mechanical issues, or their memory cards reached capacity due to vegetation growth or camera malfunction, so we calculated the daily detection rate for each month by dividing the number of detections in each month by the number of active trap nights in the month (Lashley et al., 2018). This calculation is similar to the

commonly used detections per 100 trap nights, used to standardize camera trap data for comparison purposes (Kelly and Holub, 2008; Harmsen et al., 2021). This method provides standardization for inconsistent numbers of trap nights across sites but assumes that the detection probability did not change over a month. Preliminary analyses revealed this assumption to be valid in our study, so an experimental unit was removed only when the camera was not active for an entire month.

2.4. Covariates

In community-level camera trap studies, accounting for differences in microsite vegetation characteristics is important for reducing detection bias of different species (Hofmeester et al., 2019). In South Texas, woody cover is important for predicting site use by a variety of species, including carnivores, ungulates, and others (Lombardi et al., 2020a; Yamashita et al., 2021; Lombardi et al., 2022; Sergeyev et al., 2023). Therefore, incorporating a metric of woody cover is essential to account for microsite effects on beta diversity and detection rates. We used a freely available LiDAR point cloud dataset collected in 2018 to calculate canopy height in a 10 m radius around each site (Sergeyev et al., 2024). We used the program LP360 (GeoCue Group, Inc., Madison, AL, USA) to create a digital surface model and digital elevation model of the study area using a pixel size of 1.5 m. We then calculated canopy height (m) using ArcGIS Pro (ESRI, Redlands, CA, USA) and computed the median canopy height of all pixels within 10 m of camera locations.

2.5. Statistical methods

2.5.1. PERMANOVA analyses

To assess the impacts of traffic volume and distance on the beta diversity and detection of mammals (30 min period for independent events), we used PERMANOVA (Anderson, 2001, 2017). PERMANOVA provides an ideal platform for assessing impacts of environmental variation on beta diversity because it provides an effective, statistically powerful method for modeling multivariate community composition and detection rates (Legendre et al., 2005; Anderson et al., 2011). PERMANOVA is more powerful than equivalent parametric tests ([multivariate] analysis of variance) when assumptions of normality cannot be satisfied (Anderson, 2017).

To assess beta diversity, we analyzed the community of mammals that could be captured on camera traps, excluding rodents (hereafter mammal community), as well as three subsets of the mammal community based on functional and taxonomic groupings. The mammal community included 21 species and two unknown categories (Table 1). The subsets included the native mammal community plus feral hog and nilgai (excludes exotic and most non-native species; hereafter native community; 16 species), the carnivore community (10 species), and the ungulate community (eight species plus one unknown category). We also ran single-species analyses on 12 species found on both ranches and had at least 100 total detections (most commonly detected species in the study area): American badger (*Taxidea taxus*; hereafter badger), bobcat (*Lynx rufus*), cottontail, coyote (*Canis latrans*), feral hog, javelina (*Pecari tajacu*), nilgai, nine-banded armadillo (*Dasypus novemcinctus*; hereafter armadillo), northern raccoon (*Procyon lotor*; hereafter raccoon), striped skunk (*Mephitis mephitis*), Virginia opossum (*Didelphis virginiana*; hereafter opossum), and white-tailed deer (*Odocoileus virginianus*).

We analyzed models within a randomized block design with repeated measures on each road. These designs were combined, and the full experiment was analyzed using a split-split-plot arrangement of factors, with traffic volume, distance, and month as main plot, subplot, and subsubplot factors, respectively. Transect, its interaction with traffic volume, and its crossed interaction with distance nested in traffic volume were included as random effects in the model. This design was analyzed with respect to each response variable using PERMANOVA with a covariate in the program Primer v7 (Primer-E, Albany, Auckland,

Table 1

List of mammal species identified in camera traps in the road effect zone and which analyses they were included in: entire mammal community (C1), native mammal community plus feral hog and nilgai (C2), carnivore community (C3), ungulate community (C4), and single-species analyses (S1–12).

Common name	Scientific name	C1	C2	C3	C4	S1–12
Addax	<i>Addax nasomaculatus</i>	X			X	
Armadillo	<i>Dasypus novemcinctus</i>	X	X			X
American badger	<i>Taxidea taxus</i>	X	X	X		X
Bobcat	<i>Lynx rufus</i>	X	X	X		X
Coyote	<i>Canis latrans</i>	X	X	X		X
Domestic cattle	<i>Bos taurus</i>					
Domestic cat	<i>Felis catus</i>	X		X		
Domestic dog	<i>Canis familiaris</i>	X		X		
Domestic horse	<i>Equus caballus</i>	X			X	
Eastern cottontail	<i>Sylvilagus floridanus</i>	X	X			X
Feral hog	<i>Sus scrofa</i>	X	X		X	X
Grey fox	<i>Urocyon cinereoargenteus</i>	X	X	X		
Javelina	<i>Pecari tajacu</i>	X	X		X	X
Long-tailed weasel	<i>Mustela frenata</i>	X	X	X		
Mexican ground squirrel	<i>Ictidomys mexicanus</i>	X	X			
Nilgai	<i>Boselaphus tragocamelus</i>	X	X		X	X
Northern raccoon	<i>Procyon lotor</i>	X	X	X		X
Ocelot	<i>Leopardus pardalis</i>	X	X	X		
Scimitar-horned oryx	<i>Oryx dammah</i>	X			X	
Rodent spp.	<i>Rodentia</i> spp.					
Striped skunk	<i>Mephitis mephitis</i>	X	X	X		X
Unknown mammal	<i>Mammalia</i> spp.	X				
Unknown ungulate	<i>Artiodactyla</i> spp.	X			X	
Virginia opossum	<i>Didelphis virginiana</i>	X	X			X
Waterbuck	<i>Kobus ellipsiprymnus</i>	X			X	
White-tailed deer	<i>Odocoileus virginianus</i>	X	X		X	X

New Zealand). We calculated a zero-adjusted Bray-Curtis similarity matrix using an adjustment of 0.03 detections/day (1 detection in a 31-day month), the smallest non-zero value in the species matrix (Faith et al., 1987; Clarke et al., 2006). We calculated distance among centroids to ensure that the error term for each level of the split plot was appropriate (Anderson, 2017). Median canopy height was included at the traffic volume and distance levels of the split-split-plot. PERMANOVA can be greatly affected by the relative difference in the number of detections of different species, with more abundant species driving patterns of beta diversity. To account for this, we square-root transformed the mammal community, native community, and ungulate community data before calculation of the similarity matrix to reduce the influence of cottontail, nilgai, and white-tailed deer and allow rare species (e.g., carnivores) to have greater influence on beta diversity (Legendre and Legendre, 2012). For the carnivore community and single-species analyses, we did not transform data because they did not contain any hyperabundant species relative to others in the set (Legendre and Legendre, 2012). We tested simple main effects and simple effects with PERMANOVA and pairwise PERMANOVA analyses; these analyses do not combine error terms when appropriate but rather partition the data into subsets for permutation.

We used principal coordinates analysis (PCO) to assess whether significant differences were due to differences in location or dispersion, visualize multivariate analyses, and assess species associations with the levels of each factor of interest (Legendre et al., 2005; Anderson, 2017). We computed the distance among centroids that correspond to combinations of significant factor levels and used PCO for visualizations. To assess species associations, we calculated the Pearson correlation coefficient between species detections and each PCO axis (Legendre and Gallagher, 2001). For univariate analyses, we calculated the mean number of detections and standard errors using the *Mixed* procedure with a Toeplitz or autoregressive correlation structure to model random effects using SAS v9.4 software (SAS Institute Inc., Cary, NC, USA). All plots were created using the package *ggplot2* in Program R (Wickham,

2016).

3. Results

Camera traps were active for 12 months and captured 21 species of mammal—almost all known target species in the study area, apart from black-tailed jackrabbit (*Lepus californicus*; Table 1; Schmidly and Bradley, 2016, Schmidly et al., 2023). Black-tailed jackrabbits are found in the study area (TJY, ZMW, JVL unpublished data) but prefer habitats that were not captured by our camera traps (agricultural areas, deserts, shrublands; Simes et al., 2015). We retained 1154 out of 1176 experimental units due to camera malfunctions and vegetation growth. Within a particular transect and distance, no more than two experimental units were excluded from the analysis.

3.1. Beta diversity results

We found an interaction between traffic volume and distance (pseudo-F = 1.4989, $p = 0.0410$, permutations = 9864) and between traffic volume and month (pseudo-F = 2.8457, $p = 0.0001$, permutations = 9848) for the mammal community composition (Table 2). Within the traffic volume/distance interaction, there were differences in traffic volume at the 50 m (pseudo-F = 2.7347, $p = 0.0239$, permutations = 9951), 250 m (pseudo-F = 6.1124, $p = 0.0019$, permutations = 9947), and 450 m (pseudo-F = 7.0991, $p = 0.0037$, permutations = 9958) distances (Fig. 2A). There were no differences in distance within either traffic volume level. Within all months, there were differences in traffic volume (Fig. 3A; for full test statistics and p -values, see Appendix A).

Within the native community subset, we found an interaction between traffic volume and distance (pseudo-F = 1.4203, $p = 0.0669$, permutations = 9886) and between traffic volume and month (pseudo-F = 2.7652, $p = 0.0001$, permutations = 9855; Table 2). Within the traffic volume/distance interaction, we found differences in traffic volume at the 50 m (pseudo-F = 2.7309, $p = 0.0244$, permutations = 9955), 250 m (pseudo-F = 5.9731, $p = 0.0026$, permutations = 9935), and 450 m (pseudo-F = 6.8174, $p = 0.0024$, permutations = 9939) distances (Fig. 2B). We found no differences in distance within either level of traffic volume on the native mammal community composition. Within month, we found differences in traffic volume in all months except for June and July 2022 (Fig. 3B; for full test statistics and p -values, see Appendix A).

Within the carnivore subset, we found an interaction only between traffic volume and month (pseudo-F = 3.0460, $p = 0.0001$, permutations = 9878; Table 2). Within month, we found differences in traffic volume in nine of the 12 months (Fig. 3C; for full test statistics and p -

values, see Appendix A). There was no effect of distance on the carnivore community composition.

Within the ungulate subset, we found an interaction between traffic volume and month (pseudo-F = 2.7989, $p = 0.0001$, permutations = 9882; Table 2). Within month, we found differences in traffic volume in 10 of 12 months (Fig. 3D; for full test statistics and p -values, see Appendix A). There was no effect of distance on the ungulate community composition.

3.2. Single-species results

There was only an effect of month for number of detections of armadillo (pseudo-F = 6.6277, $p = 0.0001$, permutations = 9811), bobcat (pseudo-F = 6.7540, $p = 0.0001$, permutations = 9921), and white-tailed deer (pseudo-F = 4.0361, $p = 0.0001$, permutations = 9900; Table 3). There was an interaction between traffic volume and month for badger (pseudo-F = 3.5812, $p = 0.0001$, permutations = 9927), coyote (pseudo-F = 3.2142, $p = 0.0001$, permutations = 9906), feral hog (pseudo-F = 3.05434, $p = 0.0001$, permutations = 9929), nilgai (pseudo-F = 5.6636, $p = 0.0001$, permutations = 9888), opossum (pseudo-F = 5.1068, $p = 0.0001$, permutations = 9916), and raccoon (pseudo-F = 4.1628, $p = 0.0001$, permutations = 9920; Table 3). There was an interaction between distance and month (pseudo-F = 1.5191, $p = 0.0013$, permutations = 9833) and traffic volume and distance (pseudo-F = 2.3468, $p = 0.0231$, permutations = 9946) for feral hog (Table 3). Finally, there was a three-way interaction between traffic volume, distance, and month for cottontail (pseudo-F = 1.3315, $p = 0.0053$, permutations = 9757), javelina (pseudo-F = 1.4852, $p = 0.0025$, permutations = 9841), and striped skunk (pseudo-F = 1.3730, $p = 0.0131$, permutations = 9812; Table 3).

Within month, there was a difference in traffic volume in eight months for number of detections of badger, seven months for coyote, one month for feral hog, nine months for nilgai, two months for opossum, and one month for raccoon (Fig. 4). For feral hog, there was a difference in distance in one month, with the 1050 m distance being different from the 250 m, 450 m, 650 m, and 850 m distances (Fig. 5). Additionally for feral hog, there were differences in traffic volume at the 250 m and 450 m distances and between the 450 m and 1050 m distances on the low traffic volume road and between the 50 m distance and 250 and 450 m distances on the high-volume road (Appendix B). For cottontail, there were interactions between traffic volume and distance in two months and differences in distance in an additional four months (Appendix B). In no month was there a difference in traffic volume alone. For javelina, there was an interaction between traffic volume and distance in two months, an effect of distance alone in two months, and an effect of traffic volume alone in nine months. For striped skunk, there was an interaction between traffic volume and distance in one month and a difference in traffic volume alone in two months. For a detailed description of the results, including all test statistics and associated p -values, see Appendix A.

4. Discussion

Our results suggest that traffic volume may play a significant role in determining the beta diversity and number of detections of several mammal species living around roads; effects of distance, however, were only manifested at the mammal community and native community levels. By assessing how beta diversity varied around roads, we provide insights into how mammals respond to roads and how differences in road properties may impact future road mitigation efforts for mammals.

Traffic volume was an important factor impacting beta diversity and species detection in our study, as it affected the beta diversity of all subsets of the community and detections of all but three species (armadillo, bobcat, and white-tailed deer). Within beta diversity analyses, there was clear differentiation in both location and dispersion of beta diversity for all community subsets, indicating that increased

Table 2

Summary of statistically significant treatment effects for the community-level analyses: entire mammal community (mammals), native mammal community plus feral hog and nilgai (natives), carnivore community (carnivores), and ungulate community (ungulates). Traffic volume (low, high) is the level of traffic of each study road, distance (50, 250, 450, 650, 850, 1050, and 1250 m) is the distance from the road, and month (May 22 to Apr 23) is the sampling month.

Community	Traffic volume	Distance	Month
Mammals	Depends on Month	Depends on Traffic Volume	Depends on Traffic Volume
	Depends on Distance		
Natives	Depends on Month	Depends on Traffic Volume	Depends on Traffic Volume
	Depends on Distance		
Carnivores	Depends on Month	No Effect	Depends on Traffic Volume
Ungulates	Depends on Month	No Effect	Depends on Traffic Volume

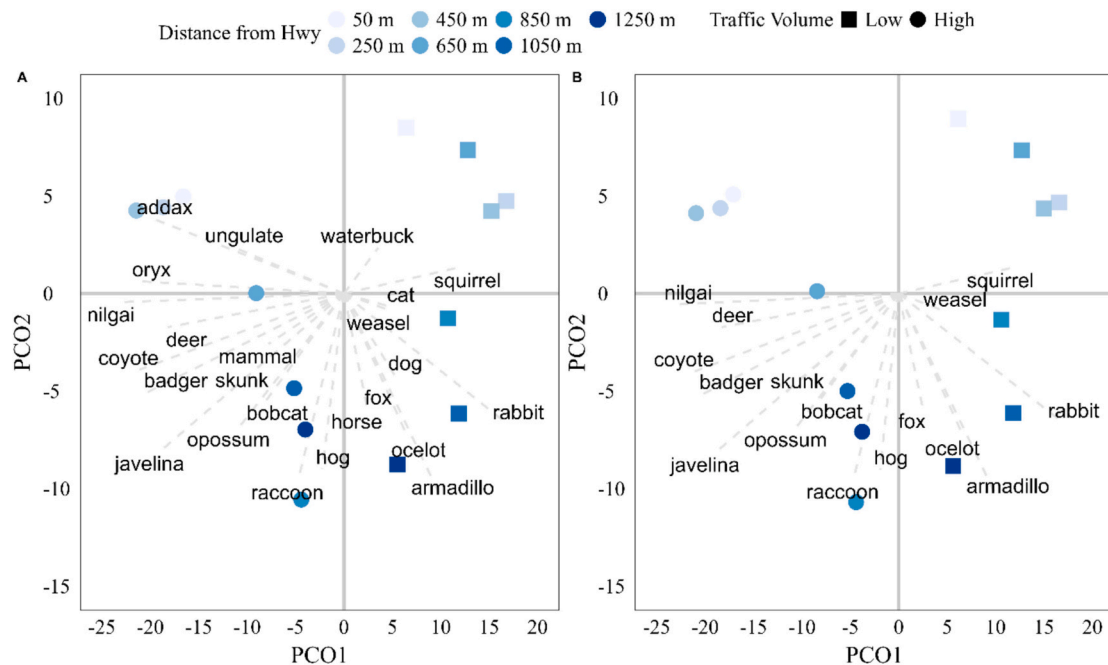


Fig. 2. Principal coordinates analysis (PCO) ordination for the effect of the interaction between distance and traffic volume on the (A) entire mammal community and (B) native mammal community plus feral hog and nilgai. Grey lines represent the Pearson correlation coefficient between the number of detections of a species and each PCO axis.

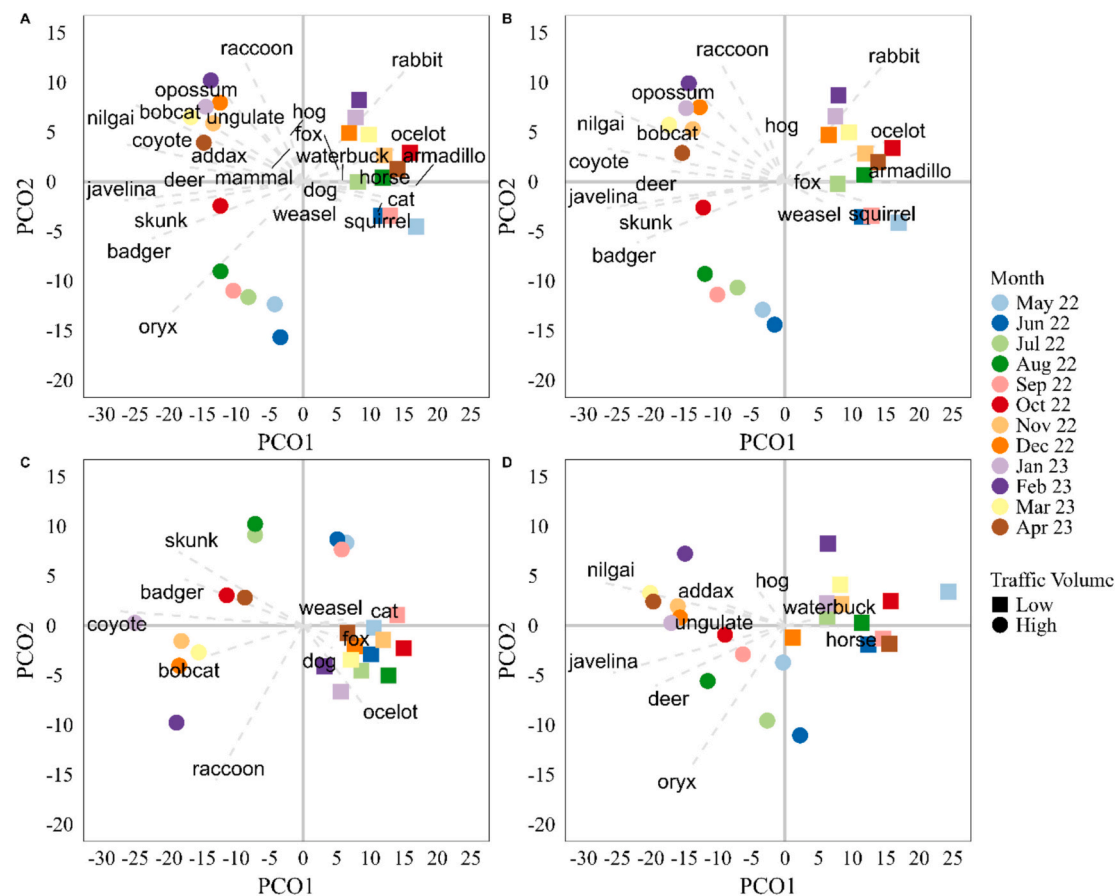


Fig. 3. Principal coordinates analysis (PCO) ordination for the effect of the interaction between traffic volume and month on the (A) entire mammal community, (B) native mammal community plus feral hog and nilgai, (C) carnivore community, and (D) ungulate community. Grey lines represent the Pearson correlation coefficient between the number of detections of a species and each PCO axis.

Table 3

Summary of statistically significant treatment effects for the individual species analyses: nine-banded armadillo (armadillo), American badger (badger), bobcat, eastern cottontail (cottontail), coyote, feral hog, javelina, nilgai, Virginia opossum (opossum), northern raccoon (raccoon), striped skunk, and white-tailed deer. Traffic volume (low, high) is the level of traffic of each study road, distance (50, 250, 450, 650, 850, 1050, and 1250 m) is the distance from the road, and month (May 22 to Apr 23) is the sampling month.

Species	Traffic volume	Distance	Month
Armadillo	No Effect	No Effect	Yes
Badger	Depends on Month	No Effect	Depends on Traffic Volume
Bobcat	None	No Effect	Yes
Cottontail	Depends on Distance and Month	Depends on Traffic Volume and Month	Depends on Traffic Volume and Distance
Coyote	Depends on Month	No Effect	Depends on Traffic Volume
Feral hog	Depends on Distance	Depends on Traffic Volume	Depends on Traffic Volume
	Depends on Month	Depends on Month	Depends on Distance
Javelina	Depends on Distance and Month	Depends on Traffic Volume and Month	Depends on Traffic Volume and Distance
Nilgai	Depends on Month	No Effect	Depends on Traffic Volume
Opossum	Depends on Month	No Effect	Depends on Traffic Volume
Raccoon	Depends on Month	No Effect	Depends on Traffic Volume
Striped skunk	Depends on Distance and Month	Depends on Traffic Volume and Month	Depends on Traffic Volume and Distance
White-tailed deer	No Effect	No Effect	Yes

disturbance around the high-volume road may cause some species to adjust their usage of the REZ. These differences in beta diversity were likely driven by the loss of disturbance-sensitive species, especially carnivores, around the high-volume road. The general increase in detections of non-native nilgai around the high-volume road may have also contributed to the differences in beta diversity; however, a preliminary analysis had indicated no difference in results when nilgai and feral hogs were excluded, so we believe that this change was primarily driven by the loss of native carnivores. Principal coordinates analysis indicated that there was likely a difference in dispersion between traffic volume levels. Although PERMANOVA is sensitive to both differences in location and dispersion, differences in both location and dispersion are indicative of road impacts on the community. Increased variability in activity is a known response to increased disturbance, and therefore, the increased variability observed in community composition around roads is in line with the disturbance response of animals to humans (Tablado and Jenni, 2017). Despite the limitations of examining only two traffic volume levels (with different road characteristics), our study found similar results to previous works. The density and abundance of anurans (Fahrig et al., 1995) and birds (Reijnen et al., 1996) and the movement of mammals (Dennehy et al., 2021) have all been shown to be negatively affected by higher traffic volumes. Interestingly, we detected similar negative effects of traffic volume in beta diversity, but not always at lower traffic volumes than these previous studies, indicating that changes in community structure may be a more sensitive metric than species-level analyses. Therefore, additional research is needed to identify how road characteristics, including changes in traffic volume, impact beta diversity around roads.

Contrary to our expectations, we found a limited effect of distance to road on beta diversity and species detections. At the broader community levels, the community composition around the two roads was similar starting at 650 m from each road, indicating that at this distance, roads

may stop influencing community structure. Interestingly, though, we did not find differences in beta diversity among distances along each road. A previous study used occupancy modeling to examine how the abundance of mammals in Brazil was affected by distance to roads and found similar mixed results to our study (Alberici et al., 2024) indicating that individuals living around roads likely use the entire area around the road, as has been found in ocelots in Texas (Veals et al., 2022). We found that the number of detections per species generally increased with distance, indicating that mammals may use areas near roads less often than areas farther from roads (McKinney, 2008). Although roads are known to influence home range placement of mammals (Riley et al., 2003; Riley et al., 2021; Veals et al., 2022), road presence may be mediated by utilizing areas near roads less often than other parts of the home range.

Whereas we cannot say exactly how far the road effect zone extends for beta diversity or any particular species, the impact of disturbance (i.e., traffic volume) on beta diversity seems to decrease between 450 and 650 m from the road. This may indicate that the relative effects of traffic volume on beta diversity extend a limited distance from the road. While it is possible that our sampling occurred entirely within the REZ for most mammals (Andrasi et al., 2021; Lombardi et al., 2023), our study nonetheless demonstrates how variability in traffic volume can impact mammal use of the REZ.

Interestingly, exotic species did not have much influence on the native mammal community, as exemplified by the similarity in response to roads by the mammal community and native community. Species-level analyses showed differences primarily in traffic volume—a likelier, easier-to-detect, and stronger impact on mammals (Grilo et al., 2015; Mata et al., 2017) – indicating that finer-scale impacts on beta diversity, such as those from distance, may not appear in species-level analysis. In our study, we were only able to conduct single-species analyses of the most common species in the study area. This has important conservation implications because species-specific studies may not have the power to detect road impacts on rare and threatened species (Huijser and Bergers, 2000). Providing an estimate of how beta diversity varies around roads may help identify how roads could impact these species. In our study area, changes in beta diversity due to traffic volume and distance were primarily due to loss of rare species rather than turnover, indicating that rare species are likely more impacted by roads than common species. Additionally, using subsets of the community to examine subsets of beta diversity allowed us to identify how different groups of species respond to roads and how these groups of species contribute to the overall community-level response to traffic and distance.

We conducted this study along only two highways and on two ranches in South Texas, which limits our inferences about traffic volume to these two sites. While road traffic volume was the primary difference between the two ranches on which we conducted our study, we recognize that slight differences in ranch management (hunting and cattle operations), soil types (and therefore vegetation communities), and human activity may have affected the relative detection rates of each species around each road. For example, badgers were detected more frequently near the high-volume road than the low-volume road, possibly because the presence of fine sandy soils near the high-volume road promoted fossorial behavior unique to badgers among our study species (Duquette and Gehrt, 2014). Additionally, ranch management activities, particularly hunting and cattle management, may have altered mammal behavior in the REZ, which may have affected the observed response of the mammal community to roads. While none of our sites were near ungulate feeding stations, hunting practices, including the use of feed programs, can support non-target species such as raccoons and coyotes, potentially increasing the abundance of those species around the high-volume road (Campbell et al., 2013). However, given the clear differences in community composition for all subsets of communities, the greater variability in the community composition seen around the high-traffic volume road suggests impacts of greater disturbance on wildlife. Additional work is required to examine the

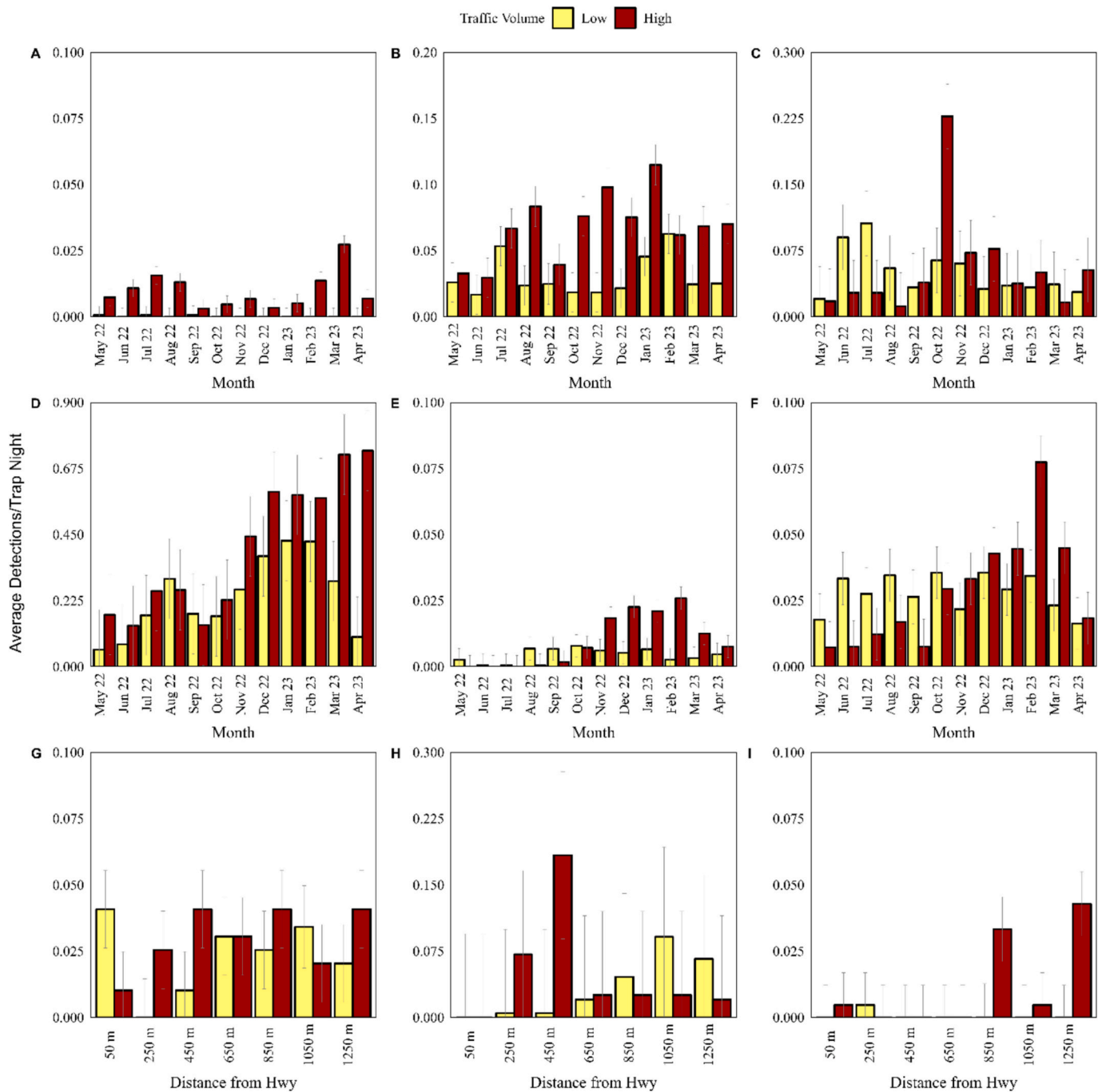


Fig. 4. Conditional effects plots of traffic volume on the average number of detections per trap night of (A) American badger, (B) coyote, (C) feral hog, (D) nilgai, (E) Virginia opossum, (F) northern raccoon, (G) eastern cottontail, (H) javelina, and (I) striped skunk. For A–F, a significant interaction only occurred between traffic volume and month, so number of detections is only shown between traffic volume and month. For G–I, a significant interaction occurred among traffic volume, distance, and month, so the interaction between traffic volume and distance is shown within one level of month: Feb 2023 for G and H, and Jun 2022 for I. For complete plots showing differences in all months, see Appendix B.

confounding influences of cattle and ranch management practices (e.g., cattle rotations, stocking rates, prescribed fire, hunting) on mammal use of the REZ.

Additionally, seasonal variation in animal behavior could impact the relationship we found between traffic volume, distance, and the mammal community. Our study, being one year in duration, was unable to parse the effects of seasonality on the relationship between roads and beta diversity. However, we believe that our results are indicative of the overall effects of traffic volume and distance on beta diversity because there was a clear difference in beta diversity among traffic volumes

within every month studied. Additional studies on long-term relationships between roads and beta diversity may help to reveal dynamic relationships between vehicle traffic, temperature, and precipitation on mammal beta diversity within the REZ.

5. Conclusions

Despite our limited inferential ability, our study indicated that traffic volume may play a significant role in determining beta diversity around roads and that the REZ for the mammal community of South Texas may

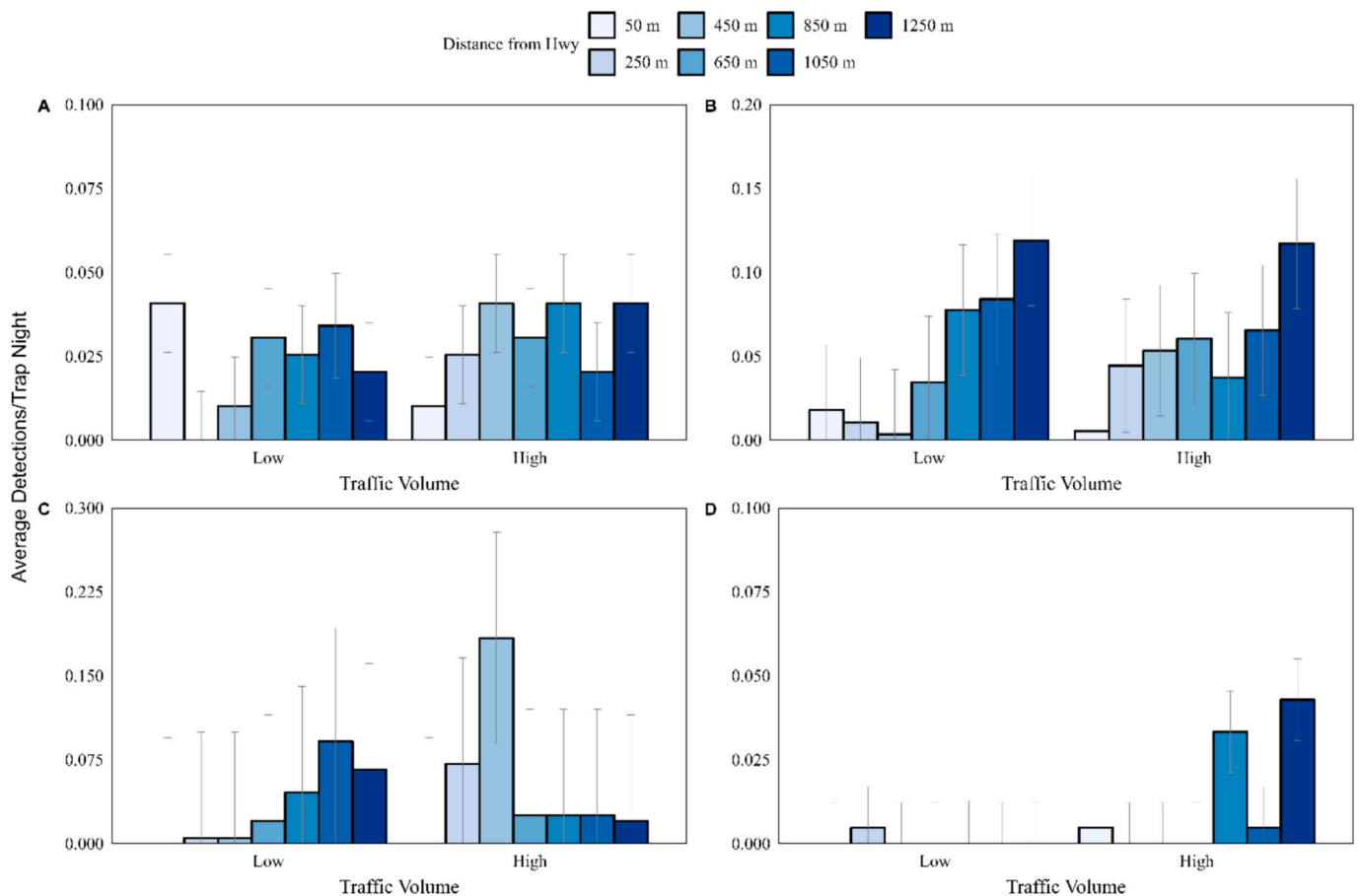


Fig. 5. Conditional effects plots of distance on the average number of detections per trap night of (A) feral hog, (B) eastern cottontail, (C) javelina, and (D) striped skunk. For B–D, a significant interaction occurred among traffic volume, distance, and month, so the interaction between distance and traffic volume is shown within one level of month: Feb 2023 for B and C and Jun 2022 for D. For complete plots showing differences in all months, see Appendix B.

extend to 450 to 650 m. Additionally, using beta diversity may provide a more sensitive approach than single-species analyses for identifying impacts of traffic volume and distance to roads on both common and rare mammals. Whereas species-specific models can provide valuable insights into responses of individual species to roads, models focusing on community diversity provide stronger support for assessing broad-scale impacts of roads on wildlife and expand our understanding of road impacts on ecosystems. Maintaining healthy wildlife communities is critically important to maintaining healthy ecosystems (Warwick, 1993; Attrill and Depledge, 1997) around roads, and more diverse communities usually contain rarer and threatened species (Gotelli and Colwell, 2001). Therefore, managing areas around roads for increased wildlife diversity is likely to promote conservation of rare species, which are often the target of road mitigation efforts and legislative policy frameworks.

CRediT authorship contribution statement

Thomas J. Yamashita: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **David B. Wester:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Zachary M. Wardle:** Writing – review & editing, Investigation, Funding acquisition. **Daniel G. Scognamiglio:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **Landon R. Schofield:** Writing – review & editing, Resources. **Michael E. Tewes:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **John H. Young:** Writing –

review & editing, Resources, Project administration, Funding acquisition. **Jason V. Lombardi:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111428>.

Data availability

Original LiDAR point cloud are freely available from the Texas Natural Resources Institute online web service at <https://data.tnris.org>, accessed 1 October 2023. Camera trap data used in this manuscript are available upon request. Code and other data for this manuscript are available on GitHub at <https://github.com/tomyamashita/BetaDiversityInRoadEffectZone>. The functions used for processing camera data are available in the cameraTrapping package on GitHub at <https://github.com/tomyamashita/cameraTrapping>.

References

- Alberici, V., Desbiez, A.L.J., Pasqualotto, N., Chiarello, A.G., 2024. Unravelling unique responses of mammal abundance to road proximity in agricultural landscapes. *Anim. Conserv.* 27, 611–625. <https://doi.org/10.1111/acv.12933>.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>.
- Anderson, M.J., 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). 115 in: In: Balakrishnan, N., Colton, T., Everitt, B., Piegorsch, W., Ruggeri, F., Teugels, J.L. (Eds.), Wiley StatsRef: Statistics Reference Online.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Andrasi, B., Jaeger, J.A.G., Heinicke, S., Metcalfe, K., Hockings, K.J., 2021. Quantifying the road-effect zone for a critically endangered primate. *Conserv. Lett.* 14, e12839. <https://doi.org/10.1111/conl.12839>.
- Attrill, M.J., Depledge, M.H., 1997. Community and population indicators of ecosystem health: targeting links between levels of biological organisation. *Aquat. Toxicol.* 38, 183–197. [https://doi.org/10.1016/S0166-445X\(96\)00839-9](https://doi.org/10.1016/S0166-445X(96)00839-9).
- Beery, S., Morris, D., Yang, S., Simon, M., Norouzzadeh, A., Joshi, N., 2019. Efficient pipeline for automating species ID in new camera trap projects. *Biodivers. Inf. Sci. Stand.* 3, e37222. <https://doi.org/10.3897/biss.3.37222>.
- Benitez-Lopez, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* 143, 1307–1316. <https://doi.org/10.1016/j.biocon.2010.02.009>.
- Blackburn, A., Heffelfinger, L.J., Veals, A.M., Tewes, M.E., Young, J.H., 2021. Cats, cars, and crossings: the consequences of road networks towards the conservation of an endangered felid. *Glob. Ecol. Conserv.* 27, e01582. <https://doi.org/10.1016/j.gecco.2021.e01582>.
- Blackburn, A., Veals, A.M., Tewes, M.E., Wester, D.B., Young Jr., J.H., DeYoung, R.W., Perotto-Baldovino, H.L., 2022. If you build it, will they come? A comparative landscape analysis of ocelot roadkill locations and crossing structures. *PLoS One* 17, e0267630. <https://doi.org/10.1371/journal.pone.0267630>.
- Campbell, T.A., Long, D.B., Shriner, S.A., 2013. Wildlife contact rates at artificial feeding sites in Texas. *Environ. Manag.* 51, 1187–1193. <https://doi.org/10.1007/s00267-013-0046-4>.
- Caravaggi, A., Banks, P.B., Burton, A.C., Finlay, C.M.V., Haswell, P.M., Hayward, M.W., Rowcliffe, M.J., Wood, M.D., 2017. A review of camera trapping for conservation behaviour research. *Remote Sens. Ecol. Conserv.* 3, 109–122. <https://doi.org/10.1002/rse2.48>.
- Clarke, K.R., Somerfield, P.J., Chapman, M.G., 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* 330, 55–80. <https://doi.org/10.1016/j.jembe.2005.12.017>.
- Clevenger, A.P., 2005. Conservation value of wildlife crossings: measures of performance and research directions. *Gaia-Ecol. Perspect. Sci. Society* 14, 124–129. <https://doi.org/10.14512/gaia.14.2.12>.
- Cooper, D.J., Wagner, J.I., 2013. Tropical storm driven hydrologic regimes support *Spartina spartinae* dominated prairies in Texas. *Wetlands* 33, 1019–1024. <https://doi.org/10.1007/s13157-013-0459-0>.
- Davis, R.S., Gentle, L.K., Mgoola, W.O., Stone, E.L., Uzal, A., Yarnell, R.W., 2022. Using camera trap bycatch data to assess habitat use and the influence of human activity on African elephants (*Loxodonta africana*) in Kasungu National Park, Malawi. *Mamm. Biol.* 103, 121–132. <https://doi.org/10.1007/s42991-022-00330-7>.
- Dennehy, E., Llaneza, L., López-Bao, J.V., 2021. Contrasting wolf responses to different paved roads and traffic volume levels. *Biodivers. Conserv.* <https://doi.org/10.1007/s10531-021-02239-y>.
- Duquette, J.F., Gehrt, S.D., 2014. Badger (*Taxidea taxus*) resource selection and spatial ecology in intensive agricultural landscapes. *Am. Midl. Nat.* 171 (1), 116–127. <https://doi.org/10.1674/0003-0031-171.1.116>.
- Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. *Ecol. Soc.* 14. <https://www.ecologyandsociety.org/vol14/iss1/art24/>.
- Elliott, L.F., Diamond, D.D., True, D., Blodgett, C.F., Pursell, D., German, D., Treuer-Kuehn, A., 2014. Ecological Mapping Systems of Texas: Summary Report. Texas Parks & Wildlife Department, Austin, Texas.
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. *Biol. Conserv.* 73, 177–182. [https://doi.org/10.1016/0006-3207\(94\)00102-V](https://doi.org/10.1016/0006-3207(94)00102-V).
- Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68. <https://doi.org/10.1007/BF00038687>.
- Fennell, M., Beirne, C., Burton, A.C., 2022. Use of object detection in camera trap image identification: assessing a method to rapidly and accurately classify human and animal detections for research and application in recreation ecology. *Glob. Ecol. Conserv.* 35, e02104. <https://doi.org/10.1016/j.gecco.2022.e02104>.
- Forman, R.T.T., Deblinger, R.D., 2000. The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. *Conserv. Biol.* 14, 36–46. <https://doi.org/10.1046/j.1523-1739.2000.99088.x>.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington D.C.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Greenberg, S., Godin, T., Whittington, J., 2019. Design patterns for wildlife-related camera trap image analysis. *Ecol. Evol.* 9, 13706–13730. <https://doi.org/10.1002/ece3.5767>.
- Grilo, C., Ferreira, F.Z., Revilla, E., 2015. No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatio-temporal scale. *Environ. Impact Assess. Rev.* 55, 54–58. <https://doi.org/10.1016/j.eiar.2015.07.003>.
- Haines, A.M., Tewes, M.E., Laack, L.L., 2005. Survival and sources of mortality in ocelots. *J. Wildl. Manag.* 69, 255–263. [https://doi.org/10.2193/0022-541X\(2005\)069<0255:SASOMI>2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)069<0255:SASOMI>2.0.CO;2).
- Harmsen, B.J., Saville, N., Foster, R.J., 2021. Long-term monitoring of margays (*Leopardus wiedii*): implications for understanding low detection rates. *PLoS One* 16, e0247536. <https://doi.org/10.1371/journal.pone.0247536>.
- Harris, G., Thompson, R., Childs, J.L., Sanderson, J.G., 2010. Automatic storage and analysis of camera trap data. *Bull. Ecol. Soc. Am.* 91, 352–360. <https://doi.org/10.1890/0012-9623-91.3.352>.
- Hofmeester, T.R., Crooms, J.P.G.M., Odden, J., Andrén, H., Kindberg, J., Linnell, J.D.C., 2019. Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecol. Evol.* 9, 2320–2336. <https://doi.org/10.1002/ece3.4878>.
- Huijser, M.P., Bergers, P.J.M., 2000. The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. *Biol. Conserv.* 95, 111–116. [https://doi.org/10.1016/S0006-3207\(00\)00006-9](https://doi.org/10.1016/S0006-3207(00)00006-9).
- Jahrsdoerfer, S.E., Leslie, D.M., 1988. Tamaulipan Brushland of the Lower Rio Grande Valley of South Texas: Description, Human Impacts, and Management Options. U.S. Fish and Wildlife Service.
- Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61, 65–71. <https://doi.org/10.2307/1937156>.
- Kays, R., Lasky, M., Allen, M.L., Dowler, R.C., Hawkins, M.T.R., Hope, A.G., Kohli, B.A., Mathis, V.L., McLean, B., Olson, L.E., Thompson, C.W., Thornton, D., Widness, J., Cove, M.V., 2022. Which mammals can be identified from camera traps and crowdsourced photographs? *J. Mammal.* 103, 767–775. <https://doi.org/10.1093/jmammal/gyac021>.
- Kelly, M.J., Holub, E.L., 2008. Camera trapping of carnivores: trap success among camera types and across species, and habitat selection by species, on salt Pond Mountain, Giles County, Virginia. *Northeast. Nat.* 15, 249–262. [https://doi.org/10.1656/1092-6194\(2008\)15\[249:CTOCTS\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2008)15[249:CTOCTS]2.0.CO;2).
- Lashley, M.A., Cove, M.V., Chitwood, M.C., Penido, G., Gardner, B., DePerno, C.S., Moorman, C.E., 2018. Estimating wildlife activity curves: comparison of methods and sample size. *Sci. Rep.* 8, 4173. <https://doi.org/10.1038/s41598-018-22638-6>.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280. <https://doi.org/10.1007/s004420100716>.
- Legendre, P., Legendre, L., 2012. Numerical Ecology, 3rd edition. Elsevier B.V., Kidlington, Oxford, UK.
- Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* 75, 435–450. <https://doi.org/10.1890/05-0549>.
- Li, X., Hu, W., Bleisch, W.V., Li, Q., Wang, H., Lu, W., Sun, J., Zhang, F., Ti, B., Jiang, X., 2022. Functional diversity loss and change in nocturnal behavior of mammals under anthropogenic disturbance. *Conserv. Biol.* 36, e13839. <https://doi.org/10.1111/cobi.13839>.
- Lombardi, J.V., MacKenzie, D.I., Tewes, M.E., Perotto-Baldovino, H.L., Mata, J.M., Campbell, T.A., 2020a. Co-occurrence of bobcats, coyotes, and ocelots in Texas. *Ecol. Evol.* 10, 4903–4917. <https://doi.org/10.1002/ece3.6242>.
- Lombardi, J.V., Perotto-Baldovino, H.L., Tewes, M.E., 2020b. Land cover trends in South Texas (1987–2050): potential implications for wild felids. *Remote Sens.* 12, 659. <https://doi.org/10.3390/rs12040659>.
- Lombardi, J.V., Sergeyev, M., Tewes, M.E., Schofield, L.R., Wilkins, R.N., 2022. Spatial capture-recapture and LiDAR-derived vegetation metrics reveal high densities of

- ocelots on Texas ranchlands. *Front. Conserv. Sci.* 3, 1003044. <https://doi.org/10.3389/fcsc.2022.1003044>.
- Lombardi, J.V., Yamashita, T.J., Blackburn, A., Young Jr., J.H., Tewes, M.E., Anderson, C.J., 2023. Examining the spatial structure of woody cover within a highway road effect zone for ocelots in Texas. *Urban Ecosyst.* 26, 1057–1069. <https://doi.org/10.1007/s11252-023-01350-y>.
- Mata, C., Ruiz-Capillas, P., Malo, J.E., 2017. Small-scale alterations in carnivore activity patterns close to motorways. *Eur. J. Wildl. Res.* 63, 64. <https://doi.org/10.1007/s10344-017-1118-1>.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation: the impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience* 52, 883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:Ubac\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2002)052[0883:Ubac]2.0.Co;2).
- McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>.
- Mori, A.S., Isbell, F., Seidl, R., 2018. β -Diversity, community assembly, and ecosystem functioning. *Trends Ecol. Evol.* 33, 549–564. <https://doi.org/10.1016/j.tree.2018.04.012>.
- Ordenana, M.A., Crooks, K.R., Boydston, E.E., Fisher, R.N., Lyren, L.M., Siudyla, S., Haas, C.D., Harris, S., Hathaway, S.A., Turschak, G.M., Miles, A.K., Van Vuren, D.H., 2010. Effects of urbanization on carnivore species distribution and richness. *J. Mammal.* 91, 1322–1331. <https://doi.org/10.1644/09-mamm-a-312.1>.
- Palecki, M., I. Durre, J. Lawrimore, and S. Applequist. 2020. NOAA's U.S. climate normals (1991–2020): Summary of monthly normals. Accessed 24 April 2022 2022.
- Reijnen, R., Foppen, R., Meeuwssen, H., 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biol. Conserv.* 75, 255–260. [https://doi.org/10.1016/0006-3207\(95\)00074-7](https://doi.org/10.1016/0006-3207(95)00074-7).
- Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in Southern California. *Conserv. Biol.* 17, 566–576. <https://doi.org/10.1046/j.1523-1739.2003.01458.x>.
- Riley, S.P.D., Sikich, Jeffrey A., Benson, J.F., 2021. Big cats in the big city: spatial ecology of mountain lions in greater Los Angeles. *J. Wildl. Manag.* 85, 1527–1542. <https://doi.org/10.1002/jwmg.22127>.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. *Science* 343, 1241484. <https://doi.org/10.1126/science.1241484>.
- Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M., Hayward, M. W., Kerley, G.I.H., Levi, T., Lindsey, P.A., Macdonald, D.W., Malhi, Y., Painter, L.E., Sandom, C.J., Terborgh, J., Van Valkenburgh, B., 2015. Collapse of the world's largest herbivores. *Sci. Adv.* 1, e1400103. <https://doi.org/10.1126/sciadv.1400103>.
- Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlihan, J.E., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S., van der Grift, A.E., 2007. The Rauschholzhausen agenda for road ecology. *Ecol. Soc.* 12 (11). <http://www.ecologyandsociety.org/vol12/iss1/art11/>.
- Sanderson, J., Harris, G., 2013. Automatic data organization, storage, and analysis of camera trap pictures. *J. Indones. Nat. Hist.* 1, 11–19.
- Schmidly, D.J., Bradley, R.D., 2016. The Mammals of Texas, 7th edition. University of Texas Press, Austin, TX, USA.
- Schmidly, D.J., Bradley, R.D., Bradley, L.C., Yancey II, F.D., 2023. Taxonomic Catalogs for the Recent Terrestrial Vertebrates (Species and Subspecies) Described from Texas. Museum of Texas Tech University, Lubbock, TX, USA.
- Scognamiglio, D.G., Yamashita, T.J., Tewes, M.E., 2023. Ocelot and Jaguarundi Monitoring Project: Evaluating the Effectiveness of Wildlife Crossings, Cattle Guards, and Fencing on Road Facilities in Cameron County. Caesar Kleberg Wildlife Research Institute, Texas A&M University, Kingsville, Kingsville, TX, USA.
- Sergeyev, M., Cherry, M.J., Tanner, E.P., Lombardi, J.V., Tewes, M.E., Campbell, T.A., 2023. Multiscale assessment of habitat selection and avoidance of sympatric carnivores by the endangered ocelot. *Sci. Rep.* 13, 8882. <https://doi.org/10.1038/s41598-023-35271-9>.
- Sergeyev, M., Crawford, D.A., Holbrook, J.D., Lombardi, J.V., Tewes, M.E., Campbell, T. A., 2024. Selection in the third dimension: using LiDAR derived canopy metrics to assess individual and population-level habitat partitioning of ocelots, bobcats, and coyotes. *Remote Sens. Ecol. Conserv.* 10, 264–278. <https://doi.org/10.1002/rse2.369>.
- Shamon, H., Maor, R., Cove, M.V., Kays, R., Adley, J., Alexander, P.D., Allen, D.N., Allen, M.L., Appel, C.L., Barr, E., Barthelmess, E.L., Baruzzi, C., Bashaw, K., Bastille-Rousseau, G., Baugh, M.E., Belant, J., Benson, J.F., Bespoyasny, B.A., Bird, T., Bogan, D.A., Brandt, L.S.E., Bresnan, C.E., Brooke, J.M., Buderman, F.E., Buzzell, S. G., Cheeseman, A.E., Chitwood, M.C., Chrysafis, P., Collins, M.K., Collins, D.P., Compton, J.A., Conner, L.M., Cosby, O.G., Coster, S.S., Crawford, B., Crupi, A.P., Darraq, A.K., Davis, M.L., DeGregorio, B.A., Denningmann, K.L., Dougherty, K.D., Driver, A., Edelman, A.J., Ellington, E.H., Ellis-Felege, S.N., Ellison, C.N., Fantle-Lepczyk, J.E., Farris, Z.J., Favreau, J., Fernandez, P., Fisher-Reid, M.C., Fitzpatrick, M.C., Flaherty, E.A., Forrester, T.D., Fritts, S.R., Gallo, T., Gerber, B.D., Giery, S.T., Glasscock, J.L., Gonatas, A.D., Grady, A.C., Green, A.M., Gregory, T., Griffin, N., Hagen, R.H., Hansen, C.P., Hansen, L.P., Hasstedt, S.C., Hernández-Yáñez, H., Herrera, D.J., Horan III, R.V., Jackson, V.L., Johnson, L., Jordan, M.J., Kahano, W., Kiser, J., Knowles, T.W., Koeck, M.M., Koroly, C., Kuhn, K.M., Kuprewicz, E.K., Lafferty, D.J.R., LaPoint, S.D., Lashley, M., Lathrop, R.G., Lee Jr., T. E., Lepczyk, C.A., Lesmeister, D.B., Lombardi, J.V., Long, R.A., Lonsinger, R.C., MacKay, P., Maher, S.P., Mason, D.S., Millsbaugh, J.J., Moll, R.J., Moon, J.B., Mortelliti, A., Mychajliw, A.M., Nagy, C.M., Neiswenter, S.A., Nelson, D.L., Nemes, C.E., Nielsen, C.K., Olson, E., O'Mara, M.T., O'Neill, B.J., Page, B.R., Parsons, E., Pease, B.S., Pendergast, M.E., Proctor, M., Quick, H., Rega-Brodsky, C.C., Rentz, M.S., Rezendes, K., Rich, D., Risch, D.R., Romero, A., Rooney, B.R., Rota, C.T., Samples, C.A., Schalk, C.M., Sekercioglu, C.H., Sergeyev, M., Smith, A.B., Smith, D. S., Sperry, J.H., Stenglein, J.L., Stokes, M.K., Stutzman, J.S., Todd, K.R., Vanek, J.P., Varga, W., Wardle, Z.M., Webb, S.L., Wehr, N.H., Whipple, L.S., Whittier, C.A., Widness, J.S., Williamson, J., Wilson, A.M., Wolf, A.J., Zimova, M., Zorn, A.S., McShea, W.J., 2024. SNAPSHOT USA 2021: a third coordinated national camera trap survey of the United States. *Ecology* 105, e4318. <https://doi.org/10.1002/ecy.4318>.
- Shindle, D.B., Tewes, M.E., 1998. Woody species composition of habitats used by ocelots (*Leopardus pardalis*) in the Tamaulipan Biotic Province. *Southwest. Nat.* 43, 273–279.
- Simes, M.T., Longshore, K.M., Nussear, K.E., Beatty, G.L., Brown, D.E., Esque, T.C., 2015. Black-tailed and white-tailed jackrabbits in the American west: history, ecology, ecological significance, and survey methods. *West. N. Am. Nat.* 75 (4), 491–519. <https://doi.org/10.3398/064.075.0406>.
- Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should beta-diversity inform biodiversity conservation? *Trends Ecol. Evol.* 31, 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>.
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., Townsend, S.E., Carbone, C., Rowcliffe, J.M., Whittington, J., Brodie, J., Royle, J.A., Switalski, A., Clevenger, A.P., Heim, N., Rich, L.N., 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Front. Ecol. Environ.* 15, 26–34. <https://doi.org/10.1002/fee.1448>.
- Swart, R.C., Pryke, J.S., Roets, F., 2019. The intermediate disturbance hypothesis explains arthropod beta-diversity responses to roads that cut through natural forests. *Biol. Conserv.* 236, 243–251. <https://doi.org/10.1016/j.biocon.2019.03.045>.
- Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* 92, 216–233. <https://doi.org/10.1111/brv.12224>.
- Tanwar, K.S., Sadhu, A., Jhala, Y.V., 2021. Camera trap placement for evaluating species richness, abundance, and activity. *Sci. Rep.* 11, 23050. <https://doi.org/10.1038/s41598-021-02459-w>.
- Taylor, B.D., Goldingay, R.L., 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildl. Res.* 37, 320–331. <https://doi.org/10.1071/wr09171>.
- Texas Department of Transportation, 2022. Texas Department of Transportation Annual Average Daily Traffic Annuals. Texas Department of Transportation, Austin, TX.
- van der Grift, E.A., van der Ree, R., Fahrig, L., Findlay, S., Houlihan, J., Jaeger, J.A.G., Klar, N., Madrián, L.F., Olson, L., 2013. Evaluating the effectiveness of road mitigation measures. *Biodivers. Conserv.* 22, 425–448. <https://doi.org/10.1007/s10531-012-0421-0>.
- van der Ree, R., Smith, D.J., Grilo, C., 2015. Handbook of Road Ecology. John Wiley & Sons, Ltd., Chichester, Sussex, UK.
- Veals, A.M., Holbrook, J.D., Blackburn, A., Anderson, C.J., DeYoung, R.W., Campbell, T. A., Young Jr., J.H., Tewes, M.E., 2022. Multiscale habitat relationships of a habitat specialist over time: the case of ocelots in Texas from 1982 to 2017. *Ecosphere* 13, e4204. <https://doi.org/10.1002/ecs2.4204>.
- Warwick, R.M., 1993. Environmental impact studies on marine communities: Pragmatical considerations. *Aust. J. Ecol.* 18, 63–80. <https://doi.org/10.1111/j.1442-9993.1993.tb00435.x>.
- Whittaker, R.H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30, 279–338. <https://doi.org/10.2307/1943563>.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *TAXON* 21, 213–251. <https://doi.org/10.2307/1218190>.
- Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, New York, USA.
- Wilson, E.O., 1985. The biological diversity crisis. *BioScience* 35, 700–706. <https://doi.org/10.2307/1310051>.
- Yamashita, T.J., Livingston, T.D., Ryer, K.W., Young Jr., J.H., Kline, R.J., 2021. Assessing changes in clusters of wildlife road mortalities after the construction of wildlife mitigation structures. *Ecol. Evol.* 11, 13305–13320. <https://doi.org/10.1002/ece3.8053>.
- Yamashita, T.J., Lombardi, J.V., Wardle, Z.M., Tewes, M.E., Young Jr., J.H., 2025. Differences in mammal community response to highway construction along a small urban-rural gradient. *Wildl. Biol.*, e01347 <https://doi.org/10.1002/wlb3.01347>.