# LANDSCAPE PREDICTORS OF MULE DEER ROAD CROSSING BEHAVIOR IN THE AMERICAN SOUTHWEST

by

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# Abstract

Road networks pose many well-documented threats to wildlife, from fragmenting habitats and restricting movement to causing mortality through vehicle collisions. For large, wide-ranging mammals like mule deer (*Odocoileus hemionus*), home range requirements and seasonal migrations often necessitate road crossings, posing threats to human safety, property, and deer survival. Research has shown wildlife road crossings and wildlife-vehicle collisions cluster in response to environmental factors. Although general relationships between crossings, collisions, and landscape features have been described, there is variation across locations and species in predictors of crossing frequency and collision risk. We aim to evaluate the extent to which various landscape, environmental, and human factors influence the location and timing of mule deer road crossings near Salt Lake City, UT. Specifically, we are interested in understanding how elevated artificial nightlight may influence deer road crossing locations. By integrating the latest NASA nightlight products with GPS collar data collected from 67 mule deer over a 7-year period (2012 to 2018), we used a resource-selection framework to assess factors influencing seasonal crossing behavior and intensities within individual seasonal home ranges at a variety of spatial scales (fine: 20m, median hourly movement: 55.33m, and median daily movement: 573.33m). Findings indicate both anthropogenic and environmental factors influence mule deer road crossings. Areas with more shrub cover and vegetative greenness (NDVI) increased the likelihood of crossing, whereas sections of road with faster speed limits reduced crossings. Artificial nightlight also had a significant influence on whether road segments were crossed. Deer avoided crossing available roads in their home ranges with elevated nightlight in both summer and winter, especially during crepuscular and nighttime periods. However, lower nightlight levels were also associated with increased risk of road mortality, as were higher speed limits and less surrounding shrub cover. Increased knowledge about factors influencing road crossing behavior, especially factors that may attract or repel human-tolerant wildlife species from roadways, presents an opportunity to mitigate collision risk while improving population management strategies for an economically and ecologically important species in an expanding metropolitan area.

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Finally, thank you to my partner and family for supporting me in my graduate school endeavors, as in all other aspects of my life- it means the world!

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# Introduction

The expansion of human populations and the associated infrastructure development has resulted in many wide-ranging wildlife species facing increased threats to their survival, such as those posed by roads (Forman and Alexander 1998; Bencin et al. 2019). Roads have been linked with numerous negative effects on mammals, from fragmenting habitats and restricting movement to causing direct mortality through vehicle collisions (Schwab and Zandbergen 2011; Neumann et al. 2012; Garrah et al. 2015; Zeller et al. 2018, 2020; Bencin et al. 2019). Research has shown that both wildlife road crossings and wildlife-vehicle collisions (WVCs) cluster on roads where certain surrounding landscape and environmental factors are present (Gunson et al. 2011; Garrote et al. 2018; Bastille-Rousseau et al. 2018). These studies indicate that animal interactions with roads can be predictable, which would in turn provide insights for wildlife managers on how best to mitigate the negative impacts of roads. With increasing human encroachment into the ranges of many wildlife species, a more comprehensive understanding of how wide-ranging species navigate expanding road networks can therefore bolster efforts to sustainably manage their populations and reduce wildlife-vehicle collisions that may otherwise become more common.

In the Intermountain West, rapid human population growth and associated land use change has led to increased concerns about potential losses of wildlife habitat connectivity and increases in human-wildlife conflict within the wildland-urban interface. These issues are of interest in Utah specifically, which was listed as the fastest growing state by population in 2016 (United States Census Bureau 2016). It has also maintained a city in the top 5 on the list of fastest growing US cities and has recently had the most growth in terms of new housing units (United States Census Bureau 2020).

This human expansion has resulted in an increasing number of WVCs as the road network stretches into previously undisturbed habitats and movement corridors (Cramer et al. 2019). In 2019, the estimated societal cost of collisions with wildlife in Utah was $138 million (Cramer et al. 2019), up from an approximate annual cost of $7.5 million between 1996 and 2001 (Bissonette et al. 2008). Of documented collisions with wildlife in the state, the vast majority are with ungulates, and specifically with mule deer (*Odocoileus hemionus*)(Cramer et al. 2019). Collisions with large ungulates not only result in vehicle damage, human injuries, and even fatalities, but also cause ecological and economic damage in terms of the value of mule deer lost, estimated at upwards of $5 million annually (Cramer et al. 2019). As a result, state organizations such as the Utah Division of Wildlife Resources (UDWR) and the Utah Department of Transportation (UDOT) have made reduction of WVCs, and specifically WVCs involving mule deer, a top management and conservation priority (Olson et al. 2015; Utah Division of Wildlife Resources 2019b, a; Cramer et al. 2019). As mule deer herd growth is also a priority of the UDWR, there is a degree of urgency to find solutions that mitigate conflicts between the growing deer and human populations (Cramer et al. 2019; Utah Division of Wildlife Resources 2019a).

Mule deer are an economically and ecologically important ungulate species (Eckrich et al. 2020) with a distribution stretching across the Intermountain West (Ditmer et al. 2021). For large, wide-ranging mammals such as mule deer, home range and movement requirements often necessitate road crossings, which causes risks to the lives of both the animals themselves and to drivers if involved in a collision (Schwab and Zandbergen 2011; Zeller et al. 2018; Hill et al. 2020; Ditmer et al. 2021). Additionally, mule deer in this region migrate seasonally from low-elevation and often urban winter ranges to higher elevation summer ranges (Sawyer et al. 2009), with strong fidelity shown to their chosen migration routes (Sawyer et al. 2009, Meisingset et al. 2013, Coe et al. 2015). These routes may be impacted and possibly even inhibited by road placement, which in severe cases can mean loss of accessible habitat and population decline (Forman and Deblinger 2000; Shepard et al. 2008; Sawyer et al. 2009; Lendrum et al. 2012; Meisingset et al. 2013). Further increasing the risk of WVCs for mule deer is that in addition to their movement and migration requirements bringing them into contact with roadways, they are often attracted to the roadside to graze on early-successional or edge habitat forage and to take advantage of salt runoff (Gunson et al. 2011; Meisingset et al. 2013; Neumann et al. 2013).

Though often considered well adapted to urban life (Fraser et al. 2019), deer are still impacted by increased human disturbance and infrastructure. Fraser et al. (2019) found that the genetic structure of mule deer populations was aligned with highway boundaries in certain areas, highlighting the limited gene flow that the barrier effect of roadways can cause. Bliss-Ketchum et al. (2016) found that Columbia black-tailed deer (*Odocoileus hemionus columbianus*) were even sensitive to nearby artificial light sources. They experimentally lit under-road passage structures, as is sometimes done to enable human use, to explore the effects of artificially lighting these crossing structures on deer usage. They found that deer traversed lit passages much less than unlit ones, affecting their habitat connectivity (Bliss-Ketchum et al. 2016). Furthermore, Ditmer et al. (2021) linked the high levels of artificial nightlight experienced by urban-adapted mule deer to increased vulnerability to predation. They also found that non-urban mule deer generally avoided areas with elevated nightlight levels (Ditmer et al. 2021). Lendrum et al. (2012) found that mule deer migrating through urban areas traveled faster and avoided roadways where possible, further showing that human development effects deer behavior. However, increased development in or near mule deer habitat has meant that it is not always possible for deer to avoid human activity and the most developed areas (Lendrum et al. 2012; Coe et al. 2018; Ditmer et al. 2021). Roadways in particular continue to be a source of conflict, adversity, and mortality for mule deer across their range, though it is still not well understood how factors related to urbanization such as artificial nightlight may augment or ameliorate these effects (Olson 2013; Coe et al. 2015; Cramer et al. 2019; Ditmer et al. 2021).

Understanding which road segments in a given area have the highest intensity of use as crossing points for mule deer could help explain their seasonal migration behavior and non-migratory movement patterns, in addition to identifying crossing hotspots and critical areas for collision mitigation or conservation intervention. Linking road crossing behavior with landscape, vegetation, and environmental factors could also provide insight into potential management opportunities and challenges. As mule deer herd growth and reduction in deer-vehicle collisions are top priorities for Utah wildlife managers (Cramer et al. 2019; Utah Division of Wildlife Resources 2019a), insights in this realm could lead to interventions such as spatially and temporally targeted placement of fences, signage, and wildlife crossing structures, which mule deer have been shown to utilize when available (Gloyne and Clevenger 2001; Sawyer et al. 2012; Bissonette and Rosa 2012). Furthermore, comparing the factors influential to the crossing behavior of mule deer with the roadway locations where their carcasses are found could provide insight into the potentially differing landscape, roadway, and environmental features that determine successful crossings versus those that end in mortality events.

Many analyses of roadway impacts examine either movement data (Meisingset et al. 2013; Olson et al. 2015; Bastille-Rousseau et al. 2018) or wildlife collision or road mortality data only (Nielsen et al. 2003; Ng et al. 2008; Clevenger et al. 2015; Ha and Shilling 2018; Laliberté and St-Laurent 2020)(but see Schwab and Zandbergen 2011, Neumann et al. 2012 and Zeller et al. 2018). Studies that have utilized both sources, such as Zeller et al. (2018), note that there are shortcomings associated with examining only one or the other, particularly when it comes to understanding the biological relevance of different road segments as it relates to collision risk. Neumann et al. (2012) found that crossing and collision sites had significantly different surrounding environmental attributes. They also found that movement data alone were insufficient at predicting collision risk, but that collision data alone overestimated the risk in certain habitats (Neumann et al. 2012). This supports the importance of examining both movement and collision data when assessing road impacts and WVC risk.

Here we will evaluate the road crossing behavior of mule deer along a subset of road segments near Salt Lake City, UT using an established metric for crossing intensity (Bastille-Rousseau et al. 2018) and GPS collar movement data from 67 mule deer over a 7-year period (2012 to 2018). We will then assess which landscape, environmental, and road factors, including the novel factor of artificial nightlight, are shared between areas of high crossing intensity and to what extent these factors could be used to indicate the likelihood that a road segment will be used for crossing. Additionally, we will use road mortality data to determine whether common factors surround road crossing and mortality locations. To date, we are aware of no such comprehensive examination of the locations and frequency with which mule deer cross roads based on movement data that has been performed for the rapidly growing greater Salt Lake City region, or any that examines the influence of artificial nightlight on mule deer road crossing behavior and mortality. Our goal with this study is to provide a predictive understanding of mule deer road crossing behavior and the associated correlates to provide managers with information to potentially deter crossings in dangerous areas and/or increase crossing probabilities in other locations, with a net result of reduced risk for human drivers and decreased mortality for this important species.

# Methods

## *Overview*

We used GPS data from collared mule deer and spatially explicit mule deer road mortality data to analyze road crossing and road mortality site characteristics in the Oquirrh Mountains and greater Salt Lake City area (Figure 1). By aggregating information on a variety of covariates (Table 1) within several different sized buffer zones around the road network (three scales: 20m, 55.33m, and 573.33m), we were able to explore the relationship between the covariates and the probability of a mule deer crossing, intensity of use, and the probability of mortality. To account for the migratory behavior of mule deer, we conducted these analyses for two distinct seasons- “summer” and “winter”. With the exception of the road mortality analysis, which was not temporally explicit, we were able to further categorize these relationships by day, crepuscular, and night periods. We explored the relationships between the covariates and our crossing and mortality response variables by fitting generalized linear/logistic mixed models by season and day period (where applicable). Using AIC (Supplementary Table S4), we then determined which of the three scales was most appropriate and focused on the results of the models at the best fit scale (Supplementary Table S5).

## *Study Area and Mule Deer Data*

Mule deer GPS data were collected from an initial set of 82 individuals in the Oquirrh Mountains and greater Salt Lake City area by the Utah Division of Wildlife Resources (UDWR) (Figure 1). GPS-locations were recorded between January 2012 and November 2018 at a median fix rate of approximately 3 hours. Duplicate data points were checked for and removed. Individuals with at least 150 GPS fixes were selected for use in our analysis. After removing these individuals, our final set had n = 67 deer (Total: 215,957,151 fixes, minimum: 153 fixes, average: 1,260 fixes, maximum: 2,149 fixes).

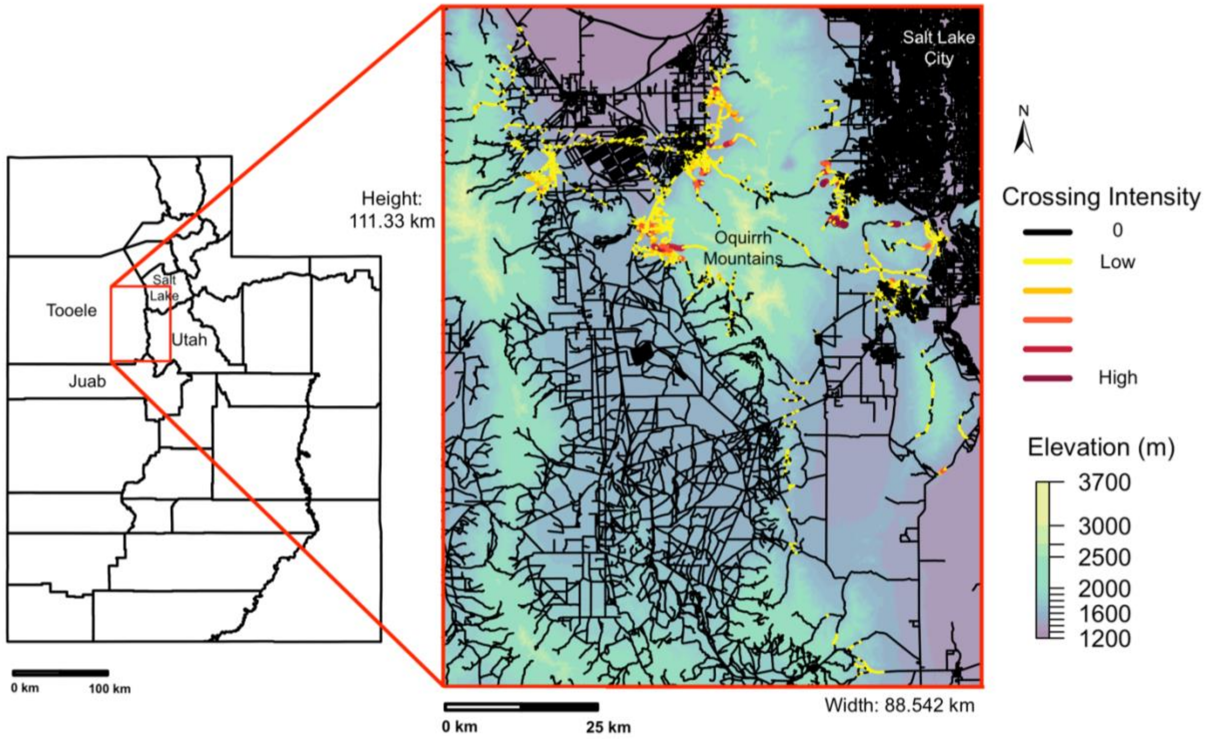

**Figure 1**: Study Area location relative to Utah county boundaries, showing its overlap with Salt Lake, Utah, Tooele, and Juab counties. The crossing intensity of mule deer across the study area is shown on the right, overlaid on the road network and elevation data for the region.

Our study region encompasses 9,857 km$^2$ and at least partially covers four counties- Salt Lake, Utah, Tooele, and Juab. The region includes a rapidly expanding metro area and is located in an ecoregion that exhibits a high degree of seasonality, variable elevation (range: 1,300 m to 3,200 m), and a gradient of human disturbance, with mule deer distributed throughout (Olson 2013). Mule deer in this region often spend the summer months in the high elevation wildlands of the Oquirrh mountains and the winter months in their more urban and low elevation winter range, located to the southwest of Salt Lake City, UT (Olson 2013; Ditmer et al. 2021). The study area is under the management of UDWR's "Central" region (Utah Division of Wildlife Resources 2022) and primarily under UDWR mule deer herd unit management plans 18, 19, and 21 (Utah Division of Wildlife Resources 2014a, b, 2020), as well as under the management of Utah Department of Transportation (UDOT) regions 2 and 3 (Utah Department of Transportation 2022).

### *Determining Seasonal Home Ranges*

We defined two distinct migration seasons for our analyses using net squared displacement in program R (R Core Team 2021) with package ‘amt’ (Signer et al. 2019). All spatial and statistical analyses were conducted in R (R Core Team 2021). Net squared displacement patterns revealed upon visual inspection that deer moved to their summer ranges around April 16 and returned to their winter ranges around October 15. We then split the deer GPS points into groups based on these seasonal divisions for each year of the study, from 2012-2018. For each individual, we calculated a seasonal 95% kernel density home range for each year using the ad hoc approach for smoothing using package ‘adehabitatHR’ (Calenge 2006). We then used the seasonal home range areas considered available to individuals and combined them using package ‘rgeos’ (Bivand and Rundel 2021) to create an aggregate range representing what was available to all individuals. Road network data came from the Utah Geospatial Resource Center (UGRC) and represents the road network in the state of Utah as of June 2021 (Utah Geospatial Resource Center 2021). This dataset includes interstates, US highways, state highways, paved and unpaved major local roads, local/neighborhood/rural roads, and service/general access roads (Utah Geospatial Resource Center 2021). By cropping the road network to the shape of each seasonal combined home range boundary, we obtained seasonal representations of the roads available to the deer for crossing each year. Roads within these “available” areas were split into segments with a maximum 500m in length (minimum: < 1m, overall summer range mean: 238.74m, overall winter range mean: 218.12m).

### *Analyzing Crossing Intensity*

For each year’s seasonal aggregated home range area, we determined “crossing” locations for each individual by assuming linear movements between two consecutive GPS fixes and finding the intersection between those straight-line paths and the road segments. To do this, we created trajectories for each deer using the ‘adehabitatLT’ package (Calenge 2006) and calculated the intersection of deer movement paths and the road network.

We calculated crossing intensity following Bastille-Rousseau et al.’s method (2018), which produces a metric standardized among road segments, removing biases due to unequal monitoring times for individual deer. Crossing intensity ($C_s$) for a particular road segment (s) is defined as:

$$C_s = \frac{\sum_{i=1}^{n_s} \frac{x_{is}}{t_i}}{n_s}$$

Where $C_s$ is the summation of the total number of steps per individual ($x_{is}$) that crossed the road segment divided by the time period they were monitored ($t_i$), divided by the total number of individuals that crossed the segment over the entire monitoring period ($n_s$) (Bastille-Rousseau et al. 2018). This results in a value representing a standardized crossing intensity for each road segment whereby monitoring time is explicitly considered in order to eliminate biased results due to unequal sampling among individuals. We implemented this by adapting code from the 'wildxing' package (Bastille-Rousseau 2021), which was developed as part of the same paper that created the crossing intensity metric (Bastille-Rousseau et al. 2018).

Modifications to the 'wildxing' code were made to include additional metadata, such as the crossing timestamps. Maintaining the timestamp of each crossing was important in order to determine the time of day the road segment was crossed, explained further in the "Assessment of Crossing Times" section below. Minor modifications of the 'wildxing' code such as this enabled the calculation of additional metrics and a more detailed characterization of road crossings.

### *Landscape and Anthropogenic Factors*

We hypothesized a variety of landscape, land cover, anthropogenic factors, and road characteristics that could influence mule deer road crossing behavior (Table 1). Spatially explicit artificial nightlight estimates were extracted from NASA's Black Marble product. This dataset derives estimates of radiance from NASA-NOAA's Suomi National Polar-Orbiting Partnership Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band using BRDF (bidirectional reflectance distribution function) correction to isolate anthropogenic sources (Román et al. 2018). We took the mean of the latest daily product at a 500m resolution across the associated year and seasons (as defined by the net squared displacement analysis) to create year-specific seasonal composites of anthropogenic nightlight radiance.

Estimates of 2010 housing density, at a sub-census block unit (100m$^2$) (National Park Service 2010), were modeled based on the United States Census Bureau (Theobald 2005). Road density for our study area was calculated from the USGS National Transportation Dataset shapefile (U.S. Geological Survey 2021). To do so, we created a blank 50m raster grid and any cell intersecting a road line segment was given a value of 1, otherwise a 0 for those cells that did not intersect a road. To convert this to a measure of density, the raster was aggregated to 1 km$^2$ such that each cell represents the proportion of each 1 km$^2$ cell with a road segment present.

Speed limit information is maintained by the Utah Department of Transportation (UDOT) and was included as part of the Road Centerlines dataset obtained from the Utah Geospatial Resource Center (Utah Geospatial Resource Center 2021). We were therefore able to associate a speed limit (in miles per hour) with each road segment. Road segment length was also included in our analysis as a control variable.

Bare Earth elevation data was obtained from USGS in raster format as a Digital Elevation Model (DEM) with a spatial resolution of 30m. The terrain roughness index was then derived by taking the mean of the absolute differences between the elevation value of a cell and the value of its 8 neighboring cells using the function ‘terrain’ in package ‘raster’ (Hijmans 2021).

Snow cover data, as defined by the percentage of the 500m resolution data covered by snow in an 8-day period, was obtained from the MODIS/Terra Snow Cover 8-Day L3 Global 500m SIN Grid (MOD10A2; from the NASA National Snow and Ice Data Center; Hall, D.K. and G.A. Riggs 2021). We created a year-specific winter composite (16 October – 15 April) by taking the mean of snow cover values for each cell. We estimated vegetative greenness using the Normalized Difference Vegetation Index (NDVI) derived from MODIS (MOD13Q1) generated every 16 days at 250m resolution (Didan 2015). From these layers we created year-specific seasonal composites (for each summer and winter, as defined above) of mean NDVI.

Land cover data at a 30m spatial resolution was obtained from the National Land Cover Dataset (NLCD) (U.S. Geological Survey 2016) and aggregated into five categories:

forest (values 41- 45), shrub/scrub (values 51, 52), developed/urban (values 21-24), agriculture (values 81, 82), and open/natural (includes herbaceous, open water, and other "open" land types; values 11, 31, 71, 72, 90, 95) based on ecological significance and/or horizontal vegetative thickness that may influence deer road crossing decisions. Although our study period spans 2012-2018, we elected to use land cover data just from 2016 in our analysis. This decision was made after analyzing land cover change in the study area over the study timeframe. We compared NLCD values from 2011-2016 and 2011-2019 to assess change. From 2011 – 2016, approximately 6.4% of pixels changed values, with the vast majority of changes being either shrub to open/natural or open/natural to shrub. Similar results were found for 2011-2019, with approximately 10.12% of pixels changing, with the majority again being shrub to open/natural or vice versa. A small percentage of pixels meaningfully changed categories, as we determined shrub to open/natural changes could amount to a change in the categorization methods and not radical changes on the ground. Because of the small percentage of pixels that changed values over our study period, and the fact that most changes did not involve developed landcover (urbanization), we elected to use the 2016 NLCD data as representative of land cover over the entire study period.

**Table 1**: Landscape, human, and environmental variables used in modeling deer road crossing behavior and mortality

| **Variable** | **Short Name** | **Description** | **Derived From Source** |
|---|---|---|---|
| Artificial Nightlight Index | Nightlight | Year-specific seasonal composites of daily average estimates of anthropogenic artificial nightlight from NASA's Black Marble product suite at a 500m spatial resolution | (Román et al. 2018) |
| Housing Density | Housing Density | Estimates of 2010 housing density at 100$m^2$ sub-census block units modeled based on U.S. Census Bureau following Theobald (2005) | (National Park Service 2010) |
| Road Density | Road Density | Density of the road network represented as the proportion of each 1 $km^2$ cell with at least one road segment when divided into 50$m^2$ pieces | (U.S. Geological Survey 2021) |
| Speed Limit | Speed Limit | Posted speed limit in miles per hour (mph) as maintained by UDOT | (Utah Geospatial Resource Center 2021) |
| Road Segment Length | Segment Length | Length (in meters) of the road segment, as represented in the dataset | (Utah Geospatial Resource Center 2021) |
| Bare Earth Elevation | Elevation | Bare Earth elevation in meters from the Digital Elevation Model (DEM) | (U.S. Geological Survey 2019) |

| | | | |
|---|---|---|---|
| Terrain Roughness Index | Terrain Roughness | Terrain roughness index represented as the mean of the absolute differences between a cell’s elevation and that of its 8 neighboring cells | (U.S. Geological Survey 2019) |
| Composite Snow Cover Index | Snow Cover | Year-specific snow cover winter composites calculated by taking the mean of each winter’s snow cover values, which represent an 8-day mean percentage snow cover in each 500m cell | (Hall and Riggs 2016) |
| Normalized Difference Vegetation Index | NDVI or vegetative greenness | Year-specific seasonal composites of mean NDVI derived from MODIS 16 day estimates at 250m spatial resolution | (Didan 2015) |
| Forest | Forest | Aggregated forest land cover types (NLCD values 41- 45) | (U.S. Geological Survey 2016) |
| Shrub/Scrub | Shrub or Shrubland | Aggregated shrub and scrub land cover types (NLCD values 51, 52) | (U.S. Geological Survey 2016) |
| Developed/Urban | Developed/Urban | Aggregated developed/urban land cover types (NLCD values 21-24) | (U.S. Geological Survey 2016) |
| Agriculture | Agriculture | Aggregated agricultural land cover types (NLCD values 81, 82) | (U.S. Geological Survey 2016) |
| Open/Natural | Open/Natural | Aggregated open/natural land cover types, including herbaceous, open water, and other “open” land types (NLCD values 11, 31, 71, 72, 90, 95) | (U.S. Geological Survey 2016) |

### *Assessment of Spatial Scale*

We used three candidate spatial scales for modeling deer road crossing decisions by extracting values of our covariate layers at three distinct buffer distances around each road segment. The first two were based on hourly and daily movement distances. We calculated the median hourly movement distance by using consecutive GPS locations with 3-hour intervals and calculating the median movement distance per hour across all individual mule deer. To calculate median daily movement, we calculated the distance between a given day’s first GPS location for each mule deer and the next subsequent location that was 24-hours after the first location considered. The resulting median distance among locations represents a daily Euclidean distance, or daily displacement distance, which does not include movements among locations occurring throughout the day. The median daily movement/displacement distance was 573.3m, and the median hourly movement distance was 55.3m, both of which we used as buffer sizes around each road segment when extracting covariate values. We considered a third scale, a buffer distance of 20m around each road segment, a “roadside” or fine-scale distance representing the values of the variables just alongside the roadways. For each season and year, we generated nonaligned systematically sampled spatial points using package ‘sp’ (Pebesma and Bivand 2005; Bivand et al. 2013) to extract and summarize covariate values within each of the three buffer sizes for each road segment (Supplementary Figure S1). For the 20m and 55.33m buffer sizes, 1,000 points were sampled, and we sampled 10,000 points for the larger 573.33m buffer size. See Supplementary Table S1 for a summary of the distribution of each covariate's summary values at the best model scale.

### *Assessment of Crossing Times*

Although we already determined seasons to consider for analyses, we also assessed the intra-daily crossing patterns of mule deer because of interest in the influence of artificial nightlight. Artificial nightlight patterns vary seasonally (e.g., differences in natural nightlight vs. artificial, changes in human activity patterns), and the time of day plays the largest role in the potential influence of artificial nightlight (e.g., daytime vs. nighttime). We assigned each mule deer crossing location a value associated with the elevation of the sun using the timestamp of the crossing and the 'solarpos' function from the 'maptools' package in R (Bivand and Lewin-Koh 2021). Solar positions were calculated for each road crossing, with values less than or equal to -20° assigned to "night", between -20° and 20° to "crepuscular", and greater than or equal to 20° to "day". These classifications for time of day were used to bin our data into three corresponding groups per season.

### *Modeling Strategy*

We developed two different sets of seasonal regression models for each time of day (day, night, crepuscular) to examine mule deer road crossing behavior. The first set of models used logistic regression and considered whether an available road segment (within an associated combined seasonal home range) had any road crossings ($y = 1$) or not ($y = 0$) as the response variable. Results from these logistic regression models indicated the features around segments that influenced the probability that a given segment was crossed. The second set of models used linear regression with a response variable of the crossing intensity among road segments that were crossed at least once by mule deer. Results from these linear regression models indicated what features influenced the intensity of crossing among crossed segments.

We examined our set of covariates for each combined season and time of day for correlation prior to modeling (Supplementary Table S2) using the 'cor' function from the 'stats' package (R Core Team 2021). When a pair of variables had a correlation magnitude greater than or equal to 0.7 in any of the subsets, we kept only one of the two for use in the analysis. Which variable was removed was manually determined by comparing the number of complete rows in the data set for each variable, whether a variable was correlated with multiple other variables, and its hypothesized importance to the model. Our final set of variables included: artificial nightlight, speed limit, terrain roughness, snow cover, NDVI, road segment length, and the land cover types of shrub, agriculture, and open/natural. All variables were scaled and centered prior to modeling and all were treated as fixed effects. We included a random effect intercept for year.

We assessed the centroid locations of the road segment crossings for spatial autocorrelation. This was done by constructing non-spatial models from which Moran's I could be calculated using the 'DHARMa' package in R (Hartig 2021). We found the set of segments crossed by deer were significantly spatially autocorrelated in the vast majority of the non-spatial models (Supplementary Table S3). We therefore accounted for spatial autocorrelation in all models using the 'glmmTMB' package to fit mixed effects models that included spatial effects (Brooks et al. 2017).

Our first set of models, which considered whether a given segment was crossed or not, used mixed effects logistic regression, with road segments being coded as 0 or 1 based on if the segment was crossed by at least one mule deer. The logistic models did not converge properly when considering the spatial structure so we accounted for the spatial distances among road segments by including the easting and northing of each road segment centroid to account for spatial effects. Our second set of models, which assessed the factors that influenced the intensity of road crossings for all road segments with a crossing intensity greater than 0, again used a mixed effects structure. We used the log value of crossing intensity as our response variable with the same group of covariates considered in the first set of models. However, we considered non-linear fits of certain covariates with crossing intensity by including natural cubic splines with 2 degrees of freedom via the 'splines' package in R (R Core Team 2021). Doing so produces two coefficients for each covariate fit using splines; these are denoted using "1" and "2" after the name in the results section below. Spatial effects were accounted for in this set of models with an exponential correlation structure using the 'exp' function and the road segment centroids (R Core Team 2021). For each set of models (seasonal by time of day), we assessed which of the candidate spatial scales best explained mule deer road crossing behavior by comparing the Akaike's Information Criterion (AIC)(Bozdogan 1987) values of the global model fits.

### *Road Mortality Analysis*

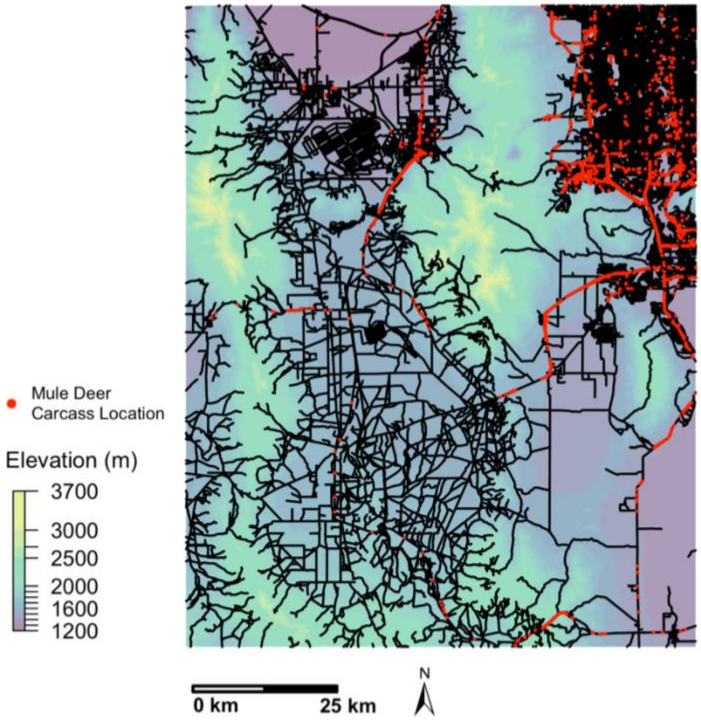

**Figure 2**: Mule deer carcass locations as reported by state contractors to the UDWR within our study area boundaries from 2012 – 2018 overlaid on the road network and elevation data for the area.

In addition to examining movement data, we used mule deer road mortality data from the State of Utah Wildlife-Vehicle Collision (WVC) Data Collector repository (Figure 2) to model mortality probability among road segments using the same set of landscape factors (Table 1). When an animal carcass on a roadway is reported to or found by state contractors, they record the species, estimated age class, and GPS coordinate location of the animal in addition to other ancillary information, which is aggregated in the WVC repository. We filtered the dataset to include only instances of mule deer road mortality within each seasonal home range during the same time period as the study (summer: n = 93, winter: n = 500). We only included roads that had at least one mule deer carcass found in a given season because carcass collection is limited primarily to highways along set routes. We were then able to associate a count of mortality events with each road segment. Using this information, we fit a mixed effects logistic regression with road mortality as the response variable (0 = no mortality events, 1 = at least one mortality even for a given road segment) and the same predictor variables and random effects structure (year as the random effect) as above to model how our set of landscape factors relates to the probability a road segment had at least one mule deer killed by vehicle collision for a given season. Unlike our crossing behavior analyses, we were unable to divide our road mortality analysis into categories related to time of day, because the time of each mortality incident was unknown (only the date a carcass was found was reported).

## Results

### *Spatial and Temporal Characteristics of Mule Deer Road Crossings*

In the summer season, all mule deer road crossings (n = 12,544) occurred during the day (29.93%) or crepuscular periods (70.07%). No summer road crossings occurred at night. In the winter season, crossings (n = 21,215) occurred during the crepuscular periods (72.84%) or at night (27.16%), with no crossings during the day (Figure 3). When comparing road segments in the winter and summer ranges, we found that the winter range was more urban, at a lower average elevation, had less rough terrain, far more artificial nightlight, and a greater number of both crossings and road mortalities (Supplementary Table S1). We found mule deer road crossing decisions were most associated with the landscape and road characteristics within the daily median movement distance of 573.33m from the crossing location (Supplementary Table S4). Full results of the 573.33m scale models are reported in Supplementary Table S5.

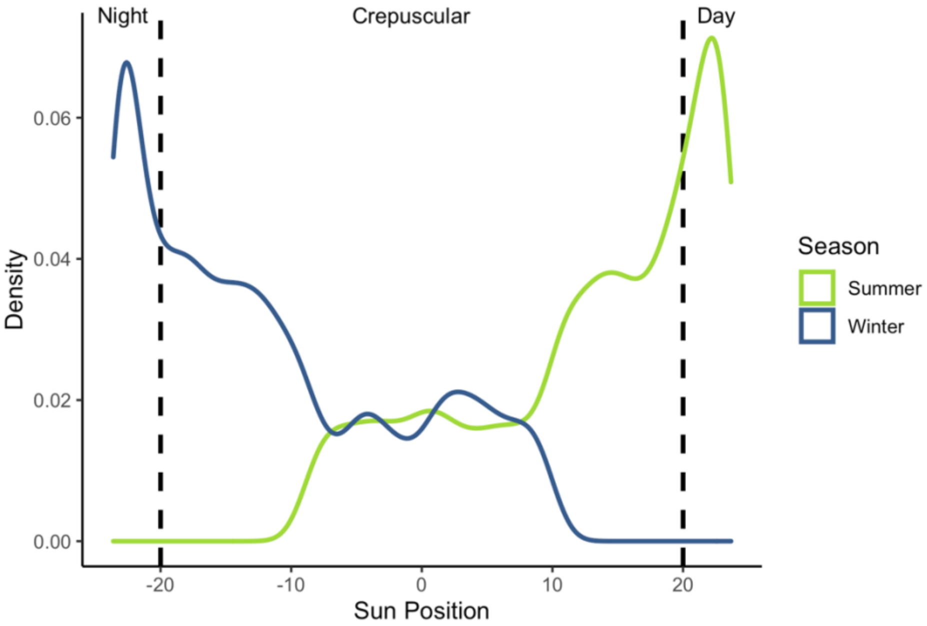

**Figure 3**. Density plot showing mule deer road crossings by time of day based on the sun's elevation (degrees up from the horizon) for n = 67 mule deer near Salt Lake City, UT recorded from 2012 - 2018. Sun positions less than -20° represent night, between -20° and 20° represent the crepuscular periods, and greater than 20° represents day.

### *Anthropogenic Factors*

Artificial nightlight had one of the greatest effects on where mule deer chose to cross the road in both summer (Fig. 4A, Fig. 5; $\hat{\beta}_{\text{crepuscular}}$ = -0.603, 95% CI = -0.821, -0.384) and winter (Fig. 4A, Fig. 5; $\hat{\beta}_{\text{crepuscular}}$ = -0.294, 95% CI = -0.423, -0.164; $\hat{\beta}_{\text{night}}$ = -0.318, 95% CI = -0.470, -0.166). Deer generally avoided crossing the brightest road segments, an effect that was strongest in darker periods, especially night and crepuscular crossings. Despite this, nightlight level had no significant influence on the intensity of mule deer use among crossed segments, except during the winter crepuscular period when, among crossed segments, deer surprisingly preferred the brighter segments. Nightlight level was also related to which road segments had mule deer mortality events, but at a higher threshold for significance ($\alpha <$ 0.1), with decreased nightlight levels associated with increased probability of mortality. This effect was much stronger in summer (Fig. 4C; $\hat{\beta}_{\text{summer}}$ = -0.528, 95% CI = -1.069, 0.013) than in winter (Fig. 4C; $\hat{\beta}_{\text{winter}}$ = -0.208, 95% CI = -0.428, 0.013).

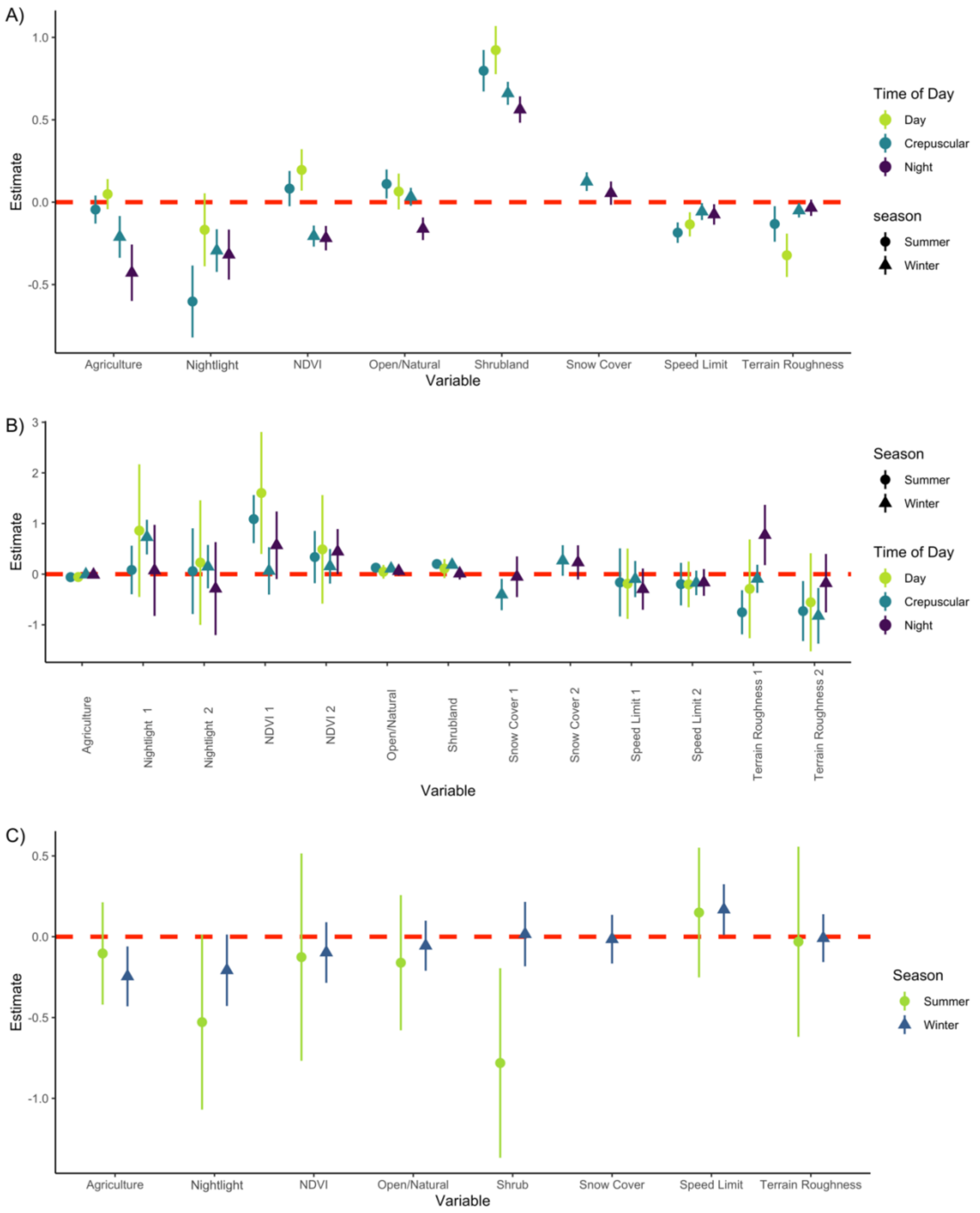

**Figure 4**: Results showing estimated coefficients and 95% confidence intervals for A) the probability of a road segment being crossed, B) the intensity of use among crossed segments and C) the probability of a road segment having at least one mule deer mortality event. Covariates are scaled and centered for the purposes of comparison. Because the crossing intensity models used natural cubic splines, some covariates in B are reported with a “1” or “2”, as two coefficients were returned.

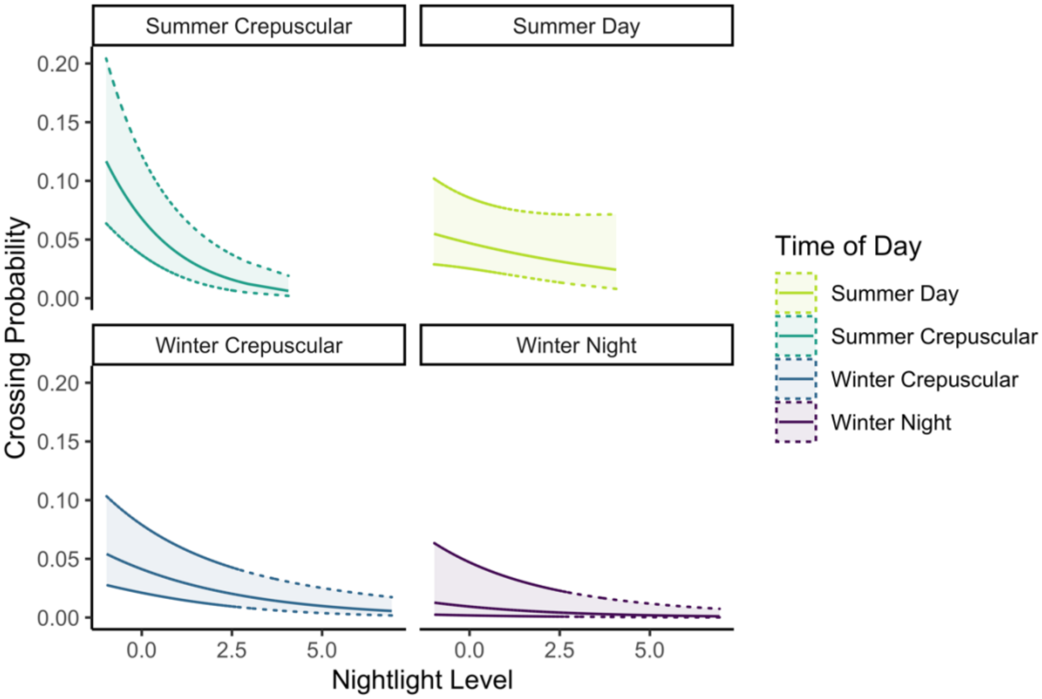

**Figure 5**: Modeled relationship and 95% confidence interval between nightlight level (scaled and centered) and the probability that a segment was crossed during the day, night, or crepuscular period for summer and winter. At all times of day for both summer and winter increased nightlight levels were associated with a lower probability that a mule deer would cross a given segment.

Higher speed limits had a positive effect on mule deer road mortality events in the winter (Fig. 4C, Fig. 6; $\hat{\beta}_{\text{winter}}$ = 0.168, 95% CI = 0.011, 0.325), despite being negatively associated with road crossings (Fig. 4A; summer: $\hat{\beta}_{\text{crepuscular}}$ = -0.185 95% CI = -0.247, -0.123, $\hat{\beta}_{\text{day}}$ = -0.135, 95% CI = -0.208, -0.061; winter: $\hat{\beta}_{\text{night}}$ = -0.074, 95% CI = -0.137, -0.012, $\hat{\beta}_{\text{crepuscular}}$ = -0.057, 95% CI = -0.108, 0.006). Speed limit did not appear to alter crossing decisions between times of day, with deer being generally more likely to cross roads that had lower speed limits at all times of day, particularly in the summer. Despite its influence on road mortality and crossing decisions, speed limit had no significant effect on the intensity of use for crossed road segments.

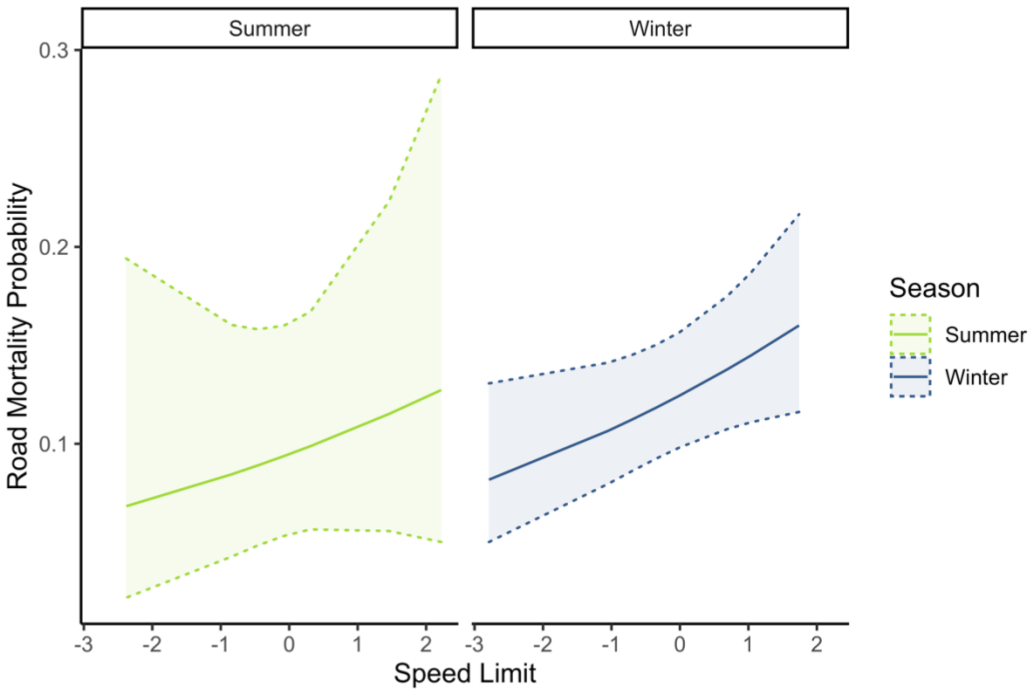

**Figure 6**: Modeled relationship and 95% confidence interval between a road segment's speed limit (scaled and centered) and the probability that at least one mule deer road mortality event occurred. In both summer and winter, higher speed limits were associated with an increased chance of mule deer road mortality.

### *Landscape Factors*

Terrain roughness was one of the most influential factors impacting intensity of mule deer use among crossed segments. In the summer and winter crepuscular periods (Fig. 4B; $\hat{\beta}_{\text{summer 1}}$ = -0.753, 95% CI = -1.188, -0.318, $\hat{\beta}_{\text{summer 2}}$ = -0.729, 95% CI = -1.321, -0.136; $\hat{\beta}_{\text{winter 1}}$ = -0.091, 95% CI = -0.369, 0.186, $\hat{\beta}_{\text{winter 2}}$ = -0.822, 95% CI = -1.372, -0.272), mule deer preferentially used road segments in areas with less rough terrain. Conversely, this was not the case during winter nighttime crossings (Fig. 4B; $\hat{\beta}_{\text{night 1}}$ = 0.774, 95% CI = 0.179, 1.369), when deer strongly preferred road segments in areas of rougher terrain. This relationship was nonlinear however, as the highest crossing probabilities during winter nights were associated with terrain roughness in a slightly decreasing way (Fig. 4B; $\hat{\beta}_{\text{night 1}}$ = -0.178, 95% CI = -0.755, 0.399). Despite its strong negative relationship with crossing intensity, terrain roughness had a smaller impact on the probability that a road segment would be crossed, reducing the probability in summer (Fig. 4A; $\hat{\beta}_{\text{day}}$ = -0.322, 95% CI = -0.454, -0.191, $\hat{\beta}_{\text{crepuscular}}$ = -0.132, 95% CI = -0.240, -0.025), and slightly reducing it in winter (Fig. 4A; $\hat{\beta}_{\text{crepuscular}}$ = -0.050, 95% CI = -0.093, -0.007). It had no significant effect on the probability of deer road mortality.

Mule deer were much more likely to cross roads with a high proportion of surrounding shrubland regardless of season and time of day. In the summer and winter, it had the strongest effect out of all variables on crossing probability (Fig. 4A, Fig. 7; summer: $\hat{\beta}_{\text{day}}$ = 0.923, 95% CI = 0.777, 1.069, $\hat{\beta}_{\text{crepuscular}}$ = 0.798, 95% CI = 0.672, 0.924; winter: $\hat{\beta}_{\text{night}}$ = 0.562, 95% CI = 0.482, 0.642, $\hat{\beta}_{\text{crepuscular}}$ = 0.661, 95% CI = 0.591, 0.730). In the summer months, the proportion of surrounding shrubland strongly decreased the probability of a deer road mortality event (Fig. 4C; $\hat{\beta}_{\text{summer}}$ = -0.781, 95% CI = -1.367, -0.195), but had no significant influence on winter mortality despite being the most impactful summer factor. During the crepuscular periods of both seasons, mule deer used roads with greater intensity that were surrounded by more shrubland (Fig. 4B; $\hat{\beta}_{\text{summer}}$ = 0.200, 95% CI = 0.122, 0.279; $\hat{\beta}_{\text{winter}}$ = 0.182, 95% CI = 0.118, 0.247).

The proportion of surrounding agricultural land was the most significant factor for winter mule deer road mortality and was also important for mule deer road crossing decisions in the winter months. Roads surrounded by more agricultural land had a lower chance of mule deer road mortality in the winter (Fig. 4C; $\hat{\beta}_{\text{winter}}$ = -0.245, 95% CI = -0.431, -0.060), but also had a lower chance that a mule deer would cross the road at that segment (Fig. 4A; $\hat{\beta}_{\text{crepuscular}}$ = -0.211, 95% CI = -0.337, -0.084, $\hat{\beta}_{\text{night}}$ = -0.428, 95% CI = -0.599, -0.257). Additionally, in the summer crepuscular period, mule deer intensity of use among crossed segments increased when surrounded by slightly less agricultural land (Fig. 4B; $\hat{\beta}_{\text{crepuscular}}$ = -0.059, 95% CI = -0.117, -0.001), but it was not a significant factor during other times of day or in the winter.

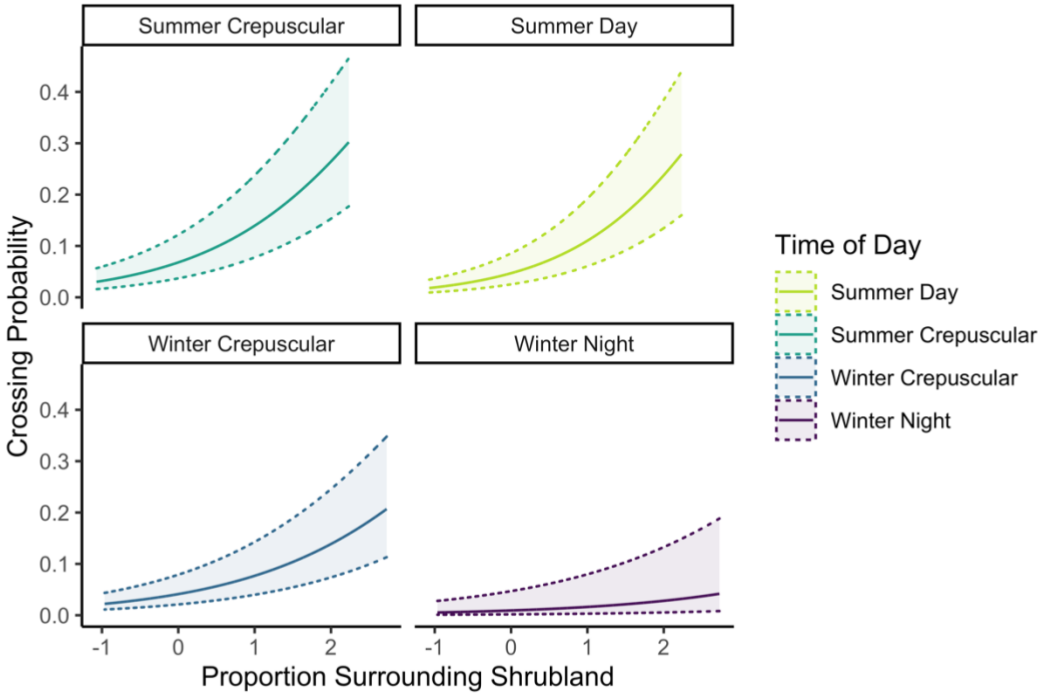

**Figure 7**: Modeled relationship and 95% confidence interval between the proportion of shrubland (scaled and centered) within a 573.33m buffer of a road segment and the probability that at least one mule deer crossed it. At all times of day in both summer and winter, higher proportions of surrounding shrubland were associated with a higher probability of a mule deer crossing a given road segment.

Surrounding open or natural land had a significant positive impact on which roads mule deer chose to cross in the summer crepuscular period (Fig. 4A; $\hat{\beta}_{\text{crepuscular}} = 0.110$, 95% CI = 0.023, 0.198) but conversely a negative impact during the winter at night period (Fig. 4A; $\hat{\beta}_{\text{night}} = -0.161$, 95% CI = -0.230, -0.093). It also had a positive effect on the intensity of crepuscular use among crossed roads in both seasons (Fig. 4B; $\hat{\beta}_{\text{summer}} = 0.128$, 95% CI = 0.065, 0.190; $\hat{\beta}_{\text{winter}} = 0.107$, 95% CI = 0.057, 0.158). There was no significant relationship between deer road mortality and surrounding open/natural land.

The average snow cover surrounding the roads had a positive impact on the chance mule deer would cross a given road during winter crepuscular periods (Fig. 4A; $\hat{\beta}_{\text{crepuscular}} =$ 0.125 95% CI = 0.068, 0.182) but a generally negative impact on intensity of winter crepuscular use among crossed roads (Fig. 4B; $\hat{\beta}_{\text{crepuscular 1}} = -0.402$, 95% CI = -0.712, -

0.092). As seen with winter terrain roughness, the relationship was non-linear, with lower intensity of use correlating with high snow cover, but higher intensity of use related to increasing snow cover (Fig. 4B; $\hat{\beta}_{\text{crepuscular 2}}$ = 0.270, 95% CI = -0.032, 0.572). Mule deer road mortality probability was not significantly related to snow cover.

NDVI, or vegetative greenness, had a strong positive relationship with summer crossing intensity (Fig. 4B; $\hat{\beta}_{\text{day 1}}$ = 1.603, 95% CI = 0.399, 2.808, $\hat{\beta}_{\text{day 2}}$ = 0.490, 95% CI = -0.582, 1.561, $\hat{\beta}_{\text{crepuscular 1}}$ = 1.087, 95% CI = 0.612, 1.562, $\hat{\beta}_{\text{crepuscular 2}}$ = 0.338, 95% CI = -0.179, 0.854), though began to saturate at higher crossing intensity values. It also had a positive relationship with winter nighttime crossing intensity ($\hat{\beta}_{\text{night 1}}$ = 0.571, 95% CI = -0.097, 1.238, $\hat{\beta}_{\text{night 2}}$ = 0.445, 95% CI = 0.000, 0.891). While NDVI also had a positive effect on which roads deer chose to cross in summer (Fig. 4A; $\hat{\beta}_{\text{day}}$ = 0.196, 95% CI = 0.070, 0.321), it had the strongest effect of all variables on the intensity of summertime use among crossed segments, with mule deer greatly preferring roads surrounded by more vegetative greenness. In contrast, NDVI had a negative impact on mule deer crossing probability in the winter months (Fig. 4A; $\hat{\beta}_{\text{night}}$ = -0.218, 95% CI = -0.293, -0.144, $\hat{\beta}_{\text{crepuscular}}$ = -0.206, 95% CI = -0.269, -0.142), as opposed to the positive relationship seen in summer. NDVI was not significantly related to mule deer road mortality.

## Discussion

Our findings support that even urban-adapted species like mule deer will selectively avoid anthropogenic disturbances such as artificial nightlight while simultaneously taking advantage of resources in or near disturbed areas. Across seasons, we found that deer avoided areas of high artificial nightlight, and selected for preferred habitat for cover and forage, such as roads with surrounding shrub cover. Similar to Neumann et al. (2012)., we found differences between the factors associated with increased mortality and increased use of road segments. We found that roads with preferred habitat or forage (such as shrub cover) saw elevated use, but lower mortality risk, whereas low levels of artificial nightlight saw elevated use and higher mortality risk. Roads with higher speed limits saw lower use but higher risk. Level terrain and increased vegetative greenness were associated with higher intensity of use but had no significant relationship with mortality risk. Noticeably, there seemed to be a deadly winter combination of preference for dark roads and necessity of crossing higher speed roads mixed with proximity to increased human activity. This may have been the reason there were five times as many mortality events in winter than in the summer over our study period.

The level of artificial nightlight had a strong influence on mule deer crossing behavior. In the crepuscular periods of both seasons and in the night in winter, mule deer crossed roads where nightlight levels were low. This reflects the work by Bliss-Ketchum et al. (2016), who found that Columbia black-tailed deer, a subspecies of mule deer, also avoided using artificially lit areas. Our mortality analysis results also show that increased nightlight levels greatly reduced the occurrence of road mortality events in both seasons, though statistically significant to a lesser degree. This implies that while deer chose the darkest locations to cross, they were also more likely to be involved in a fatal collision in these areas, where they were harder for drivers to see.

We also found mule deer crossed roads with lower speed limits in both summer and winter, though this preference was only about half as strong in winter. In the winter, we additionally found that higher speed limit roads were associated with greater risk of mortality. As their winter range is more urban, there is both a higher density of low speed limit roads for the deer to cross and increased contact with the highways that bisect the region. While high in the mountains in the summer it was likely easier for deer to avoid having to cross the highways, in the winter they were less able to do so, to their detriment as higher speed limit roads saw increased mortality risk. These findings are in line with many other studies of collision risk which also found higher speed limits associated with increased WVCs (Ng et al. 2008; Gunson et al. 2011; Meisingset et al. 2014; Garrote et al. 2018; Zeller et al. 2018; Pagany 2020) .

While surrounding shrub cover strongly increased the chance that a deer would cross a road segment in both summer and winter, in summer it also strongly decreased the chance that the segment would have mortality events associated with it. This is interesting because the summer months also saw the strongest effect of shrubland on increased crossing probability as well as a strong relationship with crepuscular crossing intensity, and yet the chances of mortality were greatly reduced when the road was surrounded by shrubland. In their review of WVC study findings, Gunson et al. (2011) found that WVCs commonly took place where roads bisected favorable cover or foraging habitat for a species. Our results contrast with this, because shrub and scrub land, which are both favorable cover and forage for mule deer (Utah Division of Wildlife Resources 2019a), was associated with decreased mortality risk, particularly in the summer. Perhaps these differences can be explained by variation in preferred habitat across species and regions and subsequent variation in the effects on motorist visibility (for example, if forest is the preferred habitat it may have reduced visibility as compared to shrubland, leading to increased crossings and increased mortality).

There are other factors that commonly appear in studies of collision risk that we were not able to assess for our study region. Annual average daily traffic (AADT) data, which provides a measure of traffic volume, was incomplete across our study area. AADT is widely cited as influencing the extent to which roads act as barriers and the risk of WVCs (Gagnon et al. 2007; Gunson et al. 2011; Coe et al. 2015; Cramer et al. 2019; Pagany 2020), so is likely an influential factor to further investigate. Measures of motorist visibility, such as road sinuosity, also affect the risk and location of WVCs and influence the amount of stopping time a driver will have once they spot an animal in the roadway (Gunson et al. 2011; Laliberté and St-Laurent 2020). Finally, distance to water or hydrologic features has been included in other studies of collision risk or habitat use (Ng et al. 2008; Clevenger et al. 2015; Coe et al. 2015; Zeller et al. 2018). We examined this factor for inclusion but found that too few hydrologic features fell within the buffer zone we used around the roadways for it to be included.

A limitation of our study results is the scope of the mortality analysis. Mule deer road mortality data were limited to ad hoc reports and carcasses found along a small number of set contracted routes, which were primarily highways. The actual number of collisions with deer resulting in animal mortality is likely much higher and occurs across a greater diversity of road types (Olson 2013; Cramer et al. 2019). This limits the ability of our mortality results to be generalizable beyond roads similar to the highways that were sampled. While some studies, such as by Snow et al. (2015), claim that the predictive power of collision models is not hindered by underreporting of WVCs, it remains true that our data represent an underestimate and may not capture all the subtleties of mule deer road mortality in our study region (Snow et al. 2015). Future studies could expand on ours by examining reports of deer-vehicle collisions in addition to carcass location data, or by supplementing state-collected data with a tailored carcass collection survey in the area of interest.

A possible pathway for expansion on our methodology would be to further integrate WVC data with movement data, as recommended by Zeller et al. (2018). This would also dovetail with the work of Cramer et al. (2019), who identified WVC hotspots based on collision and carcass data for multiple species across the entire state of Utah. Integrating movement data and mortality data into a single model would allow for identifying specific roads or regions that are of both high biological relevance and high risk for wildlife (Zeller et al. 2018).

Our findings add support for the need for collision mitigation and conservation interventions. Managers could target roadways for mitigation that see both high mortality and high use, such as roads in the winter ranges. Darker and higher speed roads are the most dangerous to deer and drivers, and roads bisecting crucial shrub habitat see high levels of use. Targeting these roads would reduce the risks associated with low driver visibility, short stopping distances, and increased deer presence. UDWR has already identified and categorized mule deer habitat areas across the state and assessed their importance (Utah Division of Wildlife Resources 2021). In our study region, crucial winter habitat is neighbored by growing metropolitan areas such as South Jordan, listed as one of the top 5 growing cities in 2020 (United States Census Bureau 2020). This combination could mean more roadways have or will expand into important mule deer habitat areas. Furthermore, with herd growth a top priority (Utah Division of Wildlife Resources 2019a), increasing deer and human populations may find themselves competing for use of similar areas, and at the very least, colliding more frequently on roadways where mitigation measures are lacking but needed.

Artificially brightening problem roads may be a novel way to reduce mule deer crossings, especially if a safer and darker crossing option exists nearby. This could be a cost-effective way to repel deer from certain roads while attracting them to others. Another approach our findings support is seasonal or nightly speed limit reductions on high mortality roads. Though some novel but limited research suggests that reduced nighttime speed limits are not effective if the road was designed for higher speeds (Riginos et al. 2022), because of the increased risks to drivers and deer it may be worth further exploring crepuscular and nightly winter speed reductions on problematic stretches of road. This type of mitigation could also be a cost-effective option in places where erecting a crossing structure is not feasible or imminent and would correlate well with observed mule deer activity periods and seasonal fluctuations in risk. Although it is often the most expensive option, wildlife crossing structures with fencing have been shown to be the most effective way to reduce collisions and increase landscape connectivity for mule deer, in some cases reducing collisions by more than 80% (Sawyer et al. 2012). These could be placed where migration or movement corridors bisect roads, or at places of high crossing intensity. Finally, our findings support that managers and future researchers should not underestimate the impact of artificial nightlight on habitat connectivity, use, and selection. It could be a powerful tool for encouraging or discouraging deer use of certain spaces and roadways, particularly in high mortality risk locations and time periods.

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# Supplementary Appendix

**Table S1**: Distribution, including upper and lower 95% confidence interval bounds, of each covariate’s calculated summary values at our determined the best fit model scale of 573.33m around each road segment, or the value associated with the road segment itself

| **Season** | **Variable** | **Distribution** |
|---|---|---|
| Summer | Nightlight (index) | Lower: -70.072, Mean: 76.6717, Upper: 223.4155<br>Min: 2.7794, Max: 381.1307 |
| Summer | Housing Density (index) | Lower: 0.3243, Mean: 6.7454, Upper: 13.1666<br>Min: 0.0000, Max: 11.1551 |
| Summer | Road Density (index) | Lower: -2.7302, Mean: 5.0457, Upper: 12.8216<br>Min: 0.0000, Max: 13.9430 |
| Summer | Speed Limit (mph) | Lower: 12.3375, Mean: 26.3822, Upper: 40.4269<br>Min: 0, Max: 65 |
| Summer | Segment Length (m) | Lower: -88.2163, Mean: 238.7439, Upper: 565.7041<br>Min: 0.0311, Max: 500 |
| Summer | Elevation (m) | Lower: 1261.6858, Mean: 1642.9477, Upper: 2024.2096<br>Min: 1372.216, Max: 2851.9923 |
| Summer | Terrain Roughness (index) | Lower: -5.8365, Mean: 7.9156, Upper: 21.6678<br>Min: 1.7262, Max: 37.9661 |
| Summer | NDVI (index) | Lower: 0.207, Mean: 0.3683, Upper: 0.5296<br>Min: 0.1794, Max: 0.6919 |
| Summer | Forest (proportion) | Lower: -0.276, Mean: 0.0615, Upper: 0.399<br>Min: 0, Max: 1 |
| Summer | Shrub (proportion) | Lower: -0.2687, Mean: 0.3243, Upper: 0.9173<br>Min: 0, Max: 1 |
| Summer | Developed/Urban (proportion) | Lower: -0.3127, Mean: 0.485, Upper: 1.2828<br>Min: 0, Max: 1 |
| Summer | Agriculture (proportion) | Lower: -0.0897, Mean: 0.0278, Upper: 0.1454<br>Min: 0, Max: 0.7146 |
| Summer | Open/Natural (proportion) | Lower: -0.2166, Mean: 0.1013, Upper: 0.4192<br>Min: 0, Max: 0.9966 |
| Winter | Nightlight (index) | Lower: -98.6245, Mean: 102.4861, Upper: 303.5967<br>Min: 2.411, Max: 813.751 |
| Winter | Housing Density (index) | Lower: -1.1443, Mean: 4.7159, Upper: 10.5761<br>Min: 0, Max: 12 |
| Winter | Road Density (index) | Lower: -1.8455, Mean: 3.93, Upper: 9.7055<br>Min: 0, Max: 13.9397 |
| Winter | Speed Limit (mph) | Lower: 5.3062, Mean: 24.511, Upper: 43.7158<br>Min: 0, Max: 65 |
| Winter | Segment Length (m) | Lower: -100.4026, Mean: 218.117, Upper: 536.6366<br>Min: 0.0175, Max: 500 |
| Winter | Elevation (m) | Lower: 1197.5148, Mean: 1549.898, Upper: 1902.2812<br>Min: 1286.7925, Max: 2851.3688 |
| Winter | Terrain Roughness (index) | Lower: -4.9839, Mean: 5.3209, Upper: 15.6258<br>Min: 1.2806, Max: 38.6979 |
| Winter | Snow Cover (index) | Lower: 5.2098, Mean: 29.6989, Upper: 54.188<br>Min: 0, Max: 77.5488 |
| Winter | NDVI (index) | Lower: 0.0852, Mean: 0.1872, Upper: 0.2891<br>Min: 0.0285, Max: 0.4741 |
| Winter | Forest (proportion) | Lower: -0.2449, Mean: 0.0387, Upper: 0.3224<br>Min: 0, Max: 1 |

| | | |
|---|---|---|
| Winter | Shrub (proportion) | Lower: -0.2693, Mean: 0.2613, Upper: 0.7919<br>Min: 0, Max: 1 |
| Winter | Developed/Urban (proportion) | Lower: -0.2325, Mean: 0.4625, Upper: 1.1574<br>Min: 0, Max: 1 |
| Winter | Agriculture (proportion) | Lower: -0.3291, Mean: 0.1391, Upper: 0.6073<br>Min: 0, Max: 1 |
| Winter | Open/Natural (proportion) | Lower: -0.2312, Mean: 0.0984, Upper: 0.428<br>Min: 0, Max: 1 |

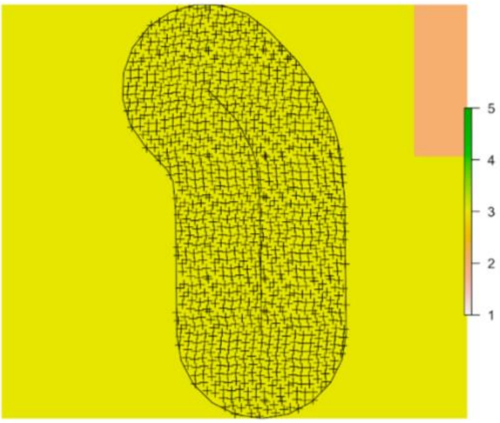

**Figure S1:** Nonaligned systematic sampling of n = 1,000 points in the 55.33m buffer around a road segment, demonstrated over land cover (NLCD) data.

**Table S2**: Correlation coefficients calculated using Pearson's r between all variables included in the regression models for crossing probability, crossing intensity, and mortality probability. Values were derived using the summary statistics calculated for each road segment aggregated for both the summer and winter ranges.

A: Summer road crossing and intensity 573.33m covariate correlation values. Red coloration shows where the threshold of |r| > 0.70 was exceeded.

| | Speed Limit | Elevation | Terrain Roughness | Road Density | VIIRS | NLCD 1 | NLCD 2 | NLCD 3 | NLCD 4 | NLCD 5 | NDVI | Segment Length |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Speed Limit | 1 | 0.03212716 | 0.10954379 | -0.07942015 | -0.07254606 | 0.08194688 | 0.11847009 | -0.1067539 | -0.04427574 | -0.02371627 | -0.02844426 | 0.15240969 |
| Elevation | 0.03212716 | 1 | 0.83849434 | -0.44210329 | -0.41922073 | 0.86291631 | 0.24631896 | -0.48449814 | -0.19908106 | -0.08611686 | 0.46997477 | 0.29664499 |
| Terrain Roughness | 0.10954379 | 0.83849434 | 1 | -0.55861768 | -0.50711174 | 0.78878696 | 0.40836981 | -0.64390808 | -0.22486834 | 0.09987112 | 0.38065218 | 0.34915453 |
| Road Density | -0.07942015 | -0.44210329 | -0.55861768 | 1 | 0.74605 | -0.37066523 | -0.69138352 | 0.86591912 | -0.04584183 | -0.47287994 | 0.18850317 | -0.43755196 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| VIIRS | -0.07254606 | -0.41922073 | -0.50711174 | 0.74605 | 1 | -0.33588406 | -0.69109385 | -0.82444969 | -0.07465199 | -0.39562614 | -0.01970112 | -0.38808729 |
| NLCD 1 | 0.08194688 | 0.86291631 | 0.78878696 | -0.37066523 | -0.33588406 | 1 | 0.08550639 | -0.41662155 | -0.16160499 | -0.11587055 | 0.47879394 | 0.26291693 |
| NLCD 2 | 0.11847009 | 0.24631896 | 0.40836981 | -0.69138352 | -0.69109385 | 0.08550639 | 1 | -0.83838836 | -0.10597277 | 0.18698582 | -0.29909452 | 0.41483392 |
| NLCD 3 | -0.1067539 | -0.48449814 | -0.64390808 | 0.86591912 | 0.82444969 | -0.41662155 | -0.83838836 | 1 | -0.02016738 | -0.49584373 | 0.14679931 | -0.52422636 |
| NLCD 4 | -0.04427574 | -0.19908106 | -0.22486834 | -0.04584183 | -0.07465199 | -0.16160499 | -0.10597277 | -0.02016738 | 1 | 0.05009857 | 0.04421592 | -0.0302003 |
| NLCD 5 | -0.02371627 | -0.08611686 | 0.09987112 | -0.47287994 | -0.39562614 | -0.11587055 | 0.18698582 | -0.49584373 | 0.05009857 | 1 | -0.33512606 | 0.27377416 |
| NDVI | -0.02844426 | 0.46997477 | 0.38065218 | 0.18850317 | 0.01970112 | 0.47879394 | -0.29909452 | 0.14679931 | 0.04421592 | -0.33512606 | 1 | -0.03743098 |
| Segment Length | 0.15240969 | 0.29664499 | 0.34915453 | -0.43755196 | -0.38808729 | 0.26291693 | 0.41483392 | -0.52422636 | -0.0302003 | 0.27377416 | -0.03743098 | 1 |

B: Winter road crossing and intensity 573.33m covariate correlation values. Red coloration shows where the threshold of |r| > 0.70 was exceeded.

| | Speed Limit | Elevation | Terrain Roughness | Road Density | VIIRS | NLCD 1 | NLCD 2 | NLCD 3 | NLCD 4 | NLCD 5 | NDVI | Snow Cover | Segment Length |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Speed Limit | 1 | 0.06712552 | 0.09482494 | 0.05478196 | 0.07496002 | 0.06122452 | 0.006039558 | 0.08082924 | -0.2092352 | 0.06443468 | 0.10005611 | -0.07836487 | 0.24786799 |
| Elevation | 0.067125523 | 1 | 0.80721507 | -0.19759259 | -0.31259981 | 0.79577577 | 0.314891484 | -0.37543073 | -0.2606113 | -0.03000619 | 0.06204006 | 0.01818568 | 0.29551547 |
| Terrain Roughness | 0.094824943 | 0.80721507 | 1 | -0.31195346 | -0.33890511 | 0.71971261 | 0.391398031 | -0.45198448 | -0.3002222 | 0.13001161 | 0.08106903 | 0.01467406 | 0.3219286 |
| Road Density | 0.054781961 | -0.19759259 | -0.31195346 | 1 | 0.54820924 | -0.22720543 | -0.429689305 | 0.70771118 | -0.1984081 | -0.32307637 | 0.135301 | -0.04063872 | -0.25557861 |
| VIIRS | 0.074960023 | -0.31259981 | -0.33890511 | 0.54820924 | 1 | -0.24613787 | -0.538149432 | 0.75372982 | -0.1406486 | -0.31123935 | -0.06892496 | -0.18088662 | -0.30099058 |
| NLCD 1 | 0.061224522 | 0.79577577 | 0.71971261 | -0.22720543 | -0.24613787 | 1 | 0.08974509 | -0.33220557 | -0.1549472 | -0.08453248 | 0.1815234 | 0.05148483 | 0.2263619 |
| NLCD 2 | 0.006039558 | 0.31489148 | 0.39139803 | -0.42968931 | -0.53814943 | 0.08974509 | 1 | -0.62240016 | -0.3221971 | 0.08279499 | -0.06305136 | 0.03021137 | 0.31563307 |
| NLCD 3 | 0.080829239 | -0.37543073 | -0.45198448 | 0.70771118 | 0.75372982 | -0.33220557 | -0.622400158 | 1 | -0.2941104 | -0.40279008 | 0.05232609 | -0.10337908 | -0.39023762 |
| NLCD 4 | -0.209235172 | -0.26061127 | -0.30022221 | -0.19840805 | -0.14064862 | -0.15494715 | -0.322197106 | -0.29411038 | 1 | -0.14849023 | -0.17629463 | 0.11503537 | -0.10869202 |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NLCD 5 | 0.064434681 | -0.03000619 | 0.13001161 | -0.32307637 | -0.31123935 | -0.08453248 | 0.082794988 | -0.40279008 | -0.1484902 | 1 | 0.08545451 | -0.03841588 | 0.27432315 |
| NDVI | 0.100056107 | 0.06204006 | 0.08106903 | 0.135301 | -0.06892496 | 0.1815234 | -0.06305136 | 0.05232609 | -0.1762946 | 0.08545451 | 1 | -0.08614212 | 0.07586084 |
| Snow Cover | -0.078364867 | 0.01818568 | 0.01467406 | -0.04063872 | -0.18088662 | 0.05148483 | 0.030211368 | -0.10337908 | 0.1150354 | -0.03841588 | -0.08614212 | 1 | 0.02925612 |
| Segment Length | 0.247867993 | 0.29551547 | 0.3219286 | -0.25557861 | -0.30099058 | 0.2263619 | 0.31563307 | -0.39023762 | -0.108692 | 0.27432315 | 0.07586084 | 0.02925612 | 1 |

C: Summer road mortality 573.33m covariate correlation values. Red coloration shows where the threshold of |r| > 0.70 was exceeded.

| | Speed Limit | Terrain Roughness | Road Density | VIIRS | NLCD 1 | NLCD 2 | NLCD 3 | NLCD 4 | NLCD 5 | NDVI | Segment Length |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Speed Limit | 1 | -0.19546524 | -0.11918375 | -0.08843352 | -0.2331017018 | 0.2036791 | -0.158000569 | -0.099405236 | 0.29031266 | -0.5056579 | 0.2717656854 |
| Terrain Roughness | -0.19546524 | 1 | -0.42843859 | -0.46138925 | 0.813657096 | 0.3035755 | -0.520888904 | -0.267471697 | -0.00249439 | 0.60520265 | 0.0989660475 |
| Road Density | -0.11918375 | -0.42843859 | 1 | 0.75288043 | -0.302507616 | -0.699774 | 0.854715141 | 0.043081842 | -0.45127575 | 0.10553757 | -0.3166800585 |
| VIIRS | -0.08843352 | -0.46138925 | 0.75288043 | 1 | -0.268368672 | -0.6967267 | 0.837530073 | 0.029524069 | -0.44253818 | -0.03034356 | -0.2437171801 |
| NLCD 1 | -0.2331017 | 0.8136571 | -0.30250762 | -0.26836867 | 1 | 0.0196687 | -0.328407509 | -0.15534123 | -0.17858699 | 0.67962293 | -0.0005046594 |
| NLCD 2 | 0.20367914 | 0.30357545 | -0.69977397 | -0.69672674 | 0.0196686977 | 1 | -0.824895566 | -0.267721884 | 0.20747682 | -0.22619015 | 0.3513397349 |
| NLCD 3 | -0.15800057 | -0.5208889 | 0.85471514 | 0.83753007 | -0.3284075093 | -0.8248956 | 1 | 0.005790068 | -0.51713072 | 0.01191917 | -0.3672030841 |
| NLCD 4 | -0.09940524 | -0.2674717 | 0.04308184 | 0.02952407 | -0.1553412305 | -0.2677219 | 0.005790068 | 1 | 0.10871094 | 0.03447041 | -0.0107315906 |
| NLCD 5 | 0.29031266 | -0.00249439 | -0.45127575 | -0.44253818 | -0.1785869885 | 0.2074768 | -0.517130725 | 0.108710941 | 1 | -0.31221452 | 0.2255992662 |
| NDVI | -0.5056579 | 0.60520265 | 0.10553757 | -0.03034356 | 0.6796229316 | -0.2261902 | 0.011919172 | 0.034470409 | -0.31221452 | 1 | -0.0780692665 |
| Segment Length | 0.27176569 | 0.09896605 | -0.31668006 | -0.24371718 | -0.0005046594 | 0.3513397 | -0.367203084 | -0.010731591 | 0.22559927 | -0.07806927 | 1 |

D: Winter road mortality 573.33m covariate correlation values. Red coloration shows where the threshold of |r| > 0.70 was exceeded.

| | Speed Limit | Terrain Roughness | Road Density | VIIRS | NLCD 1 | NLCD 2 | NLCD 3 | NLCD 4 | NLCD 5 | NDVI | Snow Cover | Segment Length |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Speed Limit | 1 | 0.19635571 | -0.34942721 | -0.16977 | 0.08870264 | 0.31849727 | -0.3867326 | -0.07179087 | 0.35327119 | -0.08634906 | -0.1014080139 | 0.4008078876 |
| Terrain Roughness | 0.19635571 | 1 | -0.11169623 | -0.2015708 | 0.59045711 | 0.59025217 | -0.3243274 | -0.37131148 | 0.01229171 | -0.09909976 | -0.0103755221 | 0.1099569615 |
| Road Density | -0.34942721 | -0.11169623 | 1 | 0.5853757 | -0.1056452 | -0.45760769 | 0.7379905 | -0.28439051 | -0.38561533 | 0.17190267 | -0.0766801125 | -0.3311532949 |
| VIIRS | -0.16977001 | -0.20157085 | 0.58537565 | 1 | -0.17147623 | -0.45989108 | 0.6660243 | -0.18077369 | -0.34611491 | -0.12205088 | -0.2386635434 | -0.1857578281 |
| NLCD 1 | 0.08870264 | 0.59045711 | -0.1056452 | -0.1714762 | 1 | 0.21031565 | -0.2084673 | -0.12967029 | -0.08880396 | 0.08569275 | 0.0621373583 | 0.0906885649 |
| NLCD 2 | 0.31849727 | 0.59025217 | -0.45760769 | -0.4598911 | 0.21031565 | 1 | -0.6566422 | -0.293341 | 0.08427158 | -0.20581668 | 0.1073617707 | 0.252954318 |
| NLCD 3 | -0.38673263 | -0.32432737 | 0.73799055 | 0.6660243 | -0.20846732 | -0.65664216 | 1 | -0.34900865 | -0.48941847 | 0.15294275 | -0.1347161528 | -0.3802898937 |
| NLCD 4 | -0.07179087 | -0.37131148 | -0.28439051 | -0.1807737 | -0.12967029 | -0.293341 | -0.3490087 | 1 | -0.0789344 | -0.10434238 | 0.1176005666 | 0.1036188916 |
| NLCD 5 | 0.35327119 | 0.01229171 | -0.38561533 | -0.3461149 | -0.08880396 | 0.08427158 | -0.4894185 | -0.0789344 | 1 | 0.11390212 | -0.0669232572 | 0.2146938423 |
| NDVI | -0.08634906 | -0.09909976 | 0.17190267 | -0.1220509 | 0.08569275 | -0.20581668 | 0.1529427 | -0.10434238 | 0.11390212 | 1 | -0.0914133315 | -0.1510224612 |
| Snow Cover | -0.10140801 | -0.01037552 | -0.07668011 | -0.2386635 | 0.06213736 | 0.10736177 | -0.1347162 | 0.11760057 | -0.06692326 | -0.09141333 | 1 | -0.0001019542 |
| Segment Length | 0.40080789 | 0.10995696 | -0.33115329 | -0.1857578 | 0.09068856 | 0.25295432 | -0.3802899 | 0.10361889 | 0.21469384 | -0.15102246 | -0.0001019542 | 1 |

**Table S3:** Summary of results of testing for spatial autocorrelation in our models using Moran's I, where the alternative hypothesis is that spatial autocorrelation is present. As most models showed significant spatial autocorrelation, we accounted for spatial effects in all.

| **Model** | **573.33m Moran's I** | **55.33m Moran's I** | **20m Moran's I** |
|---|---|---|---|
| Summer Day Crossing Intensity | observed = 0.0471, expected = -0.0017, sd = 0.0073, p-value = 2.731e-11 | observed = 0.0390, expected = -0.0017, sd = 0.0073, p-value = 2.795e-08 | observed = 0.0383230, expected = -0.0017, sd = 0.0073, p-value = 4.83e-08 |
| Summer Crepuscular Crossing Intensity | observed = -0.0047, expected = -0.0011, sd = 0.0061, p-value = 0.5605 | observed = -0.0024, expected = -0.0011, sd = 0.0061, p-value = 0.8283 | observed = -0.0009, expected = -0.0011, sd = 0.0061, p-value = 0.9759 |
| Summer Day Crossing Probability | observed = 0.0062, expected = -0.0002, sd = 0.0019, p-value = 0.0007 | observed = 0.0032, expected = -0.0002, sd = 0.0019, p-value = 0.0752 | observed = 0.0010, expected = -0.0002, sd = 0.0019, p-value = 0.505 |

| | | | |
|---|---|---|---|
| Summer Crepuscular Crossing Probability | observed = 0.0096, expected = -0.0002, sd = 0.0019, p-value = 2.679e-07 | observed = 0.0094, expected = -0.0002, sd = 0.0019, p-value = 4.003e-07 | observed = 0.0079, expected = -0.0002, sd = 0.0019, p-value = 2.19e-05 |
| Winter Crepuscular Crossing Intensity | observed = 0.0226, expected = -0.0007, sd = 0.0041, p-value = 1.606e-08 | observed = 0.0226, expected = -0.0007, sd = 0.0041, p-value = 1.753e-08 | observed = 0.0234, expected = -0.0007, sd = 0.0041, p-value = 5.293e-09 |
| Winter Night Crossing Intensity | observed = 0.0090, expected = -0.0010, sd = 0.0051, p-value = 0.04912 | observed = 0.0054, expected = -0.0010, sd = 0.0051, p-value = 0.2068 | observed = 0.0054, expected = -0.0010, sd = 0.0051, p-value = 0.2104 |
| Winter Crepuscular Crossing Probability | observed = 1.3244e-02, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 | observed = 9.5006e-03, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 | observed = 8.9089e-03, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 |
| Winter Night Crossing Probability | observed = 7.1344e-03, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 | observed = 7.3257e-03, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 | observed = 6.0911e-03, expected = -5.0904e-05, sd = 4.3290e-04, p-value < 2.2e-16 |

**Table S4**: Summary of all models fit for our data set and their associated AIC values. All models (except Summer Crossing Intensity) had a best fit scale of 573.33m, so that scale was selected for the final analysis, as well as for performing the road mortality analysis.

| **Model** | **573.33m AIC** | **55.33m AIC** | **20m AIC** |
|---|---|---|---|
| Summer Day Crossing Intensity | 1651.3 | 1652.5 | **1651.2** |
| Summer Crepuscular Crossing Intensity | 3288.7 | **3287.1** | 3295.4 |
| Summer Day Crossing Probability | **4423** | 4581.3 | 4604.9 |
| Summer Crepuscular Crossing Probability | **5464.6** | 5644.4 | 5669 |
| Winter Crepuscular Crossing Intensity | **6087** | 6109.6 | 6120.8 |
| Winter Night Crossing Intensity | **3304.8** | 3312.4 | 3315.6 |
| Winter Crepuscular Crossing Probability | **13067.7** | 13441.9 | 13508.2 |
| Winter Night Crossing Probability | **9566.6** | 9758.8 | 9819.7 |

**Table S5**: Full model results for the determined best spatial scale of 573.33m

A: Summer Day Crossing Intensity

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -3.76571 | 0.27206 | -13.841 | < 2e-16 |
| Speed Limit 1 | -0.09121 | 0.36945 | -0.247 | 0.804998 |
| Speed Limit 2 | -0.31065 | 0.22927 | -1.355 | 0.175436 |
| Terrain Roughness 1 | -0.72646 | 0.26546 | -2.737 | 0.006208 |
| Terrain Roughness 2 | -0.71746 | 0.3436 | -2.088 | 0.036792 |
| Nightlight 1 | -1.45741 | 0.26308 | -5.54 | 3.03E-08 |

| | | | | |
|---|---|---|---|---|
| Nightlight 2 | -0.71885 | 0.3056 | -2.352 | 0.018662 |
| Shrubland | -0.05619 | 0.04724 | -1.189 | 0.234259 |
| Agriculture | -0.08174 | 0.02988 | -2.736 | 0.006219 |
| Open/Natural | -0.07028 | 0.03348 | -2.099 | 0.035834 |
| NDVI 1 | 0.9769 | 0.28328 | 3.449 | 0.000564 |
| NDVI 2 | 0.20022 | 0.38902 | 0.515 | 0.606777 |
| Segment Length 1 | 0.86375 | 0.21957 | 3.934 | 8.36E-05 |
| Segment Length 2 | 0.33548 | 0.07531 | 4.455 | 8.39E-06 |

B: Summer Crepuscular Crossing Intensity

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -4.70879 | 0.22224 | -21.188 | < 2e-16 |
| Speed Limit 1 | -0.16276 | 0.34294 | -0.475 | 0.635065 |
| Speed Limit 2 | -0.19664 | 0.21454 | -0.917 | 0.359377 |
| Terrain Roughness 1 | -0.75297 | 0.22213 | -3.39 | 0.000699 |
| Terrain Roughness 2 | -0.72886 | 0.30231 | -2.411 | 0.015909 |
| Nightlight 1 | 0.08265 | 0.24466 | 0.338 | 0.735516 |
| Nightlight 2 | 0.05937 | 0.4317 | 0.138 | 0.890607 |
| Shrubland | 0.20039 | 0.03988 | 5.025 | 5.04E-07 |
| Agriculture | -0.05905 | 0.02945 | -2.005 | 0.044953 |
| Open/Natural | 0.12758 | 0.032 | 3.986 | 6.71E-05 |
| NDVI 1 | 1.08723 | 0.24239 | 4.485 | 7.28E-06 |
| NDVI 2 | 0.33771 | 0.26353 | 1.282 | 0.200014 |
| Segment Length 1 | 1.35236 | 0.22449 | 6.024 | 1.70E-09 |
| Segment Length 2 | 0.39255 | 0.08047 | 4.878 | 1.07E-06 |

C: Winter Crepuscular Crossing Intensity

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -4.05168 | 0.224123 | -18.078 | < 2e-16 |
| Speed Limit 1 | -0.096351 | 0.182326 | -0.528 | 0.59718 |
| Speed Limit 2 | -0.172429 | 0.12373 | -1.394 | 0.16344 |
| Terrain Roughness 1 | -0.091488 | 0.141771 | -0.645 | 0.51872 |

| | | | | |
|---|---|---|---|---|
| Terrain Roughness 2 | -0.8221 | 0.280623 | -2.93 | 0.00339 |
| Nightlight 1 | 0.73165 | 0.174701 | 4.188 | 2.81E-05 |
| Nightlight 2 | 0.148527 | 0.218637 | 0.679 | 0.49693 |
| Shrubland | 0.182488 | 0.033106 | 5.512 | 3.54E-08 |
| Agriculture | -0.007091 | 0.020263 | -0.35 | 0.72636 |
| Open/Natural | 0.107372 | 0.025864 | 4.151 | 3.30E-05 |
| NDVI 1 | 0.064485 | 0.23867 | 0.27 | 0.78702 |
| NDVI 2 | 0.155078 | 0.174145 | 0.891 | 0.37319 |
| Snow Cover 1 | -0.402015 | 0.15811 | -2.543 | 0.011 |
| Snow Cover 2 | 0.269884 | 0.154059 | 1.752 | 0.07981 |
| Segment Length 1 | 1.001679 | 0.155311 | 6.45 | 1.12E-10 |
| Segment Length 2 | 0.406129 | 0.049831 | 8.15 | 3.63E-16 |

### D: Winter Night Crossing Intensity

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -4.38381 | 0.26562 | -16.504 | < 2e-16 |
| Speed Limit 1 | -0.29594 | 0.20793 | -1.423 | 0.1547 |
| Speed Limit 2 | -0.16331 | 0.1349 | -1.211 | 0.2261 |
| Terrain Roughness 1 | 0.77367 | 0.30365 | 2.548 | 0.0108 |
| Terrain Roughness 2 | -0.17792 | 0.29445 | -0.604 | 0.5457 |
| Nightlight 1 | 0.07438 | 0.45892 | 0.162 | 0.8712 |
| Nightlight 2 | -0.28509 | 0.4683 | -0.609 | 0.5427 |
| Shrubland | 0.01159 | 0.05968 | 0.194 | 0.846 |
| Agriculture | -0.01215 | 0.03024 | -0.402 | 0.6879 |
| Open/Natural | 0.0605 | 0.04559 | 1.327 | 0.1845 |
| NDVI 1 | 0.57075 | 0.34045 | 1.676 | 0.0936 |
| NDVI 2 | 0.44544 | 0.22726 | 1.96 | 0.05 |
| Snow Cover 1 | -0.05134 | 0.20485 | -0.251 | 0.8021 |
| Snow Cover 2 | 0.2322 | 0.17225 | 1.348 | 0.1776 |
| Segment Length 1 | 0.97444 | 0.13632 | 7.148 | 8.79E-13 |
| Segment Length 2 | 0.36195 | 0.04764 | 7.598 | 3.01E-14 |

### E: Summer Day Crossing Probability

| **Variable** | ***β* Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -3.011 | 0.32773 | -9.187 | < 2e-16 |
| Speed Limit | -0.13473 | 0.03742 | -3.601 | 0.000318 |
| Terrain Roughness | -0.32234 | 0.06711 | -4.803 | 1.56E-06 |
| Light | -0.16764 | 0.11305 | -1.483 | 0.138113 |
| Shrubland | 0.92292 | 0.07455 | 12.38 | < 2e-16 |
| Agriculture | 0.0488 | 0.04672 | 1.044 | 0.296262 |
| Open/Natural | 0.06465 | 0.05547 | 1.165 | 0.243818 |
| NDVI | 0.1957 | 0.06414 | 3.051 | 0.00228 |
| Segment Length | 0.44123 | 0.04312 | 10.233 | < 2e-16 |
| Easting | 0.28318 | 0.09528 | 2.972 | 0.002957 |
| Northing | 0.06807 | 0.04759 | 1.43 | 0.15267 |

F: Summer Crepuscular Crossing Probability

| **Variable** | ***β* Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -2.61818 | 0.32815 | -7.979 | 1.48E-15 |
| Speed Limit | -0.18501 | 0.03169 | -5.838 | 5.27E-09 |
| Terrain Roughness | -0.1323 | 0.05499 | -2.406 | 0.0161 |
| Light | -0.60274 | 0.11139 | -5.411 | 6.26E-08 |
| Shrubland | 0.7977 | 0.06426 | 12.413 | < 2e-16 |
| Agriculture | -0.04467 | 0.04348 | -1.027 | 0.3043 |
| Open/Natural | 0.11037 | 0.04481 | 2.463 | 0.0138 |
| NDVI | 0.08225 | 0.05462 | 1.506 | 0.1321 |
| Segment Length | 0.44026 | 0.03693 | 11.921 | < 2e-16 |
| Easting | 0.18344 | 0.07806 | 2.35 | 0.0188 |
| Northing | 0.19417 | 0.04533 | 4.284 | 1.84E-05 |

G: Winter Crepuscular Crossing Probability

| **Variable** | ***β* Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -3.14692 | 0.35257 | -8.926 | < 2e-16 |
| Speed Limit | -0.057 | 0.02625 | -2.171 | 0.0299 |
| Terrain Roughness | -0.05004 | 0.02194 | -2.281 | 0.02253 |

| | | | | |
|---|---|---|---|---|
| Light | -0.29373 | 0.06608 | -4.445 | 8.78E-06 |
| Shrubland | 0.66054 | 0.03568 | 18.515 | < 2e-16 |
| Agriculture | -0.21064 | 0.06471 | -3.255 | 0.00113 |
| Open/Natural | 0.0327 | 0.02783 | 1.175 | 0.2399 |
| NDVI | -0.20575 | 0.03261 | -6.31 | 2.80E-10 |
| Snow Cover | 0.12472 | 0.02898 | 4.303 | 1.68E-05 |
| Segment Length | 0.41964 | 0.02456 | 17.089 | < 2e-16 |
| Easting | -0.07913 | 0.03616 | -2.188 | 0.02865 |
| Northing | 0.47503 | 0.04344 | 10.934 | < 2e-16 |

## H: Winter Night Crossing Probability

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -4.66621 | 0.84564 | -5.518 | 3.43E-08 |
| Speed Limit | -0.07448 | 0.03169 | -2.351 | 0.0187 |
| Terrain Roughness | -0.03397 | 0.0252 | -1.348 | 0.1777 |
| Light | -0.31827 | 0.07753 | -4.105 | 4.04E-05 |
| Shrubland | 0.56211 | 0.04078 | 13.785 | < 2e-16 |
| Agriculture | -0.42821 | 0.08736 | -4.901 | 9.52E-07 |
| Open/Natural | -0.16142 | 0.035 | -4.612 | 4.00E-06 |
| NDVI | -0.21837 | 0.03788 | -5.764 | 8.21E-09 |
| Snow Cover | 0.05481 | 0.03616 | 1.516 | 0.1296 |
| Segment Length | 0.41011 | 0.0293 | 13.997 | < 2e-16 |
| Easting | -0.08897 | 0.04151 | -2.143 | 0.0321 |
| Northing | 0.51886 | 0.05385 | 9.635 | < 2e-16 |

## I: Summer Road Mortality Probability

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -2.2572 | 0.30926 | -7.299 | 2.91E-13 |
| Speed Limit | 0.14956 | 0.20467 | 0.731 | 0.464921 |
| Terrain Roughness | -0.03096 | 0.30001 | -0.103 | 0.917795 |
| Light | -0.52842 | 0.27603 | -1.914 | 0.055576 |
| Shrubland | -0.78114 | 0.29912 | -2.611 | 0.009016 |

| | | | | |
|---|---|---|---|---|
| Agriculture | -0.10357 | 0.16148 | -0.641 | 0.52128 |
| Open/Natural | -0.16084 | 0.2133 | -0.754 | 0.450802 |
| NDVI | -0.12614 | 0.3272 | -0.386 | 0.699849 |
| Segment Length | 0.55224 | 0.16736 | 3.3 | 0.000968 |
| Easting | 0.19309 | 0.28238 | 0.684 | 0.494111 |
| Northing | 0.15511 | 0.14742 | 1.052 | 0.292717 |

J: Winter Road Mortality Probability

| **Variable** | **$\beta$ Estimate** | **Standard Error** | **z value** | **Pr (>\|z\|)** |
|---|---|---|---|---|
| Intercept | -1.949906 | 0.136437 | -14.292 | < 2e-16 |
| Speed Limit | 0.168019 | 0.079879 | 2.103 | 0.035429 |
| Terrain Roughness | -0.008784 | 0.075499 | -0.116 | 0.907379 |
| Light | -0.207505 | 0.112744 | -1.84 | 0.065695 |
| Shrubland | 0.016143 | 0.101726 | 0.159 | 0.873914 |
| Agriculture | -0.245426 | 0.094443 | -2.599 | 0.009359 |
| Open/Natural | -0.055512 | 0.078942 | -0.703 | 0.481926 |
| NDVI | -0.097677 | 0.095644 | -1.021 | 0.307133 |
| Snow Cover | -0.015282 | 0.076822 | -0.199 | 0.842317 |
| Segment Length | 0.597576 | 0.083727 | 7.137 | 9.53E-13 |
| Easting | -0.223047 | 0.090506 | -2.464 | 0.013723 |
| Northing | 0.272869 | 0.082284 | 3.316 | 0.000912 |