Frank Kaitlyn (Orcid ID: 0000-0001-9507-6312)
Ditmer Mark Allan (Orcid ID: 0000-0003-4311-3331)
Currie William S. (Orcid ID: 0000-0003-1975-0808)

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Dark roads aid movement but increase mortality of a generalist herbivore in the American Southwest

Kaitlyn M. Frank[1], Mark A. Ditmer[2], David C. Stoner[3], William S. Currie[1], Daniel D. Olson[4], Neil H. Carter[1]

[1]School for Environment and Sustainability, University of Michigan, 440 Church Street, Ann Arbor, Michigan, 48109

[2]USDA Forest Service Rocky Mountain Research Station, 240 West Prospect, Fort Collins, Colorado, 80526

[3]Department of Wildland Resources, Utah State University, 5230 Old Main Hill, Logan, Utah, 84322

[4]Utah Division of Wildlife Resources, 1594 W. North Temple, Salt Lake City, Utah 84116

Contact/Corresponding Author: Kaitlyn M. Frank (frankkm@umich.edu, 313-671-8535)

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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, home range requirements and seasonal migrations often necessitate road crossings, posing threats to human safety, property, and animal survival. Artificial nightlight, emanating from light posts and urban skyglow, is ubiquitous on and around road networks worldwide; however, its effects on road crossing behavior and the associated mortality risk for wildlife are not well understood. By integrating the latest NASA nightlight products with GPS collar data collected from 67 mule deer (*Odocoileus hemionus*) over a 7-year period (2012 to 2018), we used a resource-selection framework to assess factors influencing seasonal crossing behavior and road mortality in Salt Lake City, Utah, an expanding metropolitan area in the United States. We found deer preferred to cross the road where surrounding artificial nightlight was lower in both summer and winter seasons, especially during crepuscular and nighttime periods. However, lower nightlight levels also increased the risk of road mortality. Areas with more shrub cover and lower speed limits increased the likelihood of crossing as well as lowered the risk of road mortality. There were five times as many mortality events in winter as in summer, likely because of the combination of deer preference for dark roads mixed with proximity to both higher speed roads and increased human activity. Better understanding how a pervasive and expanding environmental pollutant like artificial nightlight may attract or repel human-tolerant wildlife species from roadways presents an opportunity to mitigate collision risk while improving population management strategies for this abundant, generalist herbivore and many other economically and ecologically important species.

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Introduction

The expansion of human populations and associated infrastructure development has reduced and degraded wildlife habitat and increased threats to survival for many wide-ranging wildlife species (Saunders et al. 1991, Forman and Alexander 1998, Bencin et al. 2019). Roads in particular are linked with numerous negative effects on mammals (Fahrig and Rytwinski 2009), such as fragmenting habitats (Fraser et al. 2019), restricting movement (Forman and Deblinger 2000, Schwab and Zandbergen 2011), and directly causing mortality through vehicle collisions (Neumann et al. 2012, Zeller et al. 2018, Bencin et al. 2019). A more comprehensive understanding of how wide-ranging species navigate expanding road networks can bolster efforts to sustainably manage populations and reduce wildlife-vehicle collisions (WVCs).

Road crossings and WVCs are spatially and temporally non-random occurrences and tend to cluster in localities where certain landscape and environmental factors are present (Gunson et al. 2011, Garrote et al. 2018, Bastille-Rousseau et al. 2018). Ungulates, for example, face increased risk of WVCs because they are attracted to common features of roadsides such as access to early-successional or edge habitat forage (Gunson et al. 2011, Meisingset et al. 2013, Neumann et al. 2013), salt runoff (Tiwari and Rachlin 2018), and snow removal (Olson et al. 2015, Stoner et al. 2021). There is also a strong seasonal component to crossings and WVCs, with variation in movement patterns due to migration (Sawyer et al. 2009, Coe et al. 2015, Kantola et al. 2019), increased mobility during breeding (or ‘rut’; Foley et al. 2015, Cunningham et al. 2022), and overlap between crepuscular activity periods and peak traffic volumes all potentially playing a role (Cunningham et al. 2022). Anthropogenic factors, such as traffic volume (Gagnon et al. 2007, Ng et al. 2008, Jacobson et al. 2016, Abraham and Mumma 2021) and speed limit (Ng et al. 2008, Gunson et al. 2011, Neumann et al. 2012, Jacobson et al. 2016, Riginos et al. 2022), can also influence both wildlife roadside behavior and collision risk. For example, Jacobson et al. (2016) note that for wildlife who use their speed and agility to exploit traffic gaps when crossing roads (e.g., ungulates), higher vehicle speeds can reduce the effectiveness of their crossing strategy, resulting in an increased risk of WVCs.

These previous studies indicate that wildlife behaviors near and when crossing roads are likely associated with how individuals perceive the benefits and costs of making movement decisions (Gunson et al. 2011, Jacobson et al. 2016, Ditmer et al. 2018). Artificial nightlight is a significant environmental cue that might affect these perceived tradeoffs. Numerous studies have shown that artificial nightlight can influence wildlife behaviors and movements, for example, by impacting their foraging and hunting strategies (Bennie et al. 2015, Shier et al. 2020, Ditmer et al. 2021b, Hoffmann et al. 2022), movement and migration paths (Bliss-Ketchum et al. 2016, Cabrera-Cruz et al. 2018), vigilance behaviors (Yorzinski et al. 2015), physiological stress levels (Bedrosian et al. 2011, Ouyang et al. 2017), and energy budgeting (Touzot et al. 2019). Both increasing and ubiquitous, artificial nightlight emanates from skyglow, headlights, streetlamps, homes, and businesses and disturbs natural light regimes worldwide (Gaston et al. 2014, Kyba et al. 2017, Gaston 2018, Sánchez de Miguel et al. 2022). Because roads are illuminated at night for driver visibility and safety (Gaston et al. 2012), we expect the influence of artificial nightlight on wildlife to grow (Gaston et al. 2014, Cox et al. 2022) as road networks expand into historically undeveloped areas. Despite this, artificial nightlight remains relatively understudied as a predictor of WVCs and crossings (but see Reed and Woodard 1981, McDonald 1991).

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To help fill this gap, we examine the influence of environmental and anthropogenic factors, including artificial nightlight levels, on road crossing behaviors and collision risk of mule deer (*Odocoileus hemionus*) near Salt Lake City, UT. We focus on mule deer for three main reasons. First, they are an economically and ecologically important ungulate species (Eckrich et al. 2020) with a distribution stretching across the Intermountain West. The rapid human population growth and associated land use change in this region has led to concerns about loss of wildlife habitat connectivity, especially migratory routes for ungulates, and increases in human-wildlife conflict (Cramer et al. 2019, Utah Division of Wildlife Resources 2019). Second, mule deer home range and movement requirements often necessitate road crossings, risking the lives of both the deer themselves and of drivers involved in collisions (Schwab and Zandbergen 2011, Zeller et al. 2018, Hill et al. 2020, Ditmer et al. 2021b). Furthermore, as WVCs with mule deer are common, their cumulative outcomes are costly. For example, in Utah, between 2008 and 2017, the average annual societal cost of collisions with wildlife—including costs related to vehicle damage, human injuries, and even fatalities—and mule deer lost was US$138 million (Cramer et al. 2019). Third, although various studies indicate that deer are sensitive to artificial nightlight, it is not well understood how this sensory pollutant affects deer road crossings and collisions (Bliss-Ketchum et al. 2016, Ciach and Fröhlich 2019, Ditmer et al. 2021b).

Here we used 7 years of mule deer GPS collar movement data (n=67 individuals) to understand their road crossing behaviors. By linking road crossing behavior with specific landscape, environmental, and road factors, including the novel factor artificial nightlight, our analysis can inform management interventions such as spatially and temporally targeted placement of fences, signage, nightlights, and wildlife crossing structures. Additionally, we

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use road mortality data to determine whether common factors surround road crossing and mortality locations. This comparison provides insight into the features that determine successful crossings versus those that end in mortality events. Our aim, therefore, is to provide a more comprehensive and predictive framework that provides managers with information to deter animal 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 wildlife.

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 three different biologically informed buffer zones around the road network (buffer scales: 20 m, 55 m, and 573 m), we were able to explore the relationship between the covariates and mule deer crossing probability, intensity of use, and mortality probability. To account for mule deer's seasonal migratory behavior, we conducted these analyses for two distinct seasons—"summer" and "winter"—and defined seasonally specific home ranges for each year. With the exception of the road mortality analysis, which used reported carcass locations per date, 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). We then used AIC (Appendix S1: Table S4) to determine which of the three buffer scales was most appropriate

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and focused on the model results at the best fit scale (Appendix S1: Table S5). All spatial and statistical analyses were conducted using R (R Core Team 2021).

Study Area and Mule Deer Data

Mule deer GPS data from an initial set of 82 individual females in the Oquirrh Mountains and greater Salt Lake City area were collected 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 three hours. Duplicate data points were identified and removed. Individuals with at least 150 GPS fixes in a given season were selected for use in our analysis, producing a final set of 67 deer (total: 171,389 fixes; minimum in a season: 153 fixes; average in a season: 739 fixes; maximum in a season: 2,149 fixes).

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 exhibiting 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 spend the summer months in the high elevation wildlands of the Oquirrh mountains and the winter months in the low elevation mixed-use landscapes comprising their winter ranges, located to the southwest of Salt Lake City, UT (Olson 2013, Ditmer et al. 2021b). The study area falls under the management of UDWR's Central region (Utah Division of Wildlife Resources 2022) and Utah Department of Transportation (UDOT) regions 2 and 3 (Utah Department of Transportation 2022). Mule deer in this region are overseen following UDWR herd unit management plans 18, 19, and 21 (Utah Division of Wildlife Resources 2014a, 2014b, 2020).

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Determining Seasonal Home Ranges

We defined two distinct migration seasons for our analyses using net squared displacement with package 'amt' (Signer et al. 2019). Visual inspection of net squared displacement patterns revealed deer moved to their summer ranges around mid-April and returned to their winter ranges around mid-October. We split the deer GPS points into groups based on these seasonal divisions for each year of the study (2012 – 2018). For each individual, we calculated a seasonal 95% kernel density home range for each year with 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 Utah road network 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 deer for crossing each year. Roads within these "available" areas were split into smaller "segments" for analysis using the 'wildxing' package (Bastille-Rousseau 2021) using a maximum length of 500m (minimum: < 1m; overall summer range mean: 238m; overall winter range mean: 218m).

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.

Following the method of Bastille-Rousseau et al. (2018), we calculated crossing intensity, a metric standardized among road segments that removes bias from unequal monitoring times for individual deer. Crossing intensity (C_s) for a particular road segment (s) is defined as (Equation 1):

Equation 1

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

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). The resulting value represents standardized crossing intensity for each road segment whereby monitoring time is explicitly considered in order to eliminate bias due to unequal sampling among individuals. We implemented this metric by adapting code from the 'wildxing' package (Bastille-Rousseau 2021).

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 below.

Landscape and Anthropogenic Factors

We hypothesized that a variety of landscape, land cover, anthropogenic factors, and road characteristics could influence mule deer road crossing behavior (Table 1). Spatially explicit artificial nightlight estimates were extracted from NASA's Black Marble product.

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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 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 not intersecting a road. To convert this to a measure of road density, the raster was aggregated to 1 km^2 such that each cell represented the proportion of each 1 km^2 cell with a road segment present.

Speed limit information, maintained by UDOT, 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 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 were obtained from USGS in raster format as a Digital Elevation Model (DEM) with a 30m spatial resolution. The terrain roughness index was then derived by taking the mean of the absolute differences between the elevation value of a cell

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and the value of its 8 neighboring cells using the function 'terrain' in package 'raster' (Hijmans 2021).

Snow cover data, defined as the percentage of each 500m cell covered by snow in an 8-day period, were 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 data we created year-specific mean NDVI seasonal composites (for summer and winter, as defined above).

Land cover data at a 30m spatial resolution were 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, horizontal vegetative thickness, and overall impacts to visibility that may influence deer road crossing decisions. Although our study period spans 2012 – 2018, we only used land cover data from 2016 in our analysis. After comparing NLCD values from 2011-2016 and 2011-2019 to assess change, we determined that the vast majority of pixels did not change values, and those that did primarily switched from shrub to open/natural or vice versa. Because only a small percentage of pixels meaningfully changed values (as we determined shrub to open/natural changes likely resulted from a change in categorization method) and since most

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changes did not involve developed landcover (urbanization), we elected to use 2016 NLCD data as representative of the entire study period.

Assessment of Spatial Scale

We used three candidate spatial scales for modeling mule deer road crossing decisions by extracting covariate values at three distinct buffer distances around each road segment. The first two distances were based on hourly and daily movement distances. We calculated the median hourly movement distance by using consecutive GPS locations within 3-hour intervals and calculating the median movement distance per hour across all individuals, which we found to be approximately 55 m. To calculate median daily movement, we calculated the distance between a given day's first GPS location for each individual and the next subsequent location occurring 24 hours later. The resulting median distance among locations of approximately 573 m represents a daily Euclidean distance, or daily displacement distance, which does not include movements among locations occurring throughout the day. We considered a third scale, a buffer distance of 20 m around each road segment, as a "roadside" or fine-scale distance representing the values of the variables immediately alongside the roads. 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 (Appendix S1: Figure S1). For the 20 m and 55 m buffer sizes, 1,000 points were sampled, and we sampled 10,000 points for the larger 573 m buffer size. See Appendix S1: Table S1 for a summary of the distribution of each covariate's summary values at the best model scale.

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Assessment of Crossing Times

In addition to analysis by season, we 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 (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 which features around segments influenced the probability a given segment was crossed. The second set of models used linear regression with a response variable of the crossing intensity among road segments crossed at least once by mule deer. Results from these models indicated what features influenced the intensity of crossing among crossed segments. For all models, we assessed the significance of each feature's relationship with the dependent variable using a threshold of $\alpha < 0.05$.

We examined our set of covariates for each combined season and time of day for correlation prior to modeling (Appendix S1: 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 calculated the centroid locations of the road segment crossings to assess spatial autocorrelation. This was done by constructing non-spatial models from which Moran's I could be calculated using the 'DHARMa' package (Hartig 2021). We found the set of segments crossed by deer were significantly spatially autocorrelated in the vast majority of the non-spatial models (Appendix S1: Table S3). Therefore we accounted for spatial autocorrelation in all models using the 'glmmTMB' package to fit mixed effects models with 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

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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 influencing the intensity of road crossings for all crossed segments, 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 by including natural cubic splines with 2 degrees of freedom via the 'splines' package (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

We used mule deer road mortality data from 2011 – 2018 from the State of Utah Wildlife-Vehicle Collision (WVC) Data Collector repository (Figure 1) 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

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with 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 (29.9%) or crepuscular periods (70.1%). No summer road crossings occurred at night. In the winter season, crossings (n = 21,215) occurred during the crepuscular periods (72.8%) or at night (27.2%), with no crossings during the day (Figure 2). When comparing road segments in the winter and summer ranges, we found that the winter ranges were more urban, at lower average elevations, had less rough terrain, had far more artificial nightlight, and had a greater number of both crossings and road mortalities (Appendix S1: Table S1). Mule deer road crossing decisions were most associated with the landscape and road characteristics within the daily median movement distance of 573 m from the crossing location (Appendix S1: Table S4).

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Anthropogenic Factors

Artificial nightlight had one of the largest effects on where mule deer chose to cross the road in both summer and winter (Figure 3A, Table 2). Deer generally avoided crossing the brightest road segments. This effect was strongest in darker periods, like night and crepuscular crossings (Figure 4). Despite this, nightlight level generally had no meaningful influence on the intensity of mule deer use among crossed segments (Table 3). There were two exceptions to this: during the winter crepuscular period, when deer surprisingly preferred the brighter segments out of those they crossed, and during the daytime in the summer, when it reduced intensity of use but would not have been visible, likely serving as a proxy for human activity. Nightlight level had a strong negative effect on the risk of deer road mortality, but the relationship had just enough variation that it was not significant. The effect of nightlight on mortality was much stronger in summer than in winter (Figure 3C, Table 4).

Higher speed limits only had a positive effect on mule deer road mortality events in the winter (Figure 3C, Figure 5, Table 4), despite being negatively associated with road crossings (Figure 3A, Table 2). Speed limit did not appear to alter crossing probability between times of day, with deer being more likely to cross lower speed limit roads at all times of day, particularly in 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 (Table 3).

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 and daytime in the summer (Figure 3B, Table 3), mule deer preferentially used road segments in areas with less rough terrain. Conversely, this was not the case during winter nighttime crossings (Figure 3B, Table 3), when deer strongly preferred road segments in areas of rougher terrain. However, this relationship was nonlinear, as deer tended to avoid crossing the roughest sections of road at night during winter (Figure 3B, Table 3). Despite its strong negative relationship with crossing intensity, terrain roughness had a smaller impact on the probability a road segment was crossed, reducing it in summer (Figure 3A, Table 2), and slightly reducing it in winter (Figure 3A, Table 2).

Mule deer were much more likely to cross road segments surrounded by a high proportion of 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 (Figure 3A, Figure 6, Table 2). In the summer months, the proportion of surrounding shrubland strongly decreased the probability of deer road mortality events (Figure 3C, Table 4), 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 (Figure 3B, Table 3).

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. Road segments surrounded by more agricultural land had a lower chance of mule deer road mortality in winter (Figure 3C, Table 4), but also had a lower chance a mule deer would cross at that segment (Figure 3A, Table 2). Additionally, in the summer daytime and crepuscular periods, mule deer intensity of use among crossed segments increased when surrounded by slightly less agricultural land (Figure 3B, Table 3), but it was not a significant factor during the winter.

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Surrounding open or natural land had a significant positive impact on which roads mule deer chose to cross in the summer crepuscular periods (Figure 3A, Table 2) but conversely a negative impact during the winter night periods (Figure 3A, Table 2). It also had a positive effect on the intensity of crepuscular use among crossed roads in both seasons and a small negative effect on daytime use in the summer (Figure 3B, Table 3).

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 (Figure 3A, Table 2) but a generally negative impact on intensity of winter crepuscular use among crossed roads (Figure 3B, Table 3). The relationship was non-linear, with the lowest intensity of use correlating with high snow cover, but higher intensity of use related to increasing snow cover (Figure 3B, Table 3).

NDVI, or vegetative greenness, had a strong positive relationship with summer crossing intensity (Figure 3B, Table 3), though began to saturate at higher crossing intensity values. It also had a positive relationship with winter nighttime crossing intensity (Figure 3B, Table 3). While NDVI also had a positive effect on which roads deer chose to cross in summer (Figure 3A, Table 2), 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 (Figure 3A, Table 2).

Discussion

We investigated how artificial nightlight—a pervasive and expanding environmental pollutant—affects patterns of road crossings and mortalities for mule deer. Our analysis led to four main insights. First, mule deer greatly preferred crossing roads where artificial

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nightlight levels were lower, but this also increased their road mortality risk. Second, although mule deer preferred to avoid crossing higher speed roads, their winter ranges were bisected by highways that increased their mortality risk when they inevitably tried to cross. Third, the proximity of mule deer winter ranges to increased human activity augmented the risks associated with their preference for dark roads and exposed them to higher speed roads that were more dangerous to cross. Finally, mule deer were more likely to cross roads surrounded by their preferred habitat, and in contrast to other species of deer in the forested eastern United States, this actually reduced their mortality risk. Similar to findings by Neumann et al. (2012), we found differences between the factors associated with increased mortality and increased use of road segments.

Artificial nightlight had a strong influence on mule deer road crossing behavior. During the crepuscular periods of both seasons and winter nights mule deer were most likely to cross roads where nightlight levels were low. Similarly, Bliss-Ketchum et al. (2016) found that a subspecies of mule deer (Columbia black-tailed deer, *Odocoileus hemionus columbianus*) also avoided using artificially lit areas at fine spatial scales. Given this, it would seem that reducing artificial nightlight levels would aid mule deer by improving landscape connectivity and habitat suitability of areas bisected by roads. However, the associated increase in mortality risk must also be considered. While deer generally chose the darkest locations to cross, they were also more likely to be involved in fatal collisions in these areas as they were harder for drivers to see at distances that could prevent collisions. Other studies support this finding: factors that reduce motorist visibility, such as road sinuosity or forest cover, are closely tied to the risk of WVCs by influencing driver reaction times (Gunson et al. 2011, Laliberté and St-Laurent 2020). Future studies could investigate

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whether strategically increasing light on problematic road segments and decreasing it on others would be effective at reducing WVCs while providing safer movement paths for wildlife that prefer darkness.

Mule deer also preferred to cross roads with lower speed limits across seasons, though this preference was only about half as strong in winter. In the summer, deer could more easily avoid high speed roads and highways because the studied population spends its summers high in the mountains where overall road density is low. As the winter range is more urban, there is both a higher density of low speed limit roads to cross and increased contact with the highways that bisect the region. This meant deer could not always preferentially avoid crossing high speed roads and faced greater morality risk. Our 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, Jacobson et al. 2016, Garrote et al. 2018, Zeller et al. 2018, Pagany 2020). Speed limit is positively associated with another commonly examined variable: annual average daily traffic (AADT) volume. Although AADT data were incomplete across our study area, it is widely cited as influencing the extent to which roads act as barriers and increasing the risk of WVCs (Gagnon et al. 2007, Gunson et al. 2011, Coe et al. 2015, Cramer et al. 2019, Pagany 2020). Therefore, it is possible that the increase in risk associated with higher speed limits in winter is reinforced by exposure to higher traffic volumes, which previous studies have linked to road mortality (van Langevelde and Jaarsma 2005, Abraham and Mumma 2021).

Noticeably, there seemed to be a deadly winter combination of mule deer preference for dark roads, increased proximity to higher speed roads, and human activity. Compounding on these characteristics, winter also brings both shorter daylight hours, with deer attempting a

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higher number of crossings at night, and the increase in deer activity and risk-taking behavior associated with the breeding season (Foley et al. 2015). Cunningham et al. (2022) found a similar winter spike in deer-vehicle collisions. They attributed this in large part to the increase in traffic volume after dark that is exacerbated by the end of daylight savings time, which aligns peak rush hour traffic flow with darkness (Cunningham et al. 2022). Our analyses also demonstrate a five-fold increase in mortality events in winter as compared to summer, supporting the findings of Cunningham et al. (2022). Deer preference for the darkest available roads during the darkest time of year, combined with their seasonal migration to ranges overlapping with human activity, helps explain this seasonal spike in WVCs during the winter period. Instituting permanent daylight savings time could mitigate some winter collision risk on high speed or dark roads by divorcing traffic volume from times of increased deer road crossing behavior (Cunningham et al. 2022).

Mule deer were, perhaps unsurprisingly, more likely to cross roads that were surrounded by shrub cover given their association with shrub and scrub plant communities in the region (Utah Division of Wildlife Resources 2019a). However, shrub cover also strongly decreased the chance a given road segment would have mortality events associated with it, particularly in the summer. This finding contrasts with a review of WVC characteristics by Gunson et al. (2011), who found WVCs commonly took place where roads bisected favorable cover or conventional foraging habitat for a species. These differences can likely be explained by variation in preferred habitat across species and regions and subsequent variation in the effects on motorist visibility. For example, while mule deer may prefer crossing roads surrounded by shrub cover, white-tailed deer (*Odocoileus virginianus*) prefer

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crossing near forest cover, where trees reduce visibility and the increase in crossings leads to increased mortality (Nielsen et al. 2003, Ng et al. 2008).

The presence of predators or the perceived risk of predation, particularly from cougars (*Puma concolor*), may also influence mule deer movement and behavior. Cougars are the primary predator of mule deer, even in the urban-wildland interface (Ditmer et al. 2021b, Stoner et al. 2021). Deer in this region may use areas with more human activity and higher nightlight levels not only for forage, but also to avoid higher predation pressure just outside of more urbanized areas (Ditmer et al. 2021b, Stoner et al. 2021). In this case, increased urbanization, nightlight, and road density could act as a predator shield (Berger 2007) for the deer, though research has shown cougars will still follow and hunt deer up to a point in the urbanization and nightlight gradient (Ditmer et al. 2021b). Cougar presence, movement, or mule deer predation locations could therefore be relevant factors that future researchers may wish to explore.

It is important to note that the mortality data used in our study were collected by contractors along a small number of collection routes (primarily highways), thus limiting our causal inferences. The actual number of collisions with deer resulting in animal mortality is likely much higher and occurs across a greater diversity of road types. While some studies, such as by Snow et al. (2015), claim 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. 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.

Our findings add support to 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 help reduce the risks associated with low driver visibility, short stopping distances, and increased deer presence. UDWR has already identified and categorized mule deer habitat 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 habitats.

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 cross at other sections. Our findings also support 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 and would correlate well with observed mule deer activity periods and seasonal fluctuations in risk. Wildlife crossing structures with fencing are the most expensive, but also most effective way to reduce collisions and increase landscape connectivity for mule deer, in some cases

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reducing collisions by more than 80% (Sawyer et al. 2012). Utilizing crossing structures in combination with artificial light and speed limit adjustments on high use or high risk road segments could help maximize their benefits to wildlife and drivers. Finally, our findings suggest that managers and researchers should not underestimate the impact of artificial nightlight on habitat connectivity, use, and selection by wildlife species (Ditmer et al. 2021a). Artificial nightlight could be a powerful tool for encouraging or discouraging movement through certain spaces and roadways, particularly in high mortality risk locations and time periods.

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DATA AVAILABILITY STATEMENT

Data used in the final models (Frank et al. 2023) are available from Figshare https://doi.org/10.6084/m9.figshare.22310314.v1. Novel code (Bastille-Rousseau 2018) is available from Zenodo: https://doi.org/10.5281/zenodo.115870.

References

Abraham, J. O., and M. A. Mumma. 2021. Elevated wildlife-vehicle collision rates during the COVID-19 pandemic. Scientific Reports 2021 11:1 11:1–10.

Bastille-Rousseau, G. 2018. BastilleRousseau/wildxing: First release of wildxing (v1.0). Zenodo. https://doi.org/10.5281/zenodo.1158705

Bastille-Rousseau, G. 2021. wildxing: An R package for optimal positioning of widlife crossing structures.

Bastille-Rousseau, G., J. Wall, I. Douglas-Hamilton, and G. Wittemyer. 2018. Optimizing the positioning of wildlife crossing structures using GPS telemetry. Journal of Applied Ecology 55:2055–2063.

Bedrosian, T. A., L. K. Fonken, J. C. Walton, A. Haim, and R. J. Nelson. 2011. Dim light at night provokes depression-like behaviors and reduces CA1 dendritic spine density in female hamsters. Psychoneuroendocrinology 36:1062–1069.

Bencin, H. L., S. Prange, C. Rose, and V. D. Popescu. 2019. Roadkill and space use data predict vehicle-strike hotspots and mortality rates in a recovering bobcat (Lynx rufus) population. Scientific Reports 9.

Bennie, J., T. W. Davies, D. Cruse, R. Inger, and K. J. Gaston. 2015. Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. Philosophical Transactions of the Royal Society B: Biological Sciences 370:20140131.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Bivand, R., and N. Lewin-Koh. 2021. maptools: Tools for Handling Spatial Objects.

Bivand, R., and C. Rundel. 2021. rgeos: Interface to Geometry Engine - Open Source ('GEOS’).

Bivand, R. S., E. Pebesma, and V. Gomez-Rubio. 2013. Applied spatial data analysis with R. 2nd edition. Springer, Springer, NY.

Bliss-Ketchum, L. L., C. E. de Rivera, B. C. Turner, and D. M. Weisbaum. 2016. The effect of artificial light on wildlife use of a passage structure. Biological Conservation 199:25–28.

Bozdogan, H. 1987. Model selection and Akaike’s Information Criterion (AIC): The general theory and its analytical extensions. Psychometrika 1987 52:3 52:345–370.

Brooks, M. E., K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Maechler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Cabrera-Cruz, S. A., J. A. Smolinsky, and J. J. Buler. 2018. Light pollution is greatest within migration passage areas for nocturnally-migrating birds around the world. Scientific Reports 2018 8:1 8:1–8.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

Ciach, M., and A. Fröhlich. 2019. Ungulates in the city: light pollution and open habitats predict the probability of roe deer occurring in an urban environment. Urban Ecosystems 22:513–523.

Author Manuscript

Author Manuscript

Coe, P. K., R. M. Nielson, D. H. Jackson, J. B. Cupples, N. E. Seidel, B. K. Johnson, S. C. Gregory, G. A. Bjornstrom, A. N. Larkins, and D. A. Speten. 2015. Identifying migration corridors of mule deer threatened by highway development. Wildlife Society Bulletin 39:256–267.

Cox, D. T. C., A. Sánchez de Miguel, J. Bennie, S. A. Dzurjak, and K. J. Gaston. 2022. Majority of artificially lit Earth surface associated with the non-urban population. Science of The Total Environment 841:156782.

Cramer, Patricia, Vásquez, Emanuel, Jones, and Allison. 2019. Identification of Wildlife-Vehicle Conflict Hotspots in Utah.

Cunningham, C. X., T. A. Nuñez, Y. Hentati, B. Sullender, C. Breen, T. R. Ganz, S. E. S. Kreling, K. A. Shively, E. Reese, J. Miles, and L. R. Prugh. 2022. Permanent daylight saving time would reduce deer-vehicle collisions. Current Biology.

Didan, K. 2015. MOD13Q1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SIN Grid V006. NASA EOSDIS Land Processes DAAC.

Ditmer, M. A., S. J. Rettler, J. R. Fieberg, P. A. Iaizzo, T. G. Laske, K. v. Noyce, and D. L. Garshelis. 2018. American black bears perceive the risks of crossing roads. Behavioral Ecology 29:667–675.

Ditmer, M. A., D. C. Stoner, and N. H. Carter. 2021a. Estimating the loss and fragmentation of dark environments in mammal ranges from light pollution. Biological Conservation 257.

Ditmer, M. A., D. C. Stoner, C. D. Francis, J. R. Barber, J. D. Forester, D. M. Choate, K. E. Ironside, K. M. Longshore, K. R. Hersey, R. T. Larsen, B. R. McMillan, D. D. Olson, A. M. Andreasen, J. P. Beckmann, P. B. Holton, T. A. Messmer, and N. H. Carter. 2021b. Artificial nightlight alters the predator–prey dynamics of an apex carnivore. Ecography 44:149–161.

Eckrich, C. A., P. K. Coe, D. A. Clark, R. M. Nielson, J. Lombardi, S. C. Gregory, M. J. O. Hedrick, B. K. Johnson, and D. W. H. Jackson. 2020. Summer Habitat Use of Female Mule Deer in Oregon. Journal of Wildlife Management 84:576–587.

Fahrig, L., and T. Rytwinski. 2009. Effects of Roads on Animal Abundance: an Empirical Review and Synthesis. Ecology and Society 14.

Foley, A. M., R. W. Deyoung, D. G. Hewitt, M. W. Hellickson, K. L. Gee, D. B. Wester, M. A. Lockwood, and K. v. Miller. 2015. Purposeful wanderings: mate search strategies of male white-tailed deer. Journal of Mammalogy 96:279–286.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst 29:207–238.

Forman, R. T. T., and R. D. Deblinger. 2000. The Ecological Road-Effect Zone of a Massachusetts (U.S.A.) Suburban Highway. Conservation Biology 14:36–46.

Frank, K. M., M. A. Ditmer, D. C. Stoner, W. S. Currie, D. D. Olson, and N. H. Carter. 2023. Dark roads aid movement but increase mortality of a generalist herbivore in the American Southwest. figshare. Dataset. https://doi.org/10.6084/m9.figshare.22310314.v1 .

Fraser, D. L., K. Ironside, R. K. Wayne, and E. E. Boydston. 2019. Connectivity of mule deer (Odocoileus hemionus) populations in a highly fragmented urban landscape. Landscape Ecology 34:1097–1115.

Author Manuscript

Gagnon, J. W., T. C. Theimer, N. L. Dodd, S. Boe, and R. E. Schweinsburg. 2007. Traffic Volume Alters Elk Distribution and Highway Crossings in Arizona. Journal of Wildlife Management 71:2318.

Garrote, G., J. Fernández-López, G. López, G. Ruiz, and M. A. Simón. 2018. Prediction of iberian lynx road–mortality in southern Spain: A new approach using the MaxEnt algorithm. Animal Biodiversity and Conservation 41:217–225.

Gaston, K. J. 2018. Lighting up the nighttime. Science 362:744–746.

Gaston, K. J., T. W. Davies, J. Bennie, and J. Hopkins. 2012. REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. Journal of Applied Ecology 49:1256–1266.

Gaston, K. J., J. P. Duffy, S. Gaston, J. Bennie, and T. W. Davies. 2014. Human alteration of natural light cycles: causes and ecological consequences. Oecologia 176:917–931.

Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2011. Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. Journal of Environmental Management 92:1074–1082.

Hall, D. K., and G. A. Riggs. 2016. MODIS/Terra snow cover daily L3 global 500m grid (ver. 6.0): National Snow and Ice Data Center Data Set MOD10A2. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado.

Hartig, F. 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hijmans, R. J. 2021. raster: Geographic Data Analysis and Modeling.

Hill, J. E., T. L. DeVault, and J. L. Belant. 2020. Research note: A 50-year increase in vehicle mortality of North American mammals. Landscape and Urban Planning 197.

Hoffmann, J., F. Hölker, and J. A. Eccard. 2022. Welcome to the Dark Side: Partial Nighttime Illumination Affects Night-and Daytime Foraging Behavior of a Small Mammal. Frontiers in Ecology and Evolution 9:940.

Jacobson, S. L., L. L. Bliss-Ketchum, C. E. de Rivera, and W. P. Smith. 2016. A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere 7:e01345.

Kantola, T., J. L. Tracy, K. A. Baum, M. A. Quinn, and R. N. Coulson. 2019. Spatial risk assessment of eastern monarch butterfly road mortality during autumn migration within the southern corridor. Biological Conservation 231:150–160.

Kyba, C. C. M., T. Kuester, A. S. de Miguel, K. Baugh, A. Jechow, F. Hölker, J. Bennie, C. D. Elvidge, K. J. Gaston, and L. Guanter. 2017. Artificially lit surface of Earth at night increasing in radiance and extent. Science Advances 3.

Laliberté, J., and M. H. St-Laurent. 2020. In the wrong place at the wrong time: Moose and deer movement patterns influence wildlife-vehicle collision risk. Accident Analysis and Prevention 135.

van Langevelde, F., and C. F. Jaarsma. 2005. Using traffic flow theory to model traffic mortality in mammals. Landscape Ecology 19.

McDonald, M. G. 1991. Moose movement and mortality associated with the Glenn Highway expansion, Anchorage Alaska. Alces: A Journal Devoted to the Biology and Management of Moose 27:208–219.

Author Manuscript

Meisingset, E. L., L. E. Loe, Ø. Brekkum, B. van Moorter, and A. Mysterud. 2013. Red deer habitat selection and movements in relation to roads. Journal of Wildlife Management 77:181–191.

Meisingset, E. L., L. E. Loe, Ø. Brekkum, and A. Mysterud. 2014. Targeting mitigation efforts: The role of speed limit and road edge clearance for deer-vehicle collisions. The Journal of Wildlife Management 78.

National Park Service. 2010. NPScape housing measure – Phase 1 metrics processing SOP: Current housing density, historic housing density, and projected housing density metrics (Natural Resource Report. NPS/NRPC/IMD/NRR—2010/251. Published Report-2165448.).

Neumann, W., G. Ericsson, H. Dettki, N. Bunnefeld, N. S. Keuler, D. P. Helmers, and V. C. Radeloff. 2012. Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. Biological Conservation 145:70–78.

Neumann, W., G. Ericsson, H. Dettki, and V. C. Radeloff. 2013. Behavioural response to infrastructure of wildlife adapted to natural disturbances. Landscape and Urban Planning 114:9–27.

Ng, J. W., C. Nielson, C. Cassady, and S. Clair. 2008. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. Human-Wildlife Conflicts 2:34–47.

Nielsen, C. K., R. G. Anderson, and M. D. Grund. 2003. Landscape Influences on Deer-Vehicle Accident Areas in an Urban Environment. The Journal of Wildlife Management 67:46.

Olson, D. D. 2013. Assessing Vehicle-Related Mortality of Mule Deer in Utah. Utah State University.

Olson, D. D., J. A. Bissonette, P. C. Cramer, K. D. Bunnell, D. C. Coster, and P. J. Jackson. 2015. How does variation in winter weather affect deer-vehicle collision rates? Wildlife Biology 21:80–87.

Ouyang, J. Q., M. Jong, R. H. A. Grunsven, K. D. Matson, M. F. Haussmann, P. Meerlo, M. E. Visser, and K. Spoelstra. 2017. Restless roosts: Light pollution affects behavior, sleep, and physiology in a free-living songbird. Global Change Biology 23:4987–4994.

Pagany, R. 2020. Wildlife-vehicle collisions - Influencing factors, data collection and research methods. Biological Conservation 251:108758.

Pebesma, E. J., and R. S. Bivand. 2005. Classes and methods for spatial data in R. R News 5.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, D. F., and T. N. Woodard. 1981. Effectiveness of Highway Lighting in Reducing Deer-Vehicle Accidents. The Journal of Wildlife Management 45:721.

Riginos, C., E. Fairbank, E. Hansen, J. Kolek, and M. P. Huijser. 2022. Reduced speed limit is ineffective for mitigating the effects of roads on ungulates. Conservation Science and Practice 4.

Román, M. O., Z. Wang, Q. Sun, V. Kalb, S. D. Miller, A. Molthan, L. Schultz, J. Bell, E. C. Stokes, B. Pandey, K. C. Seto, D. Hall, T. Oda, R. E. Wolfe, G. Lin, N. Golpayegani, S. Devadiga, C. Davidson, S. Sarkar, C. Praderas, J. Schmaltz, R. Boller, J. Stevens, O. M. Ramos González, E. Padilla, J. Alonso, Y. Detrés, R.

Author Manuscript

Armstrong, I. Miranda, Y. Conte, N. Marrero, K. MacManus, T. Esch, and E. J. Masuoka. 2018. NASA's Black Marble nighttime lights product suite. Remote Sensing of Environment 210:113–143.

Sánchez de Miguel, A., J. Bennie, E. Rosenfeld, S. Dzurjak, and K. J. Gaston. 2022. Environmental risks from artificial nighttime lighting widespread and increasing across Europe. Science Advances 8:eabl6891.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. Conservation Biology 5:18–32.

Sawyer, H., M. J. Kauffman, R. M. Nielson, and J. S. Horne. 2009. Identifying and prioritizing ungulate migration routes for landscape-level conservation. Ecological Applications 19:2016–2025.

Schwab, A. C., and P. A. Zandbergen. 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Applied Geography 31:859–870.

Shier, D. M., A. K. Bird, and T. B. Wang. 2020. Effects of artificial light at night on the foraging behavior of an endangered nocturnal mammal. Environmental Pollution 263:114566.

Signer, J., J. Fieberg, and T. Avgar. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecology and Evolution 9.

Stoner, D. C., M. A. Ditmer, D. L. Mitchell, J. K. Young, and M. L. Wolfe. 2021. Conflict, coexistence, or both? Cougar habitat selection, prey composition, and mortality in a multiple-use landscape. California Fish and Wildlife Journal 107:147–172.

Theobald, D. M. 2005. Landscape Patterns of Exurban Growth in the USA from 1980 to 2020. Ecology and Society 10.

Tiwari, A., and J. W. Rachlin. 2018. A Review of Road Salt Ecological Impacts. Northeastern Naturalist 25:123–142.

Touzot, M., L. Teulier, T. Lengagne, J. Secondi, M. Théry, P.-A. Libourel, L. Guillard, and N. Mondy. 2019. Artificial light at night disturbs the activity and energy allocation of the common toad during the breeding period. Conservation Physiology 7.

United States Census Bureau. 2020. Southern and Western Regions Experienced Rapid Growth This Decade.

U.S. Geological Survey. 2016. NLCD 2016 Land Cover (CONUS). https://www.mrlc.gov/data/nlcd-2016-land-cover-conus.

U.S. Geological Survey. 2019. USGS Digital Elevation Model 1 arc-second (30 m) GeoTiff.

U.S. Geological Survey. 2021, November 15. USGS National Transportation Dataset (NTD) for Utah 20211115 State or Territory Shapefile . U.S. Geological Survey, National Geospatial Technical Operations Center.

Utah Department of Transportation. 2022. About UDOT. https://www.udotauctions.utah.gov/about-udot.

Utah Division of Wildlife Resources. 2014a. Mule Deer Herd Unit Management Plan Deer Herd Unit #18.

Utah Division of Wildlife Resources. 2014b. Mule Deer Herd Unit Management Plan Deer Herd Unit #19.

Author Manuscript

Utah Division of Wildlife Resources. 2019. Utah Mule Deer Statewide Management Plan.

Utah Division of Wildlife Resources. 2020. Mule Deer Herd Unit Management Plan Deer Herd Unit #21.

Utah Division of Wildlife Resources. 2021, June 14. Utah Mule Deer Habitat. Utah's State Geographic Information Database (AGRC).

Utah Division of Wildlife Resources. 2022. DWR Administrative Regions. https://utahdnr.maps.arcgis.com/apps/Viewer/index.html?appid=b9e43f4b50ea4c4c932f2c3d17593e69.

Utah Geospatial Resource Center. 2021. Road Centerlines. Utah Geospatial Resource Center.

Yorzinski, J. L., S. Chisholm, S. D. Byerley, J. R. Coy, A. Aziz, J. A. Wolf, and A. C. Gnerlich. 2015. Artificial light pollution increases nocturnal vigilance in peahens. PeerJ 2015:e1174.

Zeller, K. A., D. W. Wattles, and S. DeStefano. 2018. Incorporating Road Crossing Data into Vehicle Collision Risk Models for Moose (Alces americanus) in Massachusetts, USA. Environmental Management 62:518–528.

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

Variable	Short Name	Description	Derived from
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 $100m^2$ 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 $50m^2$ 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	Seg. 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	Terr. 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

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Table 2: Model coefficients ($\hat{\beta}$) and 95% confidence intervals for summer (day, crepuscular) and winter (crepuscular, night) road crossing probability at a scale of 573 m.

Variable	**Summer**				**Winter**			
	Day		**Crepuscular**		**Crepuscular**		**Night**	
	$\hat{\boldsymbol{\beta}}$	**95% CI**	$\hat{\boldsymbol{\beta}}$	**95% CI**	$\hat{\boldsymbol{\beta}}$	**95% CI**	$\hat{\boldsymbol{\beta}}$	**95% CI**
Artificial Nightlight	-0.17	-0.39, 0.05	**-0.60**	**-0.82, -0.39**	**-0.29**	**-0.42, -0.16**	**-0.32**	**-0.47, -0.17**
Speed Limit	**-0.14**	**-0.21, -0.06**	**-0.19**	**-0.25, -0.12**	**-0.06**	**-0.11, -0.01**	**-0.07**	**-0.14, -0.01**
Terrain Roughness	**-0.32**	**-0.45, -0.19**	**-0.13**	**-0.24, -0.03**	**-0.05**	**-0.09, -0.01**	-0.03	-0.08, 0.02
Shrubland	**0.92**	**0.78, 1.07**	**0.80**	**0.67, 0.92**	**0.66**	**0.59, 0.73**	**0.56**	**0.48, 0.64**
Agriculture	0.05	-0.04, 0.14	-0.04	-0.13, 0.04	**-0.21**	**-0.34, -0.08**	**-0.43**	**-0.60, -0.26**
Open/Natural	0.06	-0.04, 0.17	**0.11**	**0.02, 0.20**	0.03	-0.02, 0.09	**-0.16**	**-0.23, -0.09**
Snow Cover	-	-	-	-	**0.13**	**0.07, 0.18**	0.05	-0.02, 0.13
NDVI	**0.20**	**0.07, 0.32**	0.08	-0.02, 0.19	**-0.21**	**-0.27, -0.14**	**-0.22**	**-0.29, -0.14**

Note: Statistically significant values appear in boldface.

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Table 3: Model coefficients ($\hat{\beta}$) and 95% confidence intervals for summer (day, crepuscular) and winter (crepuscular, night) road crossing intensity at a scale of 573 m.

Variable	**Summer**				**Winter**			
	Day		**Crepuscular**		**Crepuscular**		**Night**	
	$\hat{\beta}$	**95% CI**	$\hat{\beta}$	**95% CI**	$\hat{\beta}$	**95% CI**	$\hat{\beta}$	**95% CI**
Artificial Nightlight 1	**-1.46**	**-1.97, -0.94**	0.08	-0.40, 0.56	0.73	0.39, 1.07	0.07	-0.83, 0.97
Artificial Nightlight 2	**-0.72**	**-1.32, -0.12**	0.06	-0.79, 0.91	0.15	-0.28, 0.58	-0.28	-1.20, 0.63
Speed Limit 1	-0.09	-0.82, 0.63	-0.16	-0.83, 0.51	-0.10	-0.45, 0.26	-0.30	-0.70, 0.11
Speed Limit 2	-0.31	-0.76, 0.14	-0.20	-0.62, 0.22	-0.17	-0.41, 0.07	-0.16	-0.43, 0.10
Terrain Roughness 1	**-0.73**	**-1.25, -0.21**	**-0.75**	**-1.19, -0.32**	**-0.09**	**-0.37, 0.19**	**0.77**	**0.18, 1.37**
Terrain Roughness 2	**-0.72**	**-1.39, -0.04**	**-0.73**	**-1.32, -0.14**	**-0.82**	**-1.37, -0.27**	**-0.18**	**-0.76, 0.40**
Shrubland	-0.06	-0.15, 0.04	**0.20**	**0.12, 0.28**	**0.18**	**0.12, 0.25**	0.01	-0.11, 0.13
Agriculture	**-0.08**	**-0.14, -0.02**	**-0.06**	**-0.12, -0.00**	-0.01	-0.05, 0.03	-0.01	-0.07, 0.05
Open/Natural	**-0.07**	**-0.14, -0.00**	**0.13**	**0.07, 0.19**	**0.11**	**0.06, 0.16**	0.06	-0.03, 0.15
Snow Cover 1	...	...	...	…	**-0.40**	**-0.71, -0.09**	-0.05	-0.45, 0.35
Snow Cover 2	...	...	...	…	**0.27**	**-0.03, 0.57**	0.23	-0.11, 0.57
NDVI 1	**1.60**	**0.40, 2.81**	**1.09**	**0.61, 1.56**	0.06	-0.40, 0.53	**0.57**	**-0.09, 1.24**
NDVI 2	**0.49**	**-0.58, 1.56**	**0.34**	**-0.18, 0.85**	0.16	-0.19, 0.50	**0.45**	**0.00, 0.89**

Note: Statistically significant values appear in boldface. Because the crossing intensity models used natural cubic splines, some covariates are reported with a “1” or “2” following the variable name, as two coefficients were returned; if one of these two values was found to be significant, the variable was considered significant.

Table 4: Model coefficients ($\hat{\beta}$) and 95% confidence intervals for summer and winter road mortality probability at a scale of 573 m.

Variable	**Summer**		**Winter**	
	$\hat{\beta}$	**95% CI**	$\hat{\beta}$	**95% CI**
Artificial Nightlight	-0.53	-1.07, 0.01	-0.21	-0.43, 0.01
Speed Limit	0.15	-0.25, 0.55	**0.17**	**0.01, 0.33**
Terrain Roughness	-0.03	-0.62, 0.56	-0.01	-0.16, 0.14
Shrubland	**-0.78**	**-1.37, -0.20**	0.02	-0.18, 0.22
Agriculture	-0.10	-0.42, 0.21	**-0.25**	**-0.43, -0.06**
Open/Natural	-0.16	-0.58, 0.26	-0.06	-0.21, 0.10
Snow Cover	...	...	-0.02	-0.17, 0.14
NDVI	-0.13	-0.77, 0.52	-0.10	-0.29, 0.09

Note: Statistically significant values appear in boldface.

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Figure 1: a) Study area location relative to 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 overlaid on the road network and elevation data for the region. b) Mule deer carcass locations as reported by state contractors to the UDWR within our study area boundaries from 2011 – 2018, shown over road and elevation data.

Figure 2: 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.

Figure 3: 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. Red dashed line at x = 0 highlights the transition between positive and negative estimated coefficients. 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 4: Modeled relationship (solid line) and 95% confidence interval (dashed lines) 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.

Figure 5: Modeled relationship (solid line) and 95% confidence interval (dashed lines) between a road segment's speed limit (scaled and centered) and the probability that at least

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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.

Figure 6: Modeled relationship (solid line) and 95% confidence interval (dashed lines) between the proportion of shrubland (scaled and centered) within a 573 m 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.

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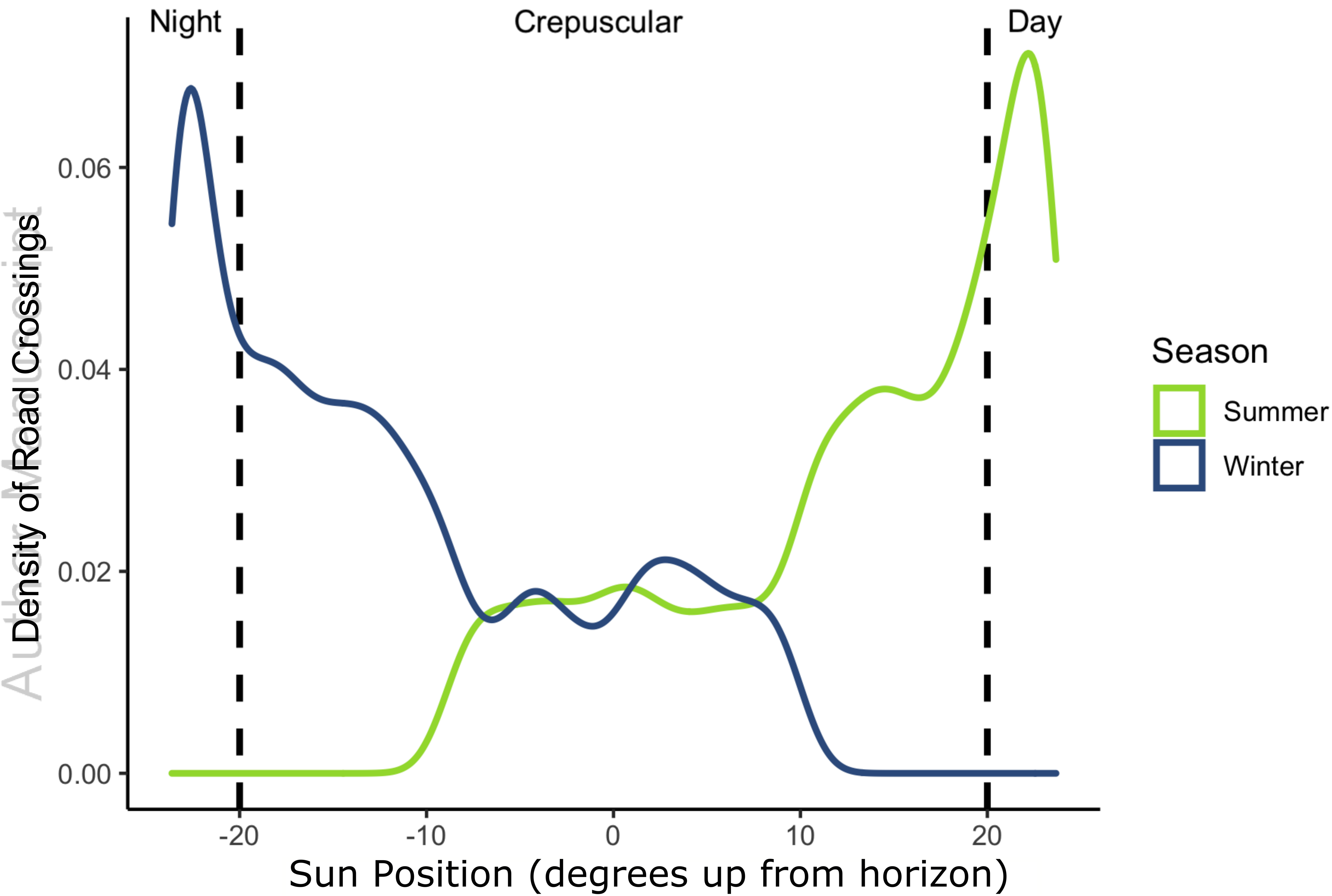

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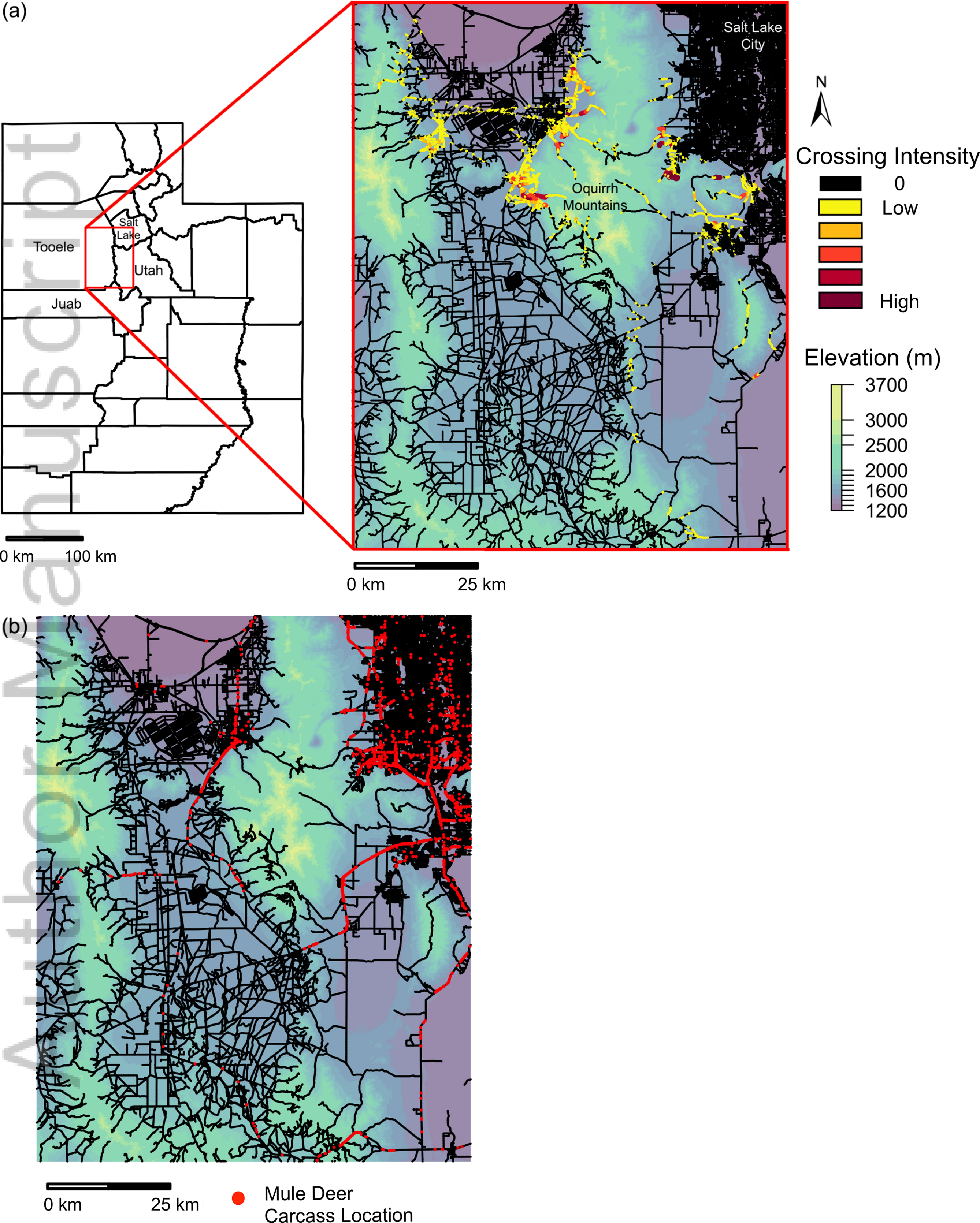

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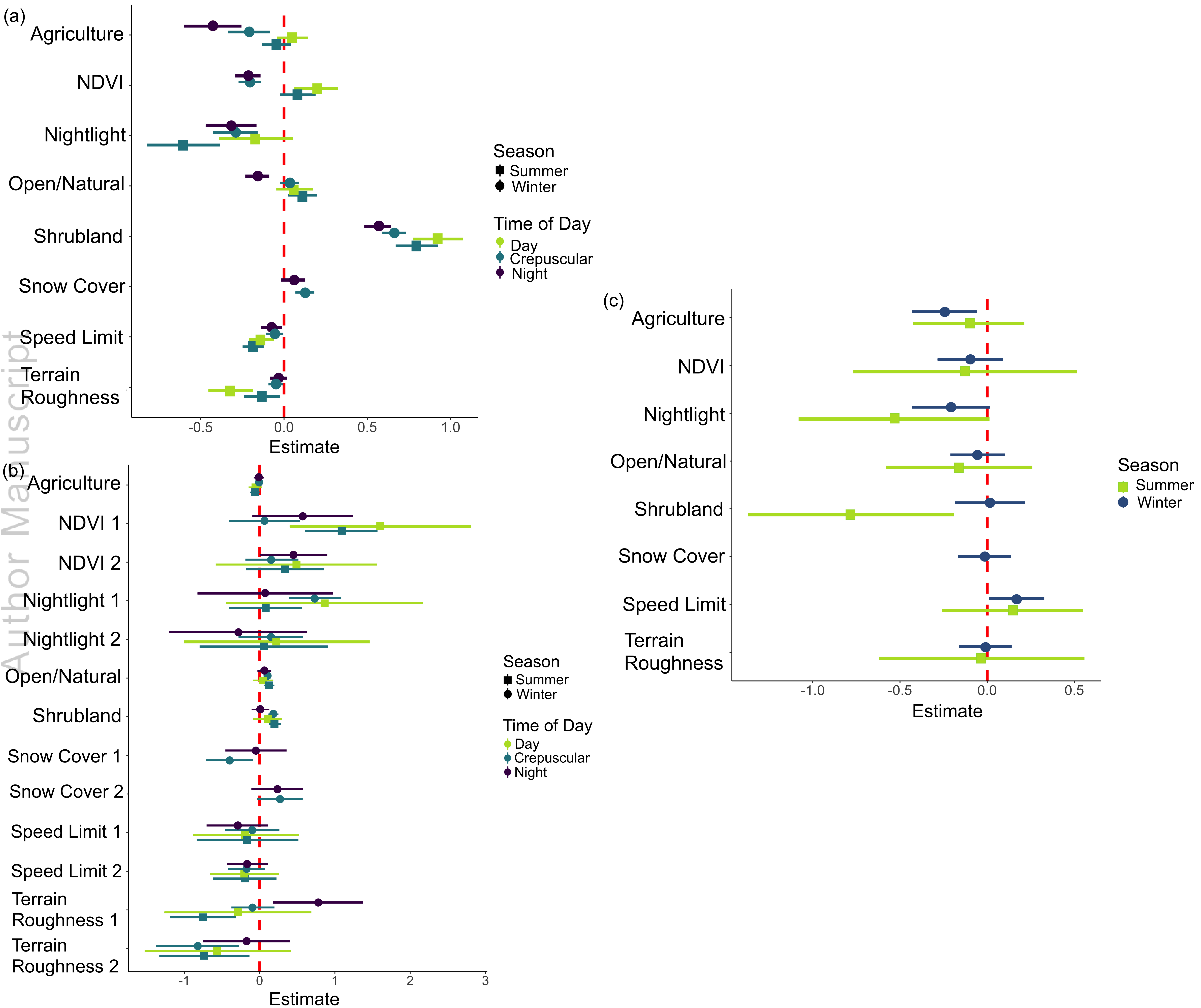

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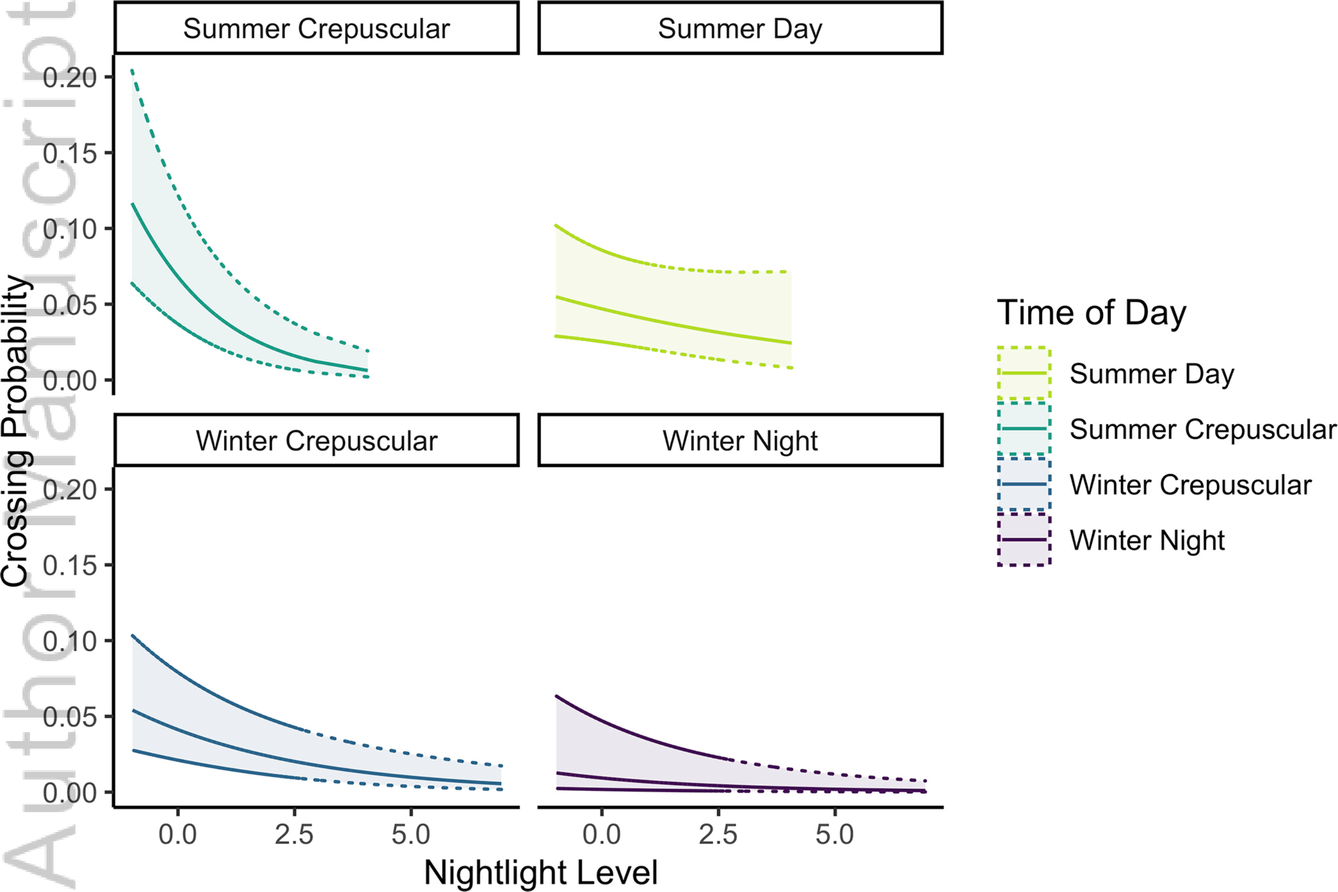

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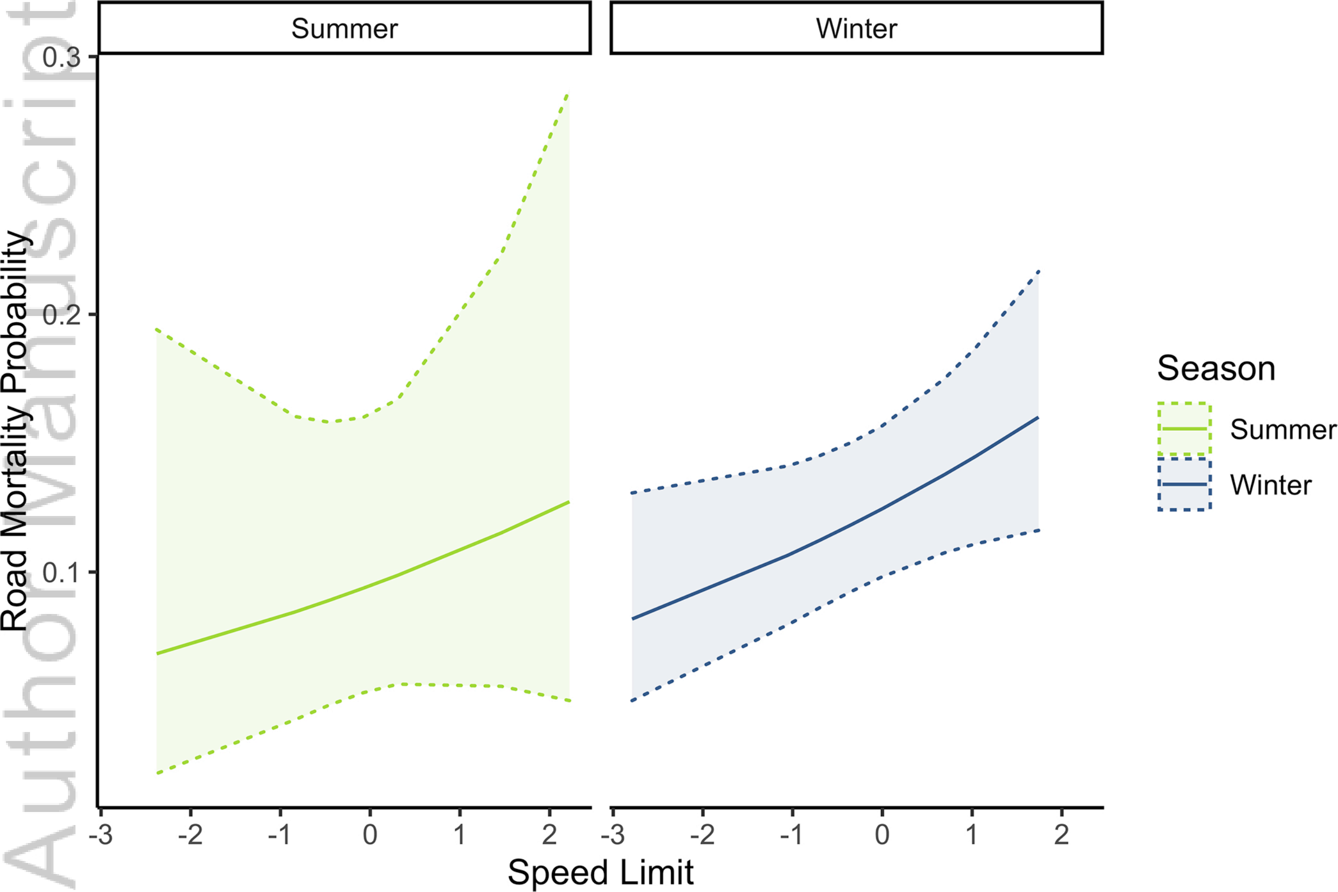

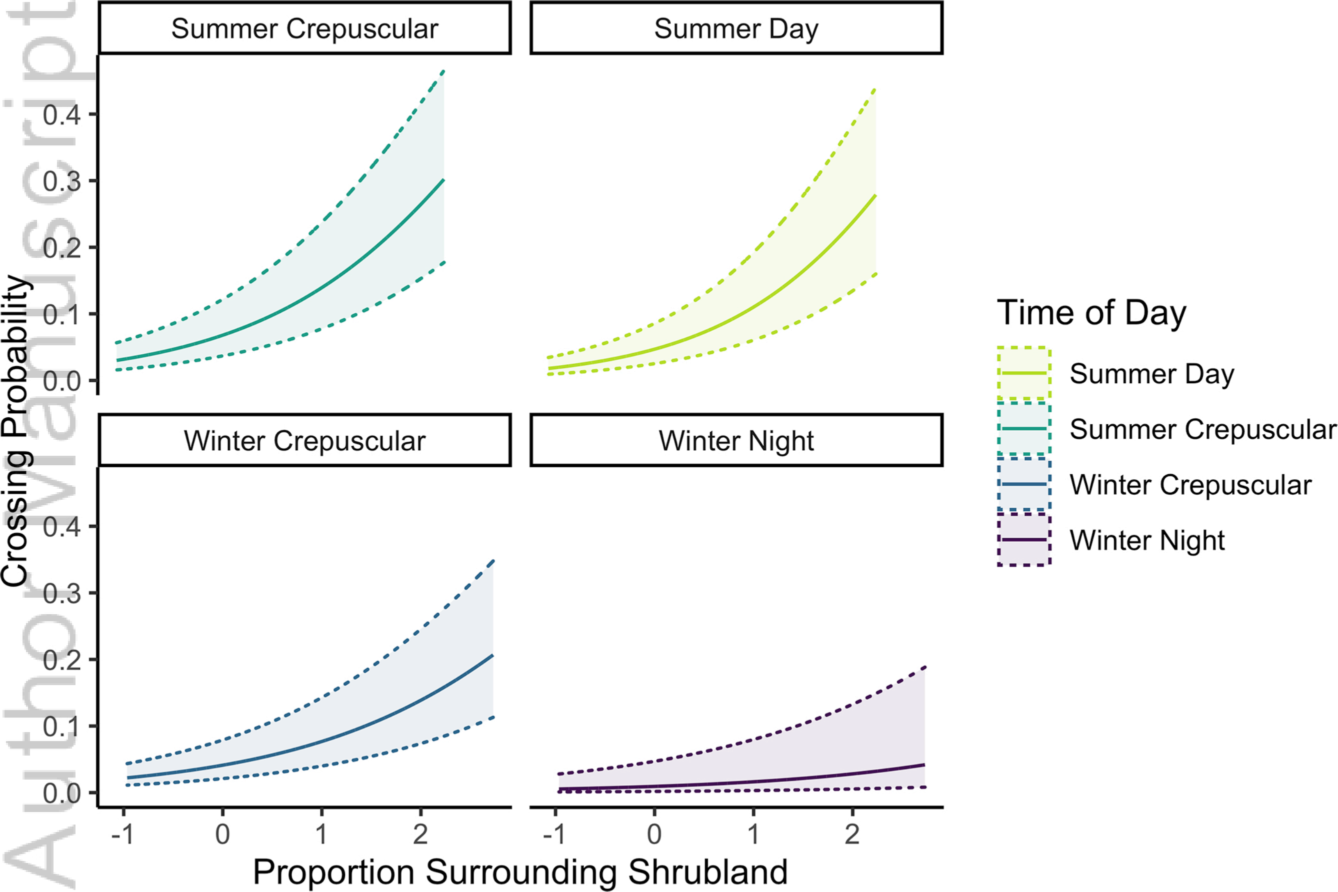

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