Wildlife mortality risk posed by high and low traffic roads

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Keywords

Road ecology, Wildlife mortality, Roadkill, Traffic volume, Wildlife-vehicle collisions, Transportation infrastructure, Habitat fragmentation, Mitigation.

Article impact statement

Low traffic roads can pose a high mortality risk for wildlife; thus, monitoring and mitigation policies are recommended to reduce roadkill.

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.14159.

Abstract

Wildlife mortality due to collisions with vehicles is considered one of the predominant negative effects exerted by roads on many species. Reducing roadkill is therefore a major component of wildlife conservation. Roadkill is affected by various factors, including road attributes and traffic volume. It was theorized that the effect of traffic volume on roadkill probability should be unimodal. However, empirical evidence of this theory is lacking. Using a large-scale roadkill database of eighteen wildlife species in Israel, encompassing 2,846 km of roads over a period of 10 years, we explored the effects of traffic volume and road attributes (e.g., road lighting, verge vegetation) on roadkill probability using a multivariate GLMM analysis. A unimodal effect of traffic volume was identified for the striped hyena (*Hyaena hyaena*), while five species demonstrated a novel quadratic U-shaped effect (e.g., golden jackal (*Canis aureus*)) and four species showed a negative linear effect (e.g., wild boar (*Sus scrofa*)). We also identified varying effects of road attributes on roadkill. For instance, road lighting and roadside trees decreased roadkill for several species, while bus stops and concrete guardrails led to increased roadkill. The theorized unimodal effect of traffic volume may only apply to large, agile species, while the U-shaped effect could be related to intraspecies variability in traffic avoidance behavior. Altogether, our study revealed that both high traffic and low traffic roads can pose a high mortality risk for wildlife. It is therefore important to monitor roadkill on low traffic roads and adapt road attributes where possible, to improve road design for wildlife. An effective roadkill reduction strategy can benefit from combining road design measures like reducing the use of concrete guardrails and median barriers, with mitigation measures that are suitable for

low traffic roads, such as wildlife detection systems combined with driver warnings, and seasonal traffic calming.

Introduction

The expanding global use of motorized transportation is accompanied by extensive development of new linear infrastructures (Laurance et al., 2015; van der Ree et al., 2015). By the year 2050, new roads amounting to 25 million km in length are expected to be built worldwide (Dulac, 2013). Roads exert various negative impacts on wildlife (Trombulak & Frissell, 2000) including habitat fragmentation (Bennett, 2017) and mortality due to wildlife-vehicle collisions (roadkill). The latter is considered one of the major impacts of roads on wildlife (Fahrig & Rytwinski, 2009), while also posing a threat to human health and incurring substantial economic costs (Gren & Jägerbrand, 2019; Ascensão et al., 2021). Globally, collisions with vehicles cause millions of incidents of animal mortality per year (Nyhus, 2016; Schwartz et al., 2020) resulting in reduced population viability of many species (Grilo et al., 2020). In a recent review on the demographic effects of road mortality on mammalian populations, it was found that roadkill is the greatest source of mortality for 28% of mammal species (Moore et al., 2023). Thus, roadkill plays a major role in the biodiversity crisis (Rytwinski & Fahrig, 2015). There is an urgent need to better understand the drivers of roadkill across landscapes, its variation among taxa, and the means to reduce roadkill (Rytwinski et al., 2016; Bartonička et al., 2018).

Many factors have been found to influence the spatial distribution of roadkill. These are broadly divided into landscape features, species traits, road attributes, traffic characteristics, and temporal factors (Aquino & Nkomo, 2021). Landscape features (e.g., land cover, topography) determine both the abundance of species and their movement patterns across the landscape, thereby affecting the occurrence of wildlife near the road (Plante et al., 2019). Species traits (e.g., locomotion type and velocity, body size, risk avoidance behavior, ecological guild) determine the tendency to avoid the road and the ability to cross safely (Jacobson et al., 2016; González-Suárez et al., 2018; Brieger et al., 2022). These responses are affected by road attributes (e.g., lighting, verge vegetation, median barriers) and traffic characteristics (e.g., traffic volume, vehicle speed), which modulate species' road avoidance behavior and mortality risk (Chen & Koprowski, 2019). The effects of some of these factors on the probability of roadkill have been studied extensively, however few studies have quantified the effects of road attributes (Pagany, 2020). The complex effects of traffic volume on roadkill probability also remain poorly understood (Grilo et al., 2015).

The probability of roadkill has been theorized to be governed by two processes that depend on traffic volume (Seiler, 2003). First, the probability that an animal will approach the road and attempt a crossing is expected to decrease as the volume of traffic increases. As vehicles pass more often, both auditory and visual disturbances increase and may prohibit an animal from approaching the road (Lima et al., 2015). In theory, this effect can vary depending on how each species reacts to perceived danger, based on four behavioral types: non-responders, pausers, speeders, and avoiders (Jacobson et al., 2016). Second, the probability of an animal colliding with a passing vehicle while crossing is expected to increase with increasing traffic volume. As vehicles approach more often, the opportunity to complete a safe crossing is diminished (Saxena et al., 2020). This effect depends on biological traits, most importantly body size and locomotion velocity (Jaarsma et al., 2006; Lin, 2016). The probability of roadkill is the product of road crossing probability, which diminishes with traffic volume, and collision probability, which increases with traffic volume. In theory, this results in a maximal roadkill probability at an intermediate traffic volume (Fig. 1). Thereby, the effect of traffic volume on roadkill probability is expected to be unimodal (Seiler, 2003).

Although the unimodal theory was suggested two decades ago, little research has been conducted to find empirical support for it, with most studies assuming a linear effect of traffic volume on roadkill probability. According to a recent review of 191 papers on wildlife-vehicle collisions (WVC), 51 studies have analyzed the effects of traffic volume on roadkill, with 75% of these finding a positive linear effect (e.g., Sadleir & Linklater, 2016) on WVC and 15% finding a negative linear effect (Pagany, 2020). In some cases, no relationship between traffic volume and roadkill was identified (Bissonette & Kassar 2008). However, of these studies only a few have analyzed traffic volume as a quadratic effect. Most studies were of small spatiotemporal scales and did not account for the confounding effects of road attributes, landscape features, temporal factors and species abundance. Seiler (2005), studying moose in Sweden, found a unimodal relationship between traffic volume and moose-vehicle collisions, which peaked at 4,000 vehicles per day. Grilo et al. (2015) studied the unimodal effect in Portugal covering large spatiotemporal scales (1,000 km of roads over six years) and traffic volumes (3,000 - 50,000 vehicles per day) for four species, however species abundances were not accounted for. A quadratic effect was found for red foxes and rabbits, but maximal roadkill probabilities occurred at very low traffic volumes, precluding the detection of a robust unimodal effect. The authors concluded that assessment of non-linear traffic effects requires large databases of traffic volumes and roadkill incidents.

Our objectives here were to evaluate the validity of the unimodal relationship between traffic volume and roadkill probability for different taxa (mammals, birds and reptiles) in Israel, while simultaneously assessing the effects of road attributes on roadkill. The latter was done to provide insights for road design aimed at reducing roadkill. Hence our study has both theoretical and applied aspects. To the best of our knowledge, no study to date has quantified the unimodal effect of traffic volume empirically using roadkill data encompassing large spatial and temporal scales, while accounting for the effects of road attributes, landscape features, temporal factors and species abundance (but see Visintin et al. [2017]).

Furthermore, no study to date has explored this relationship with sufficiently large variance in traffic volumes and for a wide variety of species. Additionally, few studies have analyzed the effects of road attributes on roadkill at a large scale and for multiple species (e.g., Canal et al., 2018). We addressed these knowledge gaps by analyzing the quadratic and linear effects of traffic volume on roadkill probability, and the effects of various road attributes, using extensive spatiotemporal data.

Our hypothesis regarding traffic volume effects on roadkill is that for species that are agile and can evade vehicles at low traffic, and also tend to avoid anthropogenic disturbances (e.g., noise or light) the effect should be unimodal, as suggested by Seiler (2003). For less agile species with a strong avoidance behavior, the effect of traffic volume on roadkill probability should be negative, as most roadkill will happen at low traffic volumes and crossing attempts will quickly decrease with increasing traffic volume. For species that show little response to traffic, the effect should be positive, because while crossing attempts will not decrease, the likelihood of collision will increase with traffic volume (Jacobson et al., 2016). The results of this research provide a better understanding of the impact of traffic volume on roadkill probability for various taxa. The study also provides important insights regarding the effects of road attributes, thereby promoting better road planning for effective mitigation of wildlife-vehicle collisions, which is essential for effective wildlife conservation.

Methods

We studied the effects of both traffic volume and road attributes on the probability of roadkill for multiple species in Israel using a multivariate GLMM model. To account for the effects of other confounding variables, we included in the statistical analysis the features of the landscape, temporal factors, and vehicle speed. Habitat suitability values were also included as a proxy for species abundance (de la Fuente et al., 2021), to account for varying species abundances along road sections.

Roadkill data

Wildlife roadkill data were reported by rangers working for the Israel Nature and Parks Authority (INPA) during the years 2008 - 2019, using the Cybertracker hand-held GPS system (Liebenberg, 2003). All roadkill occurrences were identified at the species level. Roadkill identification was done opportunistically while driving along roads, covering the entire road system of Israel. Overall, 22,155 roadkill occurrences were reported for 288 wildlife species. From these, we chose for statistical analysis only species with at least 100 roadkill occurrences, because statistical models with fewer data points did not converge numerically due to the large number of independent variables (>30 variables). Overall, eighteen species were chosen for statistical analysis, including fifteen mammals, two bird species and one reptile species (Table 1). Roadkill occurrences for these species comprise a total of 16,329 records. Total roadkill densities for these species are in the range of 0 to 2.5 occurrences per km per year, with a mean value of 0.29 (Fig. 2).

Traffic volume

Traffic volume data were available from the Israel Central Bureau of Statistics (CBS). CBS gathered data on average daily traffic volumes at the national level, for the years 2000-2020. Roads were delineated by CBS to sections between neighboring intersections, with a total of 669 road sections countrywide. Road section lengths were between 0.28 km and 122.4 km, with an average length of 6.52 km, totaling 4,364 road km over the entire country, encompassing most intercity roads in Israel. Each road section was surveyed annually by CBS for one week which was chosen randomly during each year. Traffic volume was measured using a mobile pneumatic system that registers the pressure caused by a vehicle passing over it (CBS, 2017) and published online in units of thousands of vehicles per day (CBS, 2020). We calculated the annual average daily traffic volume (AADT) for each road section. AADT values ranged from 300 to 260,000 vehicles per day, with a mean value of 25,900.

Road attributes

We surveyed road attributes at points along road sections, approximately every 150 m. This distance represents a resolution of data that is detailed enough to account for the variability

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in road attributes. Additionally, the spatial accuracy of recorded roadkill incidents was approximately within a range of 150 m from the recorded coordinates (based on maximal deviations from the road of reported roadkill locations). Therefore, a sampling of road attributes every 150 m assured that for each recorded roadkill point, a representative road data point will exist within that range. Overall, 18,838 points were surveyed, representing a total of 2,846 road km, which constitute 65.2% of road sections with traffic volume data. AADT values for the surveyed road sections ranged from 300 to 148,000 vehicles per day, with a mean value of 20,400 vehicles per day (Fig. 2). Google Street View (GSV) was used to visually identify road attributes at each surveyed point. Where GSV was not available for online surveying, we conducted surveys by driving along roads and recording the data for each point manually. Out of 18,838 surveyed points, 11,327 points were surveyed using GSV, and 7,511 points were surveyed by driving. Road attributes include features that were visually identifiable from the road and were deemed important in causing or preventing roadkill, based on past research (Pagany, 2020). We recorded the following road attributes: median barrier types, guardrail types, median vegetation types, median strip width, fence types, topography types, adjacent building types, verge vegetation types, road lighting, adjoining unpaved roads, drainage ditches, parallel paved roads, shoulder width, and the number of lanes (Table 2; See Supporting Information, Fig. S1 for visual representation of road attributes).

At some surveyed points, road attributes representing different categories of the same variable were present on each side of the road (e.g., trees on one side and perennials on the other side of the road). In these cases, we recorded two unique values, each representing one side of the road. These cases do not allow for the use of categorical variables to represent road attributes because two categories cannot be represented at a single data point. To amend this problem, we decomposed each categorical variable to a set of numerical variables using one-hot encoding, each representing a single category (Davis, 2010; Alkharusi, 2012). At points where different attributes belonging to the same categorical variable were recorded on each side, we assigned each of the respective numerical variables a value of 0.5. At points where the attributes were the same on both sides, we assigned a value of one to the respective numerical variable.

Landscape features, temporal factors and vehicle speed

Features of the surrounding landscape include the proportions of land cover types and the mean slope of the surrounding topography, each measured at a 500 m radius (following Nieszala & Klich, 2021). Temporal factors include the year, the season, and the lunar phase. Land cover data were taken from a country-wide 30 m resolution raster layer produced in 2016, developed by the organization in charge of assessing the state of nature in Israel (Hamaarag, 2020). The original raster layer is categorized into 15 land cover types. We simplified these categories into seven major types including developed areas, barren lands, grasslands, woodlands, croplands, orchards, and water bodies (See Supporting Information, Fig. S1 for visual representation of land cover types). For each land cover type, the proportion of covered area out of the total area was calculated around each surveyed point. The slope of the surrounding topography was calculated as degrees based on a country-wide 30 m resolution digital elevation model downloaded from NASA's Shuttle Radar Topography Mission (Farr & Kobrick, 2000). For each roadkill data point, the date on which the roadkill incident was reported is recorded by the Cybertracker system. We used the recorded date to extract the year, the season, and the lunar phase. Lunar phase was calculated as the illuminated fraction of the moon on the roadkill record date, using data from the Astronomical Applications Department at the United States Naval Observatory website (USNO, 2020). To account for the effects of vehicle speed on roadkill, we used the maximal speed limit for each road, available from OpenStreetMap (OpenStreetMap, 2015).

Habitat suitability as a proxy for species abundance

Habitat suitability values were used as a proxy for species abundance (following de la Fuente et al., 2021), to account for varying species abundances along road sections. A previous meta-analysis has found a consistent significant positive relationship between abundance and habitat suitability. This relationship was found in all cases regardless of scale of the study, ecological niche modeling method, or the set of variables used to derive habitat suitability (Weber et al., 2017). In our study, habitat suitability was calculated for each species using MaxEnt, a maximum entropy model (Phillips et al., 2006). Country-wide species occurrence observations, collected through systematic surveys and opportunistic reporting by various nature conservation organizations (INPA, Hammarag, and the Society for the Protection of Nature), were downloaded from BioGIS, a biological data archive maintained by the Hebrew University (BioGIS, 2020). Environmental variables for all species include land cover for the year 2016, minimum NDVI and maximum NDVI for the year 2012 (Hamaarag, 2020), elevation, slope, and aspect (Farr & Kobrick, 2000), all at a resolution of 30 m. Climatic variables include mean annual rainfall and mean annual temperature for the years 1970 – 2000 at a resolution of 1 km (Fick & Hijmans, 2017). A bias layer was used to remove the effect of sampling bias (Kramer-Schadt et al., 2013). The bias layer was produced by using the observation points of all vertebrate species in the database (BioGIS,

2020) to construct a normalized kernel-density map of observations, with values between 1 and 100 (Clements et al., 2012). Habitat suitability raster grids for each species were obtained using the standard MaxEnt configuration, with 20% of occurrence points set aside as random test points (See Supporting Information, Table S1 for model performance indices). For each surveyed point, the average habitat suitability value for each species was calculated at a circular area of 500 m radius.

Data analysis

We simultaneously quantified the effects of traffic volume and road attributes on the probability of roadkill using a generalized linear mixed model with a binomial distribution for each species. For the analysis we used the glmmTMB package in R (Brooks et al., 2017). The dependent variable was the probability (as log-odds) of occurrence of a roadkill incident in the vicinity of a surveyed data point. We defined surveyed points where a roadkill incident had occurred as those that are 150 m or less from a recorded roadkill location. This distance was chosen because the spatial accuracy of recorded roadkill data positions was estimated at 150 m, which is the maximal deviation of recorded roadkill points from road sections in the database. Because roadkill data were collected opportunistically by INPA rangers, the sampling effort could not be considered uniform for all roads. To account for this possible bias, we added a proxy variable for the sampling effort. We used an independent dataset of 37,525 reports in which rangers recorded observations of live wildlife and native plants from the road (up to 100 m from the road) during the same time period in which roadkill observations were reported. We measured the number of days in which at least one ranger was present on each road section, standardized by the road length, and used this variable as a proxy for the sampling effort on each road section.

Because roadkill data were collected opportunistically, no information regarding the individual sampling conditions (i.e., driving speeds and the number of observers per vehicle) was available. However, we can assume that in most cases, rangers were driving alone and close to the speed limit which is either 80 or 90 km/h on intercity roads. To account for variability in roadkill detectability based on road-specific driving conditions, we used a random variable that represents each road by its designated road number. The year in which each roadkill incident occurred was also included as a random variable. To prevent over-sampling of data points from areas where the focal species of the analysis is not present, we used only surveyed points that are within the geographic distribution range of each species. The distribution range was identified for each species by mapping the density of the species' occurrence points (BioGIS, 2020) using a kernel density function (Chirima & Owen-Smith, 2017) and delineating the top 90% of density values.

For each set of numerical variables representing road attributes that originated from a single categorical variable, we chose one reference variable and excluded it from the model (Table 2), to avoid perfect multicollinearity. Reference variables were those that represented absence of the attribute (e.g., no median barrier). Variables that were present at less than 1% of the surveyed points within the distribution range of each species were excluded from statistical analysis. We checked for pairwise linear correlations and found that all variable pairs had a Pearson correlation with a magnitude smaller than 0.7, which corresponds to a weak to moderate correlation (Schober et al., 2018), therefore we did not exclude any of the variables due to pairwise correlation. We also checked for multicollinearity using the variance inflation factor (VIF; Thompson et al., 2017) and removed variables with a VIF value greater than 5 to prevent multicollinearity (See Fig. 4).

For each model, we tested for spatial autocorrelation by plotting a variogram of model residuals as a function of distance between surveyed points and visually inspecting the smoothed conditional means of the variogram. We found no apparent spatial autocorrelation in the data of any model.

We tested the empirical support for a unimodal effect of traffic volume on roadkill probability for each species, by comparing the statistical model for the effects of road attributes which includes traffic volume as a linear term, to the same model with an added quadratic term for traffic volume. We used an ANOVA model to test for a significant difference between the linear and quadratic models (Jamil & Ter-Braak, 2013). In cases where the ANOVA test was significant, we checked for difference in AIC values of the linear and quadratic models. We deemed the quadratic model more informative where AIC of the linear model was greater than 2 compared to AIC of the quadratic model (Burnham & Anderson, 2004), and the extremum point of the curve was within the range of traffic volume values (Chocron et al., 2015). If the coefficient of the quadratic term was negative, the effect was defined as unimodal, and if positive, the effect was defined as U-shaped. To assess the relative importance of traffic volume in predicting roadkill, we calculated the Akaike weights for each model with a significant effect of traffic volume, compared to the same model without traffic volume (Giam & Olden, 2016).

Results

Traffic volume effects

Out of eighteen species studied, we identified six species with a significant quadratic effect of traffic volume on the probability of roadkill, and four species with a significant linear effect with no quadratic effect. While the statistical models include both traffic volume and road attributes, we present the effects of traffic volume separately for clarity (Table 3; Fig. 3). Among the species demonstrating a quadratic effect, one species exhibited a unimodal effect of traffic volume on roadkill probability, in accordance with the unimodal theory: the striped hyena (*Hyaena hyaena*), which showed a strong unimodal quadratic effect, with maximal roadkill probability at a traffic volume of 24,905 vehicles per day ($p < 0.001$, $\Delta AIC = 22.32$). Roadkill probabilities of five other species were related to traffic volume as a U-shaped curve, characterized by a minimum of roadkill probability at intermediate values of traffic. These species are the golden jackal (*Canis aureus*), red fox (*Vulpes vulpes*), southern white-breasted hedgehog (*Erinaceus concolor*), stone marten (*Martes foina*), and barn owl (*Tyto alba*). Intermediate traffic volume values corresponding to minimal probabilities of roadkill for these species were between 28,898 and 75,505 vehicles per day, with a mean value of 61,962 vehicles per day (Table 3). For four additional species, we found a significant negative linear effect of traffic volume on roadkill probability, with no significant quadratic effect. These species are the wild boar (*Sus scrofa*), European badger (*Meles meles*), rock hyrax (*Procavia capensis*), and chukar partridge (*Alectoris chukar*). For all species with significant effects of traffic volume, Akaike weights were greater than 0.98, except for the barn owl with an Akaike weight of 0.65. For the remaining eight species in the analysis, no significant effect of traffic volume on roadkill probability, either linear or quadratic, was identified.

Road attributes effects

We found multiple effects of road attributes on roadkill probability (Fig. 4; See also Supporting Information, Table S2 for full statistical analysis results). The presence of most building types on the roadside had a negative effect on roadkill probability. For medium sized mammals such as jackals, foxes, porcupines, wild boars, badgers and mongooses, the presence of residential and commercial buildings reduced the likelihood of roadkill. The presence of bus stops increased roadkill probability of four species: jackals, foxes, hares and hyraxes. Roadside fencing had no significant effect on roadkill for most species in the analysis. However, dense fences increased roadkill of hyenas, mountain gazelles and ariel gazelles. Verge vegetation had various effects on roadkill. Roadside trees caused a decrease in roadkill of foxes, hyenas, and mountain gazelles, and roadside perennials decreased foxes, hyenas, and gray wolves' roadkill. On the other hand, bushes caused increased roadkill of jackals and hedgehogs. Road lighting reduced roadkill of four species: porcupines, hares, hyenas, and partridges. Drainage ditches also reduced the roadkill probability of jackals, foxes, porcupines and wild boars.

Guardrails had significant effects on roadkill probability of various species. W-beam guardrails decreased roadkill probabilities of wild boars and hyenas, while increasing roadkill of porcupines, badgers, and martens. Concrete guardrails decreased roadkill of foxes but increased porcupines, badgers, wolves, and martens' roadkill. Similarly, median barriers had significant effects for several species, both negative and positive in direction. W-beam median barriers reduced roadkill of badgers, porcupines, hyenas, and black whipsnakes, while increasing roadkill of hares, ariel gazelles and jungle cats. Concrete median barriers reduced roadkill of jackals, porcupines, mongooses, whipsnakes, and barn owls, but increased roadkill of foxes, martens and jungle cats. Dense fencing as a mid-road barrier increased roadkill of both mongooses and partridges. A wide median strip had a positive effect on roadkill of foxes, hares, mongooses, jungle cats and partridges, and wide road shoulders were found to increase roadkill of jackals, porcupines, boars, badgers, hedgehogs, mongooses and partridges. Roadside topography affected only a small number of species with mostly negative trends in roadkill. The most prominent effect was that of high rock walls which reduced roadkill of wild boars, badgers, and hedgehogs. Maximal speed limit was found to be positively correlated with roadkill of seven species: jackals, boars, badgers, hyenas, wolves, partridges and barn owls.

Landscape features and temporal factors effects

Landscape features were found to significantly affect roadkill incidents of many species (Fig. 4). Most land cover types were negatively related to roadkill probability. Developed land cover and croplands negatively affected roadkill likelihood of ten species each, and grasslands reduced roadkill for five species. Orchards and water bodies had both negative and positive effects on roadkill for various species. Sloped terrain had a significant negative effect on roadkill probability of ten species and no positive effect. Habitat suitability, a proxy for species abundance, was a significant predictor of increased roadkill likelihood for twelve species. We found that the seasons influenced roadkill of some species. For example, in spring roadkill was more likely for five species: porcupines, hedgehogs, ariel gazelles, jungle cats and partridges. The lunar phase had no effect on most species, except for increasing porcupine roadkill.

Discussion

Traffic volume effects on roadkill

There is growing evidence that road mortality could lead to local or regional extinction of wildlife populations in many regions unless extensive mitigation actions are taken to reduce the conflict of wildlife and traffic (Ceia-Hasse et al., 2017; Grilo et al., 2021). Our large-scale study on the effects of traffic volume and road attributes on roadkill, incorporating landscape features, temporal factors, and species abundance, provides novel insights on the risk of road mortality posed to various taxa. We identified complex effects of traffic volume on roadkill probability, including unimodal, U-shaped, and negative linear effects. Our results show that although high traffic roads are considered as posing the highest risk of roadkill to wildlife, low traffic roads are also a major mortality risk for many species.

The theorized unimodal effect of traffic volume was only supported empirically for the largest carnivore species in Israel, the striped hyena. This result indicates that hyenas' road avoidance and road crossing behavior follow the patterns suggested by Seiler (2003). That is, hyenas are able to cross safely at low traffic volume roads, and avoid roads with high traffic volumes, resulting in maximal roadkill at intermediate traffic volumes. The ability to evade vehicles and move across roads safely is related to animal locomotion speed, and hyenas are a highly mobile species, known to run at speeds of up to 50 km/h (Wagner, 2006). Another possible explanation for decreased roadkill of hyenas at low traffic roads is their relatively large body size, allowing drivers to identify them in time to prevent collisions (Ford & Fahrig, 2007; González-Suárez et al., 2018). Little is currently known about the avoidance behavior of striped hyenas as related to traffic. However, as an elusive nocturnal carnivore (Wagner, 2006) it is possible that hyenas avoid roads with high traffic volumes due to high levels of light and noise disturbances.

The quadratic U-shaped effect, which is the opposite of the unimodal effect, was identified for five species: golden jackal, red fox, southern white-breasted hedgehog, stone marten, and barn owl. To the best of our knowledge, this type of response has not been reported in the literature on wildlife-vehicle collisions prior to this research, although in our study it is the predominant effect. It is possible that this is due to a lack of research which incorporates high traffic roads (AADT > 50,000 vehicles per day) and therefore the increase in roadkill on these roads has not been identified. We suggest that the U-shaped effect is caused by intraspecies variation in avoidance behavior. In theory, avoidance behavior increases with traffic volume for most individuals in the population, causing a reduction in roadkill as traffic volume increases. However, a fraction of the population could attempt to cross highways regardless of traffic volume, even when encountering intense traffic, thus behaving as non-responders (Jacobson et al., 2016). If this is the case, further increase in traffic volume will result in increasing roadkill of these non-responder individuals, while the decrease in roadkill associated with avoidance will become negligible. This will lead to an overall increase in roadkill probability at higher traffic volumes, following the initial decrease at lower traffic volumes, resulting in a U-shaped roadkill probability curve.

This hypothesized differential avoidance response may be explained by intraspecies variance in behavior, depending on the age and gender of the individual, or the urgency of motivation for crossing which can reduce avoidance behavior (Brieger et al., 2022). It is known that intraspecies variation exists in the response to human disturbances, for example in response to noise pollution (Harding et al., 2019). Another possible reason for intraspecies variation in response to traffic is behavioral adaptation to human-dominated environments. The species for which the quadratic U-shaped effect was identified in this study are all successful adapters to human-dominated landscapes (Salvati et al., 2002; Duduś et al., 2014; Gupta et al., 2016; Taucher et al., 2020). Individuals in wildlife sub-populations that persist in developed landscapes demonstrate behaviors that are distinct from their rural counterparts (Ritzel & Gallo, 2020). Specifically, individuals with an elevated level of tolerance to anthropogenic disturbances are more likely to utilize high-disturbance environments (Lowry et al., 2013). Therefore, wildlife adapted to human-dominated landscapes may be less inclined to avoid high traffic roads (Duffett et al., 2020).

The negative linear response to traffic volume, identified for the wild boar, European badger, rock hyrax and chukar partridge, is characterized by a maximal roadkill probability at low traffic volumes, followed by a continuous decrease in roadkill. This type of response indicates a strong avoidance of high traffic roads (Grilo et al., 2015). For example, European badgers tend to avoid major roads with high traffic volume, while a high frequency of badger road crossings occurs at local low-traffic roads (O'Hagan et al., 2021). Species that mostly use movement corridors that transverse low traffic roads, while avoiding high-traffic roads completely, could be less vigilant and not react quickly when a vehicle is approaching (Brieger et al., 2022), or react in unexpected ways like freezing in place or running along the road (Jacobson et al., 2016). For these species, low traffic roads that do not pose a physical or behavioral barrier to movement, encourage regular road crossings which lead to high mortality risk, although vehicle density is low. For this reason, low traffic roads that cross through high quality habitat or important movement corridors could be major roadkill hotspots. The absence of a positive linear effect of traffic volume on roadkill indicates that for the species in our study the effect of increasing traffic is not predominantly an elevated risk of collision. The predominant effect of traffic volume, based on our results, is most likely the change in animal behavior which leads to increased road avoidance.

Road attributes effects on roadkill

Road attributes affect roadkill through several possible mechanisms. A road attribute can cause attraction of wildlife to the road, or deterrence of wildlife from the road (Huijser et al., 2008). It can also impede wildlife movement towards the road or impede wildlife escape from oncoming vehicles (Clevenger & Kociolek, 2013). Another mechanism that could affect roadkill is through obstruction of the line of sight, both for wildlife and drivers (Canal et al., 2019). In some cases, several of these mechanisms could be working simultaneously. Here we discuss some of the key findings in light of these mechanisms.

Road lighting, which was found to decrease roadkill, possibly acts as a deterrent of nocturnal species. It is also possible that lighting allows the driver to identify smaller species from a distance at night, like hares and partridges, thereby reducing roadkill (Huijser et al., 2008). Guardrails decrease roadkill by acting as a deterrent for species that prefer to cross where the road is not obstructed by these structures (Pagany & Dorner, 2019). This effect was previously found for red deer, roe deer and wild boar (Malo et al., 2004). However, guardrails also increase roadkill, possibly by acting as a barrier to escape once an animal is on the road, especially for species that are not agile, like the badger or the porcupine. Median barriers showed similar results, suggesting that most species avoid road sections with median barriers due to limited visibility, thereby causing reduction in roadkill. However, for those species that are not discouraged by the barrier, crossing is more difficult, and the probability of collision increases because the possibility of evading oncoming traffic is diminished due to the barrier (Clevenger & Kociolek, 2013).

The increase in roadkill related to bus stops, found for several species, may be due to the presence of open waste containers which provide food subsidies, attracting wildlife that can benefit from this food source (Newsome et al., 2015). Drainage ditches may act as a deterrent to movement towards the road. This could be either due to the presence of water in the ditches in the wet season, or due to ditch depth and steepness, impeding movement (Seo et al., 2015). Roadside vegetation (i.e., trees, bushes or perennials) was found to have variable effects on roadkill for many species. It has been shown in previous research that roadside vegetation height has a unimodal effect on mammal roadkill (Canal et al., 2019). Short vegetation (i.e., perennials) may reduce roadkill due to better visibility for both drivers and wildlife. Medium sized bushes and shrubs may attract animals to the roadside for cover and food, while impairing visibility and thus increasing roadkill. Tall trees on the other hand are less attractive to terrestrial mammals, while maintaining visibility, thereby reducing roadkill (Canal et al., 2019).

Limitations

The main limitation of our study is the opportunistic manner by which roadkill data were collected, with certain roads possibly under-sampled compared to others (Vercayie & Herremans, 2015). While no perfect solution can be obtained for this limitation, we attempted to reduce this bias by employing a proxy variable for the sampling effort using an independent database of wildlife observations reported by rangers from the roads. We found that our results are robust when implementing this approach, with little changes to the effects of traffic volume and road attributes when correcting for the sampling bias. Due to our use of opportunistically reported data, it was also not possible to assess driving speeds and the number of observers per vehicle, to ensure a consistent sampling rate.

However, we can assume that these are very similar across most cases, as rangers usually travel alone, and the speed limit for most inter-city roads in Israel is either 80 or 90 km/h. Despite these inherent limitations, the use of opportunistic data has been recognized as an important data source for roadkill research, allowing for broader geographic coverage compared to standardized surveys (Shin et al., 2022), as is the case in our study and others (e.g., Canal et al., 2018). Using such large-scale data provides important knowledge by expanding the number of species and road characteristics that can be studied simultaneously. Nevertheless, future research can benefit from testing our findings experimentally, or using systematic sampling approaches to further establish our results and help develop effective strategies for roadkill mitigation.

It has also been suggested recently that to understand the impacts of traffic volume on roadkill, it is preferable to use exact values of traffic volume for each roadkill incident, and not yearly averaged values (Bíl et al., 2020). While this is an important research direction, using such an approach requires data collection at a fine spatiotemporal resolution and this can be challenging at large spatial and temporal scales. Our study was based on nation-wide traffic volume data that were sampled periodically, such that only a yearly averaged daily traffic volume could be used for the analysis, as previously done by Grilo et al. (2015). We acknowledge this limitation and suggest that these research approaches are complementary, and both can further the understanding of traffic-roadkill relationships. An additional possible limitation is the use of habitat suitability as a proxy for species abundance. However, it was shown that a consistent significant positive relationship exists between abundance and habitat suitability, regardless of scale of the study, ecological niche modeling method, or the set of variables used to derive habitat suitability (Weber et al., 2017).

Conclusions and conservation implications

Our study highlights the variation and complexity in the effects of traffic volume on roadkill probability for different species. These varying results support the idea that the effect of traffic volume on roadkill for each species is determined by the species' specific road avoidance behavior and crossing behavior (Seiler, 2003; Jacobson et al., 2016). For species with a negative or a U-shaped traffic-roadkill curve, mortality risk is substantial at low traffic roads where crossing attempts are most frequent. Therefore, we suggest that in areas where the populations of these species are vulnerable, a policy of conducting long-term, systematic roadkill monitoring should be implemented at low traffic roads to identify their impacts on the population (Schwartz et al., 2020). To improve conservation outcomes for the affected species, roadkill mitigation that is appropriate for low traffic roads should be used. For example, constructing underpasses or retrofitting existing drainage culverts (Brunen et al., 2020), using wildlife detection systems combined with driver warning technology (Druta & Alden, 2020), or employing seasonal traffic calming (Ascensão et al., 2022). On the other hand, for high traffic roads in human-dominated landscapes, where species that are adapted to disturbances (i.e., species with a U-shaped traffic-roadkill curve) could suffer from significantly elevated road mortality rates, different roadkill mitigation measures should be implemented. For these roads, appropriate mitigation solutions that do not interfere with traffic would be audio-visual wildlife deterrent systems (Laguna et al.,

2022) or wildlife crossing structures with accompanying fencing and jump-outs (Edwards et al., 2022).

Regarding the effects of road attributes on roadkill probability, we suggest that transportation authorities should strive to construct safer roads for wildlife based on our results, by implementing the following insights in road design. The gleaned effects of road attributes suggest that road barriers and guardrails should be avoided where possible, to decrease roadkill of vulnerable species and reduce the barrier effect. Bus stops should be managed to reduce wildlife attraction to organic waste, and road lighting can be used as a means for roadkill reduction where mortality rates are high. However, strong light pollution should be avoided in ecologically sensitive areas (Peña-García & Sędziwy, 2020). We also suggest that verge landscaping using dense bushes should be avoided, to prevent obstructions in driver visibility. Implementing these insights for road design, along with the use of appropriate mitigation measures, would combine for an effective roadkill reduction strategy, to lessen the negative impacts of both low and high traffic roads on vulnerable populations and thereby support wildlife conservation.

Acknowledgments

The authors thank the Israel Nature and Parks Authority for supporting this research.

Data availability statement

Data is available from Figshare at https://doi.org/10.6084/m9.figshare.22734062

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Tables and Figures

Table 1. List of species included in statistical modeling of factors affecting roadkill. Conservation status is at the national level within Israel. Species' roadkill percentages are relative to the total of all reported roadkill occurrences in the database (22,155 roadkill incidents).

Common name	**Scientific name**	**Class (Order)**	**Conservation status**	**Roadkills (%)**
Golden jackal	*Canis aureus*	Mammalia (Carnivora)	Least concern	5022 (22.7%)
Red fox	*Vulpes vulpes*	Mammalia (Carnivora)	Least concern	1954 (8.8%)
Indian crested porcupine	*Hystrix indica*	Mammalia (Rodentia)	Least concern	1401 (6.3%)
European badger	*Meles meles*	Mammalia (Carnivora)	Least concern	1250 (5.6%)
Southern white-breasted hedgehog	*Erinaceus concolor*	Mammalia (Eulipotyphla)	Least concern	1183 (5.3%)
Wild boar	*Sus scrofa*	Mammalia (Artiodactyla)	Least concern	918 (4.1%)
Desert hare	*Lepus capensis*	Mammalia (Lagomorpha)	Least concern	886 (4%)
Egyptian mongoose	*Herpestes ichneumon*	Mammalia (Carnivora)	Least concern	705 (3.2%)
Mountain Gazelle	*Gazella gazella*	Mammalia (Artiodactyla)	Vulnerable	621 (2.8%)
Striped hyena	*Hyaena hyaena*	Mammalia (Carnivora)	Endangered	443 (2%)
Rock hyrax	*Procavia capensis*	Mammalia (Hyracoidea)	Least concern	332 (1.5%)
Black whipsnake	*Coluber jugularis*	Reptilia (Squamata)	Least concern	318 (1.4%)
Stone marten	*Martes foina*	Mammalia (Carnivora)	Least concern	282 (1.3%)
Chukar partridge	*Alectoris chukar*	Aves (Galliformes)	Near threatened	260 (1.2%)
Barn owl	*Tyto alba*	Aves (Strigiformes)	Near threatened	260 (1.2%)
Gray wolf	*Canis lupus*	Mammalia (Carnivora)	Vulnerable	187 (0.8%)
Ariel Gazelle	*Gazella dorcas*	Mammalia (Artiodactyla)	Vulnerable	165 (0.7%)
Jungle cat	*Felis chaus*	Mammalia (Carnivora)	Vulnerable	142 (0.6%)

Table 2. List of independent variables included in the analysis of the effects on roadkill probability. Categories marked with a star were excluded from statistical modeling due to insufficient data. Abbreviations of data sources: The Israeli ecological monitoring program (Hamaarag), Israel Nature and Parks Authority (INPA), Google Street View (GSV), Shuttle Radar Topography Mission (SRTM), United States Naval Observatory (USNO), OpenStreetMap (OSM), and Israel Central Bureau of Statistics (CBS).

Categorical variables	**Categories**	**Reference category**	**Source**
Land cover	Grassland, developed, woodland, cropland, orchard, water	Barren	Hamaarag
Season	Fall, spring, winter	Summer	INPA
Median barrier	W-beam, concrete, dense fence, open fence*	No median barrier	GSV, Driving survey
Median strip	Wide, narrow, sloped*	No median strip	GSV, Driving survey
Median vegetation	Trees*, bushes*, perennials	No median vegetation	GSV, Driving survey
Topography	Upslope, downslope, high wall, low wall, chasm	Flat topography	GSV, Driving survey
Guardrails	W-beam, concrete, open fence*	No guardrails	GSV, Driving survey
Shoulders	Wide, sidewalk, narrow	No shoulders	GSV, Driving survey
Fence	Dense fence, open fence, wall	No fence	GSV, Driving survey
Building	Bus stop, agricultural, commercial, residential, gas station, other	No building	GSV, Driving survey
Verge vegetation	Trees, bushes, perennials	No verge vegetation	GSV, Driving survey
Lighting	Binary variable	No lighting	GSV, Driving survey
Unpaved road	Binary variable	No unpaved road	GSV, Driving survey
Drainage	Binary variable	No drainage	GSV, Driving survey
Parallel road	Binary variable	No parallel road	GSV, Driving survey
Continuous variables	**Value range (units)**		
Lanes	Min = 1, Max = 11 (Number of lanes)		GSV, Driving survey
Slope	Min = 0.6, Max = 27.4 (Degrees)		SRTM
Habitat suitability	Min = 0, Max = 1 (Relative suitability index)		Maxent model
Lunar phase	Min = 0, Max = 1 (Illuminated fraction)		USNO
Maximal speed limit	Min = 50, Max = 120 (km / hour)		OSM
Ranger visits per km	Min = 0.41, Max = 128.11 (Number of days / km)		INPA
Traffic volume	Min = 0.3, Max = 148 (Annual average daily traffic, in thousands)		CBS
Random variables	**Value range (units)**		
Year	Min = 2008, Max = 2019 (Year)		INPA
Road number	Min = 2, Max = 9888 (Designated road number)		OSM

Table 3. Coefficients of the effects of traffic volume on roadkill probability, for species with significant effects. Quadratic models (unimodal or U-shaped effects) include both a linear and a quadratic term, while linear models include only a linear term. ANOVA values represent the significance of the difference between linear and quadratic models for the same species. ΔAIC = AIC (linear model) – AIC (quadratic model). Extremum values are traffic volumes at which either maximal roadkill probability is reached (for unimodal curves), or minimal roadkill probability is reached (for U-shaped curves).

		Effect type	Linear term		Quadratic term		ANOVA	ΔAIC	Extremum
Species	Scientific name		Estimate	p value	Estimate	p value	p value		Vehicles / day
Striped hyena	*Hyaena hyaena*	Unimodal	1.768	2.48E-04	-0.937	9.41E-04	8.15E-07	22.32	24,905
Golden jackal	*Canis aureus*	U-shaped	-0.508	2.22E-08	0.103	6.37E-10	3.10E-09	33.12	66,400
Red fox	*Vulpes vulpes*	U-shaped	-0.545	2.73E-05	0.100	2.57E-05	4.96E-05	14.46	69,500
Southern white-breasted hedgehog	*Erinaceus concolor*	U-shaped	-1.026	1.01E-10	0.185	1.18E-10	5.17E-09	32.12	75,505
Stone marten	*Martes foina*	U-shaped	-1.002	6.52E-04	0.282	2.59E-05	9.88E-06	17.53	28,898
Barn owl	*Tyto alba*	U-shaped	-0.741	3.76E-02	0.190	2.06E-02	2.57E-02	2.97	69,505
Wild boar	*Sus scrofa*	Negative linear	-0.686	1.46E-04					
European badger	*Meles meles*	Negative linear	-0.910	4.18E-12					
Rock hyrax	*Procavia capensis*	Negative linear	-0.698	2.89E-03					
Chukar partridge	*Alectoris chukar*	Negative linear	-1.542	1.33E-04					

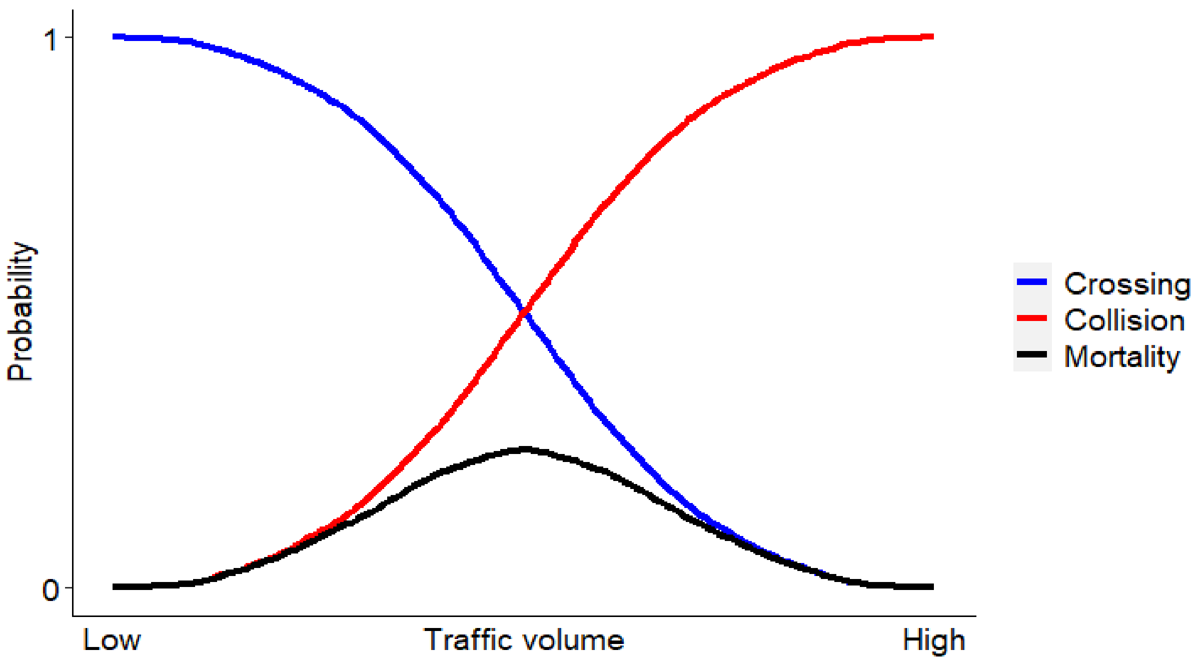

Figure 1. A conceptual model of the unimodal effect of traffic volume on the probability of wildlife road mortality due to wildlife-vehicle collisions. Road mortality probability (black) is

the product of the decreasing probability of road crossing attempts (blue) and the increasing probability of vehicle collisions with crossing individuals (red).

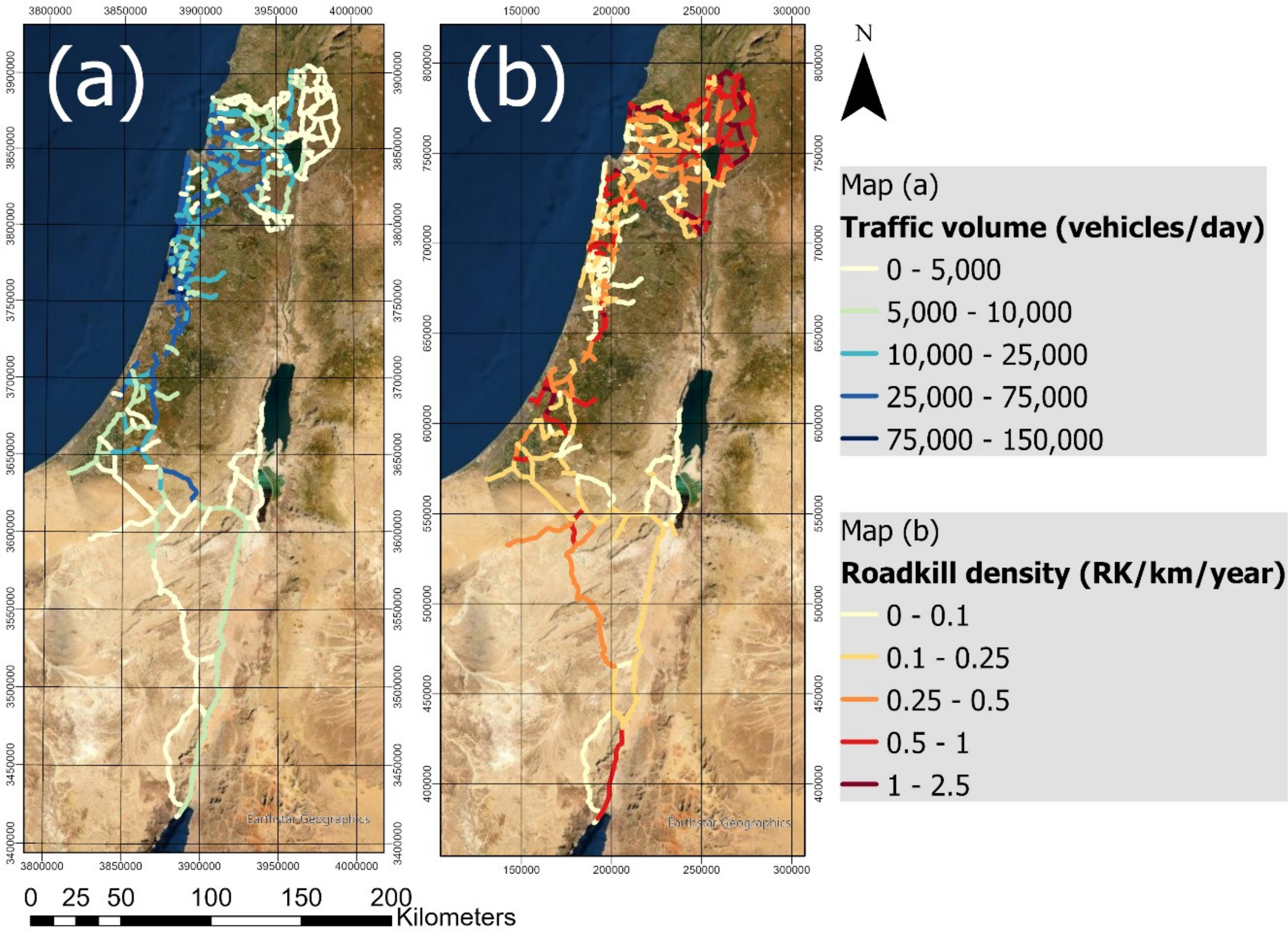

Figure 2. Country-wide traffic volume and roadkill density across Israel. (a) Annual average daily traffic volume, per road section. (b) Roadkill (RK) density of all species included in the statistical analysis, per road section.

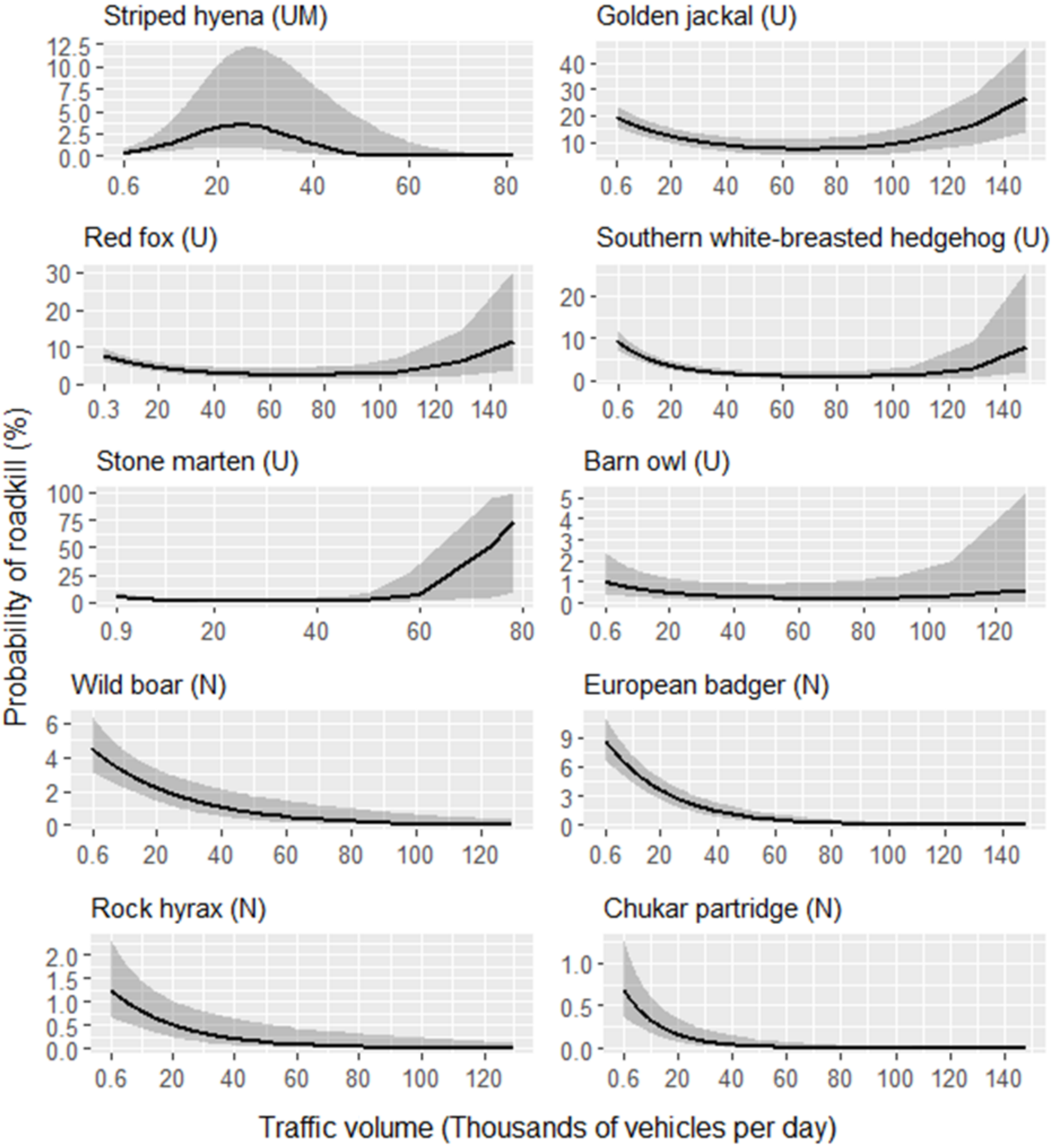

Figure 3. Significant effects of annual average daily traffic volume (in thousands of vehicles per day) on the probability of roadkill for various species (transformed from log-odds values), with 95% confidence intervals in dark gray. Effect types in parentheses: UM = Unimodal, U = U-shaped, N = Negative linear. The magnitude of roadkill probability is proportional to the ratio of the number of roadkill records to overall surveyed road data points for each species.

	Jackal	Fox	Porcupine	Boar	Badger	Hare	Hyena	Hedgehog	Wolf	Mongoose	Hyrax	Marten	Gazelle	Ariel gazelle	Jungle cat	Partridge	Barn owl	Whipsnake
Lanes (1+, 1-)	-0.07	#			0.17									#				
Median barrier - W-beam (3+, 4-)			-1.01		-1.01	0.55	-0.74							0.71	1.56			-1.99
Median barrier - concrete (3+, 5-)	-0.26	0.36	-0.37							-0.47		1.22		x	1.64		-1.31	-1.64
Median barrier - dense fence (2+, 0-)							x		x	1.03	x	x	x	x		2.13		
Median strip - wide (5+, 1-)		0.51				0.90				0.40				x	1.39	1.34	-1.59	
Median strip - narrow (1+, 3-)				-1.21		0.90	#				-2.32			x			-1.56	
Median vegetation - perennials (1+, 1-)	-0.50				0.72				x			x		x				
Topography - upslope (0+, 0-)																		
Topography - downslope (0+, 0-)																		
Topography - high wall (1+, 3-)		0.51		-0.74	-0.70			-1.00										
Topography - low wall (1+, 1-)				-1.29											3.65			
Topography - Chasm (1+, 0-)					x							2.28	x	#	x	#	#	#
Guardrails - W-beam (3+, 2-)			0.38	-0.57	0.27		-0.62					0.51						
Guardrails - concrete (4+, 1-)		-0.56	0.64		0.70				1.85			0.99		x	#			
Shoulders - narrow (2+, 0-)			0.69	#	0.36		#		#							#		
Shoulders - wide (7+, 1-)	0.41		0.56	0.28	0.62			0.49	-0.47	0.43						0.42		
Shoulders - sidewalk (0+, 0-)														#				
Fence - dense fence (3+, 1-)				-0.66			1.07						0.68	1.31				
Fence - open fence (0+, 1-)										-0.34				x				
Fence - wall (1+, 2-)	-0.74						1.58			-1.35				x				
Building - bus stop (4+, 0-)	0.45	1.25				1.08					1.18			x				
Building - agriculture (1+, 1-)		-1.01														1.64		
Building - commercial (0+, 4-)	-0.58	-0.80		-1.88					#	-0.96				x				
Building - residential (0+, 5-)	-0.84	-0.74	-0.70		-0.84					-0.75				x				
Building - gas station (0+, 0-)		x		x		x	x		x		x	x	x	x	#	x		#
Building - other (0+, 2-)	-0.56	-0.82							#					x				
Vegetation - trees (1+, 3-)		-0.88	0.24				-1.35				#	#	-0.49					
Vegetation - bushes (2+, 3-)	0.19	-0.57					-1.25	0.31									-1.23	
Vegetation - perennials (0+, 3-)	#	-0.75	#	#	#		-1.42	#	-1.41	#			#	#	#	#		#
Lighting (0+, 4-)			-0.49			-0.36	-0.48									-0.75		
Unpaved road (3+, 0-)												0.53		0.88	0.90			
Drainage (0+, 4-)	-0.23	-0.31	-0.41	-0.39										x				
Parallel road (2+, 0-)		0.65					1.06											
Land cover - grassland (1+, 5-)	0.49		-0.59	#	#	-2.78				-0.77	-1.60	-3.83				#		#
Land cover - developed (1+, 10-)		-0.80	-0.99		-1.36	-3.51			1.59				-2.66	-3.56	-3.65	-3.22	-3.07	-2.94
Land cover - woodland (2+, 2-)	0.70		#	2.16		-1.92		#			#	#	#					-1.71
Land cover - cropland (0+, 10-)	#		-1.62	-1.08	-0.90	-1.64		-1.41		#	-2.73	-4.00	-1.85		#	-2.28	#	-1.69
Land cover - orchard (5+, 6-)	0.87	0.70	-0.68	1.06	1.59		1.59		-2.76	-0.88			-2.92				-1.16	-1.19
Land cover - water (3+, 5-)	1.44	-2.86			-2.92			1.66	-11.7		-5.16		-5.30		3.95			
Slope (0+, 10-)	-0.06	-0.04	-0.05					-0.06	-0.15	-0.11	-0.06			-0.14			-0.40	-0.07
Season - fall (3+, 3-)	0.55		0.29									-0.72		0.51			-0.77	-0.88
Season - spring (5+, 1-)			0.34					0.20				-0.56		0.59	0.75	0.54		
Season - winter (3+, 1-)	0.39		0.33											0.53				-2.41
Moon phase (1+, 0-)			0.23															
Maximal speed limit (7+, 0-)	0.01			0.06	0.03		0.04		0.04							0.09	0.09	
Ranger visits per km (13+, 0-)	0.02	0.02	0.02	0.02	0.01			0.02	0.04	0.02	0.02	0.03		0.06	0.06		0.03	
Habitat suitability (12+, 1-)	0.59	1.90	2.04	1.93	1.52	1.00	3.41	2.32		1.50	4.67		-2.39		5.91			3.64

Jackal Fox Porcupine Boar Badger Hare Hyena Hedgehog Wolf Mongoose Hyrax Marten Gazelle Ariel gazelle Jungle cat Partridge Barn owl Whipsnake

Figure 4. Direction and size of significant effects of road attributes, landscape features, and temporal factors on roadkill probability for all species. Total number of positive and negative effects for each variable– are in parentheses. Blue color represents positive effects (increased roadkill), and red color represents negative effects (decreased roadkill). Cells marked with 'x' are variables that were removed due to insufficient data in each model. Cells marked with '#' are variables that were removed due to large multicollinearity (VIF > 5).