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Research Article

Predicting roadkill: a regional-scale model for the Northern Tamandua integrating environmental and road characteristics

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Abstract

Wildlife-vehicle collisions may be the most visible impact of road networks on ecosystems. It has been shown that roadkill does not randomly occur across space and is distributed depending on environmental and ecological factors, such as habitat suitability and landscape connectivity of the interest species. In Costa Rica, the Northern Tamandua (*Tamandua mexicana*) is one of the mammal species most affected by road mortality. This study aimed to predict roadkill risk for the species in northwestern Costa Rica, considering habitat suitability and landscape connectivity. Roadkill data was retrieved from a local citizen science project and collected through a field survey. Habitat suitability and landscape connectivity models were calibrated on publicly available presence data. The models were then used as input, including additional road characteristics to calibrate a maximum entropy roadkill risk model. The final model had an excellent predictive performance (AUC = 0.989) and identified 108.7 km of road sections throughout the region as high risk, mainly found on primary roads. The most significant variables in the model were road width, traffic speed and habitat suitability. Landscape connectivity did not contribute significantly to the model. This study shows that road characteristics are the main contributors to roadkill regionally and highlights the relevance of the species' ecological features, such as habitat suitability, in its prediction. Thus, such variables should be considered in the design of mitigation measures for the impacts of roads on wildlife.

Key words: Costa Rica, habitat suitability, landscape connectivity, roadkill risk model, *Tamandua mexicana*, wildlife-vehicle collision

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Introduction

Throughout the world, road infrastructures play a significant role in the fragmentation of natural habitats and the overall biodiversity crisis (Coffin 2007). Indeed, approximately a fifth of the world's land points lie within 1 km of a road as of the last decade (Ibisch et al. 2016). Besides the complete loss of the ecosystem on their path during construction, roads generate a wide variety of abiotic and biotic impacts, including habitat fragmentation, chemical, acoustic and light pollution, barrier effect, invasive species, pathogen introduction or expansion, and increased wildlife mortality due to collision with vehicles (hereafter referred to as roadkill; Coffin 2007; Van Der Ree et al. 2015; Fabrizio et al. 2019). Road impacts on natural ecosystems are not restrained to their direct vicinity.

The habitat fragmentation and barrier effect they generate often result in the loss of landscape connectivity, i.e., the rate at which the landscape facilitates or impedes the movement of ecosystemic components (Taylor et al. 1993), thus affecting wildlife populations persistence and other ecological processes (Jackson and Fahrig 2011; Girardet et al. 2015). In extreme cases, the loss of landscape connectivity can even result in the genetic differentiation and extinction of segregated populations (Riley et al. 2006; Ceia-Hasse et al. 2017).

The most notorious impact of roads on biodiversity is arguably wildlife roadkill, a phenomenon that has been increasing globally in recent decades (Pagany 2020). Grilo et al. (2020) report that approximately 29 million mammals die annually due to roadkill in Europe alone, and Dornas et al. (2012) estimated an annual rate of 14.7 (± 44.8) million vertebrate deaths by roadkill in Brazil. Depending on the species, these numbers can significantly decrease genetic diversity and seriously threaten the viability of local wildlife populations (Jackson and Fahrig 2011; Ceia-Hasse et al. 2017; Oddone Aquino and Nkomo 2021). To develop effective mitigation measures, several studies have turned their eyes to studying the factors responsible for wildlife roadkill risk (Coelho et al. 2012; Grilo et al. 2011; Roger et al. 2012; Girardet et al. 2015; Visintin et al. 2016; Gonçalves et al. 2018; Fabrizio et al. 2019) and have found that roadkill is not randomly distributed across space.

In fact, roadkills are often concentrated in a way that reflects road and landscape characteristics as well as species movement and dispersal patterns at various spatial and temporal scales (Malo et al. 2004; Danks and Porter 2010; Santos et al. 2013; Visintin et al. 2016; Valerio et al. 2023). In particular, landscape connectivity and species habitat suitability have proven to play a significant role in the detection of roadkill hotspots (Grilo et al. 2011; Roger et al. 2012; Girardet et al. 2015; Visintin et al. 2016; Fabrizio et al. 2019; Valerio et al. 2023). Those studies and the roadkill risk models they provide are valuable tools for wildlife managers and decision-makers, given that they allow identifying key localities for mitigation measures or further studies (Rudnick et al. 2012).

The interest in road ecology research in Central America emerged only recently and has become increasingly popular in the last decade (Pinto et al. 2020; Silva et al. 2021). In a country like Costa Rica, with its extensive protected areas network harboring 6.5% of the global biodiversity (MINAE 2018), research to reduce and mitigate the impact of roads is of primary importance. Indeed, Costa Rica has one of the densest road networks in the world (MINAE 2018) and increasing traffic flow makes road impacts a central topic in conservation (Arévalo et al. 2017; Sánchez-Hernández 2018). One of the mammals most affected by roadkill in the region is the Northern Tamandua *Tamandua mexicana* (Pilosa: Mymecophagidae), Saussure 1860, both nationally and regionally. Many studies on roadkill in Costa Rica have listed it as the most encountered in surveys, excluding rodents and chiropters (Alfaro and Quesada 2015; Alfaro and Quesada 2016; Arévalo et al. 2017; Medrano-Vizcaíno et al. 2022; Villalobos-Hoffman et al. 2022; Granados-Rodriguez et al. 2024). Although the IUCN Red List of Threatened Species has listed *T. mexicana* in the Least Concern category (Ortega-Reyes et al. 2014), road mortality figures in the main threat faced by the species across its range. The actual magnitude and severity of the effects of roads on the species are unknown, which represents a serious threat to populations at regional and local levels (Ortega-Reyes et al. 2014). Moreover, only one study in Costa Rica has focused on trying to predict roadkill risk for this species but omitted environmental factors (Gutiérrez-Sanabria 2017).

Therefore, this study aimed at predicting roadkill risk for *T. mexicana* at a regional level in the Tempisque Conservation Area, Costa Rica, through a prediction model based on habitat suitability and landscape connectivity, as well as road characteristics. Specifically, this study intends to (a) characterize the spatial distribution of *T. mexicana* roadkills in the region; (b) identify road sections with high roadkill risk with precision; and (c) analyze the contribution of environmental (habitat suitability and landscape connectivity) and road variables to the prediction of roadkill risk for the species. As other authors have found, roadkill risk is expected to increase when habitat suitability and landscape connectivity are high (Grilo et al. 2011; Roger et al. 2012; Girardet et al. 2015; Visintin et al. 2016; Fabrizio et al. 2019; Valerio et al. 2023). The focus was directed to this specific area because of its ecological diversity, the lack of research conducted in it and because it is part of the National System of Conservation Areas. This is the first study utilizing those specific environmental and ecological variables to predict roadkill risk on Costa Rican roads.

Methods

The study was conducted from June to August 2023 in the entire national road network of the Tempisque Conservation Area (ACT) in northwestern Costa Rica. Presence data on *T. mexicana* in the region was used to produce a habitat suitability model (HSM) and a landscape connectivity model (LCM) for the species in the ACT. Both models were then used with the other variables to produce a roadkill risk model (RRM) based on collected roadkill data.

Study area

The study area corresponded to the terrestrial limits of the ACT, comprising the whole Nicoya peninsula geographical unit, as well as the western Tempisque plains (Fig. 1), covering a total area of 5126 km^2. Topography in the region is varied, with mountains, plains and valleys from sea level to 1018 m of elevation. The whole study area is located within the accepted distribution of *T. mexicana* (Ortiz-Malavasi 2014).

The climate in the region ranges from tropical dry to humid with a distinct dry season. The region encompasses the life zones of tropical dry forest, tropical moist forest, tropical wet forest and premontane wet forest (Holdrigde 1978, as well as some transition zones. The region hosts a variety of ecosystems, such as riverine, palustrine and lacustrine wetlands; tropical dry forests; tropical moist and wet forests; semi-deciduous and deciduous forests; mangroves; coastal forests; grasslands; plantation forests; and agricultural landscapes. Additionally, 23 protected areas of various categories are found within the study area. The total length of the road network is 6307 km (85.1% local roads, 14.9% national roads; see Fig. 1) with an average density of 1.23 km/km^2 (Ortiz-Malavasi 2014).

Species data

Presence data for the species was obtained from the Global Biodiversity Information Facility (GBIF 2023) for the whole distribution range and filtered to retain records of living individuals based on human and machine observations. Opportunistic sightings made during the study in the area were also included

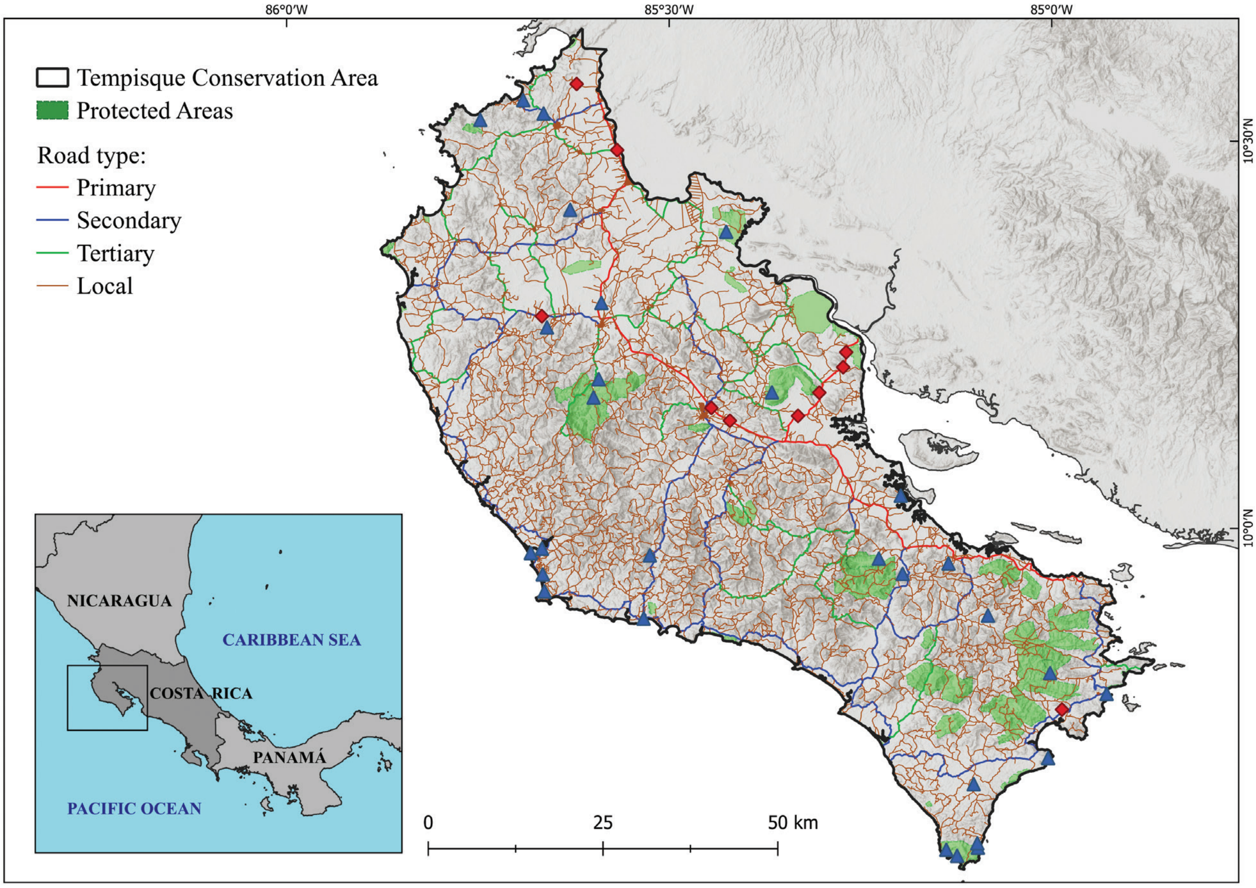

Figure 1. Terrain map of the study area. The study area boundaries are shown as the ACT terrestrial boundaries. The protected areas (excluding their maritime extension) are shown in green. Blue triangles represent occurrence data for living tamanduas in the study area. Red diamonds show roadkill occurrences. Roads are classified by category. The local roads are not part of the national network but are shown to enable a better understanding of the area.

in the dataset. Roadkill data was collected through a series of surveys between June and August 2023. Each national road in the area (973 km in total) was surveyed at least two times at a speed of 40–60 km/h. Local roads were not included in this study as they support low traffic volumes and evidence exists showing that high traffic volume significantly increases roadkill rates (Grilo et al. 2015; Santos et al. 2018)

Finally, roadkill records of *T. mexicana* available in the iNaturalist project “Fauna atropellada en las carreteras de Costa Rica” (iNaturalist 2023) for the study area, as well as GBIF records that showed an image of a road-killed individual and did not correspond to any of the iNaturalist records, were included to maximize the amount of data. A total of 558 presence and 10 roadkill georeferenced locations were obtained after filtering.

Habitat suitability model (HSM)

The HSM of the species in the study area was calibrated using one topographic and three vegetation predictors: slope, land cover type, mean canopy height and normalized difference vegetation index (NDVI). Since there is no detailed information on the ecological requirements of *T. mexicana* apart from the fact it tends to favor forested areas (Wainwright 2007; Navarrete and Ortega

2011), those variables were selected because of their easy obtention and relevance to distinguish major vegetation types. Land cover type was retrieved from the National Forest Inventory of Costa Rica (SINAC 2015). Mean canopy height (in meters) was obtained from the product derived by Potapov et al. (2020) from the Global Ecosystem Dynamics Investigation (GEDI-NASA). Regarding the NDVI, an index that describes vegetation thickness through an estimation of primary productivity (Spisni et al. 2012), it was calculated using satellite imagery produced by Landsat-8 (USGS) for the month of June 2023. Slope was derived from the STRM-USGS digital elevation model (DEM; Farr et al. 2007). All predictors were rasterized at a spatial resolution of 30 m using the QGIS software (QGIS.org 2023).

Since the study area represents only a small portion of the species' global distribution range and the fact that it is a generalist species, a two-level hierarchy was used to produce the HSM. In fact, habitat modeling is severely biased when only a small portion of a species' range is considered (Raes 2012; Guisan et al. 2014). Consequently, a first HSM was fitted for the species at a 1 km spatial resolution considering its entire distribution range. This first model was calibrated using the bioclimatic variables of WorldClim v2.0 (Fick and Hijmans 2017) and the elevation data of the STRM-USGS DEM. Duplicate occurrence records of the species were eliminated using a 1 km threshold in the NICHETOOLBOX software (Osorio-Olvera et al. 2016) resulting in 550 data points. To avoid an eventual multicollinearity between the variables, the variance inflation factor (VIF) was calculated for the dataset using the *raster* package in R (Hijmans and van Etten 2023), setting the threshold at 5 (Zuur et al. 2010). The elevation and 8 bioclimatic variables were retained as a result (see Suppl. material 1). The model was generated using the maximum entropy model in the MAXENT software (Phillips et al. 2023), with 500 iterations and 100 replicates, a random test sample of 25%, 10000 background points, bootstrap resampling and aleatory seed.

The resulting models were validated using the area under the curve (AUC) criteria and the 10 best models were then averaged in QGIS. According to these criteria, maxent model predictions can be considered excellent (AUC > 0.9), good (0.8 < AUC < 0.9), reasonable (0.7 < AUC < 0.8) or bad (AUC < 0.6), with an AUC < 0.5 meaning that the model predictions are no better than random (Phillips et al. 2006). The aforementioned local predictors were then used to refine the first HSM to the study area (Di Febbraro et al. 2015) at a 30 m spatial resolution, considering 36 presence records of the species in the area. Modelling settings for a validation method for the final HSM remained unchanged. All the variables used presented a VIF < 5.

Landscape connectivity model (LCM)

The LCM for *T. mexicana* in the study area was constructed according to circuit theory, which assumes that the individual lacks knowledge of their habitat beyond their immediate surroundings and does not require extensive knowledge of the studied population, like movement and dispersal patterns (Dickson et al. 2019 Diniz et al. 2020. A conductivity map of the area was built using the CIRCUITSCAPE software (Anantharaman et al. 2020), whose algorithm considers a set of nodes and a resistance surface to calculate the cost of moving through a given area. (McRae et al. 2008).

Instead of using a reclassification of land cover as a set of resistance values, i.e., values representing the difficulty of movement of an individual, a method that would require expert knowledge of the species (Fabrizio et al. 2019), the HSM was converted to a resistance surface. Resistance values were calculated with the formula used by Zhang et al. (2021) considering a high suitability threshold of 0.75 (tenth percentile training presence of the HSM). This formula converts each cell of a habitat suitability map with a value below the chosen threshold to a resistance value between 1 and 1000. The resistance of cells with a habitat suitability value above the threshold is set to 1 (Zhang et al. 2021, see Suppl. material 1).

In addition, to avoid the bias in the estimation of conductivity value between nodes when they are placed inside the study area (Koen et al. 2014), 43 nodes equidistant by 10 km were placed along a 10 km buffer around the study area (903 unique pairs). The resulting cumulative current map based on the nodes' pairwise analysis was considered as the final LCM.

Roadkill risk model

A maximum entropy model was used to predict roadkill risk probability for *T. mexicana* in the study area, as this algorithm only requires presence data. In this case, roadkill records were used as the presence data as done by other authors (Fabrizio et al. 2019; Wright et al. 2020). The HSM and LCM were used as the biological predictors for the model. On top, data on road width (in meters), average vehicle speed (in km/h) and average daily traffic (in vehicles per day) were retrieved from the Anuario de Informacion de Tránsito 2018 (MOPT 2018) and used as non-biological predictors. The Euclidian distance to urban settlements (in meters) was also added as a non-biological predictor and was calculated in QGIS from the National Atlas of Costa Rica (Ortiz-Malavasi 2014).

All predictors were rasterized at a 30 m spatial resolution, and the absence of multicollinearity was checked by imposing a VIF < 5. Similarly to the HSM, the model was generated in the MAXENT software, with 500 iterations and 100 replicates, a random test sample of 25%, bootstrap resampling and random seed. According to the home range size of *T. mexicana* (Navarrete and Ortega 2011), 10000 background points were constrained in a 250 m buffer around the road network (Fabrizio et al. 2019). A final consensus model was built by averaging the 10 replicate models with the highest AUC. Finally, roadkill risk hotspots were isolated when the road section presented a value above 0.75 in the RRM. This value corresponded to the tenth percentile training presence value of the roadkill risk records used in the RRM. To analyze the contribution of variables to the model, the permutation test provided by the MAXENT software was considered. This test measures the drop in AUC of the consensus model when one variable is omitted, indicating how much the model relies on it, and does not heuristically depend on the model (Phillips et al. 2006).

Results

No road-killed individuals were found during the surveys and 6 records were retrieved from the iNaturalist platform, as well as 4 records from the GBIF portal. Of the total roadkill records obtained, 70% were found to have occurred on primary roads and the remaining 30% on secondary roads. The highest roadkill density occurred around the Tempisque River estuary, in the vicinity of Barra Honda National Park (see Fig. 1). The HSM models showed a good predictive performance both at global and local levels, with an average AUC of 0.879 ± 0.011 and 0.826 ± 0.036, respectively. The average AUC of the 10 best replicates used as a consensus model was 0.896 ± 0.003 at the global level and 0.890 ± 0.021 at the local level. The final HSM for *T. mexicana* in the ACT showed that most of the suitable habitat was confined to coastal regions and low elevations, as well as valleys and topographically flat areas characterized by high canopy and dense vegetation. LCM highlighted valleys and other low-elevation areas, with a higher potential towards the southeast of the area and the vicinity of the Nicoyan Gulf (see Suppl. material 1).

The RRM showed excellent prediction performance scores with an average AUC of 0.949 ± 0.022, with the 10 best replicates used as a consensus model averaging an AUC of 0.989 ± 0.005. The model predicted a higher roadkill risk on primary roads located in the low elevation areas of the northern and eastern regions of the ACT, as well as some isolated sections on secondary and tertiary roads to the northern, western and southern extremes of the study area (Fig. 2A). In general, roads crossing more mountainous areas showed low roadkill risk. A total of 108.7 km of the national roads in the study area were identified as roadkill hotspots (Fig. 2B). Habitat suitability showed a positive relation to roadkill risk as hypothesized and, in general, all non-biological predictors showed a positive relation to roadkill risk. Landscape connectivity showed a slightly positive relation to roadkill risk according to the RRM variable importance (Fig. 3). However, this result varied greatly during replications, and landscape connectivity proved to be the variable with the lowest contribution to the model (0.2%). The highest contributing variables to the model were road width, average vehicle speed and habitat suitability (Fig. 4). Average daily traffic showed a lower contribution (2.7%) and the distance to urban settlements showed a low contribution value (0.5%).

Discussion

The model highlighted the importance of habitat suitability in predicting roadkill risk for *Tamandua mexicana* in the Tempisque Conservation Area. More importantly, the model showed that road width and traffic speed are the primary factors explaining the species' road mortality on the national road network in this area. Landscape connectivity, in turn, was not retrieved as a relevant factor for roadkill risk prediction. However, the results demonstrate that roadkill risk is high in specific localities of the study area. In fact, 11.2% of the total national road extent in the ACT can be considered as roadkill risk hotspots for the species of interest, with most sections concentrated in the northern and eastern parts of the peninsula, some of which coinciding with predictions made by Gutiérrez Sanabria (2017).

Despite the small size of the dataset obtained during the process, the model presented an excellent predictive performance, with an AUC > 0.9 (Swets 1988; Phillips et al. 2006). The fact that no roadkill was recorded during the survey period can be attributed to some behavioral aspects of *T. mexicana*. The species tends to travel more frequently and over greater distances during the dry season when resources are scarcer and ants and termites, its main food source, are less abundant (Nadjar and de la Ossa 2013; Arguedas and Ovares 2019). Also, many studies have concentrated their efforts on a particular or a few road

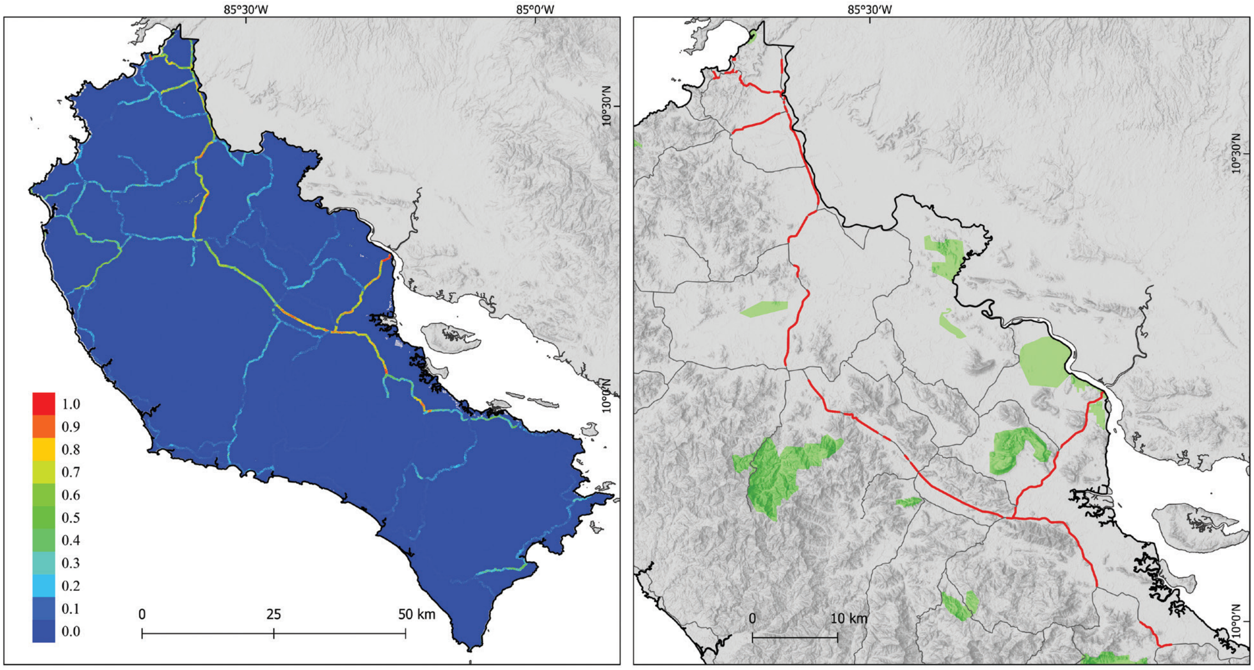

Figure 2. Roadkill risk model of *Tamandua mexicana* in the study area. The general roadkill risk model (A) is shown for the entire area. Risk increases towards red, the scale indicating roadkill probability of occurrence. Detail on roadkill risk hotspot (B) is provided in bold red, corresponding to road section with a roadkill probability of occurrence equal or greater than 75%. Terrain and protected areas are shown to give context to the roadkill hotspots.

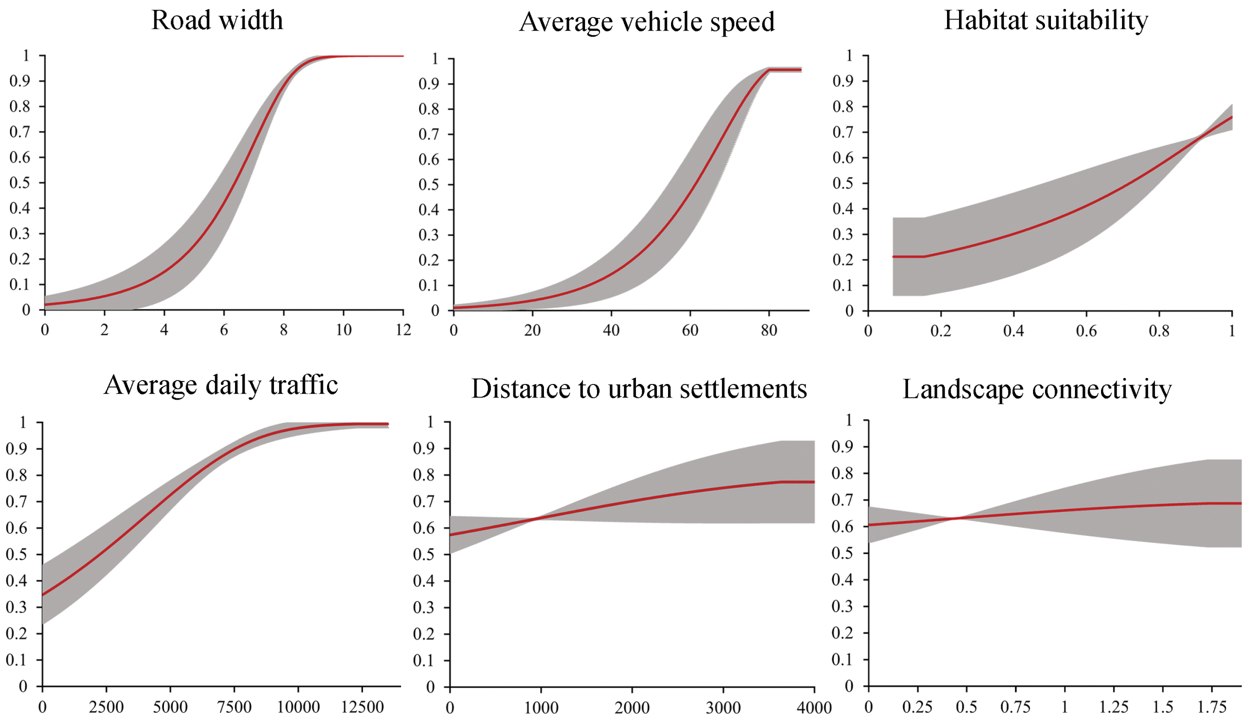

Figure 3. Response curves of the variables used in the roadkill risk model. The graphics show how each variable (horizontal axis) affects the probability of roadkill occurring (vertical axis). The red line corresponds to the average of the 100 model replicates and the grey area represents the standard deviation between them. Units in the horizontal axis are as mentioned in the methods section.

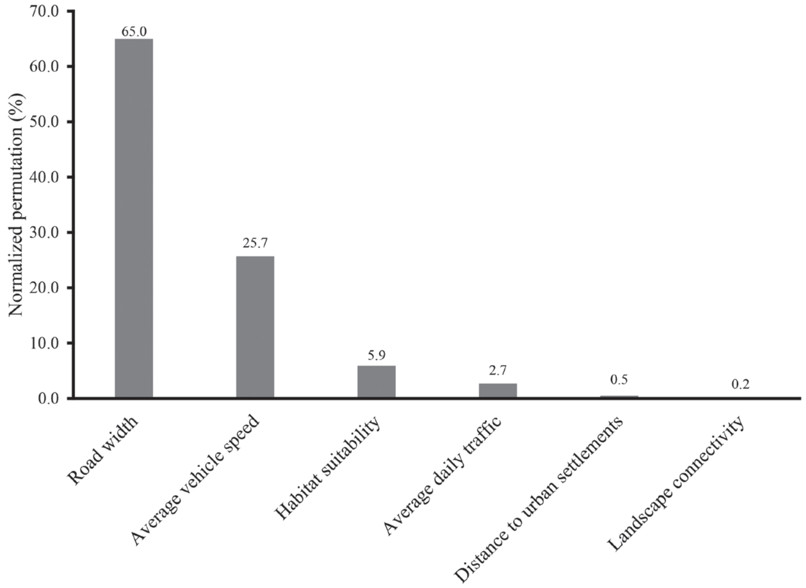

Figure 4. Contribution of each variable to the roadkill risk model. Percentage values represent the average change for the 100 replicates in the model AUC when the variable is omitted, giving its relative contribution to the final model.

sections instead of a regional scale network (Artavia et al. 2015; Girardet et al. 2015; Arévalo et al. 2017; Monge-Velázquez and Saénz 2022), so logistical limitations may have played a significant role here and increasing the survey effort is necessary to obtain more data.

Regarding the relative contribution of the variables to the model predictions, the fact that road width and traffic speed prevail makes sense when considering that *T. mexicana* is a slow and awkwardly moving animal on the ground (Emmons 1990). Besides being unable to gallop fast enough to avoid potential threats (e.g., a moving vehicle), *T. mexicana* adopts a defensive tripod posture and stays still when threatened (Navarrete and Ortega 2011). This behavior makes it particularly vulnerable when crossing wide roads with fast moving vehicles. The relevance of habitat suitability in the model is consistent with the conclusion made by several other authors. As a matter of fact, habitat suitability has been shown to contribute significantly to roadkill risk models of several species or groups with varied morphological traits, behaviors, and ecological requirements (Girardet et al. 2015; Kang et al. 2016; Fabrizio et al. 2019; Wright et al. 2020; Valerio et al. 2023). In addition, the response curves for road width, average vehicle speed and average daily traffic showed a positive relation with roadkill risk up to a “deadly trap” threshold (ca. 100% roadkill probability, see Fig. 3). This has been observed directly for multiple other taxa (Grilo et al. 2015; Santos et al. 2018) and indirectly, for example, in the case of the European badger *Meles meles* (Carnivora: Mustelidae) by Fabrizio et al. (2019), where a road type classification was used as a proxy to road width and traffic volume.

Furthermore, the strictly positive relation between roadkill risk and habitat suitability for *T. mexicana* coincides with the conclusions made by Girardet et al. (2015), who showed that roadkill risk for the roe deer *Caproelus caproelus* (Artiodactyla: Cervidae) is linearly correlated with the proportion of available habitat in the immediate vicinity of the road, and Wright et al. (2020), who found similar results for the European hedgehog *Erinaceus europaeus* (Euliopotyphla:

Erinaceidae). On the other hand, using a similar methodology, Fabrizio et al. (2019) found that the relationship between habitat suitability and roadkill risk is not linear for the European badger, a medium-sized mammal and generalist species similarly to *T. mexicana*, but was positive until a tipping point. The exact relationship between habitat suitability and roadkill risk is then species-dependent and often reflects on behavioral aspects such as dispersal patterns and new habitat exploration, as well as biological aspects of the species like reproduction (Fabrizio et al. 2019; Wright et al. 2020).

Landscape connectivity has been established as an important factor in predicting roadkill risk by several studies (Santos et al. 2013; Girardet et al. 2015; Kang et al. 2016; Fabrizio et al. 2019; Valerio et al. 2023). However, in this case, landscape connectivity did not contribute significantly to the roadkill risk model (0.2% contribution) and no clear relationship between roadkill risk and landscape connectivity was found. Some authors have also considered landscape connectivity as a direct product of a taxon's habitat suitability (Santos et al. 2013; Kang et al. 2016; Valerio et al. 2023) and, consequently, differentiating the role of both variables in roadkill risk prediction can be difficult (Fabrizio et al. 2019). Moreover, different methods produce different results when evaluating the complex concept of landscape connectivity (Diniz et al. 2020). In the present case, using a land cover resistance surface where each cover type is reclassified with a resistance value could result in a more significant variable and produce a different roadkill risk model, but the rate at which certain land cover type hinders or facilitate the movement of *T. mexicana* has not been studied. Furthermore, landscape connectivity can impact roadkill risk differently at different scales (Kang et al. 2016). Finally, the fact that the study area is mainly rural, a context where high habitat suitability patches might be a crucial component for the species, could explain the predominance of habitat suitability over landscape connectivity in the final roadkill risk model (Girardet et al. 2015).

The model generated in this study supports the hypothesis that habitat suitability is an important factor in roadkill risk for *T. mexicana* in the study area, and that roadkill risk increases when habitat suitability does. On the contrary, the model does not support the similar hypothesis for landscape connectivity, at least not at a regional level. Also, the model shows the importance of the road infrastructure characteristics on the species mortality by vehicle collision. Ultimately, it is pertinent to recognize the limitations of the results, especially regarding the size of the roadkill dataset. Indeed, the short period and monitoring protocol may have impacted the obtention of data on roadkill, and the use of citizen science data (i.e., in this case constituting the entire dataset for the HSM and RRM) can produce spatial bias (Van Strien et al. 2013) that was not necessarily accounted for. Thus, systematized surveys spanning a greater period and an increased knowledge of the species' ecology and behavior would produce more accurate models. Nonetheless, this study identified key sections for mitigation measures at a regional scale and calls for finer scale efforts to identify exact locations for their implementation.

Conclusions

Mortality by vehicle collision in the northern tamandua in the Tempisque Conservation Area is mainly influenced by road infrastructure and the habits of drivers. Despite that, this study shows that habitat suitability is an important factor for predicting roadkill risk and should be considered in similar studies whenever possible. The results also allow us to confirm that northern tamandua roadkills are not randomly distributed across the landscape, but the data and methods used cannot be used to define the role of landscape connectivity in explaining their distribution. We invite other authors and wildlife and conservation managers to incorporate this type of prediction model in their wildlife-vehicle collision mitigation measures, as they can be valuable in determining the location to build wildlife crossing infrastructure.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SB. Data curation: SB. Formal analysis: SB. Investigation: SB. Methodology: SB. Project administration: SB. Supervision: EA-H. Validation: EA-H. Writing – original draft: SB. Writing – review and editing: SB, EA-H.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary data

Authors: Silvio Boyat, Esmeralda Arévalo-Huezo

Data type: docx

Explanation note: Further details on the methods used.

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