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Research article

Tell me where you go, and I'll tell you where you die: landscape connectivity as a tool to predict amphibian roadkill risk

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ABSTRACT

Human overpopulation, development, and consequent activities such as land conversion and linear infrastructure expansion, are currently some of the main threats to biodiversity. Amphibians are especially affected because they depend on both aquatic and terrestrial habitats to complete their life cycles, which can be negatively impacted by roads, due to reduced landscape connectivity. Understanding animal movement across the land-scape may improve the prioritisation of sites to implementing mitigation measures. We assessed landscape connectivity using circuit theory, for two amphibian species (the Iberian spadefoot toad and the Iberian ribbed newt) on a Mediterranean landscape in Southern Portugal. We addressed the following question: Can landscape connectivity predict amphibian roadkill risk? Our connectivity models assigned higher current movement corridors to heterogeneous habitats composed of sparse forests combined with low-management agricultural areas and good networks of higher-density water bodies. We found a positive correlation between high-connectivity road segments and roadkill for both species, proving that landscape connectivity can be a valuable tool to predict locations with higher roadkill probability.

We acknowledge that maintaining a heterogeneous landscape, with a higher density of short-distance water bodies that connect highly suitable habitats is important for amphibians. The identification of corridors with increased amphibian movement probability provides useful insights for road agencies to implement amphibianoriented roadkill mitigation measures.

1. Introduction

Habitat loss and fragmentation, as a result of human activities such as land conversion, urban development, and linear infrastructure expansion, are currently among the largest threats to biodiversity (Forman and Alexander, 1998; Baguette et al., 2013). Amphibians are particularly affected as their complex life cycles imply both terrestrial and aquatic habitats, placing this taxonomic group at a higher conservation risk when compared to others (Blaustein et al., 1994; Beebee and Griffiths, 2005; Matos et al., 2012; Joly, 2019). Amphibians are sensitive to the loss or alteration of these two different habitats, as well as to the connectivity between them (Becker et al., 2010). In terrestrial habitats, linear infrastructures, such as roads, are responsible for habitat loss and fragmentation. Roads also introduce a barrier effect that affects key processes for maintaining population dynamics (e.g., migration and dispersal movements; Glista et al., 2008; Semlitsch, 2008; Sillero, 2008), and cause direct mortality through vehicle collision – a negative impact to which amphibians are especially vulnerable (Glista et al., 2008; Carvalho and Mira, 2011; Beebee, 2013; Pinto et al., 2023). Aquatic habitats, such as small water bodies are reproduction sites for many amphibian species, and when these sites are close to roads, high amphibian mortality rates are commonly reported (Ascensão and Mira, 2005; Santos et al., 2007; Schmidt and Zumbach, 2008; Cooke, 2011; Pinto et al., 2023).

There is broad consensus that preserving these aquatic habitats is of utmost importance, particularly because of the biodiversity they harbour, but also for their contribution to ecosystem services. European legislation (e.g. Habitats Directive 92/43/EEC and European Water

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Framework Directive) was implemented to protect these sites across the continent (Biggs et al., 2017; Hill et al., 2018). In the western Mediterranean Basin, many of these smaller water bodies dry up during the summer months, which represents an increased challenge to water-dependent species that naturally remain close to these habitats all year round (Pinto et al., 2023). Other species, less water-dependent, only use these habitats during the breeding season. These movements to and from water bodies (migration and/or dispersal events) involve navigating, on many occasions, through a more or less inhospitable landscape matrix (Joly, 2019; Cayuela et al., 2020).

Landscape connectivity is the degree of landscape that facilitates or hinders movement between resource patches (Taylor et al., 1993). It is of extreme relevance for amphibians breeding in water bodies, whose populational structure is often considered to be organised in metapopulations - distinct populations occurring in the same region exchanging individuals through dispersal (Hanski, 1998; Marsh and Trenham, 2001). The joint effect of roads and landscape fragmentation can increase the isolation of breeding populations, particularly of less vagile species (Carr and Fahrig, 2001), leading to a higher probability of extinction due to lower demographic and genetic input (Zeller et al., 2012; Baguette et al., 2013). However, such effect can be reduced, for example, by: 1) maintaining corridors or small remnant patches (Bodin and Saura, 2010; Saura et al., 2014; Bishop-Taylor et al., 2015) that facilitate movement across the landscape; and 2) installing roadkill mitigation measures to provide safe crossing between well-connected patches (Jarvis et al., 2019; Boyle et al., 2021). This is particularly relevant for amphibian populations since they frequently experience local extinctions, even in non-fragmented landscapes (Trenham et al., 2003). Nevertheless, the application of roadkill mitigation measures (usually costly structures) mostly relies on studies that solely consider the association between roadkill records and spatial variables characterising road and landscape features, not considering landscape connectivity. Notably, despite the increase in landscape connectivity research in the last decade (Dickson et al., 2019) and its known relevance in population dynamics (Cushman, 2006; Ribeiro et al., 2011), few studies have combined landscape connectivity with road ecology (Santos et al., 2013; Fabrizio et al., 2019; Valerio et al., 2023). Such studies are even scarcer when fine spatial resolutions or small-sized animals are considered. Assessing landscape connectivity for amphibians is especially difficult due to the lack of movement data, which limits the knowledge of the different species' habitat preferences and restricts the implementation of effective conservation measures (Cushman, 2006). This challenge is particularly concerning in highly seasonal dynamic landscapes impacted by anthropogenic and environmental changes, where quantifying landscape connectivity could help to maintain the viability of populations (Nowakowski et al., 2017). In addition, the combination of habitat suitability and landscape connectivity offers a cost-effective alternative or complement to overcoming the challenges of collecting movement data in the field (Valerio et al., 2019). The inclusion of environmental data at fine spatial resolutions may also reduce uncertainties in prioritising sites where roadkill mitigation measures should be implemented or improved. In this study, we analysed whether roadkill probability increases with landscape permeability by assessing landscape connectivity using circuit theory, for an anuran species, the Iberian spadefoot toad (Pelobates cultripes); and an urodele, the Iberian ribbed newt (Pleurodeles waltl) on a Mediterranean landscape in Southern Portugal. The Iberian spadefoot toad is a generalist anuran with distinct terrestrial and aquatic stages (Recuero, 2014), contrasting with the more aquatic behaviour of the Iberian ribbed newt during adulthood, characteristic of many urodeles in our study area. Notably, terrestrial movements of the Iberian ribbed newt remain largely uncharacterised (Salvador, 2014). Both species are common in the South of the country (Speybroeck et al., 2016) and are particularly affected by road mortality, representing two of the most road-killed amphibian species in our study area (Pinto et al., 2023). We also determined whether road segments with higher connectivity (and,

consequently, higher movement probability) are associated with higher roadkill probability, as amphibians are more likely to cross roads at sites with increased connectivity (Koen et al., 2014). If so, connectivity might be used as a valuable tool to identify optimal locations for implementing roadkill mitigation measures, significantly increasing the efficiency of mitigation crossing structures when compared to methods that use only roadkill hotspots or landcover data. The ultimate goal is to provide conservation managers and road practitioners with a comprehensive evaluation of functional connectivity among terrestrial and aquatic habitats for amphibians that can be relevant to implement future conservation actions.

2. Methodology

Amphibians rely on aquatic habitats (mostly small water bodies) for reproduction (Knutson et al., 2004; Ribeiro et al., 2011); therefore, we selected water bodies within our study area to represent the core habitat patches for these species. We generated resistance surfaces from ecological niche models (Diniz et al., 2020) to calculate potential landscape functional connectivity, representing the probability of movement between suitable habitats (McRae et al., 2008). This approach enabled us to identify theoretical corridors with higher movement probability and assess whether road segments intersecting these corridors were associated with higher roadkill probability.

2.1. Study area

This study was conducted in the Alentejo region, Southern Portugal, in an area covering approximately 210.000 ha (Fig. 1). The landscape is mainly composed of Mediterranean cork (Quercus suber) and holm (Quercus rotundifolia) forests with varying tree cover and density (Pinto-Correia and Mascarenhas, 1999). It is mixed with agricultural areas in equal proportions, composing the complex agro-silvo-pastoral system known as montado (Pinto-Correia et al., 2011). These agricultural areas include mainly pastures for cattle grazing and cereal crops; however, other land uses such as orchards and permanently irrigated crops are also present at lower extents (Pinto-Correia and Mascarenhas, 1999). This landscape mosaic structure is considered one of the highest biodiverse ecosystems in the western Mediterranean Basin (Pinto-Correia et al., 2011), providing habitat for 13 of the 20 existing amphibian species in the country (Speybroeck et al., 2016). The topography is generally flat with gentle slopes ranging from 100 m to 400 m a.s.l. The climate is typically Mediterranean, with hot and dry summers (with mean temperatures between 16.5 °C and 31 °C in August) and mild and wet winters (mean temperatures ranging from 5.8 °C to 12.8 °C in January). The region is also marked by differences in precipitation between the different seasons (mean precipitation - Spring: 174 mm; Summer: 34 mm; Autumn: 181 mm; Winter: 240 mm) with mean annual precipitation reaching 650 mm (Évora, 1871-2008; IPMA, 2021). This region is also crossed by a well-established road network, comprising one highway and several national and municipal roads, including the main transportation corridor connecting Lisbon to Madrid. All these characteristics contribute to amphibian threats (including increased roadkill rates) and were the main reason for the choice of conducting the study at this location.

2.2. Water body surveys

The amphibian surveys were carried out between March and May (period of higher larvae activity in our study area) over 3 years (2016, 2017 and 2019) across a range of selected water bodies (n = 130, Fig. 1), from temporary ponds to medium-sized water reservoirs (min = 14 m²; max = 68,228 m²). Amphibian larvae sampling was done through dipnet sweeping, each one approximately 1–3 m long. For each of the sampled water bodies, we calculated its area on a GIS software (QGIS; QGIS Development Team, 2022; v3.24.1); the number of sweeps



Fig. 1. – Study area in Southern Portugal, with the main land cover classes, as well as urban areas and larger water bodies. Major national and municipal roads and the highway are also represented. Sampled water bodies (n = 130) are depicted as white circles.

performed was proportional to the calculated area through categorised classes (Table S1, supplementary materials). When possible, we performed the sweeps at different depths, to increase the probability of collecting animals from different species. On each sweep, we counted and identified each larvae to the lowest possible taxonomic level. After the counts, we released the larvae into the water. We excluded rivers from our sampling as these do not represent sites of reproduction for the studied species (Recuero, 2014; Salvador, 2014).

2.3. Roadkill surveys

We performed roadkill surveys on periods of high adult activity (when most adult amphibians moved to breeding sites) along three National Road sections (EN4, EN114 and EN18) and one Municipal Road section (EM529), comprising approximately 120 km of surveyed roads. Sampling followed a standardised protocol (see Santos et al., 2011) and was performed daily. On each survey, an experienced observer drove a car at 20-40 km/h during the first morning hours (to reduce the impact of traffic and carcass removal by scavengers), scouting both sides of the road, including lanes and shoulders. All encountered road-killed animals were collected and registered. All amphibian carcasses were identified to the lowest possible taxonomic level, their geographical position recorded with a handheld GPS device (Garmin® eTrex®), and removed from the road to avoid double counting during subsequent surveys. The error in the coordinates was always lower than half of the spatial resolution of the environmental variables (30 m; see below). The data was then filtered according to the two target species and used to relate roadkill mortality to high-connectivity sites.

2.4. Ecological niche models

We built ecological niche models (ENMs) and used the presence of each amphibian species' larvae on each water body as a response variable. Due to the low number of sampled water bodies with species' presence for each sampled year, we chose not to spatially thin the data. However, any potential spatial clustering and sampling bias arising from this decision were addressed using a bias file (see supplementary materials S1.1. for a detailed description on ENM calculation).

To provide our models with the most updated information on environmental changes at a finer resolution, we used land cover and other remote sensing-derived predictors, such as vegetation indices and topographical data, with a spatial resolution of 30 m (see below). To calculate the land cover predictors, we considered the two major classes present in our study area: forest and agriculture (Fig. 1). We used CORINE Land Cover 2012; 2018 to characterise the land use during the study period and we extracted the mean percentage of each land cover to a 30 m pixel resolution raster. We have also computed the mean Enhanced Vegetation Index (EVI; Liu and Huete., 1995), which represents local dynamics in primary production, as this has been previously used to explain amphibian occurrence (Qian et al., 2007; Pinto et al., 2023, 2024). We calculated EVI from LANDSAT 8 image collections (Level 2, Tier 1; data available from the U.S. Geological Survey) with a 30 m spatial resolution for each sampling season of each year (March to May), retaining high-quality images with 0 % cloud cover for the whole study area (WRS-2 scene: path 203, row 33). We processed all composite images and calculations in Google Earth Engine (Gorelick et al., 2017). Lastly, we used a DEM (Digital Elevation Model; DGT, 2018) to derive topographical predictors (elevation and slope) as these often influence amphibian occurrence, for example, by the concentration of water in lower topographies (Santos et al., 2007). Because urban areas and roads

are not suitable habitats for amphibians (Van Buskirk, 2012), the pixels from these land cover classes were removed from all predictors before modelling. All these operations were performed using QGIS software. Table 1 summarises all the used predictors.

We calculated correlative ENMs to estimate the species' realised ecological niche (sensu Sillero, 2011) following standard procedures (Sillero et al., 2021; Sillero and Barbosa, 2021), because we were interested in identifying the most suitable sites for the species' presence to use as input to calculate landscape connectivity. Mechanistic models are not suitable for this study as they forecast the fundamental niche (only determined by abiotic factors) and not the realised one (determined by abiotic, biotic, dispersal, and historical factors; Sillero, 2011).

Before model construction, we checked the multicollinearity among predictors through the Variance Inflation Factor (VIF) (Zuur et al., 2010; Dormann et al., 2013). All variables had a correlation below the defined threshold (VIF <5).

We used the presence-background algorithm Maxent (Phillips et al., 2006, 2017) to calculate ENMs for each year and each species. We chose to model each sampled year independently as the number of sampled water bodies differed between years. We ran Maxent with the default values, randomly splitting the data into 70 % training and 30 % testing. We ran each model 15 times (for each year and species) and used as the final model the averaged model (mean model of all our 15 runs) to consider the uncertainty in the models. Maxent predicts the habitat suitability for each species through the Habitat Suitability Index (HSI), which ranges from 0 (completely unsuitable) to 1 (completely suitable). Additionally, we calculated 15 null models (for each year and each species) to evaluate the explanatory power of our models, following Raes and ter Steege (2007) methodology. This involves building null models with the same number of points as our empirical models (but randomly selected) and comparing both AUC values with the Wilcoxon rank sum test to assess the model significance. If the AUC of the empirical models is significantly higher than the AUC of the null models, these have better predictive performance (for more details on ENMs calculation, see supplementary materials S1.1.).

We performed all the statistical analyses using the software R (v 4.1.2; R Core Team, 2021) and used Maxent (v3.4.4; Phillips et al., 2006) to run the ENMs.

2.5. Landscape connectivity models

We built the landscape connectivity models (LCMs) for the analysed species with the Circuitscape software (Julia implementation v5.0; Anantharaman et al., 2019). This software relies on electrical circuit theory principles to integrate random walk pathways, where current is injected across a resistance layer to provide an accurate assessment of

Table 1

T.	ist (of predictors	s used for	building	the habitat	t suitability	models
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Predictor name and code	Description	Source	References		
Agricultural areas (agriculture)	Percentage of agricultural areas (%)	CORINE 2012, 2018	EEA		
Forest areas	Percentage of forest areas	CORINE 2012,	EEA		
(forest)	(%)	2018			
Enhanced	Mean changes in primary	USGS	Liu and		
Vegetation	production content index.		Huete		
Index (EVI)	-1 (indicates stressed		(1995)		
	vegetation) to 1 (indicates				
	healthier vegetation)				
Elevation	Elevation retrieved from	Direção Geral	DGT (2018)		
	digital elevation model	do Território			
	(meters)	(DGT)			
Slope	Elevation changes across	Direção Geral	DGT (2018)		
-	the landscape. Derived from	do Território			
	digital elevation model	(DGT)			
	(degrees)				

animal movement and gene flow over the landscape (McRae et al., 2008). This approach aids the assessment of functional connectivity among habitat patches: patches are considered connected if the landscape matrix offers lower resistance, or disconnected if resistance is high (Zeller et al., 2012). The output is the probable movement pathways of varying strengths influenced by the resistance layer, enabling the identification of corridors and other landscape elements connecting habitat patches (McRae et al., 2008).

We averaged the ENMs for the three sampled years into a single model for each species (Fig. 2) and computed a negative exponential function (Keeley et al., 2016) to represent landscape resistance. This method allows a more flexible representation of resistance by capturing non-linear permeability and adjusting to species movement constraints. We used the following equation: $R = 100 - 99x((1 - exp(-c \ge h)/(1 - exp(-c \ge h))/(1 - exp(-c \ge h))))$ (-c))), in which R represents the resistance, h the HSI and c the transformation value. We used different c values representing different relationships between resistance and suitability (c = 0.25; c = 2; c = 4; c =8) (Valerio et al., 2019; Salgueiro et al., 2021). We reintegrated the urban areas and roads with the resistance maps and coded them as a high resistance layer. We assigned the highest resistance value to roads concerning the maximum resistance value of our maps (considering each transformation value; Table S2, supplementary materials), as roads are not completely impermeable to movement (Holderegger and Di Giulio, 2010). We used each resistance surface map (4 for each species) as input for the LCMs. This approach is considered effective, particularly when movement data is not available (Keeley et al., 2016; Valerio et al., 2019; Godet and Clauzel, 2021). We defined our focal nodes as the rasterised centroid of each sampled water body over the three years for each species (91 for the Iberian spadefoot toad and 63 for the Iberian ribbed newt) and unsampled water bodies scattered through the study area. We calculated the third quartile of both the area and the HSI of the sampled water bodies (1952 m² and 0.748 for the Iberian spadefoot toad and 1625 m² and 0.619 for the Iberian ribbed newt, respectively) and used these as thresholds for the selection of unsampled water bodies as focal nodes (n = 50 for the Iberian spadefoot to ad and n = 58 for the Iberian ribbed newt). Water bodies with higher values of HSI may be suitable for amphibians, and the maximum area threshold allows us to exclude water bodies that might have inappropriate dimensions (e.g. large dams for water retention) and therefore are not used by these species. We used the pairwise calculation mode, as well as eight neighbour raster cell connections, to calculate the current density between all pairs of focal nodes (McRae et al., 2008). This approach follows the assumption that amphibians randomly move across the landscape through any possible pathways between nodes (Bishop-Taylor et al., 2015; Dickson et al., 2019). After these calculations, the current density was summed into a single cumulative map representing the most permeable pathways for each species' dispersal (McRae et al., 2008).

2.6. Landscape connectivity as roadkill probability location predictor

To analyse whether locations with higher connectivity could be associated with high roadkill probability, we compared the mean values of our connectivity models with roadkill occurrence recorded in Autumn (between mid-September and mid-December) for each species throughout the entire study period. We selected this season because it corresponds to the period with the highest amphibian activity in our region when adults are moving towards breeding sites. For this, we divided the roads into 500 m contiguous segments and created a 500 m buffer around each segment. Then, we extracted the presence and absence of each species' roadkill in each road segment, as well as the mean connectivity value of each road segment. Next, we performed a Generalised Linear Mixed Model (GLMM) with binomial distribution (Bolker et al., 2009) for each species (and resistance transformation) relating the presence and absence of roadkill, with the mean connectivity values (with "Road" as a random factor). Lastly, we compared each model based on Δ AIC. All these operations were performed within



Fig. 2. – Habitat suitability averaged maps for the three analysed years with lighter-coloured areas representing higher habitat suitability (urban areas and roads were not included in this analysis). Left map concerns the Iberian spadefoot toad, while the right one is for the Iberian ribbed newt.

R software (using the packages "glmmTMB" (Brooks et al., 2017), "DHARMa" (Hartig, 2022) and "MuMIn" (Barton, 2015), for model construction, validation and selection, respectively).

3. Results

During the three-year period, we recorded 2503 Iberian spadefoot toad larvae and 272 Iberian ribbed newt larvae at the water body surveys, and 315 Iberian spadefoot toad carcasses and 463 Iberian ribbed newt carcasses at the roadkill surveys.

The ENMs revealed a moderate-to-good ability to predict species occurrence, suggesting that the selected predictors effectively characterised the potentially suitable habitats for both species (Table 2). The AUC from the empirical models were significantly higher than the AUC from the null models in all analysed years (Wilcoxon rank sum tests; Table 2). Fig. 2 shows the spatial output of the (mean) ENMs for the three years and each species. Our models revealed a similar response between both analysed species: mean EVI was the most important predictor for the years 2016 and 2019, and the percentage of forest was the most important predictor in 2017 (for detailed results of the EMNs of each species, see supplementary materials S1.2.). The LCMs for both species predicted areas of increased movement probability predominantly in the North and Northeast regions of our study area. Those sites are characterised by open *montado* forests with varying tree density, disrupted by open fields used for low-impact agriculture practices and

Table 2

AUC results for the empirical and the null habitat suitability models for the analysed years (2016, 2017 and 2019) for the Iberian spadefoot toad and the Iberian ribbed newt. Wilcoxon rank sum tests show that the AUC from the empirical models were significantly higher than the AUC from the null models for all analysed years.

Iberian spadefoot toad (Pelobates cultripes)						
Year	Empirical model	Null model	Wilcoxon rank sum test			
	AUC	AUC				
2016	0.818 (±0.03)	0.759 (±0.04)	W = 198, p < 0.001			
2017	0.817 (±0.03)	0.709 (±0.04)	W = 223, p < 0.001			
2019	0.822 (±0.03)	0.693 (±0.03)	W = 225, p < 0.001			
Iberian	ribbed newt (Pleurodel	es waltl)				
Year	Empirical model AUC	Null model AUC	Wilcoxon rank sum test			
2016	0.897 (±0.03)	0.819 (±0.04)	W = 208, p < 0.001			
2017	0.879 (±0.02)	0.742 (±0.04)	W = 225, p < 0.001			
2019	0.844 (±0.03)	0.752 (±0.06)	W = 207, p < 0.001			

cattle grazing (Fig. 3), and supplied with a good network of shortdistanced water bodies. These habitat patches, subject to less intense human interventions, provide diverse vegetation composition and shelter, which, together with the increased number of short-distanced water body networks, likely enhance movement probability. Conversely, isolated water bodies showed less probability of generating movement corridors when the surrounding landscape was composed of dense forests in higher altitude areas. Similarly, sites with low tree cover and highly agricultural landscapes in the Southeast also showed lower probabilities of movement for both species.

The GLMMs that revealed the best fit to data resulted from the moststeeper transformation (c = 8), therefore all the other transformations were discarded (see Table S3 supplementary materials for model selection). We found a positive correlation between road segments with higher connectivity and roadkill presence of both species (Iberian spadefoot toad: coef = 0.157, p = 0.005; Iberian ribbed newt: coef = 0.223, p = 0.002; Fig. 4). The GLMMs showed good levels of data fit despite their R-squared values (0.28 for the Iberian spadefoot toad and 0.30 for the Iberian ribbed newt). Further evaluation revealed that the residual plots showed no patterns for both species (Figs. S3 and S4, supplementary materials). Road segments with roadkill were associated with higher connectivity values, whereas road segments with no roadkill generally presented lower connectivity values. Table 3 presents these analyses results.

4. Discussion

Our study assessed landscape connectivity to identify potential movement corridors for two amphibian species (one anuran and one urodele) in a road-dominated Mediterranean landscape. The LCMs present convergences, particularly on the location of the most important movement corridors. Our analysis also revealed that landscape connectivity can be used as a tool to identify sites with increased roadkill probability, enabling the application of this modelling technique to draw effective conservation measures. Although research in landscape connectivity has considerably increased in recent years (Dickson et al., 2019), few studies have integrated landscape connectivity with road ecology (e.g., Santos et al., 2013; Fabrizio et al., 2019). For instance, Fabrizio et al. (2019) highlight the role of landscape connectivity in determining roadkill probability for the Eurasian badger. However, the scale used in that study does not support precise planning for small-scale mitigation measures. In contrast, our study uses fine-scale remote sensing imagery to precisely identify sites with higher connectivity and consequently increased roadkill probability. This fine-scale approach provides road agencies with the tools necessary to develop localised



Fig. 3. – Connectivity maps for the Iberian spadefoot toad (top) and the Iberian ribbed new (bottom). Vivid colours represent sites with higher connectivity and probability of movement. Sites with a higher probability of movement are mainly located in the North/Northeast open *montado* forests. Isolated water bodies are depicted as small lighter dots closer to the study area borders and in areas with less suitable habitats. In the detailed areas, it is possible to see the difference in the connectivity between transition sites, as well as isolated water bodies with no connectivity corridors, despite the apparent forested (Iberian spadefoot toad) or suitable (Iberian ribbed newt) surrounding habitats.



Relationship between connectivity and roadkill probability

Fig. 4. –Roadkill probability as a function of connectivity for the Iberian spadefoot toad (top) and the Iberian ribbed newt (bottom), according to the results of the GLMMs. Both species present a positive correlation: road sections with higher connectivity values exhibit higher probabilities of roadkill. Points represent the number of road sections with presences and absences of roadkill.

mitigation measures that enhance landscape connectivity while reducing amphibian roadkill. Similarly, Chyn et al. (2021) employ fine-resolution data to identify road segments with increased roadkill risk for reptiles in Taiwan. However, our study not only identifies road segments with high roadkill probability but also provides valuable insights into the landscape characteristics that promote connectivity across roads, offering a comprehensive framework for mitigation planning.

4.1. Landscape connectivity models

Our LCMs show the existence of distinct movement corridors for both species, yet some locations present higher movement probability than others. The existence of shared extended movement corridors is particularly evident in the North and Northeast regions of our study area, where two major areas highlight distinct corridors. These largely correspond to heterogeneous *montado* extents (habitats where

Table 3

GLMMs between roadkill and mean landscape connectivity for the Iberian spadefoot toad and Iberian ribbed newt with respective coefficients, AIC and R^2 .

	Estimate	Std. Error	z value	p- value	Confidence interval (95 %)	
Iberian spadefoot toad (P. cultripes)						
Mean connectivity	0.157	0.057	2.775	0.005	0.05; 0.27	
Model AIC	230					
\mathbb{R}^2	0.28					
Iberian ribbe	d newt (P. wali	tl)				
Mean connectivity	0.223	0.07	3.103	0.002	0.08; 1.18	
Model AIC	261					
R ²	0.30					

moderate-density oak forests are mixed with low-intensity agricultural areas). The particular way this distinctive landscape is managed (e.g. scarcely managed forest, with low intensity grazing and agriculture (Díaz, 2009)) allows for the existence of food and shelter, as well as potential stable levels of humidity that may support a greater number of amphibians.

Equally important for the presence of both species, seems to be the proximity among water bodies, particularly in highly suitable areas. The majority of the higher current density corridors seem to occur in areas with a well-established water bodies' network. Other studies have also reported that higher local water body densities with diversified habitats typically harbour larger amphibian populations (Semlitsch, 2000; Trenham et al., 2003). This is especially relevant since amphibian populations usually experience high turnover (Trenham et al., 2003). Since hydroperiod can be different, even between water bodies located at shorter distances, a well-diversified network of reproduction sites may contribute to population persistence. Ribeiro et al. (2011) reported that the structural connectivity of water body networks is of extreme importance for Mediterranean amphibians. The authors found that the number of species was related to the spatial position of a given water body concerning others nearby in the network, with central ones having higher connectivity. Joly et al. (2001) also highlighted the importance of water body networks on newt occupancy in agricultural areas in France. Yet, it is worth noting that the presence of high connectivity corridors in apparently good networks of water bodies does not guarantee amphibian occurrence. Although the water bodies' surrounding habitat may play a primary role in amphibians reaching those sites, other factors surely influence their occupancy, such as water conductivity and temperature, hydroperiod and presence of vegetation and predators, among others (Knutson et al., 2004; Denoël and Lehmann, 2006; Fortuna et al., 2006).

Conversely, isolated water bodies seem to be more difficult to access (absence of movement corridors), regardless of the surrounding landscape they are in. Fortuna et al. (2006) stated that water bodies may act as stepping stones in harsher landscapes, providing links for amphibian movement across inhospitable landscapes. This may be visible, at least for smaller distances; however, when water bodies are too distant from others, they are clearly depicted as isolated in our models. Although this is visible in areas with medium connectivity values, it is particularly evident in less connected areas with low water body densities. This may be especially alarming if the distance to reach other water bodies exceeds the dispersal capacity of the species inhabiting those isolated water bodies. In the medium/long term, this could result in local extinctions for those amphibian populations.

The lack of a solid network of water bodies in densely forested areas (for example, as in the South/Southwest part of our study area) may be the primary reason explaining the lower probability of movement (absence of high connectivity corridors) in sites that display less landscape resistance. As stated above, most of the existing water bodies are man-made artificial structures for cattle watering and crop irrigation and densely forested areas are usually less associated with these practices, which could explain the lower densities of these structures at forested areas.

4.2. Landscape connectivity as roadkill probability location predictor

Our models effectively found a significant positive relationship between road segments with higher landscape connectivity and both species' roadkill, confirming that roadkill occurs predominantly in road segments that have higher movement probability. This relationship is less evident in the Iberian spadefoot toad, perhaps due to its more generalist habitat requirements. Koen et al. (2014) also reported that amphibians are more likely to cross roads in areas of higher connectivity. By applying a high resistance value to roads (and urban areas), our connectivity models allowed us to locate sites where the current is stronger on both sides of a road, which can be interpreted as high probability crossing sites and where roadkill mitigation measures (such as underneath road tunnels and drift fences) might be more effective. We are, however, aware that connectivity might not be an isolated component in shaping the location of roadkill hotspots (Santos et al., 2013). In fact, sites with increased road mortality are not static over space and time (Medinas et al., 2021), and are known to be influenced by traffic density (Fahrig et al., 1995; Zimmermann Teixeira et al., 2017), road features (Clevenger et al., 2003; Medinas et al., 2013), and weather conditions (Carvalho et al., 2017). Yet, Pinto et al. (2024) highlighted that road segments capable of maintaining stable levels of humidity displayed more consistent amphibian roadkill patterns across various years. This apparent resilience of high-mortality road segments may constitute optimal sites for the implementation of mitigation measures to maintain or increase landscape connectivity while reducing the risk of road mortality.

5. Conclusions and study limitations

This study provides significant insights into two amphibian species' movements through habitats with varying complexity, on a road-dominated Mediterranean landscape. Our results provide implications for the implementation of roadkill mitigation measures. The use of landscape connectivity tools proved to be effective in identifying the most probable sites where these two species may be at higher roadkill risk.

We did not integrate rivers in the resistance surfaces, as unpublished data shows that our studies species occur exclusively in water bodies and do not use rivers as reproduction sites. However, these ecosystems could still play a role in facilitating amphibian movement by serving as dispersal corridors. Additionally, the non-integration of dispersal limits in our LCMs (due to lack of information about our species' dispersal distances), as well as the exclusion of potentially confounding factors (e. g., traffic volume, local habitat quality) in our GLMMs (also due to data unavailability) may have influenced our results. For instance, this could explain moderate roadkill probabilities that were associated with lower connectivity road segments. However, applying non-linear transformations to resistance surfaces likely provided a more accurate representation of how species perceive and navigate the landscape, potentially capturing roadkill patterns driven by these confounding factors.

While these limitations should be considered when interpreting the results, our approach demonstrates the direct applicability of these modelling tools as viable alternatives to extensive roadkill and population surveys, providing similar precision at considerably reduced costs when compared to more conventional approaches. With the identification of the corridors with the highest likelihood of movement, road agencies and practitioners have guidelines to implement amphibianoriented roadkill mitigation measures that have already demonstrated effectiveness in reducing amphibian roadkill probability. Therefore, it is possible to provide a connection between suitable habitat patches even in the presence of highly resistant structures such as roads. Nevertheless, the maintenance of heterogeneous landscapes (with equal proportions of both forested and agricultural areas, as well as sufficient shelter), supplied with a good network of water bodies is essential to provide continuous movement corridors for amphibian populations, assuring their persistence.

CRediT authorship contribution statement

Tiago Pinto: Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis, Data curation, Conceptualization. **Sara M. Santos:** Writing – review & editing, Supervision, Methodology, Conceptualization. **António Mira:** Writing – review & editing, Project administration, Methodology, Funding acquisition. **Neftalí Sillero:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.125273.

Data availability

Data will be made available on request.

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