



Factors determining roadkills in a mammal carnivore are road-type specific

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Abstract

Roads threaten the conservation of many wildlife species. Carnivores are one of the most susceptible groups due to their habitat requirements. We explored the roadkill patterns of European polecats (*Mustela putorius*) on motorways and roads to investigate if these patterns depend on road type, a research topic frequently neglected in the literature. We studied 85 roadkills on motorways and 73 on roads, and the corresponding number of random points with no roadkills in every road type. We characterized them with 7 habitat and 7 road-related variables. Roadkill sites were significantly associated with the abundance of rabbit burrows. However, this effect was stronger on motorways, as they provide more suitable habitat for the establishment of prey species on their wider rights-of-way, or on the road interchange islands, which provide wide unused spaces. In contrast, road interchange islands on conventional roads that are simple intersections and have narrower rights-of-way. Furthermore, roadkills occurred in areas with lower agricultural cover. Thus, natural habitats on roadsides could act as alternative foraging areas for this carnivore increasing their roadkill risk. Our results showed the need to consider the characteristics such as the availability of prey or the surrounding habitat, as well as intrinsic characteristics of the road type when studying wildlife roadkills as the road-type-mediated patterns demand-specific mitigation measures.

Keywords Linear infrastructure · *Mustela putorius* · *Oryctolagus cuniculus* · Road ecology · Roadsides

Introduction

Transportation infrastructure is one of the main threats to the conservation of many vertebrates (van der Ree et al. 2015a; Beben 2016). Although many animals die daily on roads, mammal carnivores are one of the most susceptible groups due to their low reproductive rates, large home ranges, and high mobilities (Fahrig and Rytwinski 2009; Benítez-López et al. 2010; Grilo et al. 2015a), whereas many of them are threatened (Karanth and Chellam 2009). Therefore, a better understanding of how road traits influence carnivore roadkills will help scientists and stakeholders to implement more

effective mitigation actions, and to build safer infrastructure both for drivers and wildlife.

The total length of the earth's roads currently exceeds 21 million km (Meijer et al. 2018). Moreover, it is estimated that an additional 3–4.7 million km of roads will be built by 2050 globally (Meijer et al. 2018), increasing the probability of wildlife-vehicle collisions, among other ecological disturbances. However, these impacts on wildlife can vary with road attributes (Borkovcová et al. 2012; Nowakowski et al. 2022). Interurban roads are classified into two types based on their characteristics: high-capacity roads (hereinafter "highways"), which contain two or more lanes in each direction separated by a median strip and feature high speed limits, up to 120 km/h, along with wide shoulders. And conventional roads (hereinafter, simply "roads"), with only one lane in each direction and without a median or with a single lane for both directions, typically have speed limits ranging from 50 to 90 km/h and feature narrow shoulders. In addition, motorways have fewer curves than roads and are frequently fenced or have side panels and usually fewer curves than roads (Ascensão et al. 2012). Also, motorways tend to be very busy roads and are, therefore, a greater barrier to

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wildlife movement than roads (Grilo et al. 2015b; Van der Ree et al. 2015b; Beben 2016). On the contrary, the lack of mitigation measures in conventional roads can increase roadkill risk for wildlife when they have freedom of movement, being especially risky for those species that do not identify vehicles as a risk, have slower reaction times, or move at slower speeds (Fahrig and Rytwinski 2009; Jacobson et al. 2016).

Although many carnivores are reluctant to cross roads (Clarke et al. 1998; Philcox et al. 1999; Fahrig and Rytwinski 2009; Benítez-López et al. 2010), some species are attracted to them when searching for food resources easy to obtain such as carcasses, rubbish or abundant small prey living in roadsides (Grilo et al. 2009; Barrientos and Bolonio 2009; Mata et al. 2017). Since transport corridors can provide new suitable habitats (i.e., predator-free with abundant food) for small prey species such as rodents and lagomorphs, these can reach high densities along roadsides and provide a predictable source of food for opportunistic predators (Bellamy et al. 2000; Barrientos and Bolonio 2009; Ascensão et al. 2012; de Redon et al. 2015).

This work aims to study the influence of road type characteristics on carnivore roadkill, a comparison—to the best of our knowledge—never approached before. Our model species was the European polecat (*Mustela putorius*), a habitat generalist (Cabral et al. 2005; Virgós et al. 2007) that die on roads above average compared to other sympatric carnivores (Quiles et al. 2021), accounting in some areas for more than 50% of total carnivore roadkills (Barrientos 2016). This non-natural mortality seems to be contributing to population declines in several European countries (Skumatov et al. 2016; Croose et al. 2018), including Spain (Virgós et al. 2007). Previous studies on mustelid roadkill patterns, including those on polecats, did not study roadkills on motorways (Clarke et al. 1998; Philcox et al. 1999; Russo et al. 2020), however, for this work we have enough roadkill data to compare between the two types of roads.

In Mediterranean ecosystems, European rabbits (*Oryctolagus cuniculus*) are the polecat's main prey (Virgós et al. 2007; Santos et al. 2009). Thus, we assessed the potential effects of food availability, as well as habitat and road type-related factors separating polecat roadkill location from random ones in an area of central Spain where the species is well distributed. We expect (i) rabbit abundance to be higher in polecat roadkill sites (Barrientos and Bolonio 2009; Barrientos and Miranda 2012); (ii) coverage of natural vegetation remnants to be higher around roadkill points as they provide better habitat both for this species and its prey (Lodé 1993; Calvete et al. 2004; Gea-Izquierdo et al. 2005; Zabala et al. 2005); and, finally, (iii) road type influences roadkills as different road categories have different traits. Namely, rights-of-way (the space between the road shoulder and the fence) in motorways are wider, have homogeneous

management along dozens of kilometres, and are usually fenced (Ascensão et al. 2012), which would favour their use as surrogate habitats both for polecats and their prey in agricultural-dominated landscapes, as they both easily trespass large mammals-oriented road fences (Plante et al. 2019).

Materials and methods

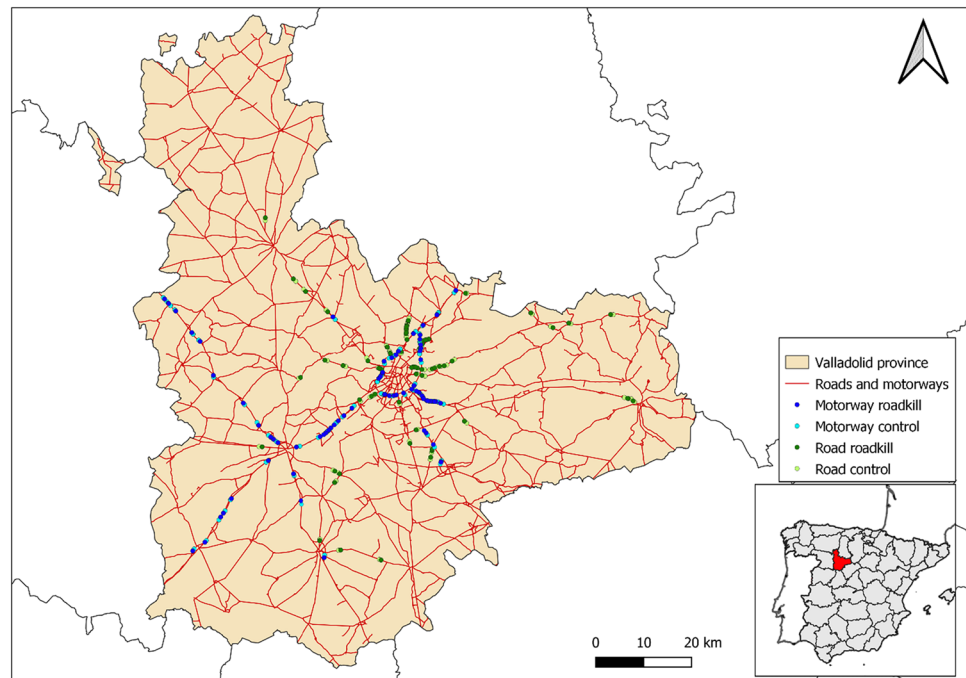
Study area

The study was carried out in Valladolid province ($\approx 8.000 \text{ km}^2$, Spain), in the centre of the northern sub-plateau of the Iberian Peninsula (Fig. 1). Valladolid has an average altitude of 700 m.a.s.l. and is the only Spanish province without mountain ranges. It has a landscape dominated by steppe-lands that have been largely replaced by intensive agricultural fields, which currently cover 75% of its surface (MITECO 2021). Natural or semi-natural lands are mainly dominated by pinewoods (*Pine* spp) or holm oak forests (*Quercus ilex*) (MITECO 2021). Climate is continental Mediterranean with an annual average temperature of 17 °C. Temperatures are highest in July (average of 22 °C), and lowest in January (average of 4° C). Precipitation ranges between 400 and 600 mm year-round, and it is more abundant during spring and autumn (Climate Data Org 2021). The study species is well distributed in the province, being a representative region to study the conservation problems of Mediterranean polecats, such as roadkills.

Study species

The European polecat is a small (800–1300 g) mustelid (Virgós et al. 2007) widely distributed throughout Europe except for Ireland, northern Scandinavia, and southern Greece or the Mediterranean islands (Skumatov et al. 2016). It is considered a habitat generalist (Cabral et al. 2005; Virgós et al. 2007), although in some studies seems to prefer certain environments such as wetlands or riparian forests (Lodé 1993; Zabala et al. 2005; Mestre et al. 2007). Polecats are opportunistic predators (Lodé 1997), and they can specialize in one prey when this is superabundant, as happens with amphibians in central and northern Europe (Jedrzejewski et al. 1993) or rabbits in Mediterranean environments (Lodé 1997; Virgós et al. 2007; Santos et al. 2009). In Spain, it is listed as "Near Threatened" (Virgós et al. 2007). According to the IUCN, polecat populations are declining, although scientific knowledge on this species is still minimal (Skumatov et al. 2016; Croose et al. 2018). Among its threats are habitat loss, competition with invasive exotic species, the decline of prey populations, hybridization with ferrets and roadkills (Birks 2000; Virgós et al. 2007; Grilo et al. 2009; Palazón et al. 2010; Costa et al. 2013; Barrientos 2015). We

Fig. 1 Province of Valladolid and sampled points. Blue points are motorway points and green are road points. The dark ones are roadkills and the light are control points



selected it as target species because it is very susceptible to roadkill, this mortality source representing up to 50% of juvenile mortality (Mañas et al. 2016). Eighty-eight percent ($n=918$) of the records from a Spanish citizen science project corresponded to roadkills (Carmona, unpublished data).

Sampling design

The roadkill data were collected by G.C. as part of the project (Distribución, Ecología y Conservación del turón en la Península Ibérica). This project aims to expand the knowledge on the European polecat's ecology and conservation status on the Iberian Peninsula. The data used for this work were obtained from roadkills found opportunistically by experienced volunteers. Roadkills were GPS referenced and verified by experts (certified by photo or in-situ). With this procedure we avoid the main limitation of citizen science, the data reliability. Ultimately, roadkill data for 85 polecats on motorways and 73 on roads across the province of Valladolid were selected from February 2019 to January 2021. We included one random point (i.e., control point with no roadkills) for each roadkill (see Russo et al. 2020). Random points were generated inside an area of a 1.5 km radius centred on each roadkill point, equivalent to the average home range described for the polecat (Baghli et al. 2005; Rondinini et al. 2006). To avoid redundancies, we established an exclusion area of 200 m between control points and roadkills.

Our response variable was ROADKILL (i.e., roadkill *versus* control point). We used 15 explanatory variables (Table 1) to explain their differences in average values

between roadkill and control points (Barrientos and Bolonio 2009). Data for these variables were collected between January and May 2021. The study variables contained three categories, namely road-type, habitat-related, and road-related: (i) ROAD classified the two road categories (motorways *vs.* roads). This is the main novelty of our study since previous works with carnivores either did not consider roadkills on motorways or indicated that those were very rare events, likely because the high traffic flow discourages animals from attempting to cross these large infrastructure (Clarke et al. 1998; Philcox et al. 1999; Barrientos and Bolonio 2009; Russo et al. 2020); (ii), habitat-related variables. We estimated the coverage of CROP COVER, FOREST COVER, and NON-USE COVER using the SigPac V 4.5 Viewer (SigPac 2022), with the "measure/circle" tool. We selected a sampling area with a radius of 50 m from the centre of each point (either roadkill or control point), following Barrientos and Bolonio, (2009). To make comparable measures in motorways and roads, the area corresponding to each habitat category was averaged for the two sides of the road, ignoring the area occupied by the pavement and the median strip (in the case of motorways), as well as those corresponding to buildings. The distance to the nearest URBAN, BUILDING, and WATER was measured with SigPac (SigPac 2022) using the length measuring tool. The variable NUMBER OF BURROWS was used as a surrogate of rabbit abundance (Palomares 2001), and this variable was measured in the field. We counted the number of rabbit burrows inside of a semicircle of 50 m diameter around each roadkill and control point (Barrientos and Bolonio 2009), on a randomly selected side of the infrastructure. The reason for using a

Table 1 Explanatory variables to characterise the roadkill points *versus* control points, their units, and their intervals between the minimum, average and maximum values

Variable	Description (unit of measurement) Category	Range (min–average–max)	
		Motorway	Road
ROAD	Type of road		
Habitat variables			
CROP COVER	Cultivated cover in an area of a radius of 50 m (%)	0-27-80	0-50-95
FOREST COVER	Forest cover in a 50 m radius area (%)	0-9-75	0-4-70
NON-USE COVER	Non-used cover in a 50 m radius area (%)	15-65-100	5-45-100
URBAN	Distance to the nearest town (m)	1-1423-5890	1-1287-5870
BUILDING	Distance to the nearest building (m)	5-336-1800	1-340-1780
WATER	Distance to the nearest river or body of water (m)	1-1563-9000	12-921-7500
NUMBER OF BURROWS	No. of rabbit burrows in a radius of 50 m	0-6-30	0-3-30
Road variables			
PASS	Distance to nearest culvert or underground pass (m)	1-557-3000	5-1172-3000
WIDTH	Pavement width (m)	19.58-23.3-42.11	4.6-9.2-24.79
SHOULDER	Width of the right-hand verge (m)	1.58-2.2-3.2	0.1-1.0-3.12
UNBROK LINE	Continuous line in 100 m section of point (%)	0-1.2-100	0-54-100
EMBANKMENT	Product of the height of the roadside with its width (m ²)	0-39-400	0-3-56
FENCE	Distance from the end of the shoulder to the fence (m)	0-8-50	0-0.2-8
ROAD INTERCHANGE ISLAND	Distance to the nearest road interchange island (m)	1-531-1500	1-1114-1500

semicircle was that crossing the motorways was impossible, which would have increased the workload. Additionally, both sides are not always accessible. Consequently, we opted to randomly sample only a semicircle and applied this methodology to roads as well. We used a GPS device (Garmin eTrex 30x) to define the 50 m diameter area during fieldwork; and (iii) road-related variables. The variables nearest PASS, road WIDTH, SHOULDER width, nearest ROAD INTERCHANGE ISLANDSPEED and percentage of UNBROK LINE were measured with SigPac (2022) with the length measuring tool. The variable EMBANKMENT surface was measured in the field. The variable distance to FENCE, when possible, was measured using the Google Earth Pro program or the SigPac V 4.5 Viewer. If this was not possible, we measured it on the field. We did not include traffic intensity as an explanatory variable because it highly correlates with others we included, like road width (see also Barrientos and Bolonio 2009). Furthermore, due to the proximity of paired control points (in a radius of 1,500 m), control and roadkill points had the same values.

Statistical analysis

Before model fitting, we performed a correlation matrix to identify highly correlated explanatory variables to avoid overfitting. We excluded those highly correlated with each of the PC factors, discarding the remaining variables with correlations > 0.6 (i.e., NON-USE COVER, WIDTH, FENCE and EMBANKMENT) (Table S1). In this way, it

was possible to use the original variables, which facilitated interpreting the results from an ecological point of view. We adjusted generalized estimating equations models (GEE) where our response variable was ROADKILL. We used a Bernoulli-distributed response variable to classify roadkill (1) and control (0) observations. GEE models improve the standard errors estimates for linear models and fit better with clustered data such as repeated measurements studies and other correlated observations (Overall and Tonidandel 2004; Fieberg et al. 2009). GEE is a semiparametric method because while we impose linearity, we do not fully specify its distribution. This approach is the most suitable in our case because we analysed paired observations where every roadkill has one associated control point. The assumptions for GEE are similar to the assumptions for GLMs: 1) the response is correlated or clustered, 2) there is a linear relationship between predictors and a transformation of the response, described by the link function and 3) the working covariance has some structure (see Koper and Manseau 2009). We included the habitat-related variables and road characteristics as explanatory variables in the models, as well as two interactions (NUMBER OF BURROWS \times ROAD and ROAD INTERCHANGE ISLAND \times ROAD) to explore the differences between road types. We considered that our sample size ($n = 158$) was enough to include up to 15 predictors in our saturated model, following the recommendations of Collart and Guisan 2023. We conducted a model selection procedure which generated models with all the possible combinations of the independent variables

and the interactions mentioned above as well as including a null model. A comparison of the model set's quality was conducted using Quasi Information Criterion (QIC). This method assesses each model and ranks them according to QIC. Delta QIC is measuring the difference in QIC between different models. When differences (Δ) between several models had a $QIC < 2.0$, we considered these models as a set of confidence models with similar statistical support and we calculated the weights (Burnham and Anderson 2002). Then, we conducted a model averaging only with the resulting models of $\Delta QIC \leq 2$ (Burnham and Anderson 2002). We obtained the averaged coefficients and the relative importance for each predictor. Finally, we calculated the coefficient of determination (pseudo- R^2) (Zheng 2000) for the selected models and estimated the model coefficients of the interaction terms using post-hoc simple-slope pairwise comparisons (Russell et al. 2021).

We used the statistical software R v.4.1. (R Development Core Team 2021) and the packages Hmisc v.4.7–2 to study the correlations between variables (Harrell 2021), geepack v.1.3.9 to analyze the data using the GEE method (Højsgaard et al. 2006), MuMIn v.1.43.17 to generate the model selection (Barton 2020) and emmeans v.1.6.3 (Russell et al. 2021).

Results

After running the correlation matrix (Table S1), we decided not to include 4 variables in the model building. The variables NON-USE COVER and CROP COVER were negatively correlated (Table S1), and we included CROP COVER in the subsequent model building. The variables, WIDTH and FENCE were removed because they were positively correlated with ROAD INTERCHANGE ISLAND (Table S1). Finally, the variables EMBANKMENT and NUMBER OF BURROWS were positively correlated (Table S1), and we maintained NUMBER OF BURROWS because it is directly related to one of our hypotheses.

Model selection provided a set of 29 models with $\Delta QIC \leq 2$ (Table S2). CROP COVER, FOREST COVER, NUMBER OF BURROWS and ROAD INTERCHANGE ISLAND were included in all the best models and had the highest relative importance (100%). Least important were URBAN (included in 62% of the models), SHOULDER (51%), WATER (34%), PASS (31%), BUILDING (27%) and UNBROK LINE (24%) (Table 2). CROP COVER, BUILDING, WATER, SHOULDER and ROAD INTERCHANGE ISLAND had a negative effect on roadkills, and FOREST COVER, URBAN, NUMBER OF BURROWS, PASS and UNBROK LINE were positively related to roadkill points (Table 2). Interactions were selected in all the best models. Roadkill probability increased with the distance to ROAD INTERCHANGE

Table 2 Beta standardized coefficients (BSC), standard errors (SE) and relative importance (RI) of habitat and road-type variables selected after weighted model averaging

Variable	BSC	SE	RI
CROP COVER	− 1.09	0.25	1.00
FOREST COVER	0.69	0.30	1.00
URBAN	0.32	0.16	0.62
BUILDING	− 0.03	0.22	0.27
WATER	− 0.01	0.17	0.34
NUMBER OF BURROWS	0.66	0.23	1.00
PASS	0.06	0.18	0.31
SHOULDER	− 0.37	0.31	0.51
UNBROK LINE	0.35	0.32	0.24
ROAD INTERCHANGE ISLAND	− 1.04	0.35	1.00
NUMBER OF BURROWS X ROAD TYPE	1.08	0.58	1.00
ROAD INTERCHANGE ISLAND X ROAD TYPE	0.97	0.31	1.00

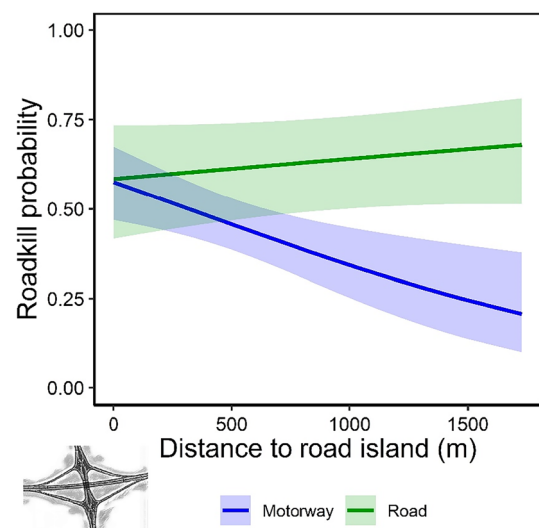


Fig. 2 Effects of the distance of road interchange island in interaction with road type on roadkill probability see the importance of this interaction in Table 2. Bands represent 95% confidence intervals. See how the probability of roadkill is higher near the road island on motorways, but on roads it remains constant

ISLAND in conventional roads but decreased in motorways [coeff. \pm SD = 0.09 ± 0.12 vs. -0.47 ± 0.18] (Fig. 2). NUMBER OF BURROWS affected positively to roadkill probability on both types of ROAD [0.31 ± 0.12 vs. 1.45 ± 0.58], but this effect was higher in conventional roads (Fig. 3).

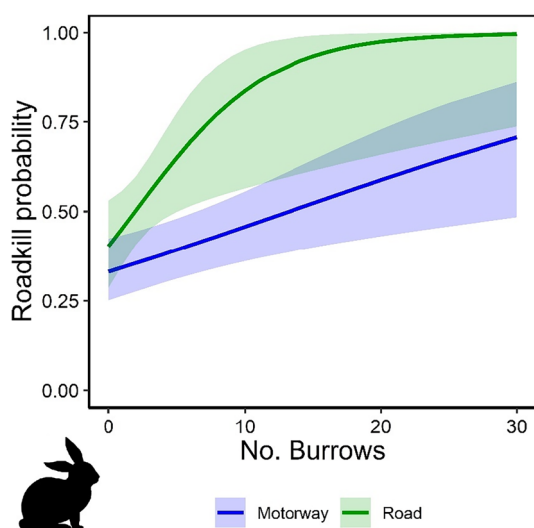


Fig. 3 Effects of the number of rabbit burrows in interaction with road type on roadkill probability, see the importance of this interaction in Table 2. Bands represent 95% confidence intervals. See how the probability of roadkill increases where the number of burrows is higher on both types of roads

Discussion

Our study shows that some ecological and road-intrinsic factors influenced roadkills of a mammal carnivore. Our target species, the European polecat, was frequently recorded as roadkill both on roads and motorways contrary to previous works on carnivore roadkills, that concentrated roadkills on roads (Clarke et al. 1998; Philcox et al. 1999; Barrientos and Bolonio 2009; Russo et al. 2020). Roadkills on motorways were closer to road interchange islands but, in conventional roads, the distance of roadkills and control points to crossroads were similar. Rabbit abundances were consistently higher and crop cover consistently lower around roadkills regardless of the road type.

The reason behind the contrasting roadkill patterns between road types could be the availability of food in surrounding areas related to the physical features of road types. Rabbits avoid cultivated areas to establish their burrows to prevent them from being destroyed during tillage (Calvete et al. 2004; Gea-Izquierdo et al. 2005), and they find in the rights-of-way an optimal area to breed (Barrientos and Bolonio 2009). Whereas roadkills were associated with a higher number of rabbit burrows both in motorways and roads, this pattern was stronger for motorways. Motorway roadsides are wider, homogeneous along hundreds of kilometres, are usually fenced, and commonly include large embankments that provide a suitable breeding substrate for several prey species (Ascensão et al. 2012, 2015; Villemey et al. 2018). We found that the distance to road interchange islands was one of the most influential variables on motorways. These intersections

often create islands of available habitat between the main motorway and the entrance and exit lanes that can be colonised by prey, which could lead to predator roadkill hotspots, at least for those species that do not avoid roads as they do not recognize vehicles as potential threats (Jacobson et al. 2016). In contrast, inlets and outlets in conventional roads are often very simple structure, most of them consist of road crossings that rarely create potential habitats for prey.

Other influential variables were those related to land cover. The study area is mainly composed of a highly disturbed environments dominated by intensive agriculture. Carnivores generally avoid areas of intensive human use and prefer mosaics of semi-natural habitats (Pita et al. 2009; Pereira and Rodriguez 2010). Thus, any patch with remaining natural vegetation becomes essential for most of them, even if it is located on roadsides (Barrientos and Bolonio 2009; Ascensão et al. 2012). Roadkills were associated with lower agriculture cover in the vicinity of the road and, therefore, with larger percentage of natural habitat characterized by grasslands or areas with moderate shrub cover, which are also more favourable for prey (Calvete et al. 2004; Gea-Izquierdo et al. 2005; Serrano et al. 2009; see also the negative correlation between these variables in Appendix S1).

Roadsides, especially those of motorways, act as corridors connecting habitat patches for many wildlife species (Huijser and Clevenger 2006; Ascensão et al. 2015). This may be of great importance in landscapes dominated by intensive agriculture like our study area (Sabino-Marques and Mira 2011; Ascensão et al. 2012; Kautz et al. 2021). Roads do not offer such an optimal environment as their margins are narrower, being, therefore, less suitable corridors. Thus, it is necessary to deepen our knowledge of the ecology of carnivores habiting in right of way. Previous studies suggest that large differences in the use of road vicinity arise within species belonging to this guild. As a general pattern, human-habituated species like foxes or stone martens made more intensive use of the motorway vicinity, whereas badgers and cats were indifferent or slightly reluctant to these potential habitat corridors (Mata et al. 2017).

Our study can help to understand the ecological processes behind roadkills and to identify the most dangerous sections for carnivores in each road type. This step is essential to implement mitigation measures to reduce roadkills in these sections (Russo et al. 2020). The installation of underpasses, especially where prey is abundant, such as at road entrances and exits on motorways, could be a useful measure to mitigate roadkill. Additionally, these should be complemented by more efficient fencing to help reduce the crossing of medium-sized mammals. Also, proper maintenance of these areas to ensure visibility of the margins of roads could improve drivers' reaction times when crossing an animal. Another potential mitigation measure could involve covering soil on embankments with concrete to prevent the

proliferation of dens in the most problematic areas. Furthermore, exploring the effectiveness of these mitigation actions requires an understanding of their benefits in improving population persistence rates (Barrientos et al. 2021).

Finally, we acknowledge several caveats associated with our study that are important to consider. First, the use of volunteer-based data has been criticized for potential issues such as errors in the identification of species or inaccuracies in observations. However, as commented above, we controlled them by checking records on the road when they were doubtful (see Results section). Second, our sample sizes were relatively small, but comparable to similar studies (e.g., Barrientos and Bolonio 2009). In this sense, it is important to note that population densities of carnivores are generally low, and waiting for more data could delay conservation decision-making. Additionally, we recognize that our sampling procedure based on opportunistic roadkill encounters may be limiting our ability to predict the effect of road type in some ways. However, studies based on citizen science are difficult to program over time and thus achieve systematic sampling. Our data collection was concentrated in a short time frame, what reduces their heterogeneity (e.g., related to potential road upgrades or temporal changes in traffic flow) compared to other studies with more records but much longer periods of data collection (see, for instance, Russo et al. 2020).

Conclusions

The different structure of motorways and roads is important in explaining carnivore roadkill patterns. Roadsides offer optimal environments for the establishment of prey species, such as rabbits, by providing spaces unused by humans, along with cover for shelter and food. This phenomenon contributes to an increase in carnivore roadkill rates in sections where prey populations become abundant. Predators like polecats, which locally specialize on capturing prey thriving in these rights-of-way, are highly susceptible to roadkills in places like motorway road interchange islands. Those road sections surrounded by natural habitats represent potential roadkill hotspots. Our findings highlight the need to take into account the intrinsic characteristics of each road type when deciding to undertake measures to mitigate roadkills.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42991-024-00400-y>.

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Author contributions GC: Methodology, Investigation, Data Curation, Writing—Original Draft. EV: Conceptualization, Methodology, Investigation, Writing—Review and Editing, Supervision. TB: Methodology, Formal analysis, Investigation, Writing—Review and Editing, Software. RB: Conceptualization, Methodology, Investigation, Writing—Original Draft, Supervision.

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Data availability The datasets generated during the current study are available from the corresponding author upon request.

Declarations

Conflict of interest We have no conflict of interest to declare.

Ethical approval We agree to have complied with the ethical standards of the Committee on Publication Ethics (COPE). We consulted extensively with the IRB of XYZ who determined that our study did not need ethical approval.

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References

- Ascensão F, Clevenger AP, Grilo C, Filipe J, Santos-Reis M (2012) Highway verges as habitat providers for small mammals in agrosilvopastoral environments. *Biodivers Conserv* 21:3681–3697. <https://doi.org/10.1007/s10531-012-0390-3>
- Ascensão F, LaPoint S, van der Ree R (2015) Roads, traffic and verges: Big problems and big opportunities for small mammals. In: van der Ree R, Smith DJ, Grilo C (eds) *Handbook of road ecology*. Wiley, Oxford, pp 325–333
- Baghli A, Walzberg C, Verhagen R (2005) Habitat use by the European polecat *Mustela putorius* at low density in a fragmented landscape. *Wildl Biol* 11:331–339. [https://doi.org/10.2981/0909-6396\(2005\)11\[331:HUBTEP\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2005)11[331:HUBTEP]2.0.CO;2)
- Barrientos R (2015) Adult sex-ratio distortion in the native European polecat is related to the expansion of the invasive American mink. *Biol Conserv* 186:28–34. <https://doi.org/10.1016/j.biocon.2015.02.030>
- Barrientos R (2016) El turón. In: Lozano J, Lacasa M (eds) *El Libro de los Carnívoros*. Photodigiscoping, Barcelona, pp 131–137

- Barrientos R, Bolonio L (2009) The presence of rabbits adjacent to road increases polecat road mortality. *Biodivers Conserv* 18:405–418. <https://doi.org/10.1007/s10531-008-9499-9>
- Barrientos R, Miranda JD (2012) Can we explain regional abundance and road-kill patterns with variables derived from local-scale road-kill models? Evaluating transferability with the European polecat. *Divers Distrib* 18:635–647. <https://doi.org/10.1111/j.1472-4642.2011.00850.x>
- Barrientos R, Ascensão F, D'Amico M, Grilo C, Pereira HM (2021) The lost road: do transportation networks imperil wildlife population persistence? *Perspect Ecol Conserv* 19:411–416. <https://doi.org/10.1016/j.pecon.2021.07.004>
- Barton K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17 <https://CRAN.R-project.org/package=MuMIn>. Accessed 7 Feb 2022
- Beben D (2016) Crossings construction as a method of animal conservation. *Transp Res Proc* 14:474–483. <https://doi.org/10.1016/j.trpro.2016.05.100>
- Bellamy PE, Shore RF, Ardeshir D, Treweek JR, Sparks TH (2000) Road verges as habitat for small mammals in Britain. *Mamm Rev* 30:131–139. <https://doi.org/10.1046/j.1365-2907.2000.00061.x>
- Benítez-López A, Alkemade R, Verweij PA (2010) The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol Conserv* 143:1307–1316. <https://doi.org/10.1016/j.biocon.2010.02.009>
- Birks JDS (2000) The recovery of the polecat, *Mustela putorius*, in Britain. In: Griffiths HI (ed) *Mustelids in a modern. World management and conservation aspects of small carnivore: human interactions*. Backhuys Publishers, Leiden, pp 141–152
- Borkovcová M, Mrtka J, Winkler J (2012) Factors affecting mortality of vertebrates on the roads in the Czech Republic. *Transp Res Part D: Transp Environ* 17:66–72. <https://doi.org/10.1016/j.trd.2011.09.011>
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media, New York
- Cabral MJ, Almeida J, Almeida PR, Dellinger T, Ferrand de Almeida N, Oliveira ME, Palmeirim JM, Queiroz AI, Rogado L, Santos-Reis M (2005) *Livro Vermelho dos Vertebrados de Portugal*. Instituto da Conservação da Natureza, Lisboa.
- Calvete C, Estrada R, Angulo E, Cabezas-Ruiz S (2004) Habitat factors related to wild rabbit conservation in an agricultural landscape. *Land Ecol* 19:531–542. <https://doi.org/10.1023/B:LAND.0000036139.04466.06>
- Clarke GP, White PCL, Harris S (1998) Effects of roads on badger *Meles meles* populations in south-west England. *Biol Conserv* 86:117–124. [https://doi.org/10.1016/S0006-3207\(98\)00018-4](https://doi.org/10.1016/S0006-3207(98)00018-4)
- Climate Data Org (2021) Climate data of Valladolid. <https://es.climate-data.org/europe/espana/castilla-y-leon/valladolid-581/#climate-table>. Accessed 9 April 2022
- Collart F, Guisan A (2023) Small to train, small to test: Dealing with low sample size in model evaluation. *Ecol Inform* 75:102106
- Costa M, Fernandes C, Birks JDS, Kitchener AC, Santos-Reis M, Bruford MW (2013) The genetic legacy of the 19th-century decline of the British polecat: evidence for extensive introgression from feral ferrets. *Mol Ecol* 22:5130–5147. <https://doi.org/10.1111/mec.12456>
- Croose E, Duckworth JW, Ruetter S, Skumatov DV, Kolesnikov VV, Saveljev AP (2018) A review of the status of the Western polecat *Mustela putorius*: A neglected and declining species? *Mammalia* 82:550–564. <https://doi.org/10.1515/mammalia-2017-0092>
- de Redon L, Le Viol I, Jiguet F, Machon N, Scher O, Kerbiriou C (2015) Road network in an agrarian landscape: Potential habitat, corridor or barrier for small mammals? *Acta Oecol* 62:58–65. <https://doi.org/10.1016/j.actao.2014.12.003>
- Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. *Ecol Soc* 14:21. <https://doi.org/10.5751/ES-02815-140121>
- Fieberg J, Rieger RH, Zicus MC, Schildcrout JS (2009) Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. *J Appl Ecol* 46(5):1018–1025
- Gea-Izquierdo G, Muñoz-Igualada J, San Miguel-Aynaz A (2005) Rabbit warren distribution in relation to pasture communities in Mediterranean habitats, consequences for management of rabbit populations. *Wildl Res* 32:723–731. <https://doi.org/10.1071/WR04129>
- Grilo C, Bissonette JA, Santos-Reis M (2009) Spatial-temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. *Biol Conserv* 142:301–313. <https://doi.org/10.1016/j.biocon.2008.10.026>
- Grilo C, Zanchetta Ferreira F, Revilla E (2015b) No evidence of a threshold in traffic volume affecting road-kill mortality at a large spatio-temporal scale. *Environ Impact Assess Rev* 55:54–58. <https://doi.org/10.1016/j.eiar.2015.07.003>
- Grilo C, Smith DJ, Klar N (2015a) Carnivores: struggling for survival in roaded landscapes. In: van der Ree R, Smith DJ, Grilo C (eds) *Handbook of road ecology*. Wiley, Oxford, pp 300–312. <https://doi.org/10.1002/9781118568170.ch35>
- Harrell FE Jr (2021) With contributions from Charles Dupont and many others. (2021). *Hmisc: Harrell Miscellaneous*. R package version 4.5–0 <https://CRAN.R-project.org/package=Hmisc>. Accessed 7 Feb 2022
- Højsgaard S, Halekoh U, Yan J (2006) The R package geepack for generalized estimating equations. *J Stat Softw* 15:1–11. <https://doi.org/10.18637/jss.v015.i02>
- Huijser MP, Clevenger AP (2006) Habitat and corridor function of rights-of-way. In: Davenport J, Davenport JL (eds) *The ecology of transportation: managing mobility for the environment*. Springer, Dordrecht, pp 233–254. https://doi.org/10.1007/1-4020-4504-2_11
- Jacobson SL, Bliss-Ketchum LL, de Rivera CE, Smith WP (2016) A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere* 7:4. <https://doi.org/10.1002/ecs2.1345>
- Jedrzejewski W, Jedrzejewska B, Brzezinski M (1993) Winter habitat selection and feeding habits of polecats (*Mustela putorius*) in Bielowieza National Park, Poland. *Zeits Säuget* 58:75–83
- Karanth K, Chellam R (2009) Carnivore conservation at the cross-roads. *Oryx* 43:1–2. <https://doi.org/10.1017/S003060530843106X>
- Kautz T, Fowler N, Petroelje T, Beyer D, Svoboda N, Belant J (2021) Large carnivore response to human road use suggests a landscape of coexistence. *Glob Ecol Conserv* 30:2351–9894. <https://doi.org/10.1016/j.gecco.2021.e01772>
- Koper N, Manseau M (2009) Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. *J Appl Ecol* 46:590–599
- Lodé T (1993) Stratégies d'utilisation de l'espace chez le Putois européen *Mustela putorius* L. dans l'ouest de la France. *Rev Ecol (terre Vie)* 48:305–322
- Lodé T (1997) Trophic status and feeding habits of the European polecat *Mustela putorius* L. 1758. *Mamm Rev* 27:177–184. <https://doi.org/10.1111/j.1365-2907.1997.tb00447.x>
- Mañas S, Gómez A, Asensio V, Palazón S, Pödra M, Casal J, Ruiz-Olmo J (2016) Demographic structure of three riparian mustelid species in Spain. *Eur J Wildl Res* 62:119–129. <https://doi.org/10.1007/s10344-015-0982-9>
- Mata C, Ruiz-Capillas P, Malo J (2017) Small-scale alterations in carnivore activity patterns close to motorways. *Eur J Wildl Res* 63:64. <https://doi.org/10.1007/S10344-017-1118-1>

- Meijer JR, Huijbregts MA, Schotten KC, Schipper AM (2018) Global patterns of current and future road infrastructure. *Environ Res Lett* 13:064006. <https://doi.org/10.1088/1748-9326/aabd42>
- Mestre FM, Ferreira JP, Mira A (2007) Modelling the distribution of the European polecat *Mustela putorius* in a Mediterranean agricultural landscape. *Rev Ecol-Terre Vie* 62:35–47. <https://doi.org/10.3406/revoc.2007.1343>
- MITECO (2021) Cuarto inventario forestal nacional, Valladolid. Catálogo de Publicaciones de la Administración General del Estado. Available in: https://www.miteco.gob.es/content/dam/miteco/es/biodiversidad/temas/inventarios-nacionales/ifn4_valladolid_tcm30-536205.pdf. Accessed 17 Jan 2022
- Nowakowski K, Ważna A, Kurek P, Cichoński J, Bojarski J, Gabryś G (2022) Long arm of motorway—the impact of fenced road on the mortality of European badgers. *Environ Manage* 69:429–437
- Overall JE, Tonidandel S (2004) Robustness of generalized estimating equation (GEE) tests of significance against misspecification of the error structure model. *Biom J* 46(2):203–213
- Palazón S, Pérez M, Batet A, Arjona L, Rafart E, Malo C, Ruiz-Olmo J (2010) Situación actual y evolución de la población de turón (*Mustela putorius* L., 1758) en Catalunya: 1950–2008. *Galemys* 22:91–112
- Palomares F (2001) Comparison of 3 methods to estimate rabbit abundance in a Mediterranean environment. *Wildl Soc Bull* 29:578–585
- Pereira M, Rodriguez A (2010) Conservation value of linear woody remnants for two forest carnivores in a Mediterranean agricultural landscape. *J Appl Ecol* 47:611–620. <https://doi.org/10.1111/j.1365-2664.2010.01804.x>
- Philcox CK, Grogan AL, MacDonald DW (1999) Patterns of otter *Lutra lutra* road mortality in Britain. *J Appl Ecol* 36:748–762. <https://doi.org/10.1046/j.1365-2664.1999.00441.x>
- Pita R, Mira A, Moreira F, Morgado R, Beja P (2009) Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. *Agric Ecosyst Environ* 132:57–65. <https://doi.org/10.1016/j.agee.2009.02.008>
- Plante J, Jaeger J, Desrochers A (2019) How do landscape context and fences influence roadkill locations of small and medium-sized mammals? *J Environ Manag* 235:511–520. <https://doi.org/10.1016/j.jenvman.2018.10.093>
- Quiles P, Ascensão F, D'Amico M, Revilla E, Barrientos R (2021) Are road-kills representative of wildlife community obtained from atlas data? *Hystrix* 32:89–94. <https://doi.org/10.4404/hystrix-00396-2020>
- R Development Core Team (2021) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3–900051–07–0 <https://www.R-project.org/>. Accessed 6 May 2022
- Rondinini C, Ercoli V, Boitani L (2006) Habitat use and preference by polecats (*Mustela putorius* L.) in a Mediterranean agricultural landscape. *J Zool (Lond)* 269:213–219. <https://doi.org/10.1111/j.1469-7998.2006.00073.x>
- Russell VL, Buerkner P, Herve M, Love J, Singmann H (2021) Package ‘emmeans’. R Package Version 1.5.4
- Russo LF, Barrientos R, Fabrizio M, Di Febbraro M, Anna L (2020) Prioritizing road-kill mitigation areas: a spatially explicit national-scale model for an elusive carnivore. *Divers Distrib* 26:1–11. <https://doi.org/10.1111/ddi.13064>
- Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. *Biol Conserv* 147:87–98. <https://doi.org/10.1016/j.biocon.2011.11.023>
- Sabino-Marques H, Mira A (2011) Living on the verge: are roads a more suitable refuge for small mammals than streams in Mediterranean pastureland? *Ecol Res* 26(2):277–287. <https://doi.org/10.1007/s11284-010-0781-4>
- Santos MJ, Matos HM, Baltasar C, Grilo C, Santos-Reis M (2009) Is polecat (*Mustela putorius*) diet affected by “mediterraneity”? *Mamm Biol* 74:448–455. <https://doi.org/10.1016/j.mambio.2009.08.007>
- Serrano S, Dalibor J, Alberto M, Vidus-Rosin A (2009) Density and habitat use by the European wild rabbit (*Oryctolagus cuniculus*) in an agricultural area of northern Italy. *Hystrix*. <https://doi.org/10.4404/hystrix-19.2-4424>
- SIGPAC (2022) Sistema de información geográfica de parcelas agrícolas. <https://sigpac.mapama.gob.es/feqa/visor/>. Accessed 29 Mar 2022
- Skumatov D, Abramov AV, Herrero J, Kitchener A, Maran T, Kranz A, Sándor A, Saveljev A, Saviour-Soubelet A, Guinot-Ghestem M, Zuberogoitia I, Birks JDS, Weber A, Melisch R, Ruetze S (2016) *Mustela putorius*. The IUCN Red List of Threatened Species 2016. <https://www.iucnredlist.org/species/41658/45214384>. Accessed 22 Jan 2022
- van der Ree R, Smith D, Grilo C (2015a) The ecological effects of linear infrastructure and traffic. In: van der Ree R, Smith DJ, Grilo C (eds) Handbook of road ecology. Wiley, Oxford, pp 1–9. <https://doi.org/10.1002/9781118568170.ch1>
- van der Ree R, Gagnon JW, Smith DJ (2015b) Fencing: a valuable tool for reducing wildlife-vehicle collisions and funneling fauna to crossing structures. In: van der Ree R, Smith DJ, Grilo C (eds) Handbook of road ecology. Wiley, Oxford, pp 159–171. <https://doi.org/10.1002/9781118568170.ch20>
- Villemeay A, Jeusset A, Vargac M, Bertheau Y, Coulon A, Touroult J, Sylvie V, Castagneyrol B, Jactel H, Witté I, Deniaud N, Flamerie F, Jaslier E, Véronique R, Guinard E, Mitouard E, Ruel V, Sordello R (2018) Can linear transportation infrastructure verges constitute a habitat and/or a corridor for insects in temperate landscapes? A systematic review. *Environ Evid* 7:1–33. <https://doi.org/10.1186/s13750-018-0117-3>
- Virgós E, Cabezas-Díaz S, Lozano J (2007) *Mustela putorius*, Linnaeus, 1758. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid, pp 297–298
- Zabala J, Zuberogoitia I, Martínez-Climent JA (2005) Site and landscape features ruling the habitat use and occupancy of the polecat (*Mustela putorius*) in a low density area: a multiscale approach. *Eur J Wildl Res* 51:157–162. <https://doi.org/10.1007/s10344-005-0094-z>
- Zheng B (2000) Summarizing the goodness of fit of generalized linear models for longitudinal data. *Stat Med* 19:1265–1275

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