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The distribution of vertebrate roadkill varies by season, surrounding environment, and animal class

Jesús Arca-Rubio[1] · Gregorio Moreno-Rueda[1] · Zaida Ortega[1]

Abstract
Due to rapid human expansion in the last century, wildlife roadkill is becoming a concerning threat to biodiversity and human safety. The frequency of roadkill events depends on factors related to specific traits of the road—tortuosity or the presence of fences, among others—and the animal ecology—such as activity patterns, reproductive season, or thermoregulation. These, in turn, are related to environmental factors, with seasonal variations. Here, we assessed roadkill mortality of terrestrial vertebrates over the year. To do this, we sampled 10 road sections (of 3 km, by walk) in the south of Spain for a full year, registering the carcasses of run-over vertebrates. Then, we analysed the spatiotemporal patterns of roadkill events for the four vertebrates' classes and the effects of road traits (presence of fence, tortuosity, distance to water point) and environmental variables (mean temperature and precipitation). Mammals suffered the highest mortality by roadkill (45.72%). The frequency of collisions was independent of tortuosity, presence of fences, and precipitation, while mean temperature significantly increased the probability of collision of mammals, birds, and reptiles. There was a seasonal effect in the number of collisions, which spatial pattern depended on the class of vertebrates. All this leads us to conclude that, to reduce the impact caused by roadkill mortality on wildlife, we need specific measures to be taken timely in each critical place and for each vertebrate group.

Keywords Animal-vehicle collisions · Road ecology · Wildlife management · Mammals · Roadkill mortality

Introduction

In the last century, the development of human societies has increased with an unprecedented magnitude and speed, which has led to global changes in wildlife (Barrientos et al. 2021). Because of that, populations of most animal species are decreasing (Jackson and Fahrig 2011). The main factors impacting the population density of animals are land-use modifications, pollution, climate change, and building infrastructures that fragment the habitats (Torres et al. 2016; Jaureguiberry et al. 2022). Among those infrastructures are roads, which show one of the highest densities in Europe (Meijer et al. 2018), to an extent that 50% of the continent's land is less than 1.5 km from some road (Torres et al. 2016). These infrastructures entail changes in land use and habitat fragmentation, which hinders the flow of animals among

subpopulations within a metapopulation, reducing the viability of the populations (Benítez-Lopez et al. 2010). Moreover, collisions between the vehicles that cross these roads and wildlife that try to make their way through them are one of the main causes of wildlife mortality worldwide (Hill et al. 2019).

The frequency of animal-vehicle collisions depends on different factors related to the type of animal, environmental factors, traffic flow, and traits related to the road (Benítez-Lopez et al. 2010). Two important factors related to the species are motility (D'Amico et al. 2015) and the ability to avoid or escape from vehicles, with animals that run less often—such as amphibians—being more likely to be run over than others with a greater capacity of reaction to a vehicle—such as birds or some mammals (Mazerolle et al. 2005). Within an animal group, the risk of being hit will depend on the time of year, either because the species has different requirements depending on it, as is the case of the dependence of water sources in some amphibians and birds (Gibbs and Shriver 2005), or due to the variation of the activity periods, as may be the case of some reptiles with brumation, some mammals

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with hibernation, or amphibians with aestivation (Garriga et al. 2017; Fernández-López et al. 2022). In the latter, the probability of being run over increases in rainy periods and, particularly, after sunset, when they reach their maximum activity (Gibbs and Shriver 2005). In addition, the effects of weather conditions on roadkill risk can also be indirect, for example, by influencing the presence of possible prey on roads (Barrientos and Bolonio 2009). Considering that different variables can affect the risk of roadkill for each vertebrate group, it is necessary to determine their impact on natural populations (Roger et al. 2011). This means that the impact suffered by a very abundant species with a high reproductive capacity is not the same as that suffered by one that is very endangered and has a low reproductive rate, and this impact will also depend on the developmental stage of the individual that has been hit (Row et al. 2007).

Here, we intended to understand the variables related to the spatiotemporal patterns of roadkill of terrestrial vertebrates. Our first aim was to assess the degree of roadkill mortality of each vertebrate class (amphibians, reptiles, birds, and mammals) and identify the species that were most affected. Since they show the greatest mobility, we predict that mammals will be the group suffering the greatest number of collisions. Secondly, we aimed to understand how some traits of the road (tortuosity, presence of fencing, and distance from a water point) affect the frequency of accidents. The presence of fencing should reduce the number of accidents, at least for mammals; the effect of tortuosity is unclear, since a more convoluted road could let the driver to reduce speed but can also hinder the driver's visibility; and the distance to a water point could be related to a greater run over of amphibians and birds. Third, we aimed to explore the seasonal fluctuations on roadkill and its variation between different groups of vertebrates. We hypothesise that seasonal variations on roadkill will depend on the biology of the different vertebrate groups, with reptiles suffering a greater number of road accidents in warm months, amphibians being most run over on periods with greater precipitation and humidity, and birds and mammals showing smaller seasonal effects. Finally, we aimed to evaluate the relationship of the main environmental variables with the accidents, for each class of vertebrates. The effect of these variables will also vary among vertebrate groups, with reptiles increasing roadkill with higher temperatures, while roadkill of amphibians could be related more to greater precipitation.

Materials and methods

Study site and road survey

During a complete year, we sampled, on foot, 10 road sections located within two municipalities in southern Spain: Loja (Granada) and Archidona (Málaga) (Fig. 1). We surveyed the road sections for 12 months—starting in March 2021 and ending in February 2022—during the last weeks of each month. All road sections had the same length (3 km) and similar speed limits ($\approx$ 60 km/h throughout their length). Road sections differed on some traits, such as sinuosity and the presence of fencing (5 sections fenced and 5 unfenced).

Each month, the same researcher (JAR) walked the 10 road sections on foot. For each sampling of each road section, a round-trip walk was carried out, paying attention to the left lane in each round (including the lane itself, the hard shoulders, gutters, and culverts). Thus, the sections were always covered on the left of the road, with a reflective vest to reduce the risk of an accident. Sampling focused exclusively on terrestrial vertebrates (mammals, birds, reptiles, and amphibians). Each run-over carcass was registered using the mobile application ObsMapp (Rabadán-González et al. 2018), including species (whenever it was possible to identify it; otherwise, we recorded the lowest taxonomic level identifiable), date and time of the observation, GPS coordinates, and photography. Data were later uploaded to the observation.org platform for its subsequent use in the national SAFE programme, aiming to reduce roadkill mortality (Caballero-Díaz et al. 2021). On this platform, carcasses' pictures are reviewed by the scientific community to confirm species identification. Once a carcass was registered, it was removed from the road to avoid possible additional accidents by potential predators.

Data analysis

We analysed the effect of road traits (road sinuosity and presence of fence) and habitat traits (distance to a water point, mean temperature, and mean precipitation) on the spatiotemporal patterns of roadkill events of the four vertebrate classes (amphibians, reptiles, birds, and mammals) along seasons of the year.

The study area has a Mediterranean climate with four marked seasons that we categorised as (1) spring, from March 20 to June 21, (2) summer, from June 21 to September 23, (3) autumn, September 23 to December 21, and (4) winter, from December 21 to March 20.

We used QGIS version 3.16 (QGIS Development Team 2022) to quantify road sinuosity and distance to water points. To estimate the sinuosity or tortuosity of each road section, we digitised the road section as a linear shapefile-type layer to measure (1) its exact length and (2) the Euclidean distance between the start point and the end point of the section and estimate the tortuosity simply as the quotient between both distances (i.e. total distance / [start point − end point]). The higher the value, the greater the tortuosity of the section of the road in question. To calculate the distance of each carcass to the nearest water point, these were first digitised as
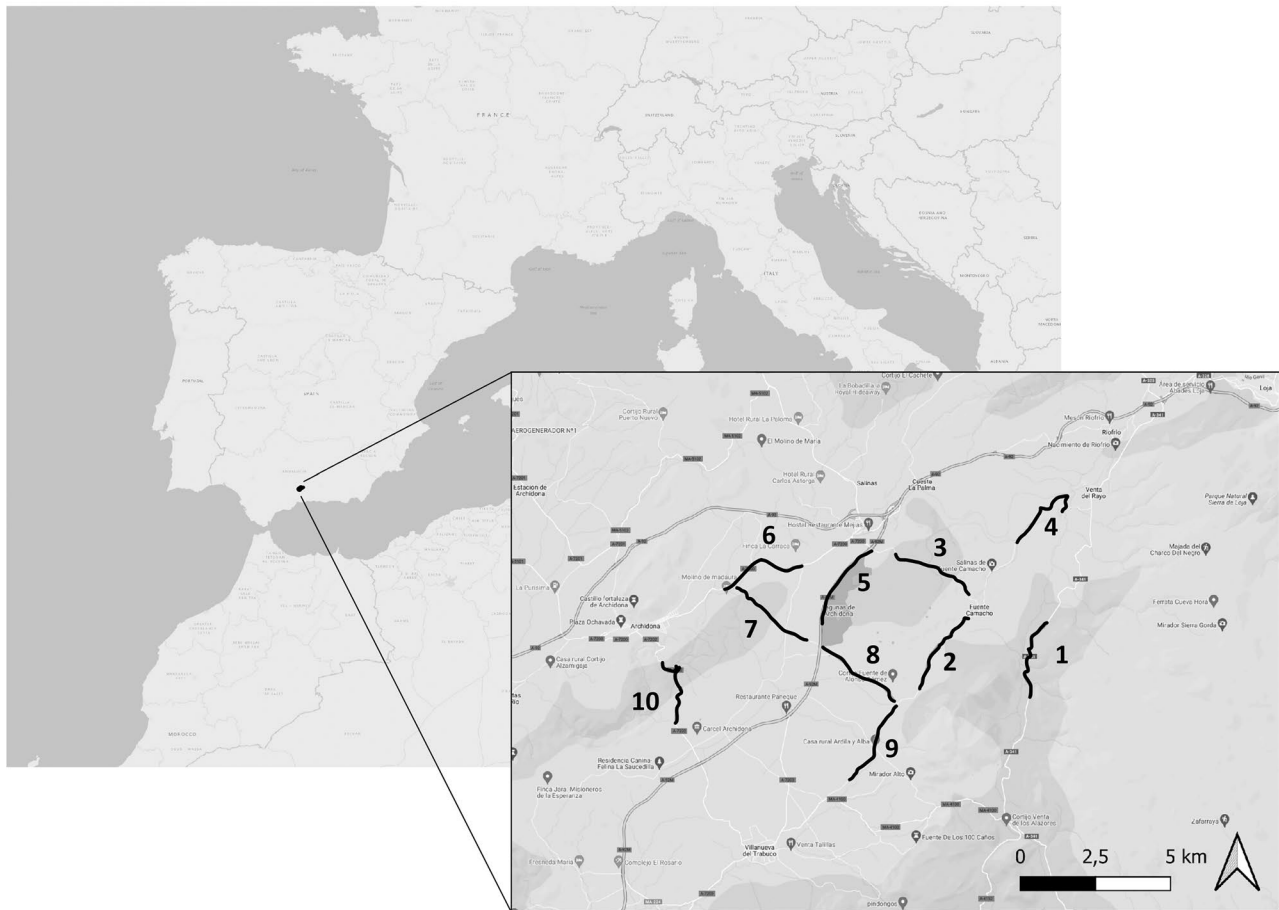
Fig. 1 Map of the study site at Loja (Granada) and Archidona (Málaga), Spain, and detail of the 10 road sections

a polygon shapefile-type layer, visually identified with the Google Hybrid plugin, selecting natural ponds and lagoons, irrigation ponds of apparently natural shores, and ignoring pools or irrigation ponds contained in walls. Once the water points had been digitised, we used the QGIS "distance to the nearest axis" tool to calculate the distance between each carcass and the closest limit to a water point.

In addition, we obtained six environmental variables from the closest meteorological station (Loja's Meteorological Station) at a monthly scale: maximum temperature (T_{max}), minimum temperature (T_{min}), mean temperature (T_{mean}), mean radiation (R_{mean}), mean precipitation (P_{mean}), and mean humidity (H_{mean}).

All data were exported to a global database, and analyses were conducted on the R programming language (R Core Team 2021). To analyse whether the number of accidents depended on road tortuosity and the presence of fencing (i.e. characteristics of the road), we fitted an N-mixture hierarchical model (Royle and Nichols 2003; Fernández-López et al. 2022) using the *unmarked* package (Fiske and Chandler 2011). In the N-mixture model, we considered the repeated

monthly sampling (12 months) of the 10 road sections, the effect of the presence of fence (fenced vs unfenced) on the animal abundance, and the additive effects of tortuosity (scaled values of this continuous variable) and presence of fence as covariates modelling the detectability of roadkill events. We included the presence of fencing in the sub-model of detectability since fenced areas could hold more abundant animal populations, because they are usually better preserved. To analyse whether the percentage of road-kill events differed for each animal class and season of the year, we fitted a Chi-square test. To delve into the effect of the season on roadkill mortality of the different classes of vertebrates, we fitted a Generalized Linear Mixed Model (GLMM) linked to a Poisson distribution on the number of collisions, with class (amphibians, reptiles, birds, mammals), season (spring, summer, autumn, winter), and their interaction as fixed terms and the road section as a random factor (random intercept), using the *lme4* package (Bates et al. 2011). Lastly, we analysed the effect of climatic variables on the probability of the hit animal being an amphibian, reptile, bird, or mammal, and we fitted a multinomial
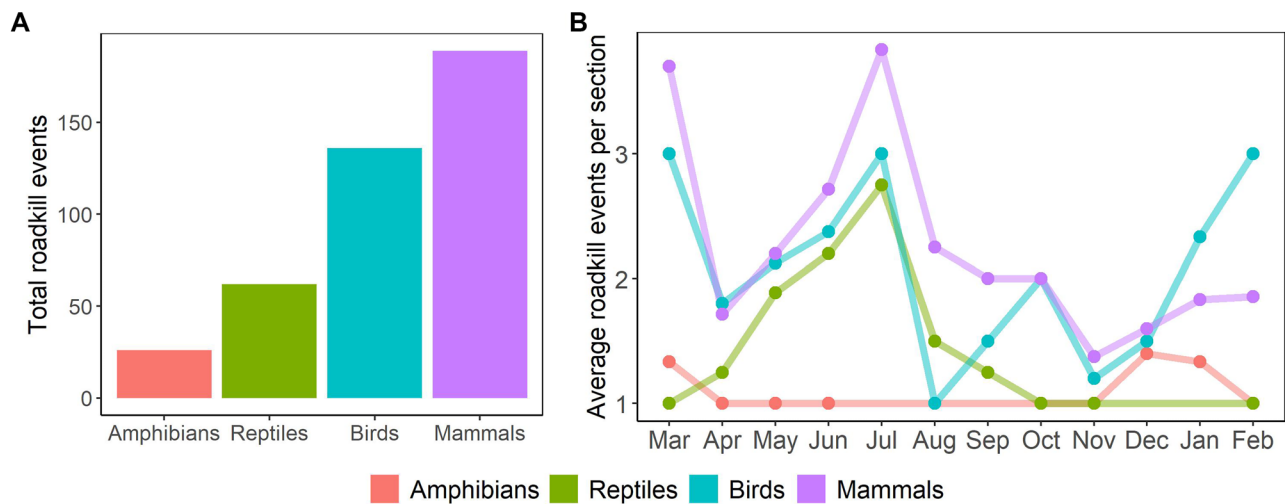
A

B

Fig. 2 **A** Total number of carcasses, **B** monthly variation on mean number of roadkill events per road section for each animal class

logistic regression model using the *nnet* package (Ripley et al. 2016). The six weather variables (T_{max}, T_{min}, T_{mean}, R_{mean}, P_{mean}, and H_{mean}) were highly correlated (r with an absolute value ≥ 0.79 for all bivariate correlations, except those related to precipitation; see correlation plot in Online Resource 1), so we decided to use only T_{mean} and P_{mean} (Pearson's correlation, $r = -0.48$) as explanatory variables in the multinomial logistic regression model. For all models, we verified that residuals followed an approximately normal distribution.

Given that the distance of the carcass to the nearest water point was not normally distributed and the variances were very heterogeneous between the different classes of vertebrates, we used a Kruskal–Wallis' test to analyse the differences in the distance to the water by class, followed by paired comparisons using Mann–Whitney U tests with Bonferroni's corrected p-values. To visualise the spatial distribution of roadkill events across vertebrate taxa and seasons, we obtained heatmaps of run-over animals in the study area for each animal class and season of the year. For plots and maps, we used the R packages *ggplot2* (Wickham 2011), *raster* (Hijmans et al. 2015), *maptools* (Bivand et al. 2022), *ggmap* (Kahle et al. 2019), and *sp* (Pebesma et al. 2012). The data and code are available in a GitHub repository (https://github.com/Zaidaortega/season_roadkill).

Results

We registered a total of 413 vertebrate carcasses, 26 amphibians (6.30%), 62 reptiles (15.01%), 136 birds (32.93%), and 189 mammals (45.76%) (Fig. 2A). Roadkill mortality varied throughout the year for the different classes of vertebrates (Fig. 2B). Among amphibian species, the most run over was

the natterjack toad (*Epidalea calamita*) ($n = 10$), in reptiles the Montpellier snake (*Malpolon monspessulanus*) ($n = 18$), in birds the common blackbird (*Turdus merula*) ($n = 21$), and in mammals the European rabbit (*Oryctolagus cuniculus*) ($n = 73$) (see Online Resource 2 for the full list of carcasses).

The N-mixture model showed that neither road tortuosity nor the presence of fence significantly affected the frequency of roadkill (Table 1).

There was a significant association between the season of the year and the animal class ($Chi^2 = 33.37$, $d.f. = 9$, $p < 0.001$) (Fig. 3A). To assess the effect of the season on each class of vertebrates, we fitted a GLMM with a Poisson error distribution family and the road section as a random factor. The model did not show any significant interaction between the season of the year and the animal class (Table 2).

Distance of the carcass to a water point differed by class (Kruskal Wallis test, $Chi^2 = 22$, $d.f. = 3$, $p < 0.001$),

Table 1 Results of the N-mixture model estimating the effect of presence of fence on animal abundance and the additive effects of road tortuosity and presence of fence on the frequency of roadkills, where the studied 10 road sections were assessed for 12 repeated sampling occasions (one per month). The presence of fence is a nominal variable (fenced vs unfenced), where fenced was the reference category for the model. Significant results are indicated in bold

Submodel	Term	Coefficient	Z	*p*-value
Abundance	**Intercept**	**2.880**	**6.482**	**< 0.001**
	Fence	0.385	0.727	0.467
Detection	**Intercept**	**−1.634**	**−3.160**	**0.016**
	Tortuosity	0.105	0.921	0.357
	Fence	−0.081	−0.134	0.894

AIC $= 549.31$

but pairwise comparisons (Mann–Whitney U tests with Bonferroni-corrected p-value) indicated that only bird carcasses were closer to water points than mammal ones ($W = 9020$, $p < 0.001$) (Fig. 3B). The number of collisions varied during the year with the oscillations of the environmental variables—mean temperature, relative humidity, and solar radiation (Fig. 4). The multinomial model showed that the probability of being run over was not related to precipitation ($p > 0.05$ in all cases), while

the mean temperature significantly affected the probability of being run over ($\beta_{\text{Reptiles}} = 0.253$, $p < 0.001$; $\beta_{\text{Birds}} = 0.099$, $p < 0.001$; $\beta_{\text{Mammals}} = 0.107$, $p < 0.001$; amphibians is the reference category) with different trends for each vertebrate class (Fig. 3C).

The spatial exploration of roadkill mortality showed a great seasonal variability in the different road sections for the different animal classes, allowing the identification of critical points for each group (Fig. 5).
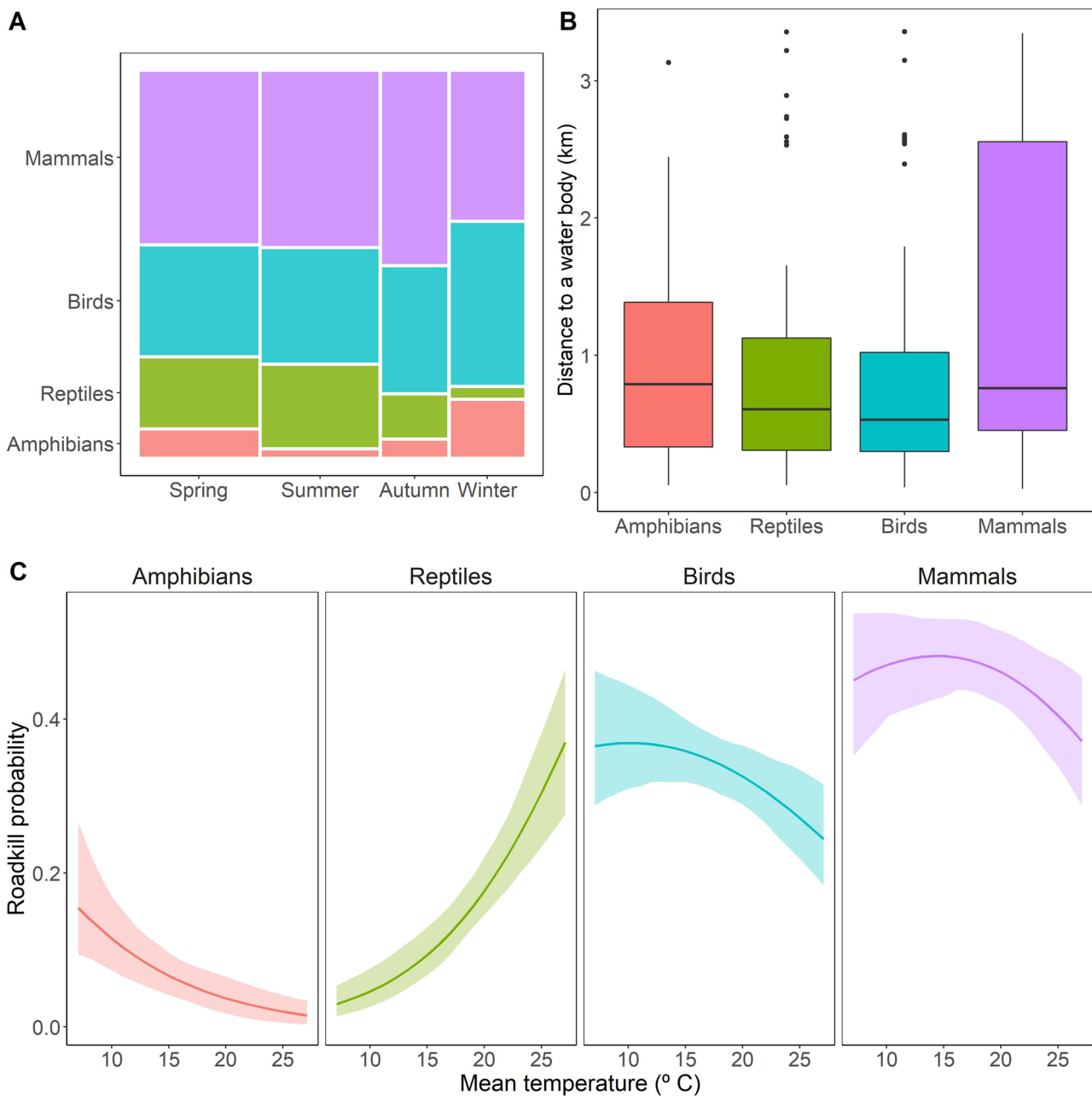

Fig. 3 A Mosaic plot of the proportion of roadkill by animal class and season. B Boxplot of distance to the closest water body for run over carcasses of each animal class. C Roadkill probability predicted by the multinomial model (mean ± 95% CI) regarding mean temperature for each animal class

Table 2 Results of the GLMM with Poisson family distribution errors, with the number of carcasses as the response variable, the main effects of the animal class (amphibian, reptile, bird, or mammal), and the study season (spring, summer, autumn, or winter), as well as their interaction, as fixed factors, and the road section as a random factor. Amphibians and spring were considered as reference levels. Significant results are indicated in bold

Term	Coefficient	Z	p-value
Intercept	0.516	1.443	0.149
Class (reptiles)	0.356	0.908	0.364
Class (birds)	**0.895**	**2.410**	**0.016**
Class (mammals)	**1.197**	**3.333**	**0.001**
Season (summer)	− 0.806	− 1.026	0.305
Season (autumn)	− 0.757	− 1.131	0.258
Season (winter)	0.133	0.301	0.763
Class (reptiles)×season (summer)	0.960	1.152	0.249
Class (birds)×season (summer)	0.832	1.018	0.309
Class (mammals)×season (summer)	0.881	1.093	0.274
Class (reptiles)×season (autumn)	0.421	0.537	0.592
Class (birds)×season (autumn)	0.300	0.417	0.677
Class (mammals)×season (autumn)	0.273	0.390	0.697
Class (reptiles)×season (winter)	− 0.835	− 0.969	0.333
Class (birds)×season (winter)	− 0.013	− 0.026	0.980
Class (mammals)×season (winter)	− 0.688	− 1.396	0.163

AIC = 503.5; BIC = 549.1, *deviance* = 469.5, *d.f.* residuals = 91 (108 observations, 10 groups). Random effects: variance = 0.151, standard deviation = 0.388

Discussion

By monthly sampling of 10 road sections along a whole year, we recorded 413 carcasses of run-over vertebrates, 45.76% of them were mammals, 32.93% birds, 15.01% reptiles, and 6.30% amphibians. This annual evaluation of roadkill mortality lets us better understand spatiotemporal patterns for each group and the variables related to them. While road sinuosity, presence of fence, and precipitation did not affect the frequency of accidents, they depended on the season, with environmental temperature modulating roadkill differently for each animal class. However, the effect of season on roadkill mortality of each animal class depended on the studied road section. Taken together, our results indicate that class-specific actions must be taken to target animals at critical sites and moments of the year.

We found that roadkill mortality varies throughout the year, with different patterns for each vertebrate class, the peak of collisions coinciding with suitable environmental conditions for each group, when they are most active (Garriga et al. 2017; Fernández-López et al. 2022). Of the 413 carcasses recorded, mammals were the most run over, with 189 animals killed on the road (45.76% of the total). Among mammal's carcasses, 73 were European rabbits (*Oryctolagus cuniculus*), which represents 17.68% of all

dead vertebrates registered in the study (Online Resource 2). This soaring roadkill mortality of rabbits may be due to different factors, such as the mobility of this species, higher than that of other vertebrates (D'Amico et al. 2015). The proximity of their burrows to the roads—since the loss of their natural habitats pushes them to construct burrows on ditches and roadsides—may also contribute to the problem (Gea-Izquierdo et al. 2005), or just simply the fact that it is a highly abundant species in the studied habitats. In any case, the high mobility of European rabbits and the proximity of their burrows to roads is concerning, since they are one of the main prey of carnivores in the Mediterranean area (Bautista et al. 2004; Barrientos and Bolonio 2009) and can attract carnivores or scavengers to the roads (Birks and Kitchener 1999), increasing their risk of collision with vehicles.

The low number of amphibian roadkill also stands out, which could be due to various causes. In the first place, detectability, since sampling has always been carried out during the daytime, and the carcasses of animals run over at night may not remain on the road the next day. As the period of greatest activity of amphibians is at night, and especially when precipitation and humidity are high (Gibbs and Shriver 2005), it is possible that at the time of sampling, either the carcasses have been run over by a lot of cars and are not visible anymore or have been predated (Mazerolle et al. 2005). In addition, the study year was dry for the area (only 187 mm^3 of precipitation), which could reduce the activity of these vertebrates and, consequently, their roadkill mortality (Jakob et al. 2003). Looking ahead to future studies, specific nocturnal sampling should be carried out to better determine the impact of road accidents on amphibians. In any case, it is important to consider that roadkill mortality strongly depends on animal abundance and its impact—from a conservation point of view—can be stronger on less abundant populations. In our case, rabbits were the most roadkilled, but this can represent a small percentage of total mortality of rabbits (compared to predation or diseases), while a smaller amount of roadkill on amphibians or reptiles could have a stronger effect in population viability.

As our aim was to understand the effect of environmental variables on the frequency of roadkill of the four vertebrate classes along the seasons of the year, we designed the study controlling the traits associated to the road section as far as possible. Some variability, nonetheless, still existed on some traits. For instance, the road sections studied traversed four different habitat types (holm oak, olive groves, broom brushes, and a mixture of these three with crop fields). Previous studies have found a dependence on roadkill frequency on habitat type (e.g. Santos et al. 2018). Although animal abundance depends on habitat type, the use of occupancy-detection models (as the N-mixture models used here) can decouple abundance from detectability (roadkill in our case; see Santos et al. 2018 and Fernández-López et al. 2022).
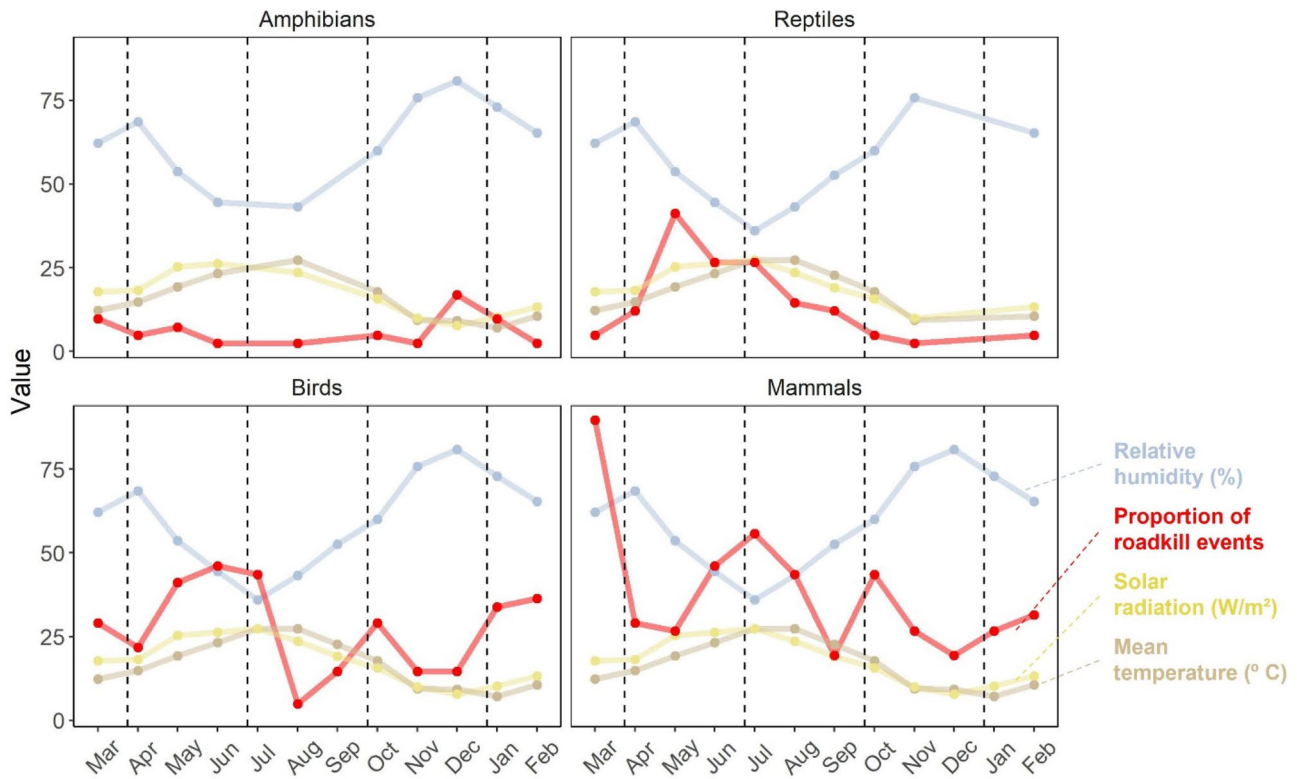
Fig. 4 For each animal class, monthly variation on roadkill events and environmental variables throughout the year. Horizontal dashed lines indicate limits between the four seasons occurring at the study area: spring (March 20–June 21), summer (June 21–September 23), autumn (September 23–December 21), and winter (December 21–March 20)

Here, we lacked enough road sections to be able to include habitat type in the models. Thus, future studies delving to assess the effect of the habitat should focus on the use of models that account for imperfect detection and include enough replicas.

Furthermore, the presence of fences and the tortuosity varied between road sections. To assess the potential effects of these two road traits on animal roadkill, we applied a hierarchical framework, fitting N-mixture models, which allowed us to separate the process of being road killed (i.e. detectability) from animal abundance. The model revealed that animal roadkill is independent of both tortuosity and the presence of fences. Despite drivers usually reducing speed in more convoluted road sections (e.g. Kanellaidis 1995), visibility also worsens in curved sections (Das et al. 2017). While the first could reduce the risk of vehicle-wildlife collision, the second would increase it (e.g. Klöcker et al. 2006). These opposite potential effects could result in the lack of relationship we found about road tortuosity and animal roadkill. On the other hand, we expected the presence of fences to reduce animal roadkills, since they would avoid the passage of many animals (McCollister and Van Manen 2010). However, most of the fenced road sections had a generalist one, which only impedes the crossing of large mammals, allowing micro and mid-mammals, as well as reptiles and amphibians, to cross it easily (Dodd et al. 2004). In addition, the fencing at most points of the study roads was in poor condition (pers. obs.), either cut or bent, causing it not to fulfil its function, and even acting as a funnel through which most vertebrates must pass (van der Ree et al. 2015). In any case, specific studies are needed to determine the potential role of fencing in the number of collisions, as well as in the fragmentation of the populations of the different groups of vertebrates.

The general analysis showed a relationship between the season and the frequency of collisions of each class of vertebrates. However, when we fit a model including the road segment as a random factor, statistically controlling for the effect of animal abundance at each segment, we see that there is no significant seasonal effect on the number of roadkill events of any of the vertebrate groups. This gives us an idea about the relevance of the variation in the number of collisions for each group of vertebrates between road segments (as we see in Fig. 5). Hence, class-specific studies are needed to detect the critical collision hotspots of each group along the year. Overall, seasonal variations are important, but it seems almost more important to identify the critical hotspots and moments of each class of vertebrates for collision prevention.
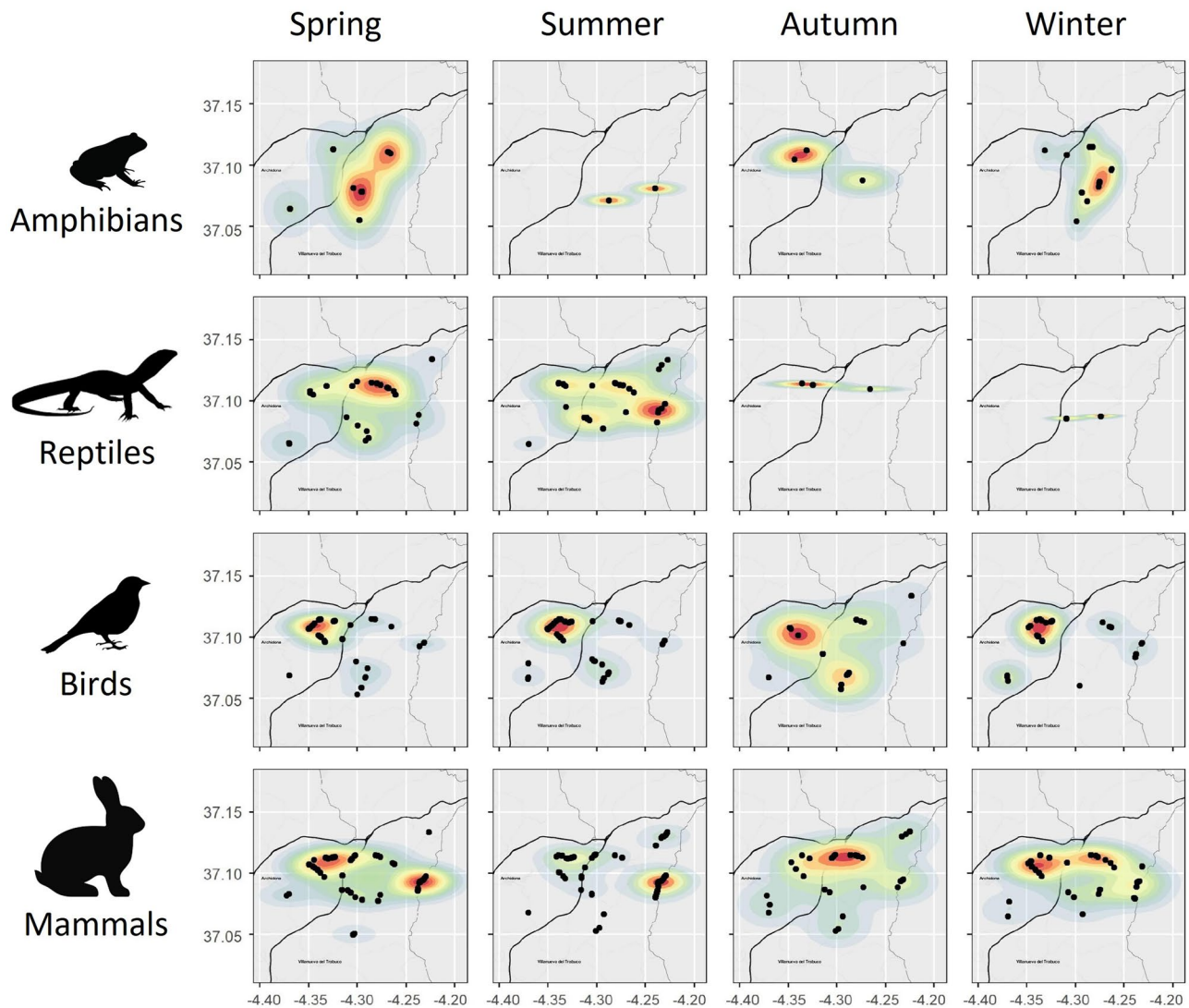
Fig. 5 Heatmaps of the density of roadkill events (where blue is minimal and red maximum frequencies) for each animal class and season

About the distance to water points, we only found a significantly shorter distance for bird carcasses in relation to mammals. Most mammal species that we have found run over are typically Mediterranean species, that is, adapted to summer drought. In addition, the intense drought experienced in 2021 (Pratt 2022) prevented most ponds from being filled during the study period. It is possible that mammals use temporary ponds and streams for hydration, so they are not necessarily associated with large perpetual water sources (Sánchez-Montoya et al. 2017). In the case of birds, the greater proximity of accidents to water masses was expected, since most species depend on water points, so they should preferably be located close to them (Pšeničková and Horák 2022). For example, the road section where we found a greater number of accidents with birds (Figs. 1 and 5) is close to rivers and ponds.

Although the seasonal effect on the number of collisions varies by road section, there are certain climatic conditions related to them, as is the case of the average temperature that significantly affected the probability of being run over for mammals, birds, and reptiles. However, precipitation did not show an effect on the probability of being hit by the different vertebrate classes. This, again, could be due to the scarcity of precipitation in the study area and period, which could have been even below a threshold from which we could find effects. Despite this, we can see that the number of amphibians being run over shows a certain relation with the increase in relative humidity and the decrease in average radiation (Fig. 4), as was found in other studies (Jakob et al. 2003). For mammals, the peak probability of being run over was around 15 °C, which is consistent with the temperatures in which most mammals show greater activity (Villafuerte et al.

1993; Zanni et al. 2021). For birds, the peak probability of being run over was around 12 °C, also a suitable temperature for bird activity (Khaliq et al. 2014). Meanwhile, this peak was around approximately 27 °C for reptiles, which coincides with temperatures in late spring and summer, where periods of greater activity of this group occur (Fig. 3C) (Ortega and Martín-Vallejo 2019). Reptiles use roads as basking surfaces or to move from one side of the road to the other in search of food or shelter (Fahrig and Rytwinski 2009), which increases their risk of being run over there.

Exploring the distribution of the accidents (maps in Fig. 5), we see that amphibian roadkill mainly occurs at specific points within each road section, since these animals live near water points (Jakob et al. 2003). For example, at the beginning of the road Sect. 9, we found several carcasses around the same point (37.071302, − 4.287494), which is an outcrop of water that accumulates there and is distributed along road Sect. 8 through irrigation ditches. For reptiles, we find most accidents concentrated at road Sects. 1 and 3, both in oak forests, an optimal habitat for this group (Vignoli et al. 2017). For birds and mammals, we observe a more homogeneous distribution of accidents in all road sections. Although tortuosity was not significant, we can see that a large part of the crashes occurs in the straight sections of the road, in which the vehicles may reach a higher speed, reducing both the driver's and the animals' reaction capacity (van Langevelde and Jaarsma 2005).

Our study had a relatively small sample size regarding road sections that may preclude us to find potential effects of some studied predictors, and future studies need to include a larger sample size to be able to make more robust assessments on the comparative effects of different road- and animal-related traits on roadkill probability. Even though more specific studies are needed to determine the specific causes of collisions for each group, by assessing the seasonal patterns of roadkill mortality for each vertebrate class in this Mediterranean area and the environmental and road-related associated traits, we were able to identify critical points to intervene for each group. We showed that even in a small study area, the spatiotemporal collision patterns of amphibians, reptiles, birds, and mammals are highly variable between road sections, which pinpoints the necessity of local studies to reduce wildlife roadkill and increase human safety on the roads.

Recommendations to reduce roadkill mortality

Among prevention actions, some of them are general and some are group-specific. Fencing is one of the most used, but its efficiency in preventing animals from accessing the road depends on the size and mobility of the animal species. For example, a fence designed for large mammals will not prevent reptiles from crossing the road. But some adaptations can make a general fence to work for more than one animal group. For example, adding a metal plate embedded in the ground in a horizontal position will prevent the passage of amphibians, reptiles, and small mammals, among others (van der Ree et al. 2015). Nonetheless, a highly effective fencing will have a counterpart since it may increase the fragmentation of habitats (Pascual-Hortal and Saura 2006) and so reduce the viability of animal populations (Glista et al. 2009). However, identifying the spatiotemporal roadkill patterns of each group can help us maximise fencing benefits and reduce its costs. Once we identify roadkill mortality hotspots for each group, we can promote policies to adapt fences at these points and promote fencing maintenance, so they can fulfil their function.

Another measure is to limit the vehicle's speed (van Langevelde and Jaarsma 2005) and/or its access to certain sections in certain periods, for example, areas where amphibians frequently pass by during rainy nights. Speed can be controlled by radars, bumps, or other structures that force drivers to reduce their velocity and should be reinforced by awareness raising and education actions. For example, the SAFE plan in Spain involves people through a large citizen project in which anyone can collaborate to assess and reduce roadkill mortality (Caballero-Díaz et al. 2021).

Conclusions from the present study indicate that the type of measure must be adjusted to the specific place and group, which will maximise its effectiveness and reduce its negative effects. For example, in critical points of collision with mammals, it makes sense to set specific fencing for this class, reducing the impact it may have on the other groups. Thus, it is possible to act with different measures for each group, in addition to including radars and specific signage at each critical point.

we uploaded the full database and R scripts to a GitHub repository (https://github.com/Zaidaortega/season_roadkill).

Declarations

Conflict of interest The authors declare no competing interests.

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