Environmental Factors Determinate Roadkill Levels of the Endemic Iberian Species, Iberian Hare (Lepus Granatensis)

Jesús Duarte
Ofitecma Marbella
David Romero (davidrp_bio@hotmail.com)
University of Malaga
Pablo Rubio
Delegación de Medio Ambiente, Oficina Técnica, Mancomunidad de Municipios de 9 la Costa del Sol Occidental
Miguel Ángel Farfán
University of Malaga
Julia Fa
University of Manchester

Research Article

Keywords: Lepus granatensis, Environmental factors, roadkill levels, Iberian species, Iberian hare, Iberian Peninsula

Posted Date: June 2nd, 2021

DOI: https://doi.org/10.21203/rs.3.rs-569721/v1

Environmental factors determinate roadkill levels of the endemic Iberian species, Iberian hare (*Lepus granatensis*)

Jesús Duarte[1§], David Romero[2*§], Pablo J. Rubio[3], Miguel A. Farfán[2#], Julia E. Fa[4#]

[1] Ofitecma Marbella, Av. Ramón y Cajal 17, 29601 Marbella, Spain.

[2] Biogeography, Diversity and Conservation research group, Department of Animal Biology, Faculty of Sciences, University of Málaga, E-29071 Málaga, Spain.

[3] Delegación de Medio Ambiente, Oficina Técnica, Mancomunidad de Municipios de la Costa del Sol Occidental, Calle de Bonanza s/n, 29604 Marbella Spain.

[4] Manchester Metropolitan University, Division of Biology and Conservation Ecology, Manchester, United Kingdom.

*Corresponding author; Email: davidrp@uma.es.

[§]*ex aequo contribution of both authors*

[#]*co-senior author*

Abstract

Lepus granatensis is an Iberian Peninsula endemic species and one of the most important small game species. We surveyed Iberian hare-vehicle accidents in roads network in southern Spain, analysing the Mediterranean landscape, the main habitats of this species. We recorded roadkill of roads during 6-month, compared hare roadkill densities to hare hunting yields. We analyzed the spatial patterns and factors that could be influencing the hare road kill. We detected blackspots of hare road kill in areas with high landscape heterogeneity and included embankments, intersections roads and high traffic intensity. The hare roadkill ranged between 6% and 41% of the annual harvest of hares killed on neighbouring hunting estates. We therefore consider

it highly relevant to take into account the hare road kill, especially in hare hunting areas, suggesting to gamekeepers and managers addressing the issue of road kill of hares. It would be necessary that hunting quotas be adjusted in territories where the additive effect of these non-natural hare mortalities converge. Results point to future directions for applied research in road ecology, which would include demographic compensation and roadkill mitigation. Our methodology could be of wide use to identify lagomorphs' road kill blackspots by analysing environmental spatial patterns.

Introduction

Roads have a widespread impact on wildlife populations through landscape fragmentation, loss of connectivity, and the emergence of corridors favouring anthropogenic species or predators, as well as by direct mortality from roadkill (1), identified as one of the main threats to the conservation of mammals in the world (2). Roads can cause the decline of the carrying capacity of a species through habitat destruction and modification in boundaries of up to 100 meters on both sides of the roads (3). Human activity and traffic intensity near the road can also disturb the adjoining habitats (4). Environmental disruption by the roads are interrupting biological activities that require the movement of animals, such as reproduction, feeding, or dispersal, resulting in genetic isolation (5; 6) and affecting the demographic characteristics, their spatial distribution and abundance of species (7; 8).

A large number of species are affected by road collisions, from large vertebrates, mesocarnivores (9; 10; 11) to smaller species (12; 13; 14; 15). Road mortality affecting the European hare (*Lepus europaeus*) (16; 8; 17) as well as other non-Mediterranean hare species (18; 19; 20) has been published. However, detailed analyses of road mortality of these are scarce.

The Iberian hare (*Lepus granatensis*) is endemic to the Iberian Peninsula (21). Hares are largely nocturnal, medium-sized lagomorphs that inhabit pastureland, farmland, plains, and forests, as well as scrubland areas in mountains in the northern range of their distribution (22). The ecological role of the Iberian hare is essential for the configuration and maintenance of Mediterranean landscape ecosystems (21). On the other hand, we expected that currently spatial configuration of the Mediterranean ecosystem could be determinate the areas of hare roadkill aggregation (13). Although hares are important game animals (23), little is known about their population biology and demography (24; 25; 26; 27). Specifically, although recently new policies are being proposed for the wildlife manager, only a few studies have quantified non-hunting mortality rates, and very few have proposed to analyse the additive effect of hunting and roadkill on game species (28). Between 13% and 38% of the hare populations studied are known to be affected by predation, disease, and environmental events (i.e. floods) (29; 30). Although it is known that roadkill has adverse effects on wildlife (6; 13), few studies have specifically addressed Iberian hare roadkill. Sánchez-García et al. (30) suggested that in the north of its distribution range in Spain, only a small part of its mortality (9%) is due to roadkill. Hare roadkill is likely to be more frequent in southern Spain, where there are large areas dedicated to growing cereals, sunflowers, grapes, and olives (31).

Seiler et al. (17) emphasized the relevance of roadkill for some game species, such as hares, suggesting that the ratio of collisions to annual harvests should be taken into account in the management of populations. In Andalusia (a region in the south of Spain), the average annual hare harvest can range from 0.8 hares/km^2 to 20.9 hares/km^2 (32). In fact, almost 250 000 hares are hunted per year (33), which clearly shows the economic importance of this species. It is relevant to understand the ecological factors that increase mortality in hare populations, given the taxonomic importance of this endemic species and the significant role it plays in the ecology and rural economy of this region. Demographic compensation is a frequent response in short-lived species (34) such as the Iberian hare. Therefore, roadkill, as a type of additive mortality, must be taken into account in management or hunting plans for this species.

Identifying relationships between road-kill hare patterns and landscape is essential to propose mitigation measures for conservation purposes. This study assessed Iberian hare roadkill within a large distribution area in southern Spain. We hypothesised that, apart from hunting activities, road mortality may be a significant cause of death of this species and thus affect its population ecology. We quantified roadkill rates and compared them to the harvesting rates recorded on neighbouring hunting estates. We also identified blackspots with high roadkill rates and the factors likely to be associated with these. Finally, we propose management measures for the conservation of these populations, applicable to other territories and scales.

Material and methods

Study Area

The study was conducted in Antequera County (37º 10' N, 4º 37' W), located in northeast Malaga province (Andalusia, southern Spain) during 2003. The area's climate is continental Mediterranean, with mean temperatures of 26 ºC in August and 9 ºC in January. Annual rainfall is 550 mm, concentrated between October and May. Summers are dry and hot, and winters cold. Days with snow are rare, although frost may occur in winter since nighttime temperatures may fall to below -3ºC (35).

The area is a relatively flat (400 - 550 m.a.s.l.) fertile plain, mainly covered by farmland (more than 80%). Road density in the area was 26.9 km per 100 km2 (36). Olive groves, vineyards, sunflower fields and cereal lands or other dry herbaceous crops are typical crops. Natural vegetation is concentrated along the adjoining hills or small habitat islands within or between crops. These are dominated by scattered holm oak (*Quercus rotundifolia*), wild olives (*Olea europaea* var. *sylvestris*) and dense scrubland consisting of rockroses (*Cistus* spp.), lentisc (*Pistacia lentiscus*) and various Labiatae (37). Other natural vegetation types are present along hedges, crop boundaries and road borders where there is a predominance of an annual herbaceous and nitrophilous plant community (38). Hare abundance in the study area was relatively high. The habitat in the region is considered very favourable for hares and is amongst the most auspicious for the species in Andalusia (39).

Data collection

We selected a total of seven main roads within the study area to perform our roadkill counts (Table 1). The sampled area comprised a square of 30 km sides which included a total length of 55.7 km of roads that cross seven municipalities (Fig. 1). All roads were comparable, containing two lanes, one in each direction, an asphalt surface 6-7 meters wide and with sides of 1-2 meters wide. Maximum speed in all these roads was 90-100 km/h, although some sections had speed limits. The mean traffic intensity for 2006 was nearly 1,000 vehicles/day, ranging from 500 to 2,000 (36). All roads were unfenced, thus allowing wildlife movement and access to the surrounding vegetation. There were verges with vegetation between the roads and the surrounding cropland. We excluded highways because these are all fenced, within which we did not detect roadkills during a prior sampling.

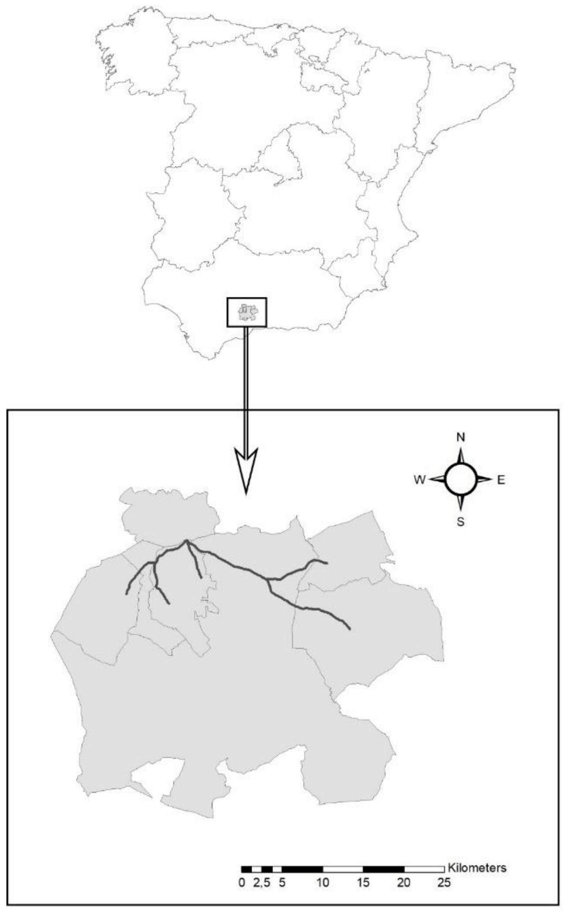

Fig. 1 Location of the study area in the northeast of Malaga province to the southern of Spain. Stretches of highways analysis for hare roadkills (55.7km).

Table 1. Features of the roads sampled in the study area. Road length is given in kilometres. Traffic volume represents the average number of vehicles/day estimated on the road (Junta de Andalucía, 2006).

Road code	Name	Length	Traffic Volume
MA-5101	Archidona - Villanueva de Algaidas	12.7	500
MA-6414	Villanueva de Algaidas - Córdoba	11.8	1000-2000
MA-6415	Córdoba - Alameda	8.9	1000-2000

MA-6409	Alameda - Los Carvajales	5.1	500-1000
MA-6410	Los Carvajales - Mollina	5.8	500-1000
MA-6408	Los Carvajales - Fuente de Piedra	5.7	500-1000
S/C	Alameda – Cortijo Peinado	5.7	500
	Total	55.7	

Roads were surveyed weekly for a total period of six months, between March 1, 2003 and July 31, 2003. This is the period of maximum reproductive activity for hares in the region (26). Three surveyors were present in each survey (always the same during the study period to avoid inter-observer biases). Surveys were driven in a car vehicle at 10 km/h. To survey by foot was not allowed by the police in these roads. Before undertaking the first sampling, we cleaned and removed all carcasses on the sampled road sections. Surveys were carried out at dawn. We recorded the UTM coordinates of each collision point using a GPS eTrex Vista Cx (Garmin, USA). When a carcass was detected, we removed it to avoid double counting during subsequent sampling. All other wild species killed by vehicle collisions were also recorded. Kill rates were standardized as the number recorded per 100 km (19).

We investigated whether hare roadkills were aggregated in certain road sections i.e., blackspots. We considered two approaches for this estimating the possible aggregation in 100-m and 500-m road sections. These distances have been proposed to be as far as the road habitat disturbance effect reaches (4). In addition, we also computed the density of roadkills in two 100m and 500m buffer radios, as the number of hares killed per km^2.

To compare hunting bags with hares killed on roads, we used the annual hunting reports (AHRs) for the period 1993 to 2001 from 181 game estates. These were all the fame estates that in the seven municipalities which were traversed by the sampled roads. We analysed 1,282 AHRs from these game estates and estimated the hunting yield (HY) as ∑ mean annual number of hares hunted per game estate / ∑ areas of the game estates in km2 (40; 41; 42). Hunting data were taken from Farfán (32).

Roadkill modelling

The number of collisions for any target species depends on a number of factors related to road features and traffic volume (43; 44), animal behaviour and phenology (45; 46; 7). The surrounding habitat structure and landscape can also play an important part (1; 14; 47). To consider the incidence of these possible factors in our sample, we overlaid hare collision points on habitat maps derived from digital orthophotographs (scale 0.5 m/pixel) using ArcGis 9.3 software (Esri, USA). All roads containing the collision points were also digitized onto the habitat maps.

We measured variables related to road features, surrounding habitat and landscape (Table 2) at each collision point. We used two sampling levels: a buffer of 100-m radius around each collision point for the habitat level (see 48; 49) and another buffer of 500-m for the landscape level (50). At the habitat level, we estimated crops and classes of vegetation present and the surface area of each vegetation patch. We also estimated habitat diversity using the Shannon index (51). At the landscape level, we measured the ecotone length and also estimated land heterogeneity using the Baxter-Wolfe interspersion index (52; 53) along a transect perpendicular to the road.

Table 2. Variables measured to model the factors that affect hare-vehicle collision locations. Road features were measured at each collision point. The habitat level variables were measured in a 100-m radius buffer around any hare accident point whereas the landscape level variables at a 500-m radius buffer. P/A, presence/absence.

Code	Definition
Road features	
Traffic	Traffic volume estimated in the road (vehicles/day; classes: 1 <500; 2, 500-1000; 3, 1000-2000)
Cross	Distance to nearest crossroad (m)
Embankment	Presence of embankment (road above surrounding land) (P/A)
Slope	Presence of lateral cutting (road below surrounding land) (P/A)
Ditch	Presence of marginal ditch (P/A)
Habitat level	
Crops	Total surface covered by crops (ha)
Natural	Total surface covered by natural vegetation (ha)
Diversity	Patch diversity (Shannon index), crops and natural vegetation
Landscape level	
Ecotone	Total ecotone length (km)
Heterog	Landscape heterogeneity (Baxter-Wolfe interspersion index)

We also generated random points without hare-vehicle collisions on these roads as controls in the statistical tests. We applied the same procedures as used with the buffers and environmental variable measurements.

Data analysis

We tested if the spatial pattern of collisions in road sections fitted a pattern expected at random through the Wald-Wolfowitz run test (54). If the random hypothesis was rejected, we estimated a spatial index of dispersion as the variance/mean ratio. If this ratio yielded values >1 hares roadkills were dispersed as contagiously objects (55) in those road sections.

To detect potential multicollinearity between variables, we developed a correlation matrix and obtained a Spearman's rank correlation coefficient (rho). Based on this value, the coefficient of determination (R^2) and the value of the Variance

Inflation Factor (VIF) were calculated to measure possible collinearity between variables (VIF >5, 56), removing one of the variables involved in the cases. Only those that captured the effects of any set of highly correlated variables were allowed to continue. The VIF statistic was calculated as:

$$VIFi = 1 / (1 - R2i).$$

We generated predictive models for hare roadkills using a GLMM with a binomial error distribution and a logit link function (57) to test if the probability of detecting a hare collision was related to any of the road and environmental factors. The different roads sampled were the random factor, collision points were the presences and the random point without collisions the absences. We selected the model with the lowest Akaike's Information Criterion (AIC) (58). The SPSS 24.0 software package (IBM, USA) was used for the statistical analysis. Means are given with their standard errors.

Results

A total of 1,336.8 km of roads were sampled during the study period. The field effort involved 171.9 observer-hours. Over a period of 6 months, we recorded a total of 162 dead animals; 68.5% Iberian hares, 17.9% wild rabbits, 4.9% other mammals, 5.6% birds, and 3.1% reptiles (Table 3). Of the 111 hares found dead near the roads, only 80 could be clearly attributed to a vehicle collision; these were taken into account for further analysis. We estimated a standard kill rate for the area of 6.0 hares/100 km.

Table 3. List and frequencies of the species found during sampling animal-vehicle accidents in the study area (March-July 2003).

Species	n	%
Mammals		
Iberian hare (*Lepus granatensis*)	111	68.52
Wild rabbit (*Oryctolagus cuniculus*)	29	17.90
Rodents (*Rattus sp.*)	2	1.23
Western hedgehog (*Erinaceus europaeus*)	2	1.23
Red fox (*Vulpes vulpes*)	2	1.23
Common genet (*Genetta genetta*)	1	0.62
Western polecat (*Mustela putorius*)	1	0.62
Birds		
Little owl (*Athene noctua*)	6	3.70
Short-toed eagle (*Circaetus gallicus*)	1	0.62
Red-necked nightjar (*Caprimulgus ruficollis*)	1	0.62
Mallard (*Anas platyrhynchos*)	1	0.62
Reptiles		
Montpellier snake (*Malpolon monspessulanus*)	3	1.85
Other snakes	2	1.23
Total	162	

Hare roadkills were not randomly distributed neither in 100-m road sections (test Wald-Wolfowitz; $N = 552$; $Z = -5,782$; $p < 0,001$) nor in 500-m sections (test Wald-Wolfowitz; $N = 113$; $Z = -4,024$; $p < 0,001$) suggesting the possible existence of black spots. However, the variance/mean ratio was only >1 in the 500-road sections (0.71 ± 0.12 hares killed per section; s2 = 1,21) confirming the existence of black spots at least in road sections from this size onwards. A total of 68.7% of the hare accidents were concentrated in 18.8% (10.5 km) of the road network sampled (Fig. 2).

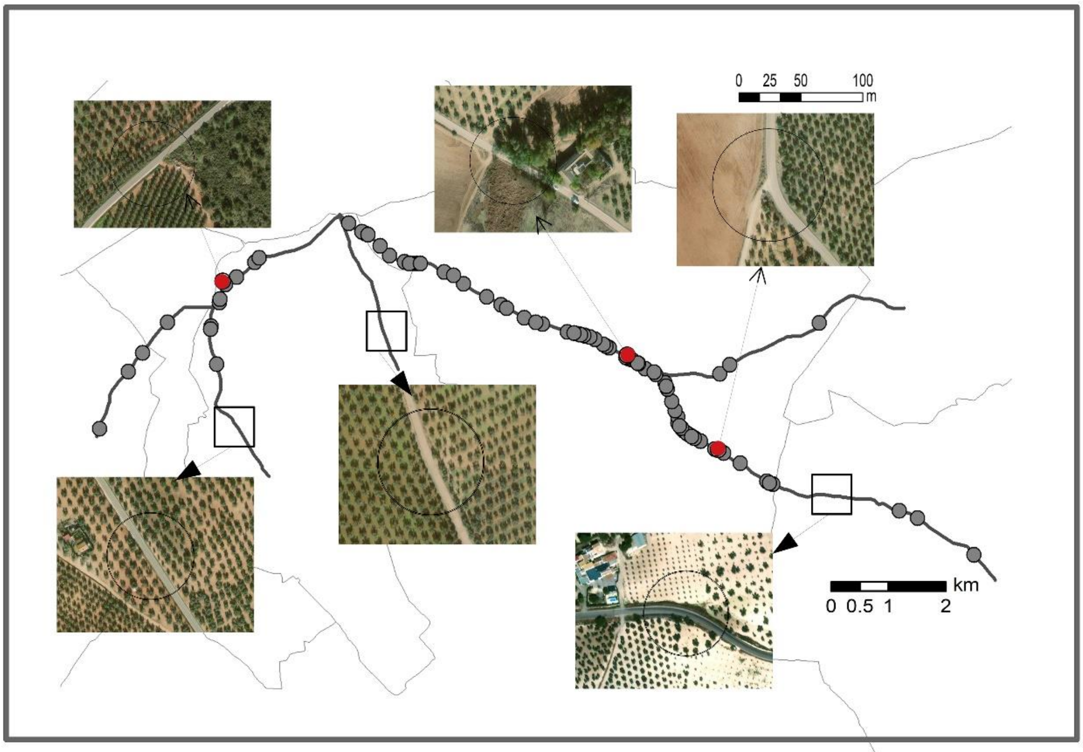

Fig. 2 Spatial study context. Grey and red circles indicate the points with hare roadkill events; the red circles, those hare roadkill points that we have added a photograph with the around 100m buffer habitat (showing heterogeneous habitats). Rectangles indicate some points without hare roadkill detected which we have added a photograph with the 100m buffer habitat (showing homogeneous habitats).

Density of hares killed on the roads was 4.6 ± 0.5 hares/km2 in 100-m buffers and 0.9 ± 1.4 hares/km^2 in 500-m buffers. The hunting yield in neighbouring game estates was 15.1 ± 14.8 hares/km^2. Therefore, roadkills can account between 8% – 40% of hares hunted in the area (Table 4).

Table 4. Hare accident density in the study area and ratio to hare hunting yields in neighbouring hunting estates (period 1993-2001). Means ± standard error and 95% confidence intervals estimation. NAHR = Number of annual hunting reports analysed; NGE = Number of game estates.

	Hares/km^2 (95% C.I.)	Roadkills / Hunting yields (%)
100-m Buffer (N = 552)	4.6 ± 0.5 (3.6 – 5.6)	39.7 (37.1 - 41.5)
500-m Buffer (N = 113)	0.9 ± 1.4 (0.6 – 1.2)	7.8 (6.2 - 8.9)
Hunting yields (N_{AHR} = 485; N_{GE} = 71)	11.6 ± 0.96 (9.7 ± 13.5)	

The test for multicollinearity did not show any VIF >5. The best model (AICc = 811.473) classified correctly 92.5% of the accidents (n = 80) and 88.9% of the random points without collisions (n = 81). The accident points were significantly associated mainly with the landscape heterogeneity and secondly with the road (embankments, crossroads and traffic volume). A highly heterogenous landscape, the presence of embankments, a nearby crossroad, and high traffic volume were the main factors influencing the hare accidents (Table 5).

Table 5. Results of the GLMM model fitted to differentiate between hare-vehicle collision points and random points without collisions. Model coefficients are shown with their standard error and Wald significance test. The random factor was the road sampled. Significant P values were considered at P < 0.05.

Source of variation	**ß ± SE**	**d.f.**	**Wald**	**P**
Landscape heterogeneity	1.547 ± 0.347	1	19.899	< 0.001
Presence of embankment	2.729 ± 0.616	1	19.661	< 0.001
Distance to nearest crossroad	-0.207 ± 0.073	1	8.094	0.005
Traffic volume in the road	2.789 ± 0.740	2	7.493	0.001

Discussion

Implications of the hare's roadkill on its conservation

Our results indicated that in the study area more than half of all reported vertebrate roadkills were Iberian hares. This frequency is higher than that observed numbers for ungulates or other medium and large-sized mammals (59; 1) and for other hare species (19; 20). The standard kill rate is also almost five times higher than for other studied hare species (18; 17) and noticeably striking in contrast with the percentage of mortality reported by Sánchez-García et al. (30) for the species' road accidents in the north of Spain. We also found that almost two-thirds of the hare roadkill were concentrated in road blackspots. Such spatial aggregation has also been reported for other mammal species (13; 60; 61). Given that mortality is concentrated in clearly defined road sections and are not at random points, mitigation measures (i.e. fencing, culvert design, verge management, crossing structures) could then be focused on these clusters (62).

However, the question arises of whether these results are representative of other areas in which the species is present. Our conclusions are limited due to the short study period and a lack of replicates. In this sense the results must be considered just as preliminary with regards to the species' road ecology. Further, smaller animals are readily missed during driven surveys, which could skew the frequencies of roadkill reported (63). Even so, we are confident that our data suggests that road mortality of hares is not insignificant and must be taken into account. Two-lane roads make up 89.4% of all Andalusian roads (36), hence the roads sampled in our study are representative of secondary roads throughout Andalusia. Fertile plains in Andalucía represent 31.1% of the regional landscape (64) as well as olive groves, vines and cereals cover 26.6% of the soils (65). Therefore, the landscape conditions, soil use, and road network in the study area are typical of almost a third of the region.

An important third limitation of the study arises from research evidences published some years after our sampling period. Santos et al. (66) shown that small mammal carcasses, like lagomorphs, do not persist on roads more than one to two days, being lower specially in summer due to same factor as scavengers, weather conditions or people removing them. This suggest that for a study like ours the optimal monitoring frequency should have been daily and not weekly. Further, this divergence in the weekly vs daily sampling could involve an important false negative rate in the estimated hotspots, missing “true” hotspots (67). In the case of lagomorphs, these authors suggest an underestimation of about 40% which implies that our estimated roadkill mortality rate is much lower than real, and some hotspots were missed. In any case, this divergence evidences the relevance of hare road mortality in the area and enhances our results because an underestimation supposes a higher source of additional mortality and bias to hunting planning.

An additional consideration about the representativeness of our results is related to hare density. It has been argued that road casualty counts are not correlated to population densities and that traffic flow is the most important explanatory variable considering variance in road accidents for certain taxa (68; 69). However, although traffic has a role to play, in the case of wild rabbits a density dependent relation between roadkills and the population living in wider landscapes has been shown (70; 71). This direct relationship may suggest something similar is affecting the Iberian hare. In fact, this relationship is true for hare hunting yields (72) since higher hare densities and more yields in fertile plains in which dry wood crops and irrigated herbaceous crops are intensively managed (23) such as in our study area.

Finally, although our study period was short it agrees with the species’ maximum reproductive activity. D’Amico et al. (46) has highlighted the relevance of phenology as the most important factor affecting temporal roadkill patterns in small mammals as well as Canal et al. (63) showed that these kinds of patterns were repeated over years and ecoregions in a same region as Andalucía. Therefore, it is likely that our results may be repetitive in similar conditions of environments, road features and hare population status, showing the existence of an unknown hare mortality rate and giving them relevance for the species management (73).

Hunting and roadkill hares; a risk of additive mortality

Roadkill data have been used to improve species management planning both in endangered (74; 75) and game species (76; 77; 78). Different authors has emphasized the general value of roadkill monitoring and its applications in some relevant ecological fields (i.e. source of information for population trends, dominance patter in species composition, mapping invasive species or contaminants and diseases; 73; 79). However, vehicle-accident data for smaller game species are often neglected for these species' management planning (71).

In the case of hunting, the consideration of sources of additional mortality is fundamental because of its effects on the species' population dynamics (80; 34) and could affect extraction rates (81). Some authors consider vehicle collision mortality as an additive source of mortality (82; 83) and even a population sink (84). Therefore, hares killed in collisions may represent individuals that would not die if this cause of mortality did not exist. Moreover, hunting mortality is considered partially compensatory (i.e. to have died due to another reason if individuals not hunted) whenever harvest rates are low (85). However, at higher harvest rates hunting mortality may also be additive. In such situations, harvest management should also take into account unnatural sources of mortality and these controlled.

Iberian hare population trends have changed significantly since our study period. It is assumed that Iberian hare populations have decreased almost 49% from 2012 to present (86). In Andalusia these authors have also estimated a 16% global reduction in the species' hunting yields. In Málaga province alone, hunting yields have dropped from 5.7 hares/km^2 (period 1993-2002; 32) to 1.7 hares/km^2 (period 2017-2018; 85). In such conditions, even a small road mortality rate should be considered relevant and likely additive, especially when new diseases are also threating the species (87; 88).

It has been argued that the high reproductive potential of the Iberian hare facilitates recruitment to populations and could make up high hunting pressures even in low density scenarios (27). In such situations or where high densities of hares exist or it is possible that the number of hare road-killed could be insignificant. However, when populations are declining and diseases are also affecting these, road kills should be considered since even a lower number of accidents would have a clear density dependent relationship. The combination of natural mortality, diseases and roadkills as well as ineffective hunting plans could drive populations into collapse. Regrettably, demographic compensation via increased fecundity of remaining Iberian hare populations is an understudied topic in road-dominated environments despite of possibly play a central role in the population growth and hare-vehicle accidents.

Factors causing hare-vehicle collisions

As other authors detected for other lagomorph species (*L. europaeus* in Brazil) (2), landscape heterogeneity is the main factor influencing Iberian hare fatalities. Mixed patches of forested areas with pastureland or farmland create habitat mosaics where an increase of resource availability for wildlife tends to increase the presence of species and then the likelihood of crossing nearby roads (11; 1). The proximity of forests to open areas is also a key factor in collisions (89). Road borders and verges may act as feeding areas for some species (14) as well as they occur during regular animal movement in their home range (90).

Forested areas in our study area are made up by olive groves, a woody crop that allow water to become available to smaller species due to their widespread trickle irrigation systems, as well as providing food resources (91). It is also worth considering that weather conditions or seasonal variations affecting food availability influence roadkill rates (92). This is a likely effect in the dry summers of the study area that could push hares to cross roads looking for available water. Vineyards also provide refuge, water and food. It should be noted that the Iberian hare follows a heterogeneous habitat selection pattern and move frequently between habitat patches (22). Therefore, hares may cross roads in points of high landscape heterogeneity in search of food (i.e.: herbaceous crop shoots, weeds or early summer grapes); looking for roadside vegetation or road verges (8); because of changes in food availability due to harvesting (93), drove by farm works or machinery (94); or simply because it's the rooting season and they are looking for mates in high diversity patches.

We identified the presence of embankments as the second factor favouring hare accidents. Some authors have suggested that embankments may act as barriers that prevent animals from crossing the road (95), and collisions occur when the road and the adjacent landscape are at the same level (96). However, the difference in level in the case of the sampled roads was always less than 1 m and in most cases was even less than 0.5 m. We think that these differences do not prevent hares from accessing roads but can slow their ability to react if encountered by a vehicle, increasing the likelihood of a collision.

Coinciding with the findings of other authors, the majority of collision points were near crossroads (2; 3). The effect of crossroads differs between mammals and may be related to the size of the animal involved. Ungulate collision points are far from crossroads (95), which may suggest avoidance of these road sections or simply that large ungulates are easier to see and avoid by vehicles in these open areas. Fence gaps or ends at intersections may favour medium or large sized mammals' fatalities near crossings (44). However, smaller size species are less visible and use road verges to hide out (97) being more difficult to avoid the collision near these intersections. Small mammals can also dig or pass easily under the fences, in case of roads fenced. Finally, higher traffic volume is positively associated, as already known, to wildlife fatalities (98). This is one the reasons why some roads are fenced: to make them safer avoiding humans and wildlife access them.

Possible mitigation strategies as conservation measures

Possible mitigation measures for Iberian hare accidents ranges from improve habitat connectivity on either side of the roads or to funnel animals to crossing structures (99; 100); to manage speed limits and traffic in the sections affected by roadkills, fencing with adequate mesh sizes or removing vegetation in road verges and bands of 50 m to 100m free of vegetation at both sides of the road (100). However, most of these measures are perceived as costly in already existing roads, appear to have little influence on improving the situation (102; 103), need appropriate and constant maintenance (104) or may be contentious as, if inappropriately placed, fences could exacerbate barrier effects and have even greater negative impacts for the population than roadkills (105). Further, it should also consider individual variability in behavioural response to roads (45) and be undertaken in the blackspots or carried out seasonally during the roadkill seasonal peaks (46). Focusing mitigation measures on blackspots in new roads can be useful, but in older roads these sections may not be the best option due to population depression (106).

Other optimal solutions must be sought (62; 28). In diminished hare populations, roads act as a clear threat and the creation of reserves without further fragmentation have been recommended (8). The Andalusian network of protected areas is already quite extensive but does not include plains and cultivated lands, where the Iberian hare is mostly present. Hunting estates in the region may act as areas for the protection of this species. Therefore, one possible mitigation measure arises from a demographic point of view because hunting allows to regulate a species population ecology when a sustainable harvesting is carried out. Given the economic and viability obstacles that may arise in areas where most roads are old and go through private farmlands or hunting estates, we propose to consider compensate the hunting rates with the road accidents in the area as a first step in the mitigation strategy of Iberian hare-vehicle accidents. This means that hare killed on roads should be taken into account in hunting plans without forgetting other mitigation measures. Therefore, we encourage careful consideration when assessing the local population status of Iberian hares that include traffic and road mortality, before estimate hunting quotas. In addition, given that hare hunting may accrue economic benefit for the local estates, a proposed solution in an inter-disciplinary field like road ecology must consider also whether reducing hunting quotas has any repercussions for estates' profit.

Conclusions

Finally, the results and discussion point to future directions for theoretical and applied research in road ecology, which would include demographic compensation and roadkill or the assessment of specific mitigation measures to protect lagomorphs. Due to the Iberian hare distribution as well as the common design of two-lane roads, we consider also that our methods and results could help to the management of roads and associated landscape throughout the national territory. In summary, this work proposes a method that allows detecting favorable spatial configuration observing a priori the spatial structure of a territory as preventive tools, and a propose a modification in the management of hunting quotes only in territories with that favorable spatial configuration by hare road kill blackspots. So, the implementation of these measures could contribute to conserve an endemic Iberian lagomorph species and indirectly also to maintaining Mediterranean landscape ecosystems.

References

1. Carvalho, F. & Mira, A. Comparing annual vertebrate road kill over two time periods, 9 years apart: a case study in Mediterranean farmland. *Eur. J. Wildl. Res.* **57**, 157−174 (2011).
2. Freitas, S. R., Oliveira, N., Ciocheti, G., Vieira, M.V., Matos, D. M. & Silva Matos, D. M. How landscape features influence road-kill of three species of mammals in the Brazilian savanna? *Oecol. Aust.* **18**, 35−45 (2015).
3. Forman, R. T. & Deblinger, R. D. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conserv. Biol.* **14**, 36−46 (2000).
4. Coffin, A. W. From roadkill to road ecology: A review of the ecological effects of roads. *J. Transp. Geogr.* **15**, 396−406 (2007).
5. Goosem, M. Fragmentation impacts caused by roads through rainforests. *Curr. Sci.* **93**, 1587−1595 (2007).

6. Van der Ree, R., Smith, D. J. & Grilo, C. In: *Handbook of road ecology*. (ed. John Wiley & Sons) (2015).

7. Grilo, C., Reto, D., Filipe, J., Ascencão, F. & Revilla, E. Understanding the mechanism behind road effects: linking occurrence with road mortality in owls. *Anim. Conserv.* **17**, 555−564 (2014).

8. Roedenbeck, I. A. & Voser, P. Effects of roads on spatial distribution, abundance and mortality of brown hare (*Lepus europaeus*) in Switzerland. *Eur. J. Wildl. Res.* **54**, 425−437 (2008).

9. Putman, R. J. Deer and road traffic accidents: options for management. *J. Environ. Manag.* **51**, 43−57 (1997).

10. Madsen, A. B., Strandgaard, H. & Prang, A. Factors causing traffic killings of roe deer *Capreolus capreolus* in Denmark. *Wildl. Biol.* **8**, 55−61 (2002).

11. Ng, J. W., Nielsen, C., Cassady, St. & Clair, C. Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. *Human-Wildl. Conflic.* **2**, 34−47 (2008).

12. Philcox, C. K., Grogan, A. L. & Macdonald, D. W. Patterns of otter *Lutra lutra* road mortality in Britain. *J. App. Ecol.* **36**, 748−762 (1999).

13. Clevenger, A. P., Chruszcz, B. & Gunson, K. E. Spatial patterns and factors influencing small vertebrate fauna roadkill aggregations. *Biol. Conserv.* **109**, 15−26 (2003).

14. Ascensão, F., Clevenger, A. P., Grilo, C., Filipe, J. & Santos-Reis, M. Highway verges as habitat providers for small mammals in agrosilvopastoral environments. *Biodiv. Conserv.* **21**, 3681−3697 (2012).

15. Serronha, A., Mateus, A. R. A., Eaton, F., Santos-Reis, M. & Grilo, C. Towards effective culvert design: monitoring seasonal use and behaviour by Meditteranean mesocarnivores. *Environ. Monit. Assess* **185**, 6235−6246 (2013).

16. Heigl, F., Stretz, C. R., Steiner, W., Suppan, F., Bauer, T., Laaha, G. & Zaller, J. G. Comparing road-kill datasets from hunters and citizen scientists in a landscape context. *Remote Sens.* **8**, 832 (2016).

17. Seiler, A., Helldin, J. O. & Seiler, C. Road mortality in Swedish mammals: results of drivers' questionnaire. *Wildl. Biol.* **10**, 225−233 (2004).

18. Caro, T. M., Shargel, J. A. & Stoner, C. J. Frequency of medium-sized mammal road kills in an agricultural landscape in California. *Am. Midl. Nat.* **144**, 362−369 (2000).

19. Fudge, D., Freedman, B., Crowell, M., Nette, T. & Power, V. Road-kill of mammals in Nova Scotia. *Can. Field Nat.* **121**, 265−273 (2007).

20. Lee, G., Tak, J. H. & Pak, S. I. Spatial and temporal patterns on wildlife road-kills on highway in Korea. *J. Vet. Clin.* **31**, 282−287 (2014).

21. Palacios, F. On the taxonomic status of the genus Lepus in Spain. *Acta Zool. Fenn.* **174**, 27−30 (1983).

22. Tapia, L., Domínguez, J. & Rodríguez, J. Modelling habitat use by Iberian hare Lepus granatensis and European wild rabbit *Oryctolagus cuniculus* in a mountainous area in northwestern Spain. *Acta Theriol.* **55**, 73−79 (2010).

23. Farfán, M. A., Duarte, J., Vargas, J. M. & Fa, J. E. Effects of human induced land-use changes on the distribution of the Iberian hare. *J. Zool.* **286**, 258−265 (2012).

24. Alzaga, V., Torres, J., Villanúa, D., Cormanzana, A., Lenaroz, I. & Mateo-Moriones, A. Conocimientos científicos importantes para la conservación y

gestión de las tres especies de liebre de la península Ibérica: deficiencias y retos para el futuro. *Ecosistemas* **22**, 13−19 (2013).

25. Alves, P. C., Gonçalves, H., Santos, M. & Rocha, A. Reproductive biology of the Iberian hare, *Lepus granatensis*, in Portugal. *Mammalian Biology* **67**, 358−371 (2002).

26. Farfán, M. A., Vargas, J. M., Real, R., Palomo, L. J. & Duarte, J. Population parameters and reproductive biology of the Iberian hare Lepus granatensis in southern Iberia. *Acta Theriol.* **49**, 319−335 (2004a).

27. Fernández, A., Soriguer, R., Castién, E. & Carro, F. Reproductive parameters of the Iberian hare *Lepus granatensis* at the edge of its range. *Wildl. Biol.* **14**, 434−443 (2008).

28. Martínez-Abraín, A., Jiménez, J. & Oro, D. New policies for a new wildlife: A road map for the wildlife manager of the future. *Biol. Conserv.* **236**, 484−488 (2019).

29. Carro, F., Beltrán, J. F., Márquez, F. J., Pérez, J. M. & Soriguer, R.C. Supervivencia de la liebre ibérica en el parque nacional de Doñana durante una época de inundaciones. *Galemys* **14**, 31−38 (2002).

30. Sánchez-García, C., Alonso, M. E., Bartolomé, D. J., Pérez, J. A., Larsen, R.T. & Gaudioso, V. R. Survival, home range patterns, probable causes of mortality, and den-site selection of the Iberian hare (Lepus, Leporidae, mammalia) on arable farmland in north-west Spain. *Italian J. Zool.* **79**, 590−597 (2012).

31. ESYRCE. Encuesta sobre Superficie y Rendimientos. Ministerio de Agricultura, Pesca y Alimentación. Subdirección General de Análisis, Coordinación y Estadística. Gobierno de España. Catálogo de Publicaciones de la

Administración General del Estado: https://cpage.mpr.gob.es. N.I.P.O.: 003-19-051-9 (2019).

32. Farfán, M. A. Evaluación de la gestión de la caza en Andalucía. Un ensayo de comarcalización cinegética. In: *PhD thesis, Universidad de Málaga (2010).*

33. Junta de Andalucía. In: *Informe de Medio Ambiente en Andalucía 2018*. Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible, Sevilla (2018).

34. Péron, G. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. *J. Anim. Ecol.* **82**, 408−417 (2012).

35. Capel-Molina, J. J. In: *Los climas de España. Oikos-Tau Barcelona* (1981).

36. Junta de Andalucía. In: *Plan de aforos de la red principal de carreteras de Andalucía 2006*. Mapa de Tráfico. Provincia de Málaga. Consejería de Obras Públicas y Transporte-Dirección General de Carreteras, Sevilla (2006).

37. Nieto, J. M., Pérez, A. & Cabezudo, B. Biogeografía y series de vegetación de la provincia de Málaga (España). *Acta Bot. Malac.* **16**, 417−436 (1991).

38. García, A. & Cano, E. In: *Malas hierbas del olivar giennense*. Diputación Provincial de Jaén, Jaén (1995).

39. Vargas, J. M., Farfán, M. A., Guerrero, J. C., Barbosa, A. M. & Real, R. Geographical and environmental correlates of big and small game in Andalusia (southern Spain). *Wildl. Res.* **34**, 498−506 (2007).

40. Farfán, M. A., Vargas, J. M., Guerrero, J. C., Barbosa, A. M. & Real, R. Distribution modeling of wild rabbit hunting yields in its original area (S Iberian Peninsula). *Italian. J. Zool.* **75**, 161−172 (2008).

41. Delibes-Mateos, M., Farfán, M. A., Olivero, J., Márquez, A. L. & Vargas, J. M. Long-term changes in game species over a long period of transformation in the Iberian Mediterranean landscapes. *Environ. Manage.* **43**, 1256−1268 (2009).

42. Delibes-Mateos, M., Farfán, M. A., Olivero, J., Vargas, J. M. Impact of land-uses changes on red-legged partridge conservation in the Iberian Peninsula. *Environ. Conserv.* **39**, 337−346 (2012).

43. D'Amico, M., Périquet, S., Román, J., Revilla, E. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *J. Appl. Ecol.* **53**, 181−190 (2016).

44. Cserkesz, T., Ottleez, B., Cserkesz, A. & Farkas, J. Interchange as the main factor determining wildlife-vehicle collision hotspots on the fenced highways: spatial analysis and applications. *Eur. J. Wildl. Res.* **59**, 587−597 (2013).

45. Ascensão, F., Grilo, C., LaPoint, S., Tracey, J., Clevenger, A. P. & Santos-Reis, M. Inter-individual variability of Stone Marten behavioral responses to a highway. *Plos One* **9**, e103544 (2014).

46. D'Amico, M., Román, J., de los Reyes, L. & Revilla, E. Vertebrate road-kill patterns in Mediterraean habitats: who, when and where. *Biol. Conserv.* **191**, 234−242 (2015).

47. Santos, S. M., Lourenço, R., Mira, A. & Beja, P. Relative effects of road risk, habitat suitability, and connectivity on wildlife roadkills: the case of the Tawny Owls (*Strix aluco*). *Plos One* **8**, e79967 (2013).

48. Malo, J. E., Suárez, F. & Díez, A. Can we mitigate animal-vehicle accidents using predictive models? *J. App. Ecol.* **41**, 701−710 (2004).

49. Villalba, P., Reto, D., Santos-Reis, M., Revilla, E. & Grilo, C. Do dry ledges reduce the barrier effect of roads? *Ecological Engineering* 57: 143−148 (2013).

50. Duarte, J., Farfán, M. A., Fa, J. E. & Vargas, J. M. Habitat-related effects on temporal variations in red-legged partridge *Alectoris rufa* abundance estimations in olive groves. *Ardeola* **61**, 31−43 (2014a).

51. Magurran, A. E. In: *Measuring biological diversity*. (Blackwell, Malden, 2004).

52. Baxter, W. L. & Wolfe, C. W. The interspersion index as a technique for evaluation a bobwhite quail habitat. In: *National Quail Symposium Proceedings*. 158−165 (1972).

53. Litvaitis, J. A., Titus, K. & Anderson, E. M. Measuring vertebrate use of terrestrial habitats and food. In: *Bookhoud* (ed. T.A., Research and management techniques for wildlife and habitats: The Wildlife Society Bethesda) 254−274 (1996).

54. Zar, J. H. In: *Biostatistical analysis. 4th* (ed. Prentice hall, Upper Saddle River, 1999).

55. Fowler, J. & Cohen, L. In: *Practical statistics for field biology*. (Wiley, New York, 1992).

56. O' Brien, R. M. A caution regarding rules of thumb for variance inflation factors. *Qual. Quant.* **41**, 673−690 (2007).

57. Crawley, M. J. GLIM for ecologists. (Blackwell, London, 1993).

58. Akaike, H. Information theory and an extension of the maximum likelihood principle. In: *Proceedings of the Second International Symposium on Information Theory*. (eds. Petrov B. N., Csaki F.) 267−268 (Akade-miai Kiado Hungary, 1973).

59. Caletrio, J., Fernández, J.M., López, J. & Roviralta, F. Spanish national inventory on road mortality of vertebrates. *Global Biodiv.* **5**, 15−18 (1996).

60. Pfeifer-Coelho, I., Coelho, A.V.P. & Kindel, A. Roadkill of vertebrate species in two highways through the Atlantic forest biosphere reserve, southern Brazil. *Eur. J. Wildl. Res.* **54**, 689−699 (2008).

61. Ruiz-Capillas, P., Mata, C. & Malo, J. How many rodents die on the road? Biological and methodological implications from a small mammals' roadkill assessment on a Spanish motorway. *Ecol. Res.* **30**, 417−427 (2015).

62. Polak, T., Rhodes, J. R., Jones, D. & Possingham, H. P. Optimal planning for mitigating impacts of roads on wildlife. *J. Appl. Ecol.* **51**, 726−734 (2014).

63. Canal, D., Camacho, C., Martín, B., de Lucas, M. & Ferrer, M. Magnitude, composition and spatiotemporal patterns of vertebrate roadkill at regional scales: a study in southern Spain. *Animal Biodivers. Conserv.* **41**, 281−300 (2018).

64. Moreira, J. M., Rodríguez, M., Zoido, F., Moniz, C., Venegas, C. & Rodríguez, J. In: *Atlas de Andalucía.* Tomo II. (Consejerías de Medio Ambiente y Obras Públicas y Transportes de la Junta de Andalucía, Andalucía, España, 2005).

65. Ministerio de Agricultura, Pesca y Alimentación. In: *Encuesta sobre superficies y Rendimientos (ESYRCE) de cultivos*. Resultados nacionales y autonómicos. (Gobierno de España, España, 2019).

66. Santos, S. M., Carvalho, F. & Mira, A. How long do the dead survive on the roads? Carcass persistence probability and implications for road-kill monitoring surveys. *Plos One* **6**, e:25383 (2011).

67. Santos, S. M., Marques, J. T., Lourenço, A., Medinas, D., Barbosa, A. M., Beja, P. & Mira, A. Sampling effects on the identification of roadkill hotspots: implications for survey design. *J. Env. Manag.* **162**, 87−95 (2015).

68. Driessen, M. M., Mallick, S. A. & Hocking, G. J. Habitat of the eastern barred bandicoot, Perameles gunnii, in Tasmania: An analysis of road-kills. *Wildl. Res.* **23**, 721−727 (1996).

69. Fahrig, L., Pedlar, J. H., Pope, S. E., Taylor, P. D. & Wegner, J. F. Effect of Road Traffic on Amphibian Density. *Biol. Conserv.* **73**, 177−182 (1995).

70. Bright, P. W., Balmforth, Z. & MacPherson, J. L. The effect of changes in traffic flow on mammal road kill counts. *App. Ecol. Env. Res.* **1381**, 171−179 (2015).

71. George, L. J., MacPherson, J. L., Balmforth, Z. & Bright, P. W. Using the dead to monitor the living: can road kill counts detect trends in animal abundance? *App. Ecol. Env. Res.* **9**, 27−41 (2011).

72. Farfán, M. A., Guerrero, J. C., Real, R., Barbosa, M. A. & Vargas, J. M. Caracterización del aprovechamiento cinegético de los mamíferos en Andalucía. *Galemys* **16**, 41−59 (2004b).

73. González-Gallina, A., Benítez-Badillo, G., Hidalgo-Mihart, M. G., Equihua, M. & Rojas-Soto, O. R. Roadkill as a complementary information source for biological surveys using rodents as a model. *J. Mammal.* **97**, 145−154 (2016).

74. Hobday, A. J. & Minstrell, M. L. Distribution and abundance of roadkill on Tasmanian highways: human management options. *Wildl. Res.* **35**, 712−726 (2008).

75. Bencin, H. L., Prange, S., Rose, C. & Popscu, V. D. Roadkill and space use data predict vehicle-strike hotspots and mortality rates in a recovering bobcat (*Lynx rufus*) population. *Sci. Rep.* **9**, 15391 (2019).

76. Romin, L. A. & Bissonette, J. A. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. *Wildl. Soc. Bull.* **24**, 276−283 (1996).

77. Colino-Rabal, V. J., Bosch, J., Muñoz, M. J. & Peris, S. J. Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Animal *Biodivers.Conserv.* **35**, 247−252 (2012).

78. Keuling, O., Baubet, E., Duscher, A., Ebert, C., Fischer, C., Monaco, A., Podgórski, T., Prevot, C., Ronnenberg, K., Sodeikat, G., Stier, N. & Thurfjell, H. Mortality rates of wild boar *Sus scrofa* L. in central Europe. *European J. Wildl. Res.* **59**, 805−814 (2013).

79. Schwartz, A. L.W., Shilling, F. M. & Perkins, S. E. The value of monitoring wildlife roadkill. *Eur. J. Wildl. Res.* **66**, 18 (2020).

80. Schaub, M. & Lebreton, J. D. Testing the additive versus the compensatory hypothesis of mortality from ring recovery data using a random effects model. *Animal Biodivers. Conserv.* **27**, 73−85 (2004).

81. Nichols, J. D., Lancia, R. A. & Lebreton, J. D. Hunting statistics: what data for what use? *Game Wildl. Sci.* **18**, 185−205 (2001).

82. Bujoczek, M., Ciach, M. & Yosef, R. Road-kills affect avian population quality. *Biodivers. Conserv.* **144**, 1036−1039 (2011).

83. Loss, S. R., Will, T. & Marra, P. P. Estimation of bird-vehicle collision mortality on U.S. roads. *J. Wildl. Manag.* **78**, 763−771 (2014).

84. Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M. & Revilla, E. Individual spatial responses towards roads: implications for mortality risk. *Plos One* **7**, e43811 (2012).

85. Sandercock, B. K., Nilsen, E. B., Broseth, H. & Pedersen, H. C. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental

harvest on the survival and cause-specific mortality of willow ptarmigan. *J. Anim. Ecol.* **80**, 244−258 (2011).

86. Garrido, J. L., Gortázar, C. & Ferreres, J. In: *Las especies cinegéticas españolas en el siglo XXI*. Garrido (ed., Independently Published), Spain. http://hdl.handle.net/10261/217633 (2019).

87. Lopes, A. M., Marques, S., Silva, E., Magahaes, M. J., Pinheiro, A., Alves, P. C., Le Pendu, J., Esteves, P. J., Thompson, G. & Abrantes, J. Detection of RHDV strains in the Iberian hare (*Lepus granatensis*): earliest evidence of rabbit lagovirus cross-species infection. *Vet. Res.* **45**, 94 (2014).

88. Águeda-Pinto, A., Lemos de Matos, A., Abrantes, M., Kraberger, S., Risalde, M. A., Gortázar, C., McFaddem, G., Varsani, A. & Esteves, P. J. Genetic characterization of a recombinant myxoma virus in the Iberian hare (*Lepus granatensis*). *Virus* **11**, 530 (2019).

89. Nielsen, C. K., Anderson, R. G. & Grund, M. D. Landscape influences on deer–vehicle accident areas in an urban environment. *J. Wildl. Manag.* **67**, 46−51 (2003).

90. Finder, R. A., Roseberry, J. L. & Woolf, A. Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. *Landsc. Urban Plan.* **44**, 77−85 (1999).

91. Pauperio, J. & Celio, P. Diet of the Iberian hare (*Lepus granatensis*) in a mountain ecosystem. *Eur. J. Wildl. Res.* **54**, 571−579 (2008).

92. Garriga, N., Franch, M., Santos, X., Montori, A. & Llorente, G. A. Seasonal variation in vertebrate traffic casualties and its implications for mitigation measures. *Landsc. Urban Plan.* **157**, 36−44 (2017).

93. Marboutin, E. & Aebischer, N. J. Does harvesting arable crops influence the behaviour of the European hare (*Lepus europaeus*)? *Wildl. Biol.* **2**, 83−91 (1996).

94. Duarte, J., Farfán, M. A., Fa, J. E. & Vargas, J. M. Soil conservation techniques in vineyards increase passerine diversity and crops use by insectivorous birds. *Bird Study* **61**, 193−203 (2014b).

95. Hubbard, M. W., Danielson, B. J. & Schmitz, R. A. Factors influencing the location of deer–vehicle accidents in Iowa. *J. Wildl. Manag.* **64**, 707−713 (2000).

96. Clevenger, A. P. & Waltho, N. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conserv. Biol.* **14**, 47−56 (2000).

97. Rico-Guzmán, E., Cantó, J. L., Terrones, B. & Bonet, A. Impacto del tráfico rodado en el PN del Carrascal de la Font Roja ¿Cómo influyen las características de la carretera en los atropellos de vertebrados? *Galemys* **23**, 113−123 (2011).

98. Sadleir, R. M. F. S. & Linklater, W. L. Annual and seasonal patterns in wildlife road-kill and their relationships with traffic density. *New Zealand J. Zool.* **43**, 275−291 (2016).

99. Yanes, M., Velasco, J. M. & Suárez, F. Permeability of roads and railways to vertebrates: The importance of culverts. *Biol. Conserv.* **71**, 217−222 (1995).

100. Mata, C., Hervás, I., Herranz, J., Suárez, F. & Malo, J. E. Complementary use by vertebrates of crossing structures along fenced Spanish motorways. *Biol. Conserv.* **124**, 397−405 (2005).

101. Rivera, D. Dejan de registrarse atropellos de fauna tras varias medidas en una carretera extremeña. *Quercus* **407**, 38−39 (2020).

102. Bissonette, J. A. & Kassar, C. A. Locations of deer-vehicle collisions are unrelated to traffic volume or posted speed limit. *Human Wildl. Conflict* **2**, 122−130 (2008).

103. Jancke, S. & Giere, P. Pattern of otter *Lutra lutra* road mortality in a landscape abundant in lakes. *Eur. J. Wildl. Res.* **57**, 373−381 (2011).

104. Farfán, M. A., Fa, J. E., Martín-Taboada, A., García-Carrasco, J. M. & Duarte, J. Lack of maintenance of motorway fences works against their intended purpose with potential negative impacts on protected species. *Sci. Rep.* **10**, 791 (2020).

105. Olsson, M. P. O. & Widen, P. Effects of highway fencing and wildlife crossing on moose *Alces alces* movements and space use in southwestern Sweden. *Wildl. Biol.* **14**, 111-117 (2008).

106. Zimmermann, F., Kindel, A., Hartz, S. M., Michell, S. & Fahrig, L. When road-kill hotspots do not indicate the best sites for road-kill mitigation. *J. App. Ecol.* **54**, 1544−1551 (2017).

Acknowledgements

We also thank S. Coxon for his help in the English revision of the manuscript.

Declarations

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.

Conflicts of interest/Competing interests the authors declare that they have no competing interests

Availability of data and material Not applicable

Code availability Not applicable

Ethics approval Not applicable.

Consent to participate All co-authors agree.

Consent for publication All co-authors agree.

Figures

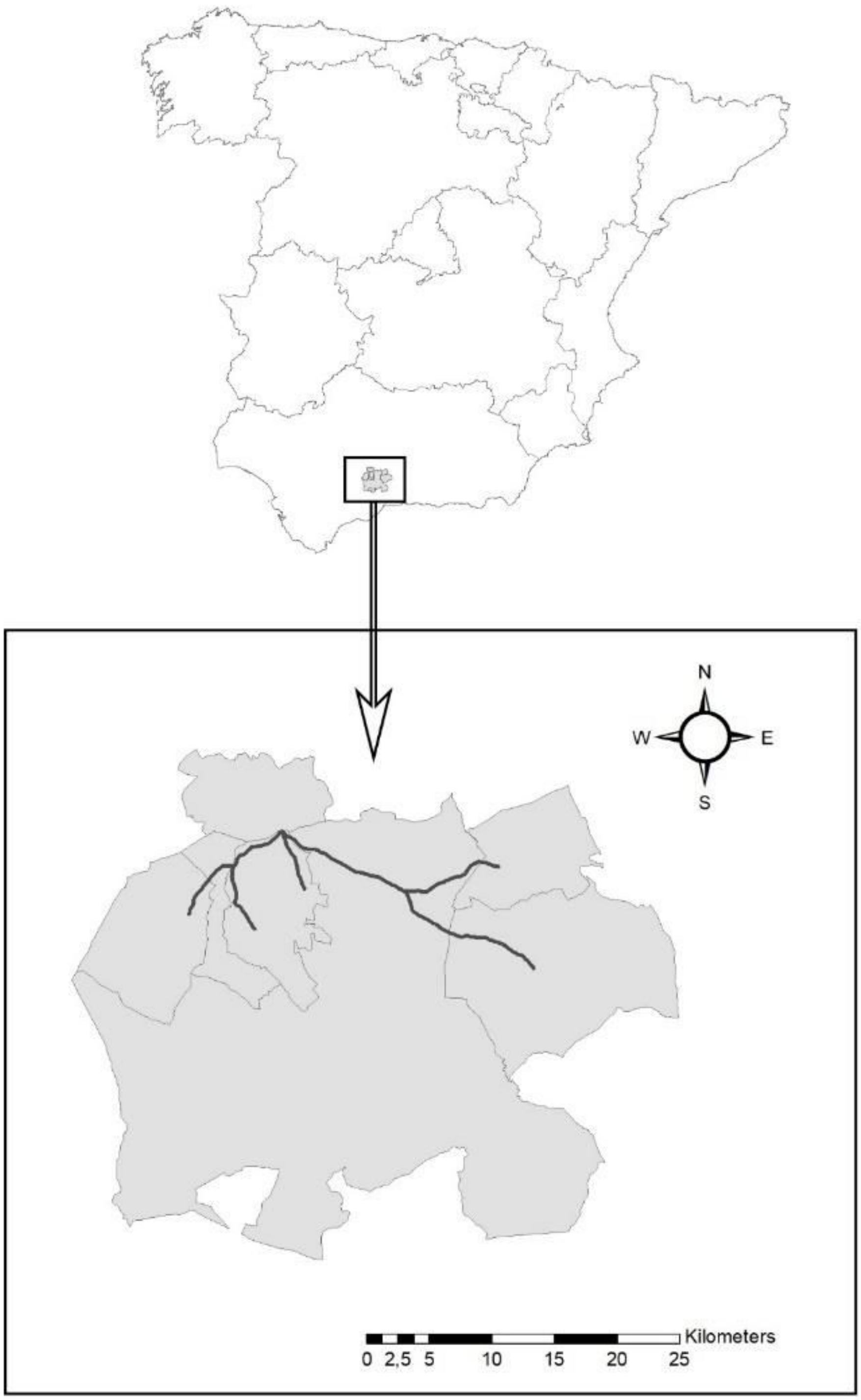

Figure 1

Location of the study area in the northeast of Malaga province to the southern of Spain. Stretches of highways analysis for hare roadkills (55.7km). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research

Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

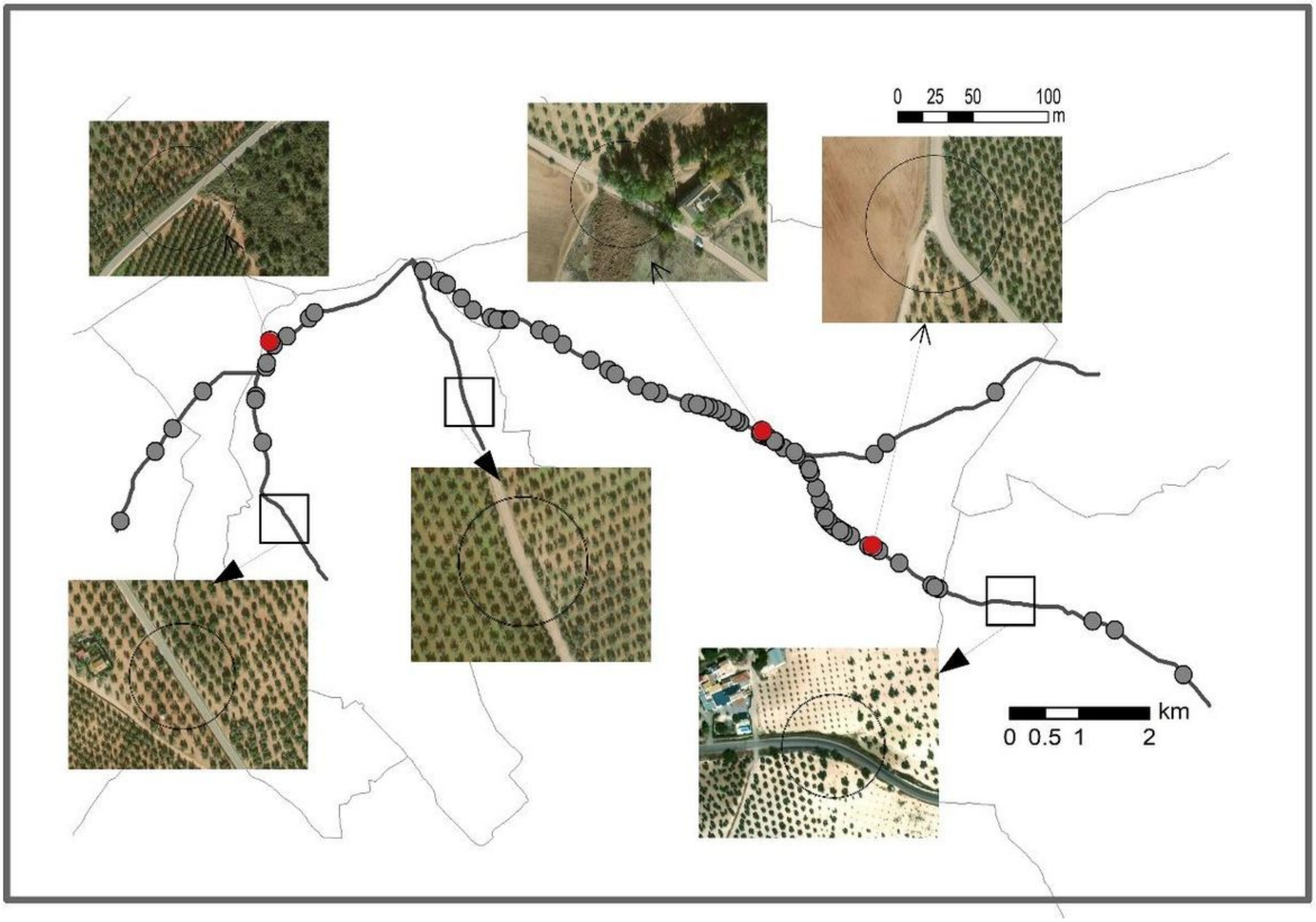

Figure 2

Spatial study context. Grey and red circles indicate the points with hare roadkill events; the red circles, those hare roadkill points that we have added a photograph with the around 100m buffer habitat (showing heterogeneous habitats). Rectangles indicate some points without hare roadkill detected which we have added a photograph with the 100m buffer habitat (showing homogeneous habitats).