

Magnitude, composition and spatiotemporal patterns of vertebrate roadkill at regional scales: a study in southern Spain

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Abstract

Magnitude, composition and spatiotemporal patterns of vertebrate roadkill at regional scales: a study in southern Spain. Although roadkill studies on a large scale are challenging, they can provide valuable information to assess the impact of road traffic on animal populations. Over 22 months (between July 2009–June 2010, and April 2011–March 2012) we surveyed 45 road sections of 10 km within a global biodiversity hotspot in Andalusia (87,000 km²), in southern Spain. We divided the region into five ecoregions differing in environmental conditions and landscape characteristics and recorded the relative magnitude, composition and spatiotemporal patterns of vertebrate (birds, mammal, amphibians, and reptiles) mortality. We used roadkill data from monthly surveys of road stretches with different speed limits, traffic volume, road design, and adjacent landscape composition. Roadkills varied over time and were not randomly distributed across ecoregions and road types. Overall, the groups most frequently encountered were mammals (54.4% of total roadkills) and birds (36.2%). Mortality rates in these two groups were higher on highways than on national or local roads, whereas those of amphibians (4.6%) and reptiles (4.3%) did not differ between road types. Except for mammals, the observed variation in vertebrate roadkills across ecoregions reflects the patterns of species richness previously described in the literature. Roadkills were concentrated over relatively short periods and this pattern was repeated over study periods and for all vertebrate classes. Our findings provide baseline information about road types, time periods and taxa with a higher probability of roadkills across an extensive region. These data represent an essential step towards the future implementation of broad-scale mitigation measures.

Key words: Wildlife vehicle collisions, Collision patterns, Collision hotspots, Mitigation measures, Non-natural mortality, Human impact

Resumen

Magnitud, composición y patrones espaciotemporales de la mortalidad de vertebrados en las carreteras a escala regional. A pesar de que los estudios a gran escala sobre mortalidad de animales en las carreteras son complejos, pueden aportar información valiosa para evaluar la incidencia del tráfico en las poblaciones de animales. Durante 22 meses (entre julio de 2009 y junio de 2010 y entre abril de 2011 y marzo de 2012), muestreamos 45 tramos de carretera de 10 km de longitud distribuidos en una zona con una gran diversidad en la región de Andalucía (87.000 km²), en el sur de España. La región se dividió en cinco ecorregiones con diferentes condiciones ambientales y características del paisaje, y se analizaron la magnitud, la composición y los patrones espaciotemporales de la mortalidad de vertebrados (aves, mamíferos, anfibios y reptiles). Usamos datos de atropellos obtenidos durante muestreos mensuales en tramos de carretera con diferentes límite de velocidad, volumen de tráfico, diseño de la carretera y composición del paisaje adyacente. Los animales atropellados fueron distintos en el tiempo y no se distribuyeron aleatoriamente entre ecorregiones ni entre tipos de carretera. En total, los grupos que se encontraron con mayor frecuencia fueron los mamíferos (el 54,4% de los atropellos registrados) y las aves (el 36,2%). La tasa de mortalidad observada en estos dos grupos fue mayor en autopistas que en carreteras nacionales o locales, mientras que la mortalidad de anfibios (el 4,6%) y de reptiles (el 4,3%) no presentó diferencias entre tipos de carretera. A excepción de los mamíferos, la variación observada de la mortalidad en las carreteras entre las diferentes ecorregiones refleja los patrones

de riqueza de especies descritos en las publicaciones científicas. Los atropellos se concentraron en períodos de tiempo relativamente cortos y este patrón se repitió en las dos temporadas de estudio y con respecto a todas las clases de vertebrados. Nuestros resultados proporcionan información de referencia sobre los tipos de carretera, los períodos de tiempo y los taxones con una mayor probabilidad de morir por atropello en una extensa región, lo que supone un paso esencial para la implementación de medidas de mitigación a gran escala.

Palabras clave: Colisiones de vehículos con animales, Patrones espaciotemporales de las colisiones, Puntos calientes de colisiones, Medidas de mitigación, Mortalidad no natural, Impacto humano

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Introduction

Linked to socio-economic development, the number of roads has increased dramatically in developed countries over the past decades. This rapid growth has led to a conflict between the need to amplify transport routes for socio-economic progress and the environmental impact caused by these infrastructures (e.g. barrier effect, habitat loss and contamination; reviewed in Forman and Alexander, 1998; Coffin, 2007; Torres et al., 2016). Collisions between vehicles and animals are an important consequence of this road-environmental conflict due to their significant socio-economic, environmental and traffic safety impact (Forman and Alexander, 1998; Forman et al., 2003; Langbein and Putman, 2006; Bissonette et al., 2008).

Every year, wildlife-vehicle collisions cause an important number of accidents, resulting in animal fatality and human injury or death, and generating a substantial economic burden due to expenses such as medical costs and material damages (Bissonette et al., 2008; Huijser et al., 2009). Although it is difficult to accurately quantify the annual number of road casualties, some studies suggest about 500,000 occur per year in Europe (Bruinderink and Hazebroek, 1996; Bissonette et al., 2008). As these studies focused mostly on large, ungulate mammals, the number of fatalities could increase by several orders of magnitude when small road-killed vertebrates are considered. For example, considering birds only, the annual estimates of roadkill could reach 27 million fatalities in some European countries (Erritzøe et al., 2003).

Traffic-related mortality is currently considered a major source of non-natural mortality in wildlife (birds: Erritzøe et al., 2003; mammals: Sáenz-de-Santa-María and Tellería, 2015; amphibians and reptiles: Colino-Rabanal and Lizana, 2012). This type of mortality may have significant effects on animal populations, such as increased inbreeding associated with isolation and reduced population size, population declines, and local extinctions (Forman et al., 2003; Coffin, 2007; Jackson and Fahrig, 2011). Traffic-related mortality may also affect the structure of animal populations because it has a differential incidence between sexes or age classes when associated with phenological events (e.g. dispersal or breeding; Mumme et al., 2000; Madsen et al., 2002; Jackson and Fahrig, 2011; Colino-Rabanal and Lizana, 2012). Traffic-related mortality has thus become an issue of major concern worldwide, as besides its potentially severe impact on natural populations, it may entail significant socio-economic costs (Forman and Alexander, 1998; Forman et al., 2003; Coffin, 2007; Bissonette et al., 2008).

In an attempt to reduce roadkill rates, a number of mitigation measures have been designed (Glista et al., 2009). However, these measures may not be universally valid because their effectiveness depends on a wide array of factors (e.g. adjacent landscape features, species involved, and their phenology). We therefore need to understand the composition, magnitude and patterns of road kill on large scales in order to optimize prevention measures (Glista et al., 2009; van der Griff et al., 2013; Rytwinski et al., 2015).

Here, we investigated the composition, seasonality and spatial patterns of vertebrate (birds, mammals, amphibian and reptiles) roadkill across an extensive Mediterranean region (Andalusia: 87,268 km² southernmost part of the Iberian Peninsula), located in one of the most important biodiversity hotspots in the world (Myers et al., 2000). Over 22 months, we monitored 45 road sections distributed across the entire region each month, constituting, to our knowledge, one of the largest surveys to date on vertebrate roadkill.

Material and methods

The study was conducted in the Autonomous Community of Andalusia, southern Spain (fig. 1) over two periods: from July 2009 to June 2010 (with the exception of September and October), and from April 2011 to March 2012. The region harbors a large diversity of species and landscapes, recognized by 30% of its territory being under some form of national or regional protection status (GIASA et al., 2006). The natural ecosystems in this region are considered highly sensitive to global change drivers, and it is predicted that they will experience dramatic biodiversity changes in the coming decades (Myers et al., 2000).

The climate in Andalusia is Mediterranean. It has a marked environmental gradient (annual rainfall varies from 170 mm/year to more than 1,800 mm/year) and a wide elevation range (from sea level to approximately 3,500 m a.s.l.). These gradients display a high degree of spatial and temporal variation in vegetation and landscape composition, including semiarid zones, forests, mountains, and marshlands. To cover such environmental diversity, we surveyed roads within different ecoregions, defined as areas characterized by similar landscape characteristics and environmental conditions (GIASA et al., 2006). The study area included five well-differentiated ecoregions: (1) lowlands and green fields of the Guadalquivir river valley (LGG: annual crops, vineyards, olive groves, mosaic crops and traditional irrigation lands); (2) medium and high mountain areas of the Baetic system (MHMB: olives groves, traditional irrigation lands, Mediterranean scrub, cork oak forests, other forests, grasslands and upland crops); (3) Atlantic and Continental biogeographic regions of Sierra Morena (ACSM: Mediterranean scrub, holm oak forests and dehesas and upland crops); (4) Atlantic and Mediterranean coastline (AMC: beach-dune systems, Mediterranean meadows, orchards and greenhouse crops); and (5) arid zones in southeastern Andalusia (AZS: sub-desert scrub and extensive steppes; fig. 1).

Besides the environmental conditions, we selected road sections according to their physical characteristics (number of lanes, speed limit and traffic volume), aiming to capture a representative picture of the entire road network of Andalusia. We grouped the road network into three categories: (1) type I, including highways characterized by a dual carriageway and 120 km/h speed limit; (2) type II, including all roads belonging to the state, regional and interregional networks except highways (hereafter, national roads); and

(3) type III, all roads belonging to the complementary regional network and provincial councils (hereafter, local roads). Both national and local roads are characterized by a single carriageway and 90 km/h speed limit. Traffic volume is assumed to decrease gradually from highways to national and local roads.

Within each of the five ecoregions, we surveyed nine road sections (three sections of each road category) of 10 km in length each month. In sum, we inspected 9,900 km (4,500 and 5,400 km in the first and second study periods, respectively) divided into 45 road segments (tables 1 in supplementary material).

The monthly surveys were carried out by two experienced observers driving a vehicle at low speed (25–30 km/h) along the roadside and with the emergency lights flashing. Surveys were conducted during the whole day. The sampling order of the surveyed sections was set at random from month to month and survey session. When a roadkill was encountered on either the paved road or the road verge, the animal was identified at the species level (whenever possible) and its location was recorded using a GPS. Carcasses were removed to avoid duplicating records during later surveys.

Several potential sources of carcass removal (e.g. scavengers, rainfall and runoff) might have biased the spatiotemporal patterns described here (reviewed in Guinard et al., 2012; Teixeira et al., 2013). We are aware that a shorter sampling periodicity is usually required to accurately estimate the accumulated number of road casualties because small animals such as amphibians and reptiles may remain on the roads for short periods of time and roadkills may be clustered in time (Guinard et al., 2012; Teixeira et al., 2013; Santos et al., 2015). This means that the number of roadkills detected do not represent the real numbers for some species, especially the small ones (Teixeira et al., 2013), and direct comparisons between species in the total number of roadkills, therefore, are meaningless. In this regard, despite their potential inaccuracy, we decided to report and interpret with caution the roadkill patterns of amphibians and reptiles since they can be useful for future studies. Note that although the actual magnitude of road mortality in Andalusia cannot be accurately determined, our survey allows us to assess the relative incidence of each road section and to explore roadkill patterns at the (eco) regional level, which is the aim of this study. Indeed, the composition and temporal mortality patterns observed in our study area are similar to those reported by other surveys conducted in the Iberian Peninsula at finer temporal resolution (i.e. weekly or fortnightly; see discussion; Frías, 1999; Grilo et al., 2009; Garriga et al., 2012; D'Amico et al., 2015). Therefore we are confident that our results reflect the true roadkill pattern in the Andalusian road network, potential differences in mortality patterns among ecoregions are assumed to be reliable.

Statistical analyses

We used chi-square goodness of fit test to test for temporal (monthly) and spatial (ecoregional) differences in roadkill frequency and to investigate roadkill

variations based on the road category and taxonomic group. Exploratory analyses showed that patterns of traffic-related mortality were similar between years both spatially (Wilcoxon paired test within ecoregions: $V = 140.5$, $P = 0.19$; or according to the type of road: $V = 11$, $P = 0.43$) and temporally (monthly: $V = 21.0$, $p = 0.54$). Data from both years were thus pooled in further analyses. Statistical analyses above were carried out in R (R Core Team, 2016).

We used the nearest neighborhood distance (NND) method (Gonser et al., 2009) to assess whether roadkills were aggregated or, conversely, independently and homogeneously distributed according to the uniform distribution over the road network. For this purpose, we tested the complete spatial randomness (CSR) hypothesis in terms of the number of roadkills at a given point set, showing, that the shortest distance from one roadkill to another roadkill was less than a parametric shortest path distance (Okabe and Sugihara, 2012). To test CSR, we applied the K function method in SANET 4.1 (Okabe et al., 2013).

We identified collision hotspots along the road network by means of a kernel density analysis (Okabe and Sugihara, 2012) using SANET V4.1 (Okabe et al., 2013). The width of the kernel function (i.e. the area of influence of each kernel function, or bandwidth) chosen for the present work was 500 m (Conruyt-Rogéon and Girardet, 2012; Morelle et al., 2013). Estimated densities were then classified using the Jenks' methods, based on minimization and maximization of variance within and between density classes, respectively (Morelle et al., 2013). Since we aimed to determine the main mortality hotspots for each taxa in the whole study area regardless of the differences in wildlife density between ecoregions, we looked for spatial aggregation in all the roadkills distributed throughout the entire road network.

Previous research suggests that Malo et al.'s method (Malo et al., 2004) should be preferred for hotspot identification (Gomes et al., 2009). As an alternative hotspot identification method, we compared the spatial pattern of fatality occurrences with that expected in a random situation, in which the likelihood of collisions for each road segment exhibits a Poisson distribution (Malo et al.'s method).

During our surveys, we found that domestic animals (dogs, *Canis lupus familiaris* and cats, *Felis silvestris catus*; see table 1) represented 18.8% of all mammals killed by vehicles. Results of the analyses excluding domestic animals were qualitatively similar to those including all data. For this reason, results from the analyses including the whole dataset are presented here.

Results

General results

A total of 1,535 animals belonging to 102 species were recorded as killed by vehicles during the two study periods (table 1). The class most frequently found dead along roads were mammals ($\chi^2_3 = 1135.8$,

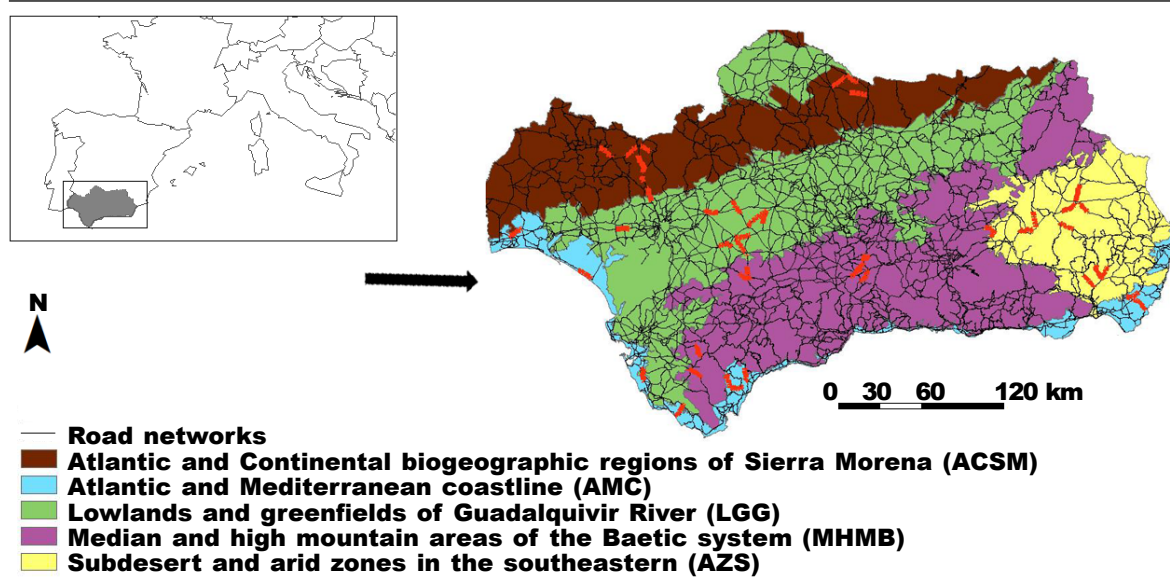


Fig. 1. Situation of the road sections and main ecological units (ecoregions) surveyed during the study period. Surveyed points (roadkill and control points) are highlighted in red.

Fig. 1. Localización de los tramos de carreteras y las principales unidades ecológicas (ecorregiones) muestreadas en el estudio. Los puntos muestreados (puntos de atropello y puntos de control) están resaltados en color rojo.

$P < 0.001$; 54.4%), followed by birds (36.2%), amphibians (4.6%), and reptiles (4.3%). Only 2.8% of roadkill could not be identified at species level due to damage and/or poor conservation condition, yet 85% ($n = 51$) of these casualties could be identified at class level (0.5% of carcasses remained undetermined at the class level; table 1).

Six of the 102 species found are threatened in Spain, listed as either 'Endangered' (*Milvus milvus*) or 'Vulnerable' (*Calandrella brachydactyla*, *Streptopelia turtur*, *Oryctolagus cuniculus*, *Salamandra salamandra* and *Mauremys leprosa*; table 1). Nine further species are listed as 'Near Threatened' in Spain (*Lanius senator*, *Lanius meridionalis*, *Asio flammeus*, *Phylloscopus trochilus*, *Mustela putorius*, *Alytes obstetricans* and *Pleurodeles waltl*) or worldwide (*Sylvia undata* and *Timon lepidus*), although the latter has not been evaluated in Spain (table 1). The incidence of traffic-related mortality for (near) threatened species was lower than six animals in all cases, with the exception of *Oryctolagus cuniculus* ($n = 298$ casualties) and *Salamandra salamandra* ($n = 11$).

Spatiotemporal patterns of roadkill

Overall, the abundance of roadkill was not uniformly distributed across months ($\chi^2_{11} = 47.4$, $P < 0.001$; fig. 2 and table 2s in supplementary material). The analyses within each vertebrate class showed a similar pattern, i.e. mortality rates differed between months (birds: $\chi^2_{11} = 22.5$, $P = 0.02$; mammals: $\chi^2_{11} = 19.9$,

$P = 0.04$; amphibians: $\chi^2_{11} = 67.9$, $P < 0.001$ and reptiles: $\chi^2_{11} = 53.3$, $P < 0.001$; fig. 2).

Spatially, the observed roadkill mortality varied markedly across ecoregions, ($\chi^2_4 = 259.4$, $P < 0.001$; fig. 3 and table 3s in supplementary material). Overall, the ecoregion with the highest number of roadkills was the Guadalquivir Lowlands (29.2%), followed by the medium and high mountain areas (26.6%), Atlantic and Mediterranean coastline (23.9%), Sierra Morena (11.5%), and the sub-desert and arid zone in southeastern Andalusia (8.8%). The number of casualties recorded also varied significantly between ecoregions for each taxonomic group ($\chi^2_{12} = 198.2$, $P < 0.001$). The highest number of road-killed mammals was recorded in the Guadalquivir Lowlands (42.4% of all detected mammals), whereas medium and high mountain areas of the Baetic system recorded the highest rate of road-killed birds (28.7% of all detected birds). Concerning amphibians and reptiles, the most hazardous ecoregions were Sierra Morena (40.8% of all detected amphibians) and the arid zone in southeastern Andalusia (28.8% of all detected reptiles; fig. 3 and table 3s in supplementary material).

The number of roadkills also varied among road types ($\chi^2_2 = 207.4$, $P < 0.001$), with the highest (50.8% of the total) vertebrate mortality recorded on highways, followed by national (31.5%) and local roads (17.7%); fig. 1s in supplementary material). This pattern was true for mammals and birds (birds: $\chi^2_2 = 84.7$, $P < 0.001$; mammals: $\chi^2_2 = 254.9$, $P < 0.001$), whereas amphibians had the lowest mortality on national roads

Table 1. Number of individuals, ecoregions and conservation status of the vertebrate species found killed by traffic along Andalusian roads between the 2009–2010 and 2011–2012 surveys. Conservation categories of the species were obtained from: (1) the Red Book of Spanish Vertebrates first published in 1992 (RB1992; Blanco and González, 1992), and then revised (RB2000) in 2002 for amphibians (Pleguezuelos et al., 2002), in 2004 for birds (Madroño et al., 2004), and in 2007 for mammals (Palomo et al., 2007); (2) CNEA, the Spanish National Catalogue of Threatened Species; and (3) IUCN (Version 2015.2). Status categories are: NE, not evaluated; DD, data deficient; K, insufficiently known; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; SI, species of special interest (for the abbreviations of ecoregions in Andalusia, see figure 1): * top roadkilled species recorded in D'Amico et al. (2015) (Huelva, South Spain); ⁱ top roadkilled species recorded in Garriga et al. (2012) (Catalonia, Northeast Spain); ⁺ top roadkilled species recorded in Frías (1999) (Toledo, Central Spain) (only birds were surveyed); and [§] top roadkilled species recorded in Grilo et al. (2009) (Alentejo, Portugal) (only nine species of medium-size carnivores were surveyed).

Tabla 1. Número de individuos, ecoregión y estado de conservación de las especies de vertebrados encontradas atropelladas en las carreteras de Andalucía durante los muestreos de 2009–2010 y 2011–2012. Las categorías de conservación de las especies se tomaron de: (1) el Libro Rojo de los Vertebrados de España, publicado por primera vez en 1992 (RB1992; Blanco y González, 1992) y luego revisado (RB2000) en 2002 para anfibios (Pleguezuelos et al., 2002), en 2004 para aves (Madroño et al., 2004) y en 2007 para mamíferos (Palomo et al., 2007); (2) CNEA, el Catálogo Español de Especies Amenazadas y (3) UICN, la Unión Internacional para la Conservación de la Naturaleza (Versión 2015.2). Las categorías de conservación son: NE, no evaluado; DD, datos insuficientes; K, insuficientemente conocida; LC, preocupación menor; NT, casi amenazada; VU, vulnerable; EN, en peligro; SI, especie de especial interés (para las abreviaturas de las ecoregiones en Andalucía, véase figura 1): * especies que sufren más atropellos mortales según D'Amico et al. (2015) (Huelva, sur de España). ⁱ especies que sufren más atropellos mortales según Garriga et al. (2012) (Cataluña, noroeste de España); ⁺ especie que sufren más atropellos mortales según Frías (1999) (Toledo, España central) (solo se estudiaron aves); [§] especies que sufren más atropellos mortales según Grilo et al. (2009) (Alentejo, Portugal) (solo se estudiaron nueve especies de carnívoros de tamaño medio).

	Conservation status				Records	Ecoregions				
	RB2000	RB1992	CNEA	IUCN		LGG	AMC	MHMB	ACSM	AZS
Mammals					835					
<i>Oryctolagus cuniculus</i> *	VU	NE	–	NT	298	111	45	109	21	12
<i>Rattus norvegicus</i> ⁱ	LC	NE	–	LC	103	25	49	24	1	4
<i>Canis lupus familiaris</i>	–	–	–	–	93	30	21	16	7	19
<i>Erinaceus europaeus</i> *	LC	NE	SI	LC	76	46	16	5	5	4
<i>Felis silvestris catus</i>	–	–	–	–	63	28	15	9	9	2
<i>Lepus</i> sp.	–	–	–	–	54	41	3	8	0	2
<i>Lepus europaeus</i>	LC	NE	–	LC	46	18	6	16	5	1
<i>Vulpes vulpes</i> * [§]	LC	NE	–	LC	30	5	2	9	5	9
<i>Lepus granatensis</i>	LC	NE	–	LC	15	9	1	4	0	1
<i>Apodemus sylvaticus</i>	LC	NE	–	LC	11	4	4	1	2	0
<i>Genetta genetta</i>	LC	NE	–	LC	8	4	2	1	0	1
<i>Herpestes ichneumon</i> [§]	LC	K	–	LC	8	2	3	3	0	0
<i>Pipistrellus pipistrellus</i>	LC	NE	SI	LC	7	3	1	3	0	0
<i>Martes foina</i> [§]	LC	NE	–	LC	6	1	1	4	0	0
<i>Mustela putorius</i>	NT	K	–	LC	4	0	2	1	0	1
<i>Eptesicus serotinus</i>	LC	K	SI	LC	3	0	0	1	1	1
<i>Meles meles</i>	LC	K	–	LC	3	0	1	0	1	1
<i>Eliomys quercinus</i>	LC	NE	–	NT	2	0	2	0	0	0
<i>Mustela nivalis</i>	LC	NE	–	LC	1	0	0	1	0	0
Undetermined mammals					4					

Table 1. (Cont.)

	Conservation status				Records	Ecoregions				
	RB2000	RB1992	CNEA	IUCN		LGG	AMC	MHMB	ACSM	AZS
Birds	555									
<i>Passer domesticus</i> ⁱ⁺	NE	NE	–	LC	70	13	30	14	8	5
<i>Sylvia melanocephala</i>	DD	NE	SI	LC	48	1	14	16	8	3
<i>Athene noctua</i> ⁺	NE	NE	SI	LC	42	16	4	10	6	6
<i>Alectoris rufa</i> ⁺	DD	NE	–	LC	41	10	4	13	13	1
<i>Turdus merula</i>	NE	NE	–	LC	30	2	9	16	2	1
<i>Sylvia atricapilla</i>	NE	NE	SI	LC	29	1	12	14	1	1
<i>Erithacus rubecula</i> *	DD	NE	SI	LC	28	6	5	6	7	4
<i>Columba livia</i>	NE	NE	–	LC	12	2	1	4	4	1
<i>Fringilla coelebs</i>	NE	NE	–	LC	12	2	1	4	1	4
<i>Galerida cristata</i>	NE	NE	SI	LC	12	1	3	5	1	2
<i>Saxicola torquata</i>	NE	NE	SI	LC	11	1	4	2	2	2
<i>Tyto alba</i>	NE	NE	SI	LC	11	4	3	2	1	0
<i>Caprimulgus ruficollis</i> *	NE	K	SI	LC	8	3	1	3	1	0
<i>Miliaria calandra</i>	NE	NE	–	LC	8	3	1	2	2	0
<i>Pica pica</i>	NE	NE	–	LC	8	0	2	2	3	1
<i>Melanocorypha calandra</i>	NE	NE	SI	LC	7	4	1	1	0	1
<i>Turdus philomelos</i>	NE	NE	–	LC	7	2	0	0	0	5
<i>Hirundo rustica</i>	NE	NE	SI	LC	8	2	2	2	0	0
<i>Alauda arvensis</i>	NE	NE	–	LC	6	3	0	1	1	1
<i>Serinus serinus</i>	NE	NE	–	LC	6	1	4	1	0	0
<i>Cisticola juncidis</i>	NE	NE	SI	LC	5	2	1	1	1	0
<i>Hirundo daurica</i>	NE	NE	SI	LC	5	1	0	0	4	0
<i>Phylloscopus collybita</i> *	NE	NE	SI	LC	5	1	4	0	0	0
<i>Bubo bubo</i>	NE	R	SI	LC	4	1	1	0	2	0
<i>Alectoris rufa</i> ⁺	DD	NE	–	LC	41	10	4	13	13	1
<i>Calandrella brachydactyla</i>	VU	NE	SI	LC	4	2	0	0	1	1
<i>Carduelis carduelis</i>	NE	NE	–	LC	4	0	1	3	0	0
<i>Jynx torquilla</i>	DD	NE	SI	LC	4	1	0	3	0	0
<i>Merops apiaster</i>	NE	NE	SI	LC	4	0	2	1	1	0
<i>Motacilla alba</i>	NE	NE	SI	LC	4	0	3	0	1	0
<i>Passer montanus</i>	NE	NE	–	LC	4	1	2	0	1	0
<i>Picus viridis</i>	NE	NE	SI	LC	4	0	0	3	0	1
<i>Streptopelia decaocto</i>	NE	NE	–	LC	4	2	2	0	0	0
<i>Asio otus</i>	NE	NE	SI	LC	3	1	0	2	0	0
<i>Bubulcus ibis</i>	NE	NE	–	LC	3	1	1	1	0	0
<i>Cuculus canorus</i>	NE	NE	–	LC	3	1	0	2	0	0
<i>Lanius senator</i>	NT	NE	SI	LC	3	0	1	2	0	0
<i>Sylvia conspicillata</i>	LC	NE	SI	LC	3	0	0	2	0	1
<i>Sylvia undata</i>	NE	NE	SI	NT	3	0	1	1	1	0
<i>Upupa epops</i>	NE	NE	SI	LC	3	1	1	1	0	0
<i>Anas platyrhynchos</i>	NE	NE	–	LC	2	1	1	0	0	0

Table 1. (Cont.)

	Conservation status				Records	Ecoregions				
	RB2000	RB1992	CNEA	IUCN		LGG	AMC	MHMB	ACSM	AZS
<i>Cettia cetti</i>	NE	NE	SI	LC	2	0	2	0	0	0
<i>Cyanopica cooki</i>	NE	NE	SI	LC	2	0	0	1	1	0
<i>Gallus gallus domesticus</i>	–	–	–	–	2	1	0	1	0	0
<i>Lanius meridionalis</i>	NT	NE	–	LC	2	0	0	1	1	0
<i>Larus argentatus</i>	NE	NE	–	LC	2	0	1	0	0	1
<i>Otus scops</i>	NE	NE	SI	LC	2	0	0	0	1	1
<i>Cyanistes caeruleus</i>	NE	NE	SI	LC	2	0	0	2	0	0
<i>Phoenicurus ochruros</i>	NE	NE	SI	LC	2	0	1	0	0	1
<i>Strix aluco</i>	NE	NE	SI	LC	2	0	1	0	1	0
<i>Sturnus unicolor</i>	NE	NE	–	LC	2	0	0	2	0	0
<i>Sturnus vulgaris</i>	NE	NE	–	LC	2	1	0	0	0	1
<i>Sylvia cantillans</i>	NE	NE	–	LC	2	0	0	1	1	0
<i>Accipiter nisus</i>	NE	K	SI	LC	1	0	0	1	0	0
<i>Asio flammeus</i>	NT	R	SI	LC	1	1	0	0	0	0
<i>Carduelis cannabina</i>	NE	NE	–	LC	1	0	1	0	0	0
<i>Carduelis chloris</i>	NE	NE	–	LC	1	0	0	0	0	1
<i>Circus cyaneus</i>	NE	K	SI	LC	1	1	0	0	0	0
<i>Corvus monedula</i>	NE	NE	–	LC	1	0	0	0	0	1
<i>Coturnix coturnix</i>	DD	NE	–	LC	1	1	0	0	0	0
<i>Delichon urbicum</i>	NE	NE	SI	LC	1	0	1	0	0	0
<i>Falco tinnunculus</i>	NE	NE	SI	LC	1	0	0	1	0	0
<i>Galerida theklae</i>	NE	NE	SI	LC	1	0	0	0	0	1
<i>Gallinula chloropus</i>	NE	NE	–	LC	1	0	1	0	0	0
<i>Garrulus glandarius</i>	NE	NE	–	LC	1	0	1	0	0	0
<i>Larus michahellis</i>	–	NE	–	LC	1	0	1	0	0	0
<i>Milvus milvus</i>	EN	NE	–	NT	1	0	0	1	0	0
<i>Parus major</i>	NE	NE	–	LC	1	0	1	0	0	0
<i>Petronia petronia</i>	NE	NE	–	LC	1	0	0	1	0	0
<i>Phylloscopus trochilus</i>	NT	NE	–	LC	1	0	0	0	0	1
<i>Streptopelia turtur</i>	VU	NE	–	LC	1	0	0	1	0	0
Undetermined birds					35					
Reptiles					71					
<i>Hemorrhois hippocrepis</i>	LC	NE	SI	LC	17	1	5	4	1	6
<i>Malpolon monspessulanus</i> [†]	LC	NE	–	LC	16	1	6	2	2	5
<i>Rhinechis scalaris</i> [*]	LC	NE	SI	LC	15	5	1	4	1	4
<i>Timon lepidus</i>	NE	NE	SI	NT	10	2	4	0	0	4
<i>Mauremys leprosa</i>	VU	NE	SI	NE	6	0	6	0	0	0
<i>Coronella girondica</i>	LC	NE	SI	LC	1	0	0	0	1	0
<i>Psammmodromus algirus</i>	LC	NE	SI	LC	1	0	0	1	0	0

Table 1. (Cont.)

	Conservation status				Records	Ecoregions				
	RB2000	RB1992	CNEA	IUCN		LGG	AMC	MHMB	ACSM	AZS
Amphibians					66					
<i>Bufo bufo</i> ⁱ	NE	NE	–	LC	35	2	14	3	10	6
<i>Salamandra salamandra</i> ⁱ	VU	NE	–	LC	11	0	0	0	11	0
<i>Pelophylax perezi</i> [*]	NE	NE	–	LC	8	1	2	4	1	0
<i>Bufo calamita</i>	LC	NE	SI	LC	7	0	2	2	3	0
<i>Alytes obstetricans</i>	NT	NE	SI	LC	3	1	2	0	0	0
<i>Pleurodeles waltl</i> [*]	NT	NE	SI	NT	3	0	2	0	1	0
Undetermined amphibians					4					
Undetermined (class)					8					

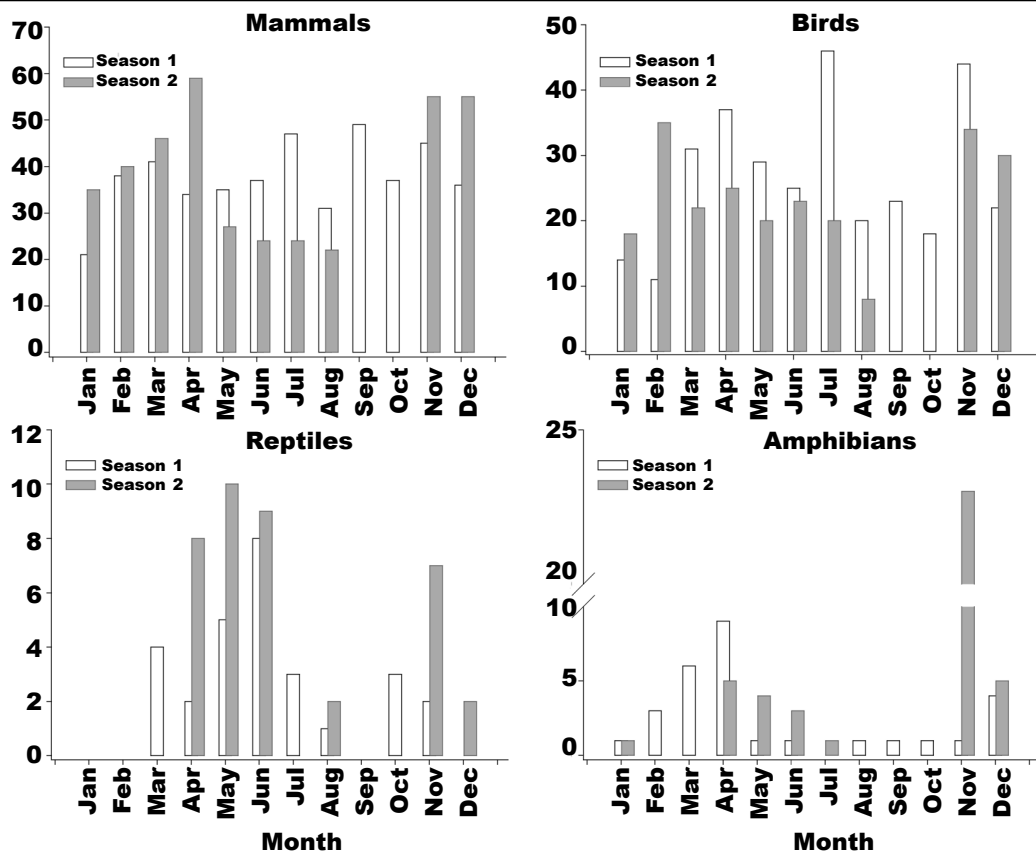


Fig. 2. Temporal variation in roadkill for each vertebrate group found on the Andalusian roads. Note that no road surveys were conducted in September or October during the first study period.

Fig. 2. Variación temporal del número de individuos atropellados encontrados en las carreteras de Andalucía para cada grupo de vertebrados. Nótese que, durante el primer período del estudio, no se realizaron muestreos en septiembre y en octubre.

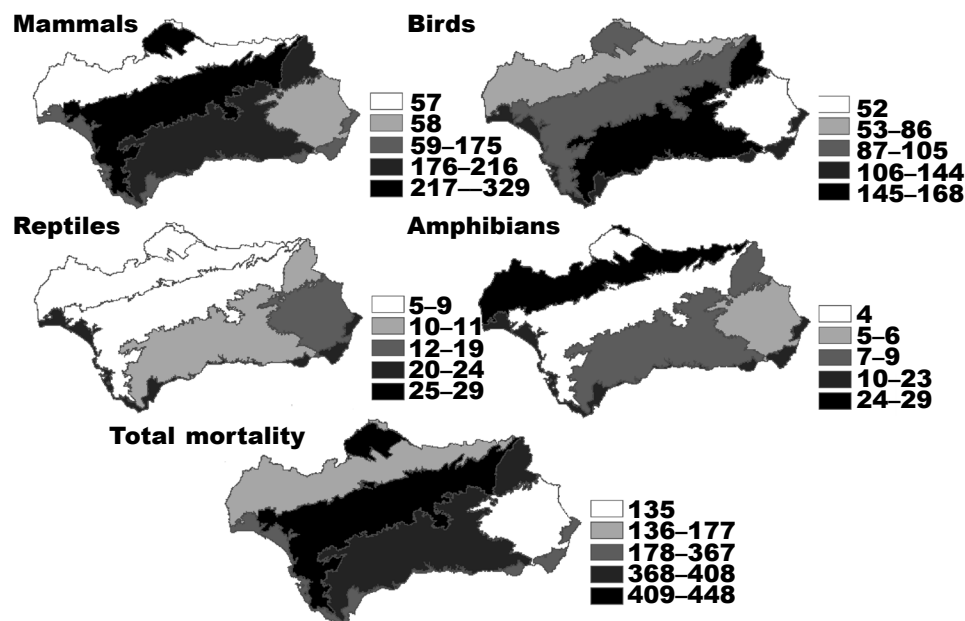


Fig. 3. Vertebrate roadkill in Andalusia according to the ecological units (ecoregions). The grey scale reflects the absolute number of roadkilled animals (Natural Breaks Classification).

Fig. 3. Número de vertebrados atropellados encontrados en Andalucía en función de las unidades ecológicas (ecorregiones). La escala gris refleja la cifra absoluta de animales atropellados (clasificación mediante umbrales naturales o de Jenks).

($\chi^2_2 = 10.5$, $P < 0.005$) and no spatial patterns were evident for reptiles ($\chi^2_2 = 1.9$, $P = 0.38$).

Roadkills were not randomly distributed across the surveyed roads. Rather they were spatially clustered, i.e., a few road sections accumulated a disproportionately large fraction of all casualties (fig. 1s in supplementary material). Moreover, we confirmed the absence of spatial randomness (CRS) with a 0.95 confidence level. Hotspots identified by Kernel and Malo et al.'s methods were spatially consistent (Spearman correlation between hotspots: $r_s = 0.58$, $p < 0.001$; fig. 4). Within vertebrate classes, roadkills were also aggregated, but the identity of the road stretches underlying such a pattern varied by taxonomic group (fig. 4 and table 1s and fig. 2s in supplementary material).

Discussion

Our extensive road survey allowed us to unravel the relative magnitude, composition and spatiotemporal patterns of vertebrate roadkill across Andalusia, a region located in a globally recognized biodiversity hotspot. Temporally, roadkills showed seasonal peaks and, spatially, some ecoregions showed disproportionately more casualties than others. Further, certain sections had higher mortality rates than others and a higher incidence on some particular taxa.

Traffic-related mortality affects a wide range of taxonomic groups and is currently considered one of the main causes of non-natural mortality of wildlife (Forman et al., 2003; Bissonette et al., 2008; Morelle et al., 2013). We recorded casualties of 102 vertebrate species during our survey, including some species listed as threatened in Spain. Based on the total number of casualties recorded in this study, one might consider the incidence of traffic-related mortality on endangered species as anecdotal. However, due to differences in species detectability, the detected numbers of casualties during the surveys do not represent the real number of roadkill for some species (Teixeira et al., 2013). Furthermore, as endangered species are characterized by low effective population sizes, the roadkill of even a few individuals may seriously threaten the long-term viability of a population (Jackson and Fahrig, 2011; Borda-de-Água et al., 2011). In effect, traffic mortality is considered a major threat for the endangered Iberian lynx, *Lynx pardinus* (Ferrerías et al., 1992; IUCN, 2015), the Florida scrub-jay, *Aphelocoma coerulescens* (Mumme et al., 2000), and several populations of turtles in the United States (Gibbs and Shriver, 2002; Andrews et al., 2008), among others. Among the threatened species recorded during our survey, we would like to draw attention to the mortality recorded for European rabbits and fire salamanders, both species listed as 'Vulnerable' in Spain. The former is a keystone species in Mediterranean ecosystems

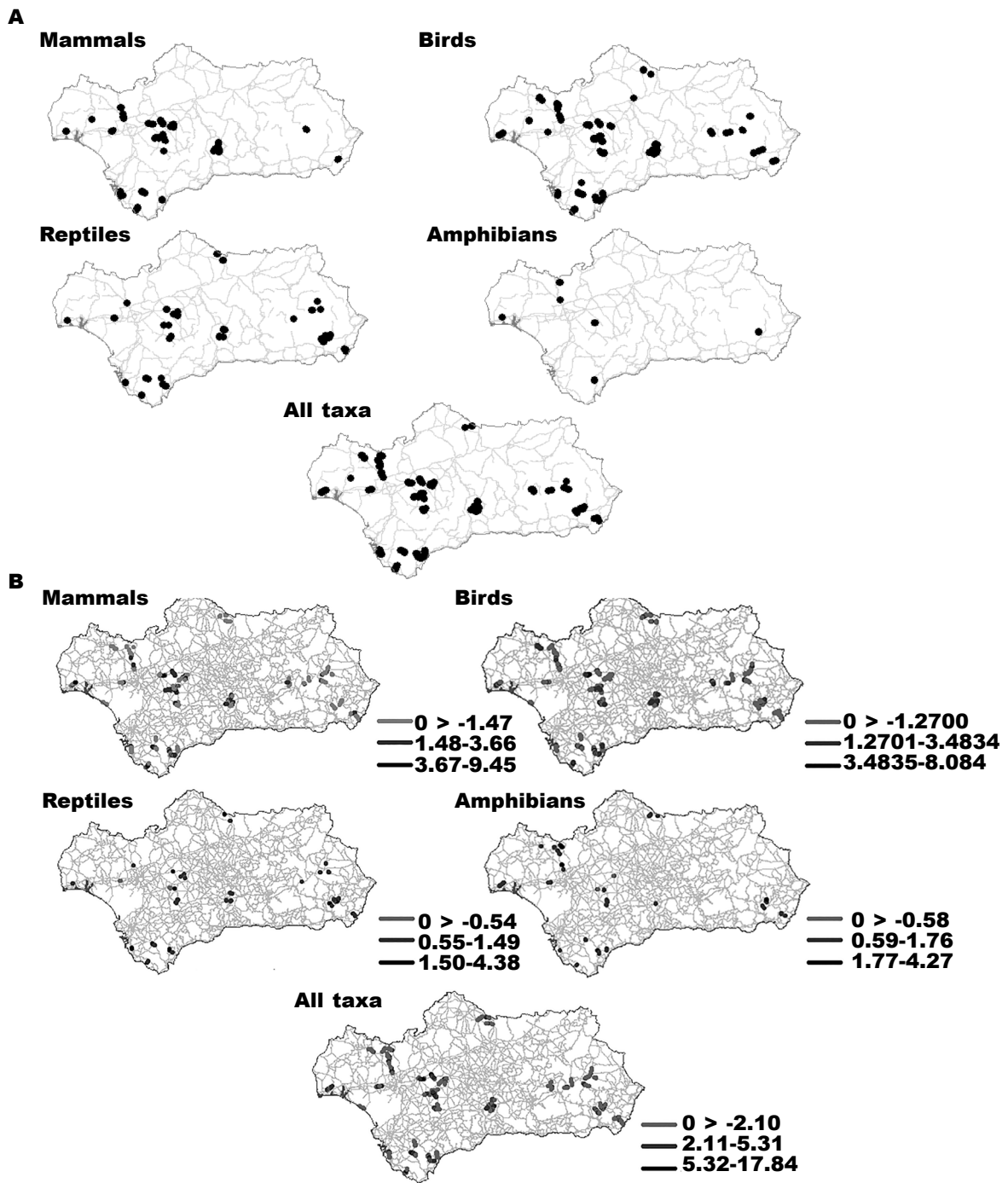


Fig. 4. Collision hotspots found on the Andalusian roads: A, Malo et al's method (Malo et al., 2004). The hotspots highlighted were defined by segments of 500-m with more than two fatalities for amphibians and reptiles (0.0003 Poisson probability), more than three fatalities for mammals (0.002 Poisson probability) and birds (0.001 Poisson probability), and more than four fatalities for all pooled taxa (0.007 Poisson probability); B, Kernel density estimation (bandwidth = 500 m; Okabe et al., 2013).

Fig. 4. Puntos calientes de colisiones en las carreteras de Andalucía: A, método de Malo y colaboradores (Malo et al., 2004). Los puntos calientes destacados fueron definidos por tramos de 500 m con más de dos atropellos mortales de anfibios y reptiles (probabilidad de Poisson de 0,0003), más de tres atropellos mortales de mamíferos (probabilidad de Poisson de 0,002) y de aves (probabilidad de Poisson de 0,001) y más de cuatro atropellos mortales cuando todos los taxones fueron analizados conjuntamente (probabilidad de Poisson de 0,007); B, estimación de la densidad Kernel (anchura = 500 m; Okabe et al., 2013).

(Delibes and Hiraldo, 1981) as it is the main prey of other key endangered species, such as the Iberian lynx and the Spanish imperial eagle *Aquila adalberti*. Despite being locally abundant in some parts of its natural range, the rabbit has suffered a sharp population decline over the last decades (70 % between the 1970s and 2000s; Virgós et al., 2007). Thus, although rabbits have high reproductive rates and probably only those inhabiting road verges are affected by roadkill, the high prevalence of rabbits recorded in our survey (298 individuals; 35 % of road killed mammals) might play a negative role in the recovery of certain rabbit populations. In the case of the fire salamander, all road-killed individuals were found within a single 2-km section (local road HU-9116/SE-6405) near a main river, suggesting all carcasses belonged to the same local population and that roadkill has a significant impact on this species in the area.

Traffic-related mortality in our survey showed seasonal peaks both across and within vertebrate groups. Several factors may have jointly contributed to shape the temporal distribution of traffic-related mortality across our study region. First, weather conditions seem to affect the incidence of roadkill, since mortality peaked in spring (March, April and May) and in autumn (October, November) and decreased in summer. The Mediterranean climate in Andalusia is characterized by a long summer drought. High temperatures and low water availability during this season often lead to a low level of activity in the studied vertebrate groups. In contrast with other regions across Spain, many areas of Andalusia, particularly those nearby to the coast, have mild autumn and winter temperatures. The moderate decrease in temperatures after summer combined with the increased water availability after the autumn rainfalls allow for high to moderate levels of activity in vertebrates in autumn and winter in Andalusia, even in cold-blooded taxa. Possibly, the annually bimodal (spring–autumn) roadkill pattern found in amphibians was largely influenced by rainfall and the typically mild temperatures in the region during these seasons. In the case of reptiles, the higher number of reptile casualties in late spring and early summer may be related to long photoperiods and high temperatures that may promote high activity levels (Colino–Rabanal and Lizana, 2012; D’Amico et al., 2015). It should be noted that the number of herpetofauna roadkills recorded was low (possibly due to different sources of carcass removal; Guinard et al., 2012; Teixeira et al., 2013; Santos et al., 2015) and, as a consequence, the mortality patterns of this group should be cautiously interpreted. Second, phenological factors such as migrations (Santos et al., 2007), breeding periods (Grilo et al., 2009; D’Amico et al., 2015), rutting seasons (Madsen et al., 2002; Zuberogoitia et al., 2014) and the hunting period (Sudharsan et al., 2006) may affect wildlife behavior and habitat use and, consequently, roadkill risk (Rytwinski and Fahrig, 2012). Phenological factors seem to be particularly important for birds, in which mortality peaks match the pre-breeding (i.e. migration) and breeding periods in spring on one hand, and autumn southward migration and the arrival of birds from northern latitudes on the other

(Andalusia is an important overwintering place for a large proportion of the Western European migratory birds; SEO/BirdLife, 2012). Regarding mammals, the number of casualties increased in spring (April) and in late autumn–early winter (October, November and December). This increase could be due to the combined effect of breeding (e.g. European hedgehogs and red foxes feeding their young in spring; Grilo et al., 2009), the subsequent dispersal of inexperienced young (e.g. red foxes in autumn), and the impact of disturbance from hunting activities on animals’ propensity to move (Sudharsan et al., 2006; Morelle et al., 2013). Overall, our results are in line with those found in previous studies in the Iberian Peninsula (e.g. Frias, 1999; Grilo et al., 2009; Garriga et al., 2012; Zuberogoitia et al., 2014; D’Amico et al., 2015) showing that roadkill patterns reflect species-specific differences in activity and mobility caused by weather, and phenological and hunting events (Santos et al., 2007; Grilo et al., 2009; D’Amico et al., 2015). Other factors, such as short- or long-term fluctuations in traffic volume (Seiler, 2005; Zuberogoitia et al., 2014; Gagné et al., 2015) or poor visibility conditions (El Faouzi et al., 2010; Mitra, 2014), may also have affected the roadkill patterns found in this study. However, given the correlative nature of our study, it is not possible to disentangle the relative contribution of the above factors to the roadkill patterns in each vertebrate group.

Roadkill patterns differed among ecoregions, with the Guadalquivir lowlands and the arid zones in southeastern Andalusia showing the highest and lowest number of roadkill, respectively. Except for mammals, the spatial variation of vertebrate roadkill is in accordance with the general patterns of species richness across ecoregions (Martin and Ferrer, 2015). Possible explanations for this unexpected result in the case of mammals include a higher attraction to roads or a reduction in the effectiveness (and/or number) of mitigation measures in areas with less species richness, as compared with more species-rich areas.

Road type (a proxy of traffic intensity and speed) was also an important predictor of roadkill, as shown in other studies (e.g. Morelle et al., 2013; Zuberogoitia et al., 2014). Overall, the highest vertebrate mortality occurred on highways, followed by national and local roads. This is in accordance with the pattern of traffic volume and speed expected for these types of roads, assumed to decrease gradually from highways to nationals and local roads. However, traffic volume and other road features may also vary at microgeographic scales, and thus confound the general patterns of roadkill mortality. For example, some particular stretches within local or national roads caused similar or even higher mortality than some sections within highways, whereas vertebrate mortality varied markedly between close sections of the same highway (e.g. 26 and 56 roadkills in two different sections of A-66; table 1). Furthermore, the overall mortality recorded in each road section varied substantially between vertebrate classes. For example, we recorded the highest mortality rates for amphibians (25.3%) on the surveyed stretch of road HU-9116, whereas no birds or reptiles were found

along this stretch. As a consequence, the areas with high risk of collision varied among vertebrate groups as shown by kernel analyses. These results imply that a large fraction of roadkill variance is not explained by traffic parameters but rather by road and landscape features and/or the spatial behavior of the affected species. For example, diverse road features, such as elevation changes, road sinuosity and the presence of road crosses, may also increase roadkill (e.g. Malo et al., 2004; Seiler, 2005; Grilo et al., 2009; Gunson et al., 2011; Zuberogitia et al., 2014). Besides this, proximity to water bodies may be related to the rate of amphibian roadkill (Santos et al., 2007; Colino–Rabanal and Lizana, 2012), whereas proximity to forested areas often increases mortality risk in ungulates (Madsen et al., 2002; Seiler, 2005; Langbein and Putman, 2006).

Overall, we have shown that roadkills in southern Spain were spatially (across regions) and temporally (throughout the year) aggregated. Our results suggest that species' behavior, landscape and road features were the main factors determining the probability of roadkill. Remarkably, the spatial pattern of mortality found (both overall and within taxa) resembles that caused by other anthropogenic infrastructures, such as power lines or wind farms, wherein few pylons or wind turbines typically account for the majority of casualties (Janss and Ferrer, 2001). Thus, as successfully shown in these research areas (Janss and Ferrer, 2001), the identification and subsequent application of mitigation measures in collision hotspots would dramatically reduce overall road mortality.

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Supplementary material

Table 1s. Ecoregion (E), road type (RT), situation of the roads, and roadkill recorded (number of casualties), separated according to taxonomic groups (M, mammals; B, birds; R, reptiles; A, amphibians): Km–O, km origin; Km–E, km end; * 10–km long sections including the same road designated with two different names, so that the official assignation of km also varies.

*Tabla 1s. Ecorregión (E), tipo de carretera (RT), situación de la carretera, y número de atropellos mortales registrados, separados por grupo taxonómico (M, mamíferos; B, aves; R, reptiles; A, anfibios): Km–O, km origen; Km–E, km final; * tramos de 10 km de una misma carretera que se designa con dos nombres diferentes, con lo que la asignación oficial de los puntos kilométricos también varía.*

Ecoregion		ID	Province	Km–O	Km–E	Taxonomic group			
Type	M					B	R	A	
Lowlands and greenfields of Guadalquivir River (LGG)									
Highways	A–92	Seville	42	52	66	19	1	4	
	A–4	Seville	497	507	51	19	0	0	
	A–49	Huelva	23	33	39	11	1	2	
National roads	A–380	Seville	0	10	51	21	2	0	
	A–407/A–456	Seville	8	38 *	57	16	2	0	
	A–364	Seville	5	15	47	8	2	1	
Local roads	JA–6108	Jaen	0	10	4	6	0	0	
	SE–7200	Seville	0	10	23	8	0	0	
	SE–8105	Seville	0	10	17	6	1	1	
Atlantic and Mediterranean coastline (AMC)									
Highways	A–49	Huelva	107	117	23	23	1	10	
	A–48	Cadiz	4	14	67	24	2	2	
	A–7	Almeria	483	493	15	13	0	1	
National roads	A–494	Huelva	42	52	2	2	0	0	
	A–405	Cadiz	23	33	8	24	6	5	
	A–377	Malaga	5	15	3	12	0	2	
Local roads	A–2227	Cadiz	0	10	33	18	8	1	
	A–2101	Cadiz	0	10	17	14	1	0	
	AL–3106	Almeria	13	23	4	8	4	1	
Atlantic and Continental biogeographic regions of Sierra Morena (ACSM)									
Highways	A–66	Huelva	755	765	5	13	0	3	
	A–66	Seville	766	776	13	13	0	0	
	A–66	Seville	782	792	21	31	1	3	
National roads	A–461	Huelva	2	12	1	3	0	1	
	N–433	Huelva	75	85	10	19	0	1	
	A–424	Córdoba	1	11	4	2	1	0	
Local roads	HU–9116/SE–6405	Huelva/Seville	1	15 *	0	0	0	18	
	CO–6103	Córdoba	1	11	2	4	0	2	
	A–3200	Córdoba	9	19	1	1	3	1	

Table 1s. (Cont.)

Ecoregion		Taxonomic group						
Type	ID	Province	Km-O	Km-E	M	B	R	A
Median and high mountain areas of the Baetic system (MHMB)								
Highways	A-381	Cadiz	43	53	49	21	4	0
	A-92M	Malaga	1	11	24	21	1	0
	A-92	Malaga	161	171	58	41	1	1
National roads	A-308	Granada	23	33	13	8	0	0
	A-406	Seville	12	22	13	25	1	1
	A-333/A-328	Malaga/Córdoba	59	69 *	18	24	3	0
Local roads	CA-5102	Cadiz	8	18	2	8	0	2
	SE-8205	Seville	0	10	2	8	1	1
Subdesert and arid zones in the southeastern (AZS)								
Highways	A-92N	Granada	10	20	5	5	1	0
	A-92N	Granada	50	60	15	9	1	0
	A-92	Almeria	365	375	9	9	3	2
National roads	A-334	Granada	11	21	13	7	0	0
	A-330	Granada	4	14	7	8	1	0
	A-349	Almeria	2	12	8	9	8	0
Local roads	GR-7100	Granada	0	10	3	3	0	0
	GR-9109	Granada	2	12	0	0	1	0
	AL-3102	Almeria	2	12	1	8	4	5

Table 2s. Temporal distribution of roadkill on the Andalusian roads according to taxonomic group and study period: M, month; P1, period 1; P2, period 2; Und., undetermined; NA, roads not surveyed in the second period in September or October.

Tabla 2s. Distribución temporal de los individuos atropellados encontrados en las carreteras de Andalucía, separados por grupo taxonómico y período de estudio: M, mes; P1, período 1; P2, período 2; Und, no determinado; NA, carreteras que no se muestrearon en el segundo período en septiembre u octubre.

M	Mammals		Birds		Reptiles		Amphibians			Total
	P1	P2	P1	P2	P1	P2	P1	P2	Und.	
1	20	35	14	18	0	0	1	1	4	93
2	38	40	11	35	0	0	3	0	0	127
3	41	46	31	22	4	0	6	0	0	150
4	34	59	37	25	2	8	9	5	0	179
5	35	27	29	20	5	10	1	4	0	131
6	37	24	25	23	8	9	1	3	0	130
7	47	24	46	20	3	0	0	1	0	141
8	31	22	20	8	1	2	1	0	0	85
9	49	NA	23	NA	0	NA	1	NA	0	73
10	37	NA	18	NA	3	NA	1	NA	0	59
11	44	55	44	34	2	7	1	23	2	212
12	35	55	22	30	0	2	4	5	2	155
Total	448	387	320	235	28	38	29	42	8	1,535

Table 3s. Spatial distribution of roadkill on the Andalusian roads according to taxonomic group and study period: P1, period 1; P2, period 2; Und., undetermined; E, ecoregion. (For abbreviations of ecoregions, see figure 1).

Tabla 3s. Distribución espacial de los individuos atropellados encontrados en las carreteras de Andalucía, separados por grupo taxonómico y período de estudio: P1, período 1; P2, período 2; Und, no determinado; E, ecorregión. (Para las abreviaturas de las ecorregiones, véase la figura 1).

E	Mammals		Birds		Reptiles		Amphibians			Total
	P1	P2	P1	P2	P1	P2	P1	P2	Und.	
LGG	141	188	57	48	5	4	0	4	1	448
AMC	100	75	80	64	8	14	10	13	3	367
MHMB	146	70	107	61	6	5	8	1	4	408
ACSM	31	26	45	41	2	3	6	23	0	177
AZS	30	28	31	21	7	12	5	1	0	135
Total	448	387	320	235	28	38	29	42	8	1535

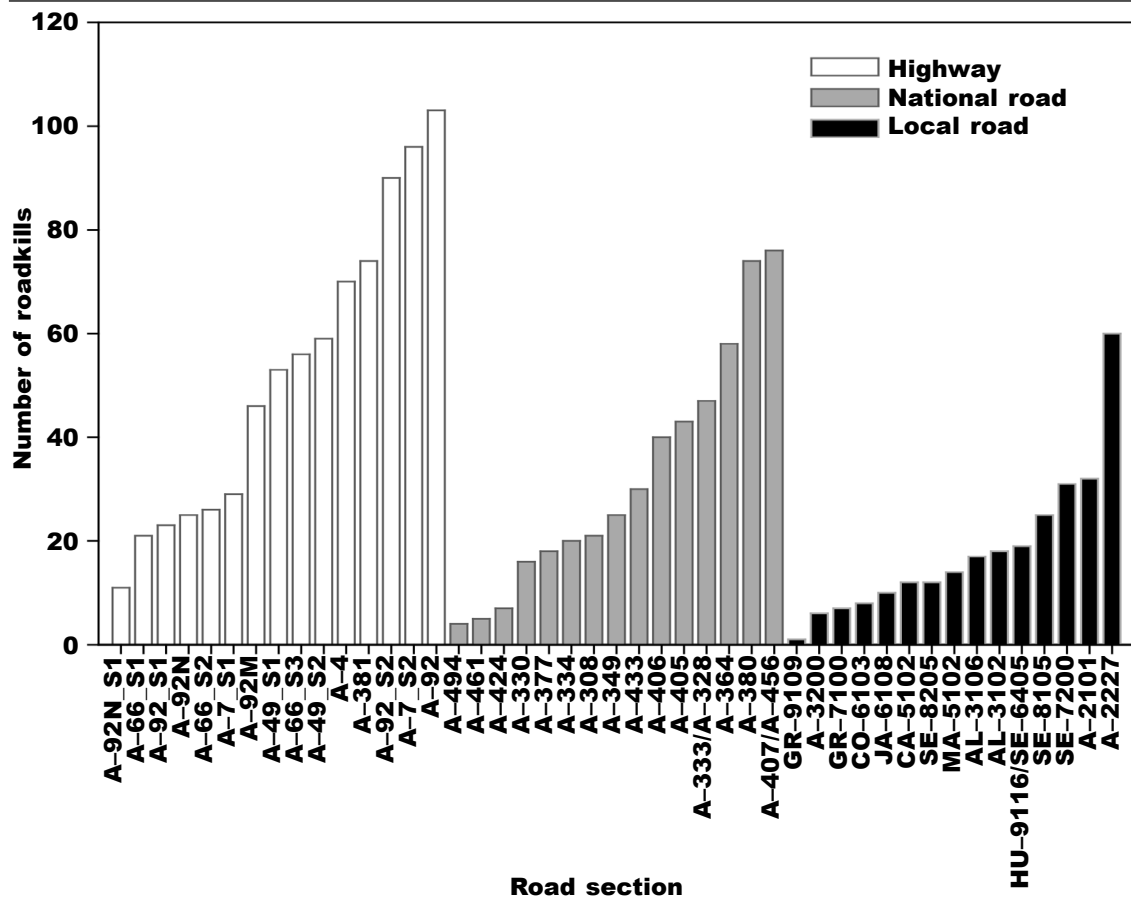


Fig. 1s. Histograms of the accumulated mortality by road section.

Fig. 1s. Histogramas de la mortalidad acumulada por tramo de carretera.

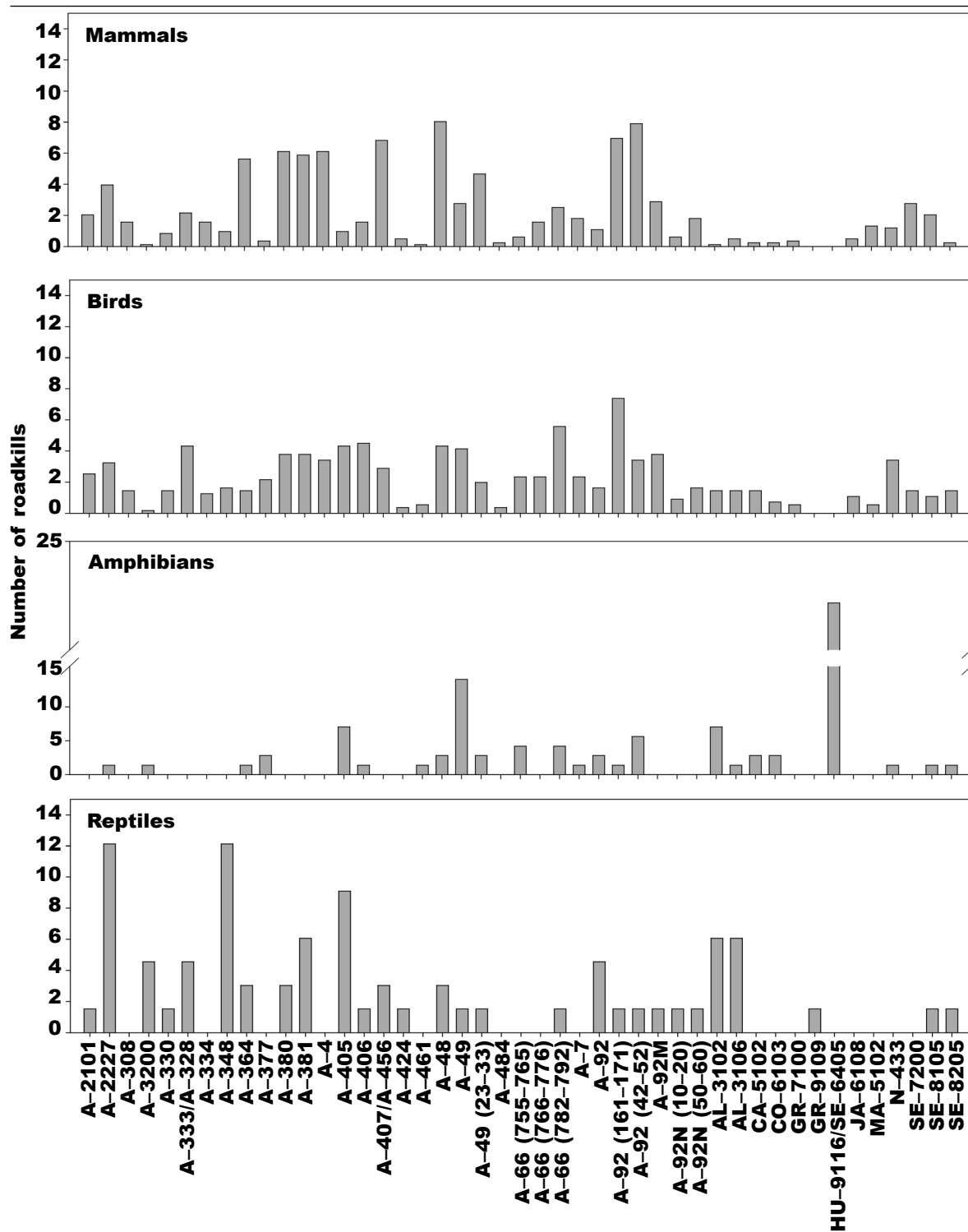


Fig. 2s. Number of vertebrate roadkills found in the Andalusian roads according to taxonomic group and road section. Y-axis was calculated as the number of roadkills detected on a section of road in relation to the total number of roadkills found for the taxonomic group. Note that the scale of y-axis varies between taxonomic groups.

Fig. 2s. Número de vertebrados atropellados encontrados en las carreteras de Andalucía, separados por grupo taxonómico y tramo de carretera. El eje de las Y indica el número de atropellos observados en cada tramo de carretera respecto al total de atropellos encontrados para el grupo taxonómico. La escala del eje de las Y difiere entre grupos taxonómicos.