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The spatial distribution of animal casualties within a road corridor: Implications for roadkill monitoring in the southern Iberian rangelands

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ABSTRACT

We assessed wildlife roadkill spatial patterns focusing on asphalt roads in southern Spanish oak rangelands (“dehesas”). Four roads in the Sierra Morena range (Andalusia) were surveyed twice during autumn-winter 2009–2010 and spring-summer 2010. Roadsides were walked on both sides across the total road length (53 km; overall length walked per season = 106 km) for each field season by 1–4 trained observers at ~1–2 km/h. Asphalt surface, road verges/shoulders, runoff ditches and road banks/slopes (neighboring habitat) were exhaustively inspected for all dead vertebrates, which were georeferenced and identified. Roadkills (N = 396) were classified into 67 species (5 amphibians, 7 reptiles, 37 birds and 18 mammals). In total, 128 (32.3%) of all roadkills were found within the road asphalt lanes, with the remaining two-thirds (268, 67.7%) outside the asphalt lanes. This pattern was consistent regardless of season and several structural attributes of roads. However, vertebrate class was determinant, with more poiquilotherms (amphibians and reptiles) being detected inside asphalt compared to birds and mammals (off-asphalt casualties were significantly more numerous). This is a strong argument in favor of recommending surveying roadkill on foot as a main survey method or complementarily to vehicle surveys.

1. Introduction

Roads and traffic are perhaps the main causal agents of animal collision with infrastructures (Coffin, 2007; Fahrig and Rytwinski, 2009; Benítez-Lopéz et al., 2010). In the field of road ecology, knowing the patterns of spatial distribution of wildlife roadkills is essential to envisage field studies for road environmental impact assessments, roadkill monitoring and to perform sound estimates of animal population losses to traffic. Such information can help implement of new road and traffic schemes with the purpose of a better ecological integration of future and extant roads (Box and Forbes, 1992). Although our knowledge of animal mortality along roads has improved, we still have little information on the fine-scaled distribution of roadkills across road surfaces and verges, and on how

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mortality among vertebrate groups varies with traffic features and road landscape integration (Gunther et al., 2001; Main and Allen, 2002; Fahrig et al., 2005). The inventory of wildlife roadkill is a basic tool to assess mortality rates in populations affected by road projects. Many studies agree that, for various reasons (removal by scavengers, sampling frequency, survey procedures, etc.), roadkill numbers often represent underestimates of actual road-caused mortality. Reliable knowledge of such animal mortality depends on the efficiency of roadkill inventories, which are subject to various sources of bias. Studies are needed to identify and reduce bias in order to implement more effective mitigation.

The studies on the rates of wildlife road accidents seek to obtain accurate estimates of the impact on animal populations, to find out the factors that determine mortality, and to reduce uncertainty in estimations (Clevenger et al., 2003; Erritzoe et al., 2003; Coffin, 2007; Loss et al., 2014). Among these factors, the effect of the attributes of road topography and road traffic, the influence of body mass and the dispersal, reproduction and foraging behaviour of the affected species and the effect of the surrounding landscape on animal mortality have been investigated (Kanda et al., 2006; Ford and Fahrig, 2007; Morelli, 2013; D'Amico et al., 2015; Barrientos et al., 2018). However, the monitoring of road mortality must manage various sources of bias in order to obtain an adequate projection of the impact of traffic on animal populations (Collinson et al., 2014; Barrientos et al., 2018).

First of all, the frequency of encounter of casualties will be influenced by seasonality, which marks the presence and abundance of certain species, their tendency to cross roads and their vagility (Carr and Fahrig, 2001; Grilo et al., 2009). Aside from typical seasonal patterns in animal abundance having a reflection in road casualties, there are differences in intrinsic vulnerability to traffic accidents. For example, flying vertebrates (birds, bats) and many insects are frequently hit at a height above pavement by passing vehicles, whereas amphibians, reptiles and many small to medium-sized mammals are mostly crushed by car wheels (Forman et al., 2003). Larger mammals like ungulates and large carnivores die mainly by collisions with the body of vehicles.

On the other hand, aside from intrinsic wildlife attributes, factors related to road design may largely determine mortality patterns (Orłowski, 2008; Morelli, 2013; Husby, 2016). For instance, the type of road profile or shape of the topographic section, can also determine the probability of being run over (Pons, 2000; Borkovcová et al., 2012).

The accuracy of observations during the roadkill surveying depends on the capacity of casualty detection on the road and its immediate vicinity (Glista et al., 2008), and this depends on several factors. Carcass detectability is to a great extent related to carcass size (or body mass) (Barrientos et al., 2018). However, the speed and number of observers also influence the ability to detect carcasses, particularly those of smaller species and in terrain configurations with low visibility (Barrientos et al., 2018). The most common survey protocols are by car (at a speed as low and constant as possible), bike surveys and on foot (Collinson et al., 2014; Heigl et al., 2017). Vehicle surveys with one or more observers are very efficient in terms of time invested and distance traveled and could, a priori, be more efficient in detecting larger species (Clevenger et al., 2003; Collinson et al., 2014; Husby, 2016). Their main drawback is that they must be performed at a certain minimum speed and at a distance from the edge of the road, which could be inadequate for recording the smaller animals (eg bats, other small mammals, most passerines, small amphibians and reptiles), or carcasses along verges (Guinard et al., 2012; Loss et al., 2014).

Other factors affecting estimates of roadkill rates include geographic region, sampling effort/size in terms of road kilometres surveyed, time invested or other measure, and periodicity of sampling. In a study which conducted surveys from vehicle in the Czech Republic, Borkovcová et al. (2012) found 328 animals for a total travelled distance of 10,000 km (an extremely low rate of 0.033 animals/km). In Norway, Husby (2016) reported 121 bird roadkills from at least 15 species for 617 survey days, along a 25 km road. Large birds like corvids and gulls were the main roadkilled species, whereas smaller passerines were far less frequent. Clevenger et al. (2003) recorded only 677 roadkills (56 species) for an impressive 65,253 km surveyed in 554 days in Canada. They surveyed roadkills from a car driving at 10–20 km/h, and did not record any casualty in 40% of survey days (Clevenger et al., 2003). For a comparatively much smaller total distance (1488 km), Glista et al. (2008), performed 496 surveys from a car at < 40 km/h in the United States (exploring asphalt surfaces plus shoulders and verges) and obtained a much more bulky estimate: 10,515 roadkills of 69 species (mostly amphibians).

Foot surveys are more work-demanding and less efficient in time, effort and distance traveled. However, this could be also an advantage because they can be more exhaustive in terms of the detectability of the smaller fauna and the possibility of finding roadkills in marginal sections of the road (verges, ditches, banks, edge habitat); we hypothesize that most wildlife casualty records tend to concentrate off the asphalt surface, often out of sight from a moving vehicle.

Here we aimed to assess and describe how vertebrate roadkills distribute across the horizontal sections of the road, under different traffic intensities and amongst different types of road cross-sections ("profiles"). Our main motivation was to describe in detail the roadkill distribution across the road structure, looking for general patterns to guide future road EIAs, inventories of wildlife species losses to traffic, and to continue improving roadkill surveys. Hence, we formulated the question of what proportion of kills can be found directly on the asphalt surface in comparison to those outside the asphalt surface. Is this distribution related to the type of road cross-section (four section types), vertebrate groups (four vertebrate groups) or traffic intensity and speed?

2. Study area and methods

We surveyed two-lane, rural asphalt roads dividing southern Spanish rangelands, or "dehesas", oak (*Quercus ilex* and *Q. suber*) woodland pastures dedicated to livestock growing, agroforestry and hunting (Fig. 1). Spanish oak rangelands are the dominant forested landscape in the southwestern part of the Iberian Peninsula ($1.3 \cdot 10^6$ ha in Andalusia, $5.8 \cdot 10^6$ ha in SW Iberian Peninsula) (García et al., 2010). Such rangeland roads traverse relatively open landscapes with gentle slopes. We selected four roads through the Sierra Morena range (Andalusia), and surveyed each segment twice for a total of 30 days of field work (end of autumn-early winter: 09/10/2009–22/01/2010; and spring-summer: 20/04/2010–20/07/2010). Mean elevation of road transects was ~400 m a.s.l.

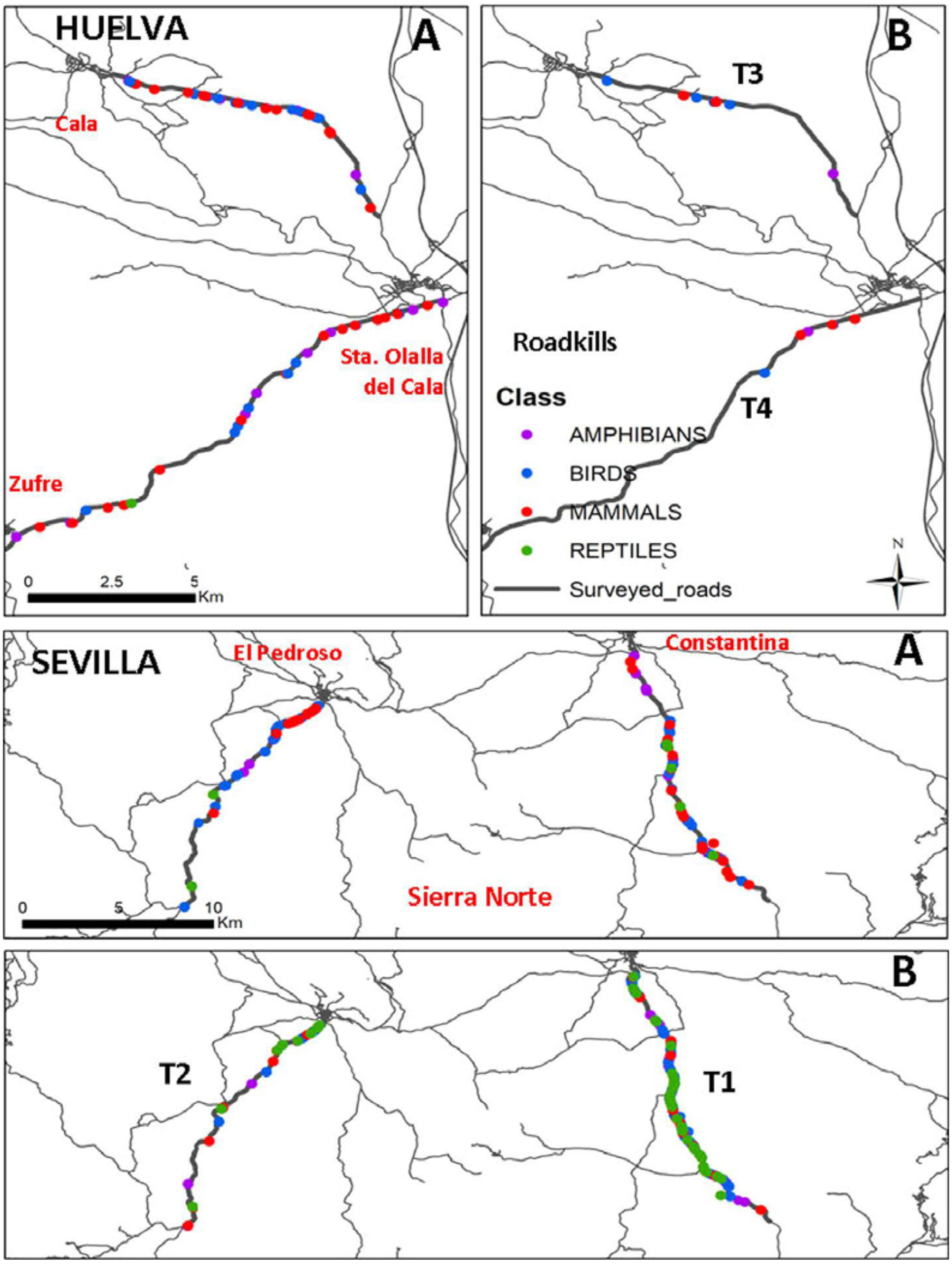

Fig. 1. Map of the study area showing distribution of roadkills along four study roads and two seasons through oak rangelands (SW Andalusia, Spain). Roadkills are shown as color points for every vertebrate class. The lines of the four surveyed roads are in bold. Above panels, Huelva province: T3: Road A-434 (Santa Olalla del Cala-Cala); T4: Road A-461 (Zufre-Santa Olalla del Cala). Bottom panels, Sevilla province: T1: Road A-455 (Lora del Río-Constantina); T2: Road A-432 (Castilblanco-Cantillana-El Pedroso). Seasons: A = Fall-winter 2009–2010, B = Spring-summer 2010.

(range: 159–583 m a.s.l.). Road width averaged 9.51 m (± 3.66 SD), and was fairly similar among roads. Roads also differed slightly regarding their moderate to low traffic intensity (Mean Daily Intensity, MDI), type of vehicles (heavy and light), and circulation speed (see Table 1 for details on the surveyed roads). For traffic intensity and speed we used data from the Servicio de Conservación y Dominio Público Viario, Sevilla (2009).

The total road length (Distance = 53 km) was walked by 1–4 trained observers at ~1–2 km/h along both roadsides (overall length walked = 106 km) and on each season (14 days in autumn-winter, 16 days in spring-summer). We inspected different road parts for all dead vertebrates. We sorted roadkill locations by road sections as follows: (1) within asphalt surface, i.e. the paved roadway; (2) road shoulders (2–3 m width), (3) run-off ditches and (4) lateral road banks or slopes up to 10 m off both asphalt edges wherever accessible. Roadkills were georeferenced with a Garmin™ GPS (model GPS 60) in UTM mode, and identified to the lowest taxonomic level possible.

Table 1
General descriptors of the studied road segments in southern Iberian dehesas (Andalusia). Average speed is shown as a range of average speeds from several segments along the surveyed roads..
Source: Servicio de Conservación y Dominio Público, Sevilla (2009)

Transect name (Road code)	Province	Road length (km)	Elevation (m a.s.l.) (min.-max.)	Mean road width (m) (± 1 SD) (min.-max.)[a]	Traffic intensity (vehicles/day) (2009)	Mean daily intensity (vehicles/day)	% heavy vehicles (2009)	Average speed (km/h)
1. Lora del Río-Constantina (A-455)	Sevilla	16	390,61 ± 51.97 (328–523)	9.92 ± 4.25 (7.82–37)	High (2000–5000)	2910	3	91–100
2. Castilblanco-El Pedroso (A-432)	Sevilla	14.7	360,29 ± 48.84 (159–404)	9.59 ± 2.89 (7.65–21.2)	High (2000–5000)	2141	8	71–80
3. Cala-Santa Olalla del Cala (A-434)	Huelva	8.5	530,94 ± 21.82 (494–583)	7.92 ± 0.13 (7.75–8.4)	Low (1000–2000)	1419	8	71–80
4. Santa Olalla del Cala-Zufre (A-461)	Huelva	14.1	421,36 ± 87.67 (268–529)	8.54 ± 2.96 (7.6–25)	Low (1000–2000)	1236	11.5	81–90

[a] Measured at casualty points.

Table 2
Distribution of the number of vertebrate roadkills among lateral road sections per category of traffic intensity and speed (data were pooled over transects and seasons) (see Fig. 2 for details of road parts and structure). See Table 1 for road codes and names.

Road	Not classified	Shoulder (earth/macadam/stones)	Shoulder (asphalt)	Asphalt lanes	Ditches	Road banks/slopes	Overall inside asphalt lanes	Overall outside asphalt lanes	Total
1. Lora del Río-Constantina	2	71	2	70	75	16	72	162	**236**
2. Castilblanco-El Pedroso		23	1	30	26	10	31	59	**90**
3. Cala-Santa Olalla del Cala		3		12	16	6	12	25	**37**
4. Santa Olalla del Cala-Zufre		11	1	11	7	3	12	21	**33**
	2	**108**	**4**	**123**	**124**	**35**	**127**	**267**	**396**

For each location of dead vertebrate, we recorded: (a) the type of cross-section of the road, establishing four categorical classes with reference to the terrain level: level (no apparent difference in level between road and surrounding habitat); raised (road right-of-way above surrounding habitat); depressed (road right-of-way under surrounding habitat); asymmetric (road and road banks were stair-shaped); (b) distance of casualties to the edge of the asphalt travelled surface; (c) road width (m) for the asphalt right-of-way. We removed carcases to avoid repeating observations.

We analysed the number of casualties found at different sections on the road right-of-way and locations off the road (Table 2). We used chi-square to test for significant differences in casualty location regarding: (a) the four types of road profiles (types of cross-section defined above: level, raised, depressed, asymmetric); (b) the four vertebrate classes; (c) the four roads surveyed, which represent four different traffic MDIs; (d) three different traffic speed ranges, and (e) the two seasons. We also used chi-square to test for significant differences in casualty presence in the four road parts described above (asphalt, shoulders, ditches and road banks/slopes), and among the four different types of road sections. Analyses were performed with the SPSS package (SPSS, vs. 17, 2008).

3. Results

3.1. Overview of roadkill data

We recorded 396 vertebrates from 67 species (75 amphibians, 55 reptiles, 164 birds and 102 mammals) from the four roads and two seasons (Fig. 1). The majority of casualties were recorded in the Sierra Norte (Seville province) along the road A-455 (Table 2 and Fig. 1). Fifty-seven species (86.4% of all species) were killed only occasionally (i.e. ≤ 5 individuals) (Appendix A). The most frequently killed species per class were the Common Toad *Bufo spinosus* (amphibians), the Ladder Snake *Rhinechis scalaris* (reptiles), the Woodchat Shrike *Lanius senator* (birds), and the Domestic Dog *Canis familiaris* (mammals) (Appendix A). Casualty numbers were similar on a daily basis in spring-summer (13.9 casualties per day of field work) and autumn-winter (12.4 casualties/day). In spring-summer, we also detected higher frequencies of roadkilled animals for “high-traffic” than “low-traffic” roads. Herpet roadkills (amphibians and reptiles) were more abundant in spring-summer, whereas mammals (especially wild carnivores) showed higher frequencies in autumn-winter. Birds were similarly abundant in both study seasons, although identity of frequent species changed due to presence of wintering vs. summering birds (*Lanius senator* in spring-summer, and *Erithacus rubecula* in autumn-winter).

3.2. Spatial patterns of casualties across the road structure

Thirty two percent (32.3%, 128 out of 396) of all casualties were detected within the asphalt surface, whereas more than two thirds (268, 67.7%) were recorded outside the asphalt surface (Fig. 2 and Table 2; see Appendix A). Most casualties were recorded up to 4 m from the road verge toward the surrounding habitats (Figs. 3 and 4), and to the centre of the asphalt surface. However, many animals were detected as far as 8 m from the asphalt surface toward the surrounding ecosystem. There were significant differences in number of total roadkills amongst the different road sections depicted in Fig. 2 ($\chi_3{}^2 = 55.482$, $p < 0.001$).

We found a significantly higher number of casualties inside the asphalt surface than outside it (shoulders, ditches and road banks/slopes) ($\chi_1{}^2 = 50.207$, $p < 0.0001$). This pattern was consistent between the two study seasons. We found no differences between seasons in the proportion of roadkills inside/outside the asphalt surface ($\chi_1^2 = 0.662$; $p = 0.416$), between types of road cross section ($\chi_3^2 = 7.576$; $p = 0.056$), road traffic intensities (MDI, $\chi_3^2 = 0.640$; $p = 0.887$) and circulation speed ($\chi_2^2 = 0.592$; $p = 0.744$). However, there was a significant difference based on vertebrate class ($\chi_3^2 = 26.631$; $p < 0.001$). Amphibians and reptiles were found in very similar proportions inside and outside (amphibians: 37 in vs 38 out; reptiles: 25 in vs 30 out) the asphalt surface, whereas birds and mammals were consistently found in higher proportions off the asphalt (birds: 48 in vs. 110 out; mammals: 18 in vs. 90 out). The detailed composition of animal species found inside and outside asphalt is shown in Appendix A.

Regarding type of road cross-section, similar roadkill numbers were recorded at “raised” (112), “asymmetric” (111) and “depressed” (94) sections, and these were all higher than for “level” road segments (79) (Appendix B). We found variability in roadkill frequency of different species depending on road cross-section. For example, European rabbits experienced relatively higher mortality at raised and level road sections, whereas foxes were more frequently found at depressed and level sections (Appendix B). We also found lower absolute roadkills in level road profiles for amphibians and reptiles. For birds, however, level and depressed profiles presented similarly low frequencies. Mammals showed slightly higher roadkill numbers at level and depressed sections. However, no significant differences in roadkills were found among these four road profiles for each of the four vertebrate classes (Amphibians: $\chi_3{}^2 = 6.55$, $p = 0.088$; Reptiles: $\chi_3{}^2 = 5.44$, $p = 0.142$; Birds: $\chi_3{}^2 = 7.66$, $p = 0.054$; Mammals: $\chi_3{}^2 = 1.61$, $p = 0.658$; All vertebrates combined: $\chi_3{}^2 = 7.45$, $p = 0.059$).

4. Discussion

Surveying roadkills across a wide band comprising asphalt surface and road lateral structures, our most interesting finding is that most casualties were detected outside the road paved surface. This pattern was consistently found for several road attributes which are recognized as important in determining roadkill rates, such as season, traffic speed and intensity (measured as MDI), and type of road section (road profile or cut type). Only the vertebrate class influenced the relative amount of casualties to be found inside vs outside the asphalt. The poiquilotherm vertebrates (amphibians and reptiles) were detected in similar numbers in and out the asphalt surface, whereas birds and mammals were found more frequently off the asphalt. The pattern of road use by poiquilotherms (seeking heat to regulate body temperature), or their ambulatory habits may partly explain their relatively higher roadkill prevalence inside

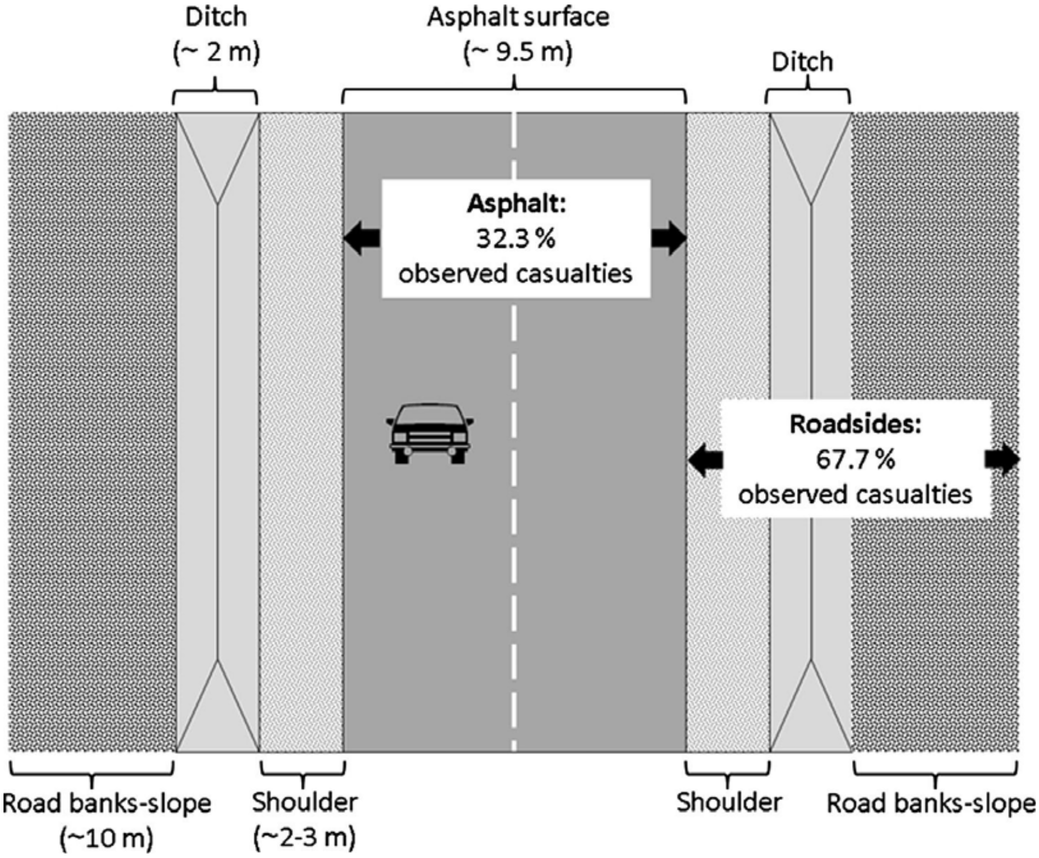

Fig. 2. Schematic view of road sections surveyed in this study (see Table 2 for details). Asphalt surface: includes all the asphalt, travelled surface or paved roadway (lanes). Shoulder: includes a lateral band (~ 2–3 m wide) mostly made of macadam granulate material on both roadsides, otherwise earth/gravel materials outside the main roadway. Ditch: excavated linear element to channel water runoff (including ditch slope, when excavated on natural terrain, and ditches made of concrete). Road bank/slope: a band of natural terrain from the upper limit of the ditch towards the habitat. Roadside: the combined surveyed width of shoulders, ditches and banks/slopes. Shown are approximate section widths (in meters) and percentage of roadkills found on asphalt and roadsides.

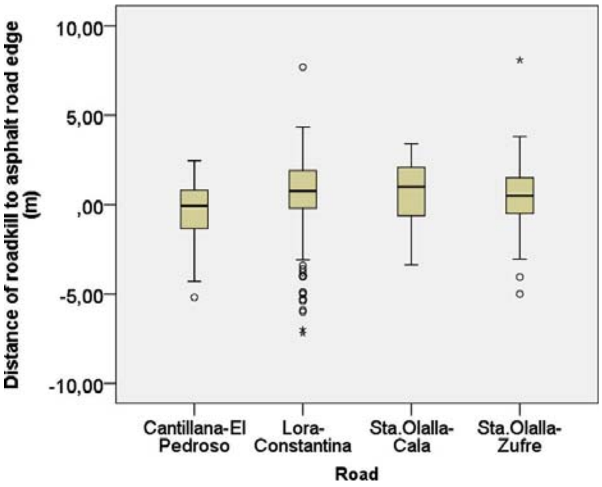

Fig. 3. Box-and-whiskers plot for distance of wildlife roadkills to asphalt edge. Negative distances depict animals killed within the asphalt surface, positive distances are for animals found off the asphalt surface. Shown are medians (horizontal lines), quartiles (percentile range 25–75%, 50% of data), minimum and maximum values (whiskers). Asterisks: Extreme values; circles: Outliers. Note the larger variation and more outlying values in the widest road and of higher traffic intensity (road Lora del Río-Constantina).

the asphalt surface (Santos et al., 2007). Besides being run over by vehicles, flying vertebrates (birds and bats), but also many amphibians, reptiles and mammals could be hit and thrown off the road, which would reduce detection rates (Glista et al., 2008). In addition, when distinguishing between roadkills in and out the asphalt surface, the probability of carcass removal or displacement due to scavenger activity after the collision cannot be ignored, and could be a source of bias in our data.

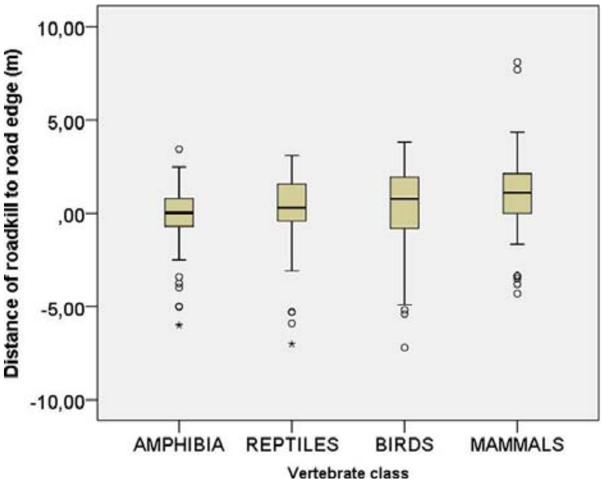

Fig. 4. Box-and-whiskers plot for distance of roadkills of the four vertebrate groups to asphalt edge. Negative distances depict animals found within the asphalt surface, positive distances are for those found off the asphalt surface. Shown are medians (horizontal lines), quartiles (percentile range 25–75%, 50% of data), minimum and maximum values (whiskers). Asterisks: Extreme values; circles: Outliers.

Many of the studies published on wildlife roadkills surveyed from a moving vehicle have found very low roadkill rates, despite high sampling effort in terms of road length and time invested. A possible implication of such results is that regional and global estimations of numbers of animals killed on roads might have been underestimated in many study cases (particularly in vehicle-based surveys), and that the actual impact of mortality due to animal-vehicle collisions is probably much higher. Underestimates can of course occur for foot-based surveys, and in fact for some animal groups, vehicle estimations could be more efficient than foot ones (Guinard et al., 2012; Collinson et al., 2014), such as for large vertebrates with larger dispersion areas.

In comparison with some of these studies (briefly reviewed in the Introduction), we found, by foot-surveying a total of only 106 km during 30 days, 396 animals of 67 species, and an overall frequency of 3.74 roadkills per kilometer. Such contrasting differences between studies would be partially due to different efficiencies of the surveying methods (i.e. car vs. walking, monitoring speed, asphalt lanes only vs. asphalt plus verges), although other factors may also be influential. Our findings suggest that more than half of the roadkilled animals, especially the smaller ones, could pass easily unnoticed in most vehicle surveys, since vehicle speed limits visual carcass detection (Langen et al., 2010).

In general, and regardless of vertebrate group, small and medium sized animals (and even the larger ones in many cases) are less likely to be noticed from a car and bike searches, even at moderate driving speeds (Pons, 2000; Slater, 2002; Teixeira et al., 2013). Vehicle censuses can be efficient in terms of time and energy invested, especially for large fauna, but carcasses along road verges are less efficiently surveyed (Guinard et al., 2012). Some studies have approached the relationship between vehicle speed and interacting variables affecting identification and bias sources (Hobday and Minstrell, 2008; Santos et al., 2011; Collinson et al., 2014). Pons (2000) and Borkovcová et al. (2012) detected/surveyed carcasses only on the road right-of-way, but not along verges, which would have increased actual roadkill figures. On the other hand, carcasses directly located on the asphalt lanes have shown lower permanency than those alongside the verges and lateral road bands (Santos et al., 2011). Hence, in our study, the consistently larger proportion of casualties detected outside the main asphalt surface (~68%) suggest that, for a more exhaustive record of animal kills, searches should be focused at least across the first 4 m off the road edge, along with simultaneous searches of the asphalt lanes.

However, our data are still conservative estimates due to low replicate temporal sampling and the high inherent variation in carcass conservation in both asphalt and verges (Slater, 2002; Santos et al., 2011; Teixeira et al., 2013; Ratton et al., 2014; Beckmann and Shine, 2015). Roadkill frequencies for some small vertebrates in our study (such as the urodelan *Triturus pygmaeus*), or small insectivorous mammals (Soricids) and bats, were probably underestimated by us (Santos et al., 2011). Roadkilled animals, and especially smaller ones, are known to be promptly consumed by scavengers. Scavenger vertebrates (raptors, foxes), roadside ant colonies and wasps abound in our study areas and might be responsible for the rapid removal of the smaller dead individuals (Frías, 1999; Bafaluy, 2000; Antworth et al., 2005). In Australia, Beckmann and Shine (2015) found that raptors removed 73% of carcasses shortly after sunrise. In our study roads, raptors (kites, kestrels, small eagles), ravens and smaller corvids (mainly Azure-winged magpies, *Cyanopica cooki*), and other avian species are suspected to remove roadkilled animals.

Finally, our results represent an argument in favor of using foot surveys as a primary source of roadkill data attempting to minimize the bias (of performing surveys at higher speeds), or at least they should be performed to complement vehicle surveys. This could help refine estimations of roadkill frequencies in EIA projects of road schemes and projections of population mortality, to improve statistical modelling and prediction of wildlife-vehicle collisions.

Patterns of casualty location vary with road section and topography, among other factors including the vertebrate group being studied (D'Amico et al., 2015; Borkovcová et al., 2012). Such variability in road structure can affect roadkill frequencies and hence it should be considered in roadkill surveys. We found a smaller number of roadkills at level road sections, the remaining three configurations accounting for the largest amount of mortality. In comparison, Borkovcová et al. (2012) found higher kill frequencies at level road segments. In our study, lower mortality frequencies for amphibians, reptiles and birds (but higher for mammals), were consistently found in level and depressed sections than in embanked ones. It can be hypothesized that asphalt surfaces might be more easily accessible by wildlife at level road sections. Also, it may be expected that animals attempting to cross level roads have a higher probability of crossing succeed, due to lower impediment of road topography (smaller barrier effect). This would be also affected by the ambulatory behaviour of particular species. Both deeply embanked and raised roads (those with steep side banks) are known to act as obstacles to animal movements (i.e. Jaarsma et al., 2006; Rico-Guzmán et al., 2011), and to increase mortality (Loss et al., 2014). However, in some cases tall embankments have been related to lower bird mortality, since they would force birds to fly over vehicle collision height (Pons, 2000).

5. Conclusions

To advance in modelling and predicting roadkill it is necessary to optimize survey protocols (Collinson et al., 2014). It is still unclear the extent to which car, bike or foot roadkill surveys differ in the degree of underestimation of wildlife roadkill frequencies. Nevertheless, it seems likely that surveys at higher speeds (i.e. from a car) miss smaller animals, especially at structurally complex road verges such as in embankments or raised sections. Since a large proportion of roadkilled animals is expected to appear off the asphalt surface, as in our study, a thorough inspection along and across road verges, apart from asphalt surfaces, ditches and remaining side structures is recommendable, especially for smaller vertebrates. Our surveyed roads differed in features such as elevation, length, traffic volume (although it can be considered as mild), and habitat configuration surrounding roads. Despite this variability among four contrasting roads, the rate of vertebrate casualties detected inside vs. outside the asphalt surfaces followed a consistent pattern. If this pattern repeats in other regions, underestimation of wildlife mortality due to traffic could be the rule. This represents a worse scenario for persistence of some wild populations in road fragmented environments. In addition, this poses an important source of roadkill location bias (at least for rural roads in montane habitats like the Spanish oak rangelands). Future studies could compare efficiencies of several roadkill surveying methods, for different animal groups and in different landscapes fragmented by roads. It would be interesting to know if our results can be repeated in other ecosystems, with contrasting faunas and by using different survey procedures. This is a necessary step for a more useful evaluation and mitigation of road mortality impact on animal populations.

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A. Vertebrate roadkills inside and outside the asphalt surface in four roads through southern Iberian rangelands

Class	Species	Inside asphalt lanes	Outside asphalt lanes	Total
Amphibians	*Anura indet.*	1	3	4
	Bufo calamita	1		1
	Bufo spinosus	24	28	52
	Hyla meridionalis	1		1
	Pelophylax perezi	8	7	15
	Triturus pygmaeus	2		2
Total Amphibians		**37**	**38**	**75**
Birds	*Alauda arvensis*		3	3
	Alectoris rufa		1	1
	Asio otus		2	2
	Athene noctua		4	4
	Buteo buteo		1	1
	Carduelis carduelis		2	2
	Carduelis spinus		1	1
	Certhia brachydactyla		5	5
	Columbiforme indet.	1		1
	Cyanistes caeruleus		2	2
	Cyanopica cooki		7	7
	Delichon urbica		1	1
	Emberiza cirlus		1	1
	Erithacus rubecula	5	6	11
	Fringilla coelebs	1		1
	Galerida cristata	2	1	3
	Hippolais polyglotta		1	1
	Lanius senator	3	13	16
	Lullula arborea		1	1
	Luscinia megarhynchos		2	2
	Merops apiaster		3	3
	Miliaria calandra	1	7	8

	Parus major	1	3	4
	Passer domesticus	8	7	15
	Passeriforme indet.	14	6	20
	Phylloscopus collybita		3	3
	Picus viridis		3	3
	Saxicola torquata	1	2	3
	Serinus serinus	5	3	8
	Sylvia atricapilla	1	1	2
	Sylvia hortensis		1	1
	Sylvia melanocephala	2	8	10
	Sylvia sp.	1		1
	Sylvia undata		1	1
	Turdus merula	1	4	5
	Turdus viscivorus	1	1	2
	Tyto alba		1	1
	Upupa epops		2	2
Total Birds		**48**	**110**	**158**
Mammals	*Apodemus sylvaticus*	6		6
	Canidae indet.		3	3
	Canis familiaris	2	33	35
	Capra hircus		1	1
	Carnivora indet.		2	2
	cf. *Barbastella barbastellus*		1	1
	Chiroptera indet.	1	3	4
	Crocidura russula		1	1
	Erinaceus europaeus		3	3
	Felis catus		12	12
	Felis cf. *silvestris*	1	1	2
	Genetta genetta		1	1
	Herpestes ichneumon		1	1
	Martes foina		1	1
	Meles meles		2	2
	Microtus duodecimcostatus		2	2
	Mustela nivalis		1	1
	Mustelidae indet.		1	1
	Oryctolagus cuniculus	6	12	18
	Rhinolophidae indet.	1		1
	Sus scrofa cf. *domestica*		1	1
	Vulpes vulpes	1	8	9
Total Mammals		**18**	**90**	**108**
Reptiles	*Acanthodactylus erythrurus*	1		1
	Blanus cinereus		2	2
	Colubridae indet.	1	1	2
	Emys orbicularis	2	6	8
	Hemorrhois hippocrepis	1	2	3
	Indet. snake	2	1	3
	Lacerta lepida	3	1	4
	Malpolon monspessulanus	1	6	7
	Rhinechis scalaris	14	11	25
Total Reptiles		**25**	**30**	**55**
Total		**128**	**268**	**396**

B. Vertebrate roadkills per type of cross section in four roads through southern Iberian rangelands

Species	Asymmetric	Depressed	Level	Raised	Total
Amphibians	**22**	**15**	**12**	**26**	**75**
Anura indet.	2	0	0	2	**4**
Bufo spinosus	13	10	12	17	**52**
Bufo calamita	1	0	0	0	**1**
Hyla meridionalis	0	0	0	1	**1**
Pelophylax perezi	5	5	0	5	**15**
Triturus pygmaeus	1	0	0	1	**2**
Reptiles	**13**	**17**	**7**	**18**	**55**
Acanthodactylus erythrurus	0	1	0	0	**1**
Blanus cinereus	0	0	2	0	**2**
Colubridae indet.	0	0	1	1	**2**
Mauremys leprosa	3	2	0	3	**8**
Hemorrhois hippocrepis	0	1	1	1	**3**

Indet. snake	0	1	0	2	**3**
Lacerta lepida	1	2	1	0	**4**
Malpolon monspessulanus	3	1	1	2	**7**
Rhinechis scalaris	6	9	1	9	**25**
Birds	**53**	**32**	**33**	**46**	**164**
Alauda arvensis	0	2	0	1	**3**
Alectoris rufa	0	1	0	0	**1**
Asio otus	0	0	1	1	**2**
Carduelis carduelis	2	0	0	0	**2**
Carduelis spinus	1	0	0	0	**1**
Apodemus sylvaticus	1	4	1	0	**6**
Athene noctua	0	1	1	2	**4**
Buteo buteo	0	0	1	0	**1**
Certhia brachydactyla	2	1	0	2	**5**
Columbiforme indet.	1	0	0	0	**1**
Cyanistes caeruleus	0	0	1	1	**2**
Cyanopica cooki	3	1	0	3	**7**
Delichon urbica	1	0	0	0	**1**
Emberiza cirlus	0	1	0	0	**1**
Erithacus rubecula	4	1	2	4	**11**
Fringilla coelebs	1	0	0	0	**1**
Galerida cristata	2	0	1	0	**3**
Hippolais polyglotta	0	0	0	1	**1**
Lanius senator	5	4	4	3	**16**
Lullula arborea	0	0	0	1	**1**
Luscinia megarhynchos	0	0	1	1	**2**
Merops apiaster	0	0	1	2	**3**
Miliaria calandra	2	2	3	1	**8**
Parus major	0	2	0	2	**4**
Passer domesticus	4	4	5	2	**15**
Passeriformes indet.	8	3	2	7	**20**
Phylloscopus collybita	2	0	0	1	**3**
Picus viridis	0	0	2	1	**3**
Saxicola torquata	1	0	0	2	**3**
Serinus serinus	5	1	2	0	**8**
Sylvia atricapilla	1	0	0	1	**2**
Sylvia hortensis	0	0	0	1	**1**
Sylvia melanocephala	4	4	0	2	**10**
Sylvia sp.	1	0	0	0	**1**
Sylvia undata	0	0	1	0	**1**
Turdus merula	1	0	2	2	**5**
Turdus viscivorus	1	0	0	1	**2**
Tyto alba	0	0	0	1	**1**
Upupa epops	0	0	2	0	**2**
Mammals	**23**	**30**	**27**	**22**	**102**
Canidae indet.	0	1	2	0	**3**
Canis familiaris	5	13	10	7	**35**
Capra hircus	0	1	0	0	**1**
Carnivora indet.	1	0	1	0	**2**
Indet. Rhinolophid bat	0	1	0	0	**1**
Chiroptera indet.	2	2	0	0	**4**
Crocidura russula	0	0	0	1	**1**
Erinaceus europaeus	0	1	1	1	**3**
Felis catus	6	2	1	3	**12**
Felis cf. *silvestris*	1	1	0	0	**2**
Genetta genetta	1	0	0	0	**1**
Herpestes ichneumon	0	1	0	0	**1**
Martes foina	1	0	0	0	**1**
Meles meles	1	0	1	0	**2**
Microtus duodecimcostatus	0	2	0	0	**2**
Mustela nivalis	0	0	1	0	**1**
Mustelidae indet.	0	1	0	0	**1**
Oryctolagus cuniculus	3	1	6	8	**18**
Rhinolophidae indet.	1	0	0	0	**1**
Sus scrofa cf. *domesticus*	0	0	0	1	**1**
Vulpes vulpes	1	3	4	1	**9**
Total	**111**	**94**	**79**	**112**	**396**

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