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Vertebrate road-kill patterns in Mediterranean habitats: Who, when and where

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ABSTRACT

Road-kill is the most recognized impact of traffic and an important threat for biodiversity. Nevertheless, most research on this topic deals with particular species or with road features, describing proximate correlates and rarely making inference on the mechanisms. Here we provide a more general approximation by describing life-history, temporal and spatial factors affecting vertebrate road-kills in Mediterranean landscapes, which are a biodiversity hotspot with little studied road impacts. During one year we recorded the casualties found on paved roads within Doñana Natural Park. We found 2368 road-kills belonging to 66 species (32% of the study area checklist), with abundant ectotherm species more likely to be road-killed. We also investigated the temporal and spatial factors affecting the road-kill patterns of different taxonomic and functional groups. The phenology of the species was the main factor affecting road-kill temporal patterns for lizards, all birds and small mammals. Additionally, rainfall events were associated with the road-kill peaks of wintering birds, whereas high temperatures were related to the increase of road-killed snakes and the decrease of road-killed amphibians. Amphibians, snakes, lizards and small passerines were mainly road-killed according with their spatial abundance. Mitigation measures such as wildlife road-crossing structures showed contradictory effectiveness for small vertebrates due to the lack of adequate drift fences. We suggest prioritizing the mitigation measures which can permanently decrease the risk of been road-killed for ectotherm species, such as specific road-crossing structures with effective drift fences on road-kill hotspots. Concurrently, group-specific temporal mitigation measures should be applied during the road-kill seasonal peaks. The present work provides recommendations to decrease road-kill impacts in Mediterranean environments, but simultaneously tries to contribute to a more general development of road ecology research, suggesting several useful guidelines to perform road-kill studies.

1. Introduction

Road-kill is the most well-known impact of traffic on wildlife (Forman and Alexander, 1998; Forman et al., 2003). In spite of the effectiveness of several mitigation efforts (*e.g.* road fences; Jaeger and Fahrig, 2004), a very large number of vertebrates die worldwide along linear infrastructures (González-Gallina et al., 2013; van der Grift et al., 2013). Road-kills are a considerable threat for populations of many species (Fahrig et al., 1995; Mumme et al., 2000; Taylor et al., 2002). They are also a relevant issue for human road safety, involving high economic costs (Conover et al., 1995; Huijser et al., 2009). As a consequence, in the last decades the number of studies focusing on road impacts has increased considerably, leading to the rise of a discipline called road ecology (Forman et al., 2003; Coffin, 2007). Most research has focused on a few emblematic species (Hobday and Minstrell, 2008; Colino-Rabanal et al., 2011), and therefore at present there is still a need for more general approximations aimed to determine life-history, temporal and spatial factors affecting road-kill probability of whole animal communities. Furthermore, most studies describing casualty patterns investigated only the role of proximate causes of road-kill (*e.g.* local road features), thus their management recommendations are difficult to translate to other localities or to other species. Casualty patterns could probably be better understood by additionally considering the role of more general predictors, such as the underlying drivers affecting road-kill probability (*e.g.* climatic factors or spatial variation of species abundance). This kind of knowledge would greatly improve our conservation efforts, helping managers to implement more suitable mitigation measures.

An example of those more general descriptors is the study of species-specific life-history traits affecting the probability of being road-killed. This is an overlooked issue in road ecology with few published studies (Ford and Fahrig, 2007; Barthelmess and Brooks, 2010; Cook and Blumstein, 2013), although the available bibliography shows the existence of relevant differences in road-kill frequency

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among species (*e.g.* Ashley and Robinson, 1996; Erritzoe et al., 2003; Orlowski and Nowak, 2006; Glista et al., 2008). An additional step should be testing the relevance of other predictors which may be potentially correlating with both road-kill probability and life-history traits, as is the case of species abundance, which has been proposed as the main underlying factor affecting road-kill probability (Ford and Fahrig, 2007; Rytwinski and Fahrig, 2010; Møller et al., 2011). The studies concerning life-history traits and road-kill probability usually focus on road-killed species, whereas unaffected species can provide valuable information on key species-specific traits and should be included in the analysis. Life-history research can improve road-kill knowledge, but at the same time it can also provide direct recommendations that can be applied to the conservation of vulnerable species for which data is not yet available. Additionally, road-kill research focused on life-history traits can improve our understanding of temporal and spatial road-kill patterns, especially if the target species are aggregated at relevant taxonomic or functional groups (*e.g.* amphibians or migrant birds) that might be differentially affected by specific climatic or environmental conditions.

Previous studies have found that temporal variations in road-kill patterns are associated with seasonal behaviors such as dispersal or migration, thus helping to predict outbreaks in the number of casualties (Smith-Patten and Patten, 2008; Lagos et al., 2012; Rodríguez-Morales et al., 2013). The climatic factors contributing to the induction of these behaviors (*e.g.* temperature or rainfall) have been suggested to be directly linked to the road-kill peaks (Puky, 2005; Andrews et al., 2006; Glista et al., 2008), but usually without statistical analyses. Conversely, understanding which temporal factors can affect seasonal behaviors and the consequent temporal variability in road-kill patterns would potentially improve mitigation measures, especially those that can be managed in time (*e.g.* limitation of traffic intensity or speed).

Finally, a central issue in road-kill research is the spatial distribution of casualties, which is probably the most investigated topic in road ecology. Most studies have usefully investigated the association between road-kill frequency and some spatial variables describing road features and/or traffic volume (Trombulak and Frissell, 2000; Jaeger and Fahrig, 2004). Nevertheless, the spatial distribution of road-kills can be affected by a large amount of landscape and road features, some of which can act simultaneously (Clevenger et al., 2001, 2003; Forman et al., 2003). It is probably for this reason that several spatial variables (*e.g.* traffic volume or surrounding habitat) have shown contradictory effects in different studies (Coelho et al., 2008; van Langevelde et al., 2009). A simultaneous evaluation of the potentially relevant predictors, obviously controlling for correlated factors, is the way to proceed.

In this study we aimed to describe the life-history, temporal and spatial factors potentially affecting casualty patterns, conducting a detailed selection of candidate predictors likely to affect road-kill probability based on available bibliography. Our first hypothesis (1) is that some species are more prone to be road-killed than others, species with particular life-history traits directly or indirectly associated with their abundance or movements. Our second hypothesis (2) is that the number of road-kills increases in time following seasonal peaks of abundance or activity. Seasonal variations of abundance and activity should in turn depend on species phenology but also on climatic predictors such as rainfall or temperature. Finally, our third hypothesis (3) is that the number of road-kills spatially increases in areas with high species density but also due to a local intensification of road-crossing events, traffic volume and vehicle speed. Finally, we assume that mitigation measures such as wildlife road-crossing structures (WCS hereafter) and road signs should locally reduce the number of road-kills. We tested these hypotheses focusing on terrestrial vertebrates in a typical Mediterranean landscape (Doñana Natural Park, south-western Spain). The Mediterranean basin is a biodiversity hotspot (Mittermeier et al., 1998; Myers et al., 2000) with an ancient and widespread road-network, affecting protected areas and threatened species (Ferreras et al., 1992; Gomes et al., 2009; Grilo et al., 2009). Road-kill studies have been mainly performed in temperate landscapes (Huijser and Bergers, 2000; Trombulak and Frissell, 2000), with few contributions from Mediterranean areas (Malo et al., 2004; Carvalho and Mira, 2011; Garriga et al., 2012). In summary, we aim to determine life-history, temporal and spatial factors affecting road-kill patterns in Mediterranean habitats in order to be able to suggest some general management and conservation recommendations for an emblematic protected area and for other Mediterranean environments. Finally, a further purpose is to provide scientists and conservation biologists with some guidelines to better understand the factors behind road-kill patterns.

2. Materials and methods

2.1. Study area

Doñana Natural Area (36°59′ N, 6°26′ W; Fig. 1) is a Biosphere Reserve with a Mediterranean climate, characterized by a mosaic of natural, rural and urban environments in which, depending on the level of protection (National and Natural parks), some human activities are allowed. The local road-network is widespread, with different types of roads and traffic intensities. We surveyed all paved roads within the Natural Park: A494 Matalascañas–Mazagón (23 km), Cabezudos road (5 km), A483-Hinojos (11 km), and A483-Villamanrique de la Condesa (16 km; Fig. 1). The A494 Matalascañas–Mazagón is a two-lane regional road, whereas Cabezudos road, A483-Hinojos and A483-Villamanrique de la Condesa are two-lane forestry/agricultural roads. On the regional road the daily traffic volume was 2347 vehicles/day and the maximum allowed speed was 100 km/h. Forestry/agricultural roads had lower traffic volumes (133 vehicles/day on Cabezudos road, 194 vehicles/day on the A483-Hinojos, and 745 vehicles/day on the A483-Villamanrique de la Condesa) and maximum speed (60 km/h; see Fig. 1 for arithmetic means and standard deviations). Almost the whole length of regional and forestry/agricultural roads are fenced (but Cabezudos road is not). There were ten WCS along the A494 Matalascañas–Mazagón, 22 along the A483-Villamanrique de la Condesa, and four along the A483-Hinojos. The surveyed roads were located in Mediterranean forest and scrubland. Local terrestrial vertebrate communities are composed by typically Mediterranean species.

2.2. Data collection

From March 2006 to February 2007 (July 2007 excluded) we surveyed driving the four roads at 15 km/h approximately twice per week (one day in the morning and one day in the afternoon, chosen at random), on both directions. The observer (always the same person) searched for road-killed animals on the road surface and along the adjacent verges and ditches, georeferencing, identifying (at class and, when possible, species level) and removing all the specimens from the road.

We used the available scientific bibliography and unpublished data of the EBD-CSIC to compile a checklist of the species present in the study area in association with the vegetation and land-uses adjacent to the roads (Appendix 1). We considered all the species included in the checklist as potential road-kill victims. For those species we selected a set of life-history predictors likely to affect road-kill probability based on available bibliography (Ford and Fahrig, 2007; Cook and Blumstein, 2013; see Appendix 1 for more details). The candidate predictors directly or indirectly described species as a function of their abundance and movement capacity. In the first case the candidate predictors were *abundance* (rare, common, or abundant), *size* (body mass), *breeding* (average number of offspring per female-year), *activity* (nocturnal or diurnal), *habitat preferences* (urban, farmlands, grasslands, scrubland/woodland and freshwater), *food habits* (carnivorous, insectivorous or herbivorous) and *territoriality* (territorial or not). In the second case the candidate predictors were *movement* (terrestrial or flying),

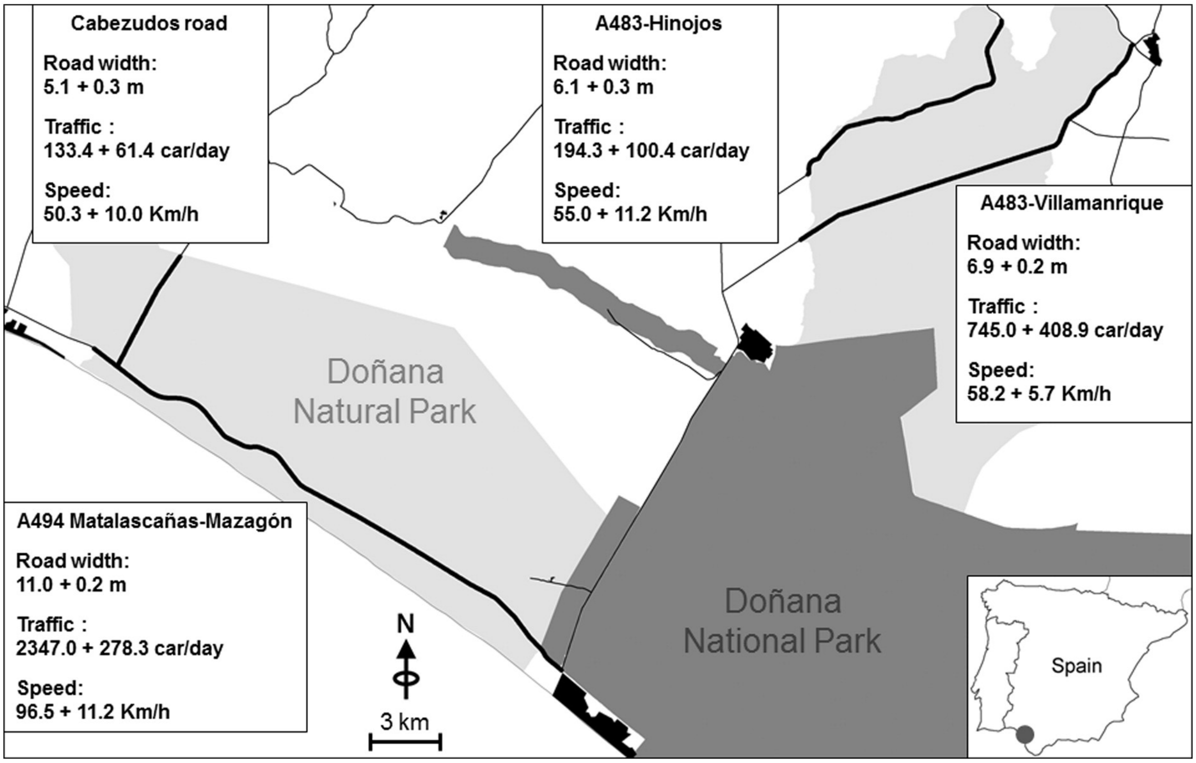

Fig. 1. Study area. Light gray areas represent Doñana Natural Park, which paved road we surveyed. Black lines represent the whole paved road-network. Bold lines are the surveyed roads: regional road A494 Matalascañas–Mazagón, and the three forestry/agricultural roads (Cabezudos road, A483-Hinojos and A483-Villamanrique de la Condesa). The arithmetic mean and the standard deviation of main road characteristics (*road width*, *traffic volume* and *maximum allowed speed*) are provided for each road.

speed (fast or slow movers) and *metabolic strategy* (ectotherms or endotherms).

In the analyses of temporal patterns we classified the road-killed species into eight taxonomic or functional groups with similar seasonal responses in abundance or activity (temporal groups hereafter): amphibians, snakes, lizards, resident birds, migrant nesting birds, migrant wintering birds, transient migrant birds and small mammals (Table 1; Appendix 2 for more details). For this analysis we selected two candidate climatic predictors which have been suggested by previous studies as affecting seasonal variations in species abundance and/or activity, and consequently road-kill temporal patterns: *rainfall* and *temperature* (Andrews et al., 2006; Glista et al., 2008; Appendix 2 for more details). Both of them were measured as the daily average of the week before each survey. Rainfall and temperature were calculated using data from the meteorological station of Palacio de Doñana. Considering that the overall traffic intensity can affect road-kill probability (Coelho et al., 2008; van Langevelde et al., 2009), we also selected a candidate predictor related with *seasonal traffic*: the average of daily traffic per season. Traffic values in the forestry/agricultural roads (Cabezudos road, A483-Hinojos, and A483-Villamanrique de la Condesa) were obtained using a magnetometer (TRAFx Vehicle Counter Generation III; sampling during one week per season). The traffic of the regional road (A494 Matalascañas–Mazagón) was obtained from the Andalusian Regional Government (sampling during one weekend and two weekdays per season at an official counter station). With the aim to control for species phenology we also included the *photoperiod variation*, a variable potentially affecting seasonal behaviors (directly or indirectly) and consequently the abundance or activity variations of a large number of species (Fryxell and Sinclair, 1988; Gwinner and Helm, 2003). Temporal increases in abundance or activity can raise road-kill probability (Grilo et al., 2009; Lagos et al., 2012; Rodríguez-Morales et al., 2013). We measured the photoperiod variation as the difference between the monthly average of the daylight of a given month and the monthly average of daylight of the following month. We obtained photoperiod variation data from the U.S. Naval Oceanography Portal (http://www.usno.navy.mil/USNO/astronomical-applications). Finally, considering that carcasses suffer temporal degradation and the removal by scavengers (Antworth et al., 2005; Santos et al., 2011), we also included a methodological variable to control for the *time elapsed since the previous survey*.

In the analyses of spatial patterns we classified the road-killed species into five taxonomic or functional groups with similar spatial behaviors (spatial groups hereafter): amphibians, snakes, lizards, small passerines and small mammals (Table 1; Appendix 3 for more details). We divided the surveyed roads (55 km in total) into 1100 sections of 50-m long with the aim to reduce spatial auto-correlation and simultaneously describe changes in spatial predictors. Each section was characterized by set of candidate predictors likely to affect local probability of wildlife road-crossing or the local variation of traffic and vehicle speed, and consequently the spatial road-kill patterns (Clevenger et al., 2001, 2003; Jaeger and Fahrig, 2004; Appendix 3 for more details). The predictors potentially affecting the spatial variation in wildlife road-crossing were related to road verges: *road verge habitat* (grass, grass with trees, grass with shrubs and trees, shrubs), presence/absence of *road-fences*, *drainage culverts* and *WCS* (which in our study area were mainly designed for medium-sized mammals). The predictors potentially affecting the spatial variations in traffic and speed were related to the road itself: *road width*, *annual average of daily traffic*, *maximum allowed speed*, and the presence/absence of *road-shoulders*, *curves*, and *vertical* or *horizontal road signs*. The characterization of road sections by spatial predictors was carried out in the field. Species abundance can also affect the spatial variations in the distribution of road-kills (Clevenger et al., 2001, 2003; Gunson et al., 2011). With the aim to control for this factor we also characterized each 50-m long section of surveyed roads by two variables which have been described as directly or indirectly affecting the species abundance: *macro-habitat*

Table 1
Road-killed species and groups. Number of road-killed individuals found and their assignation to temporal or spatial groups used in the different analyses.

Species	Number of road-kills	Temporal group	Spatial group
Amphibians			
Discoglossus galganoi	1	Amphibians	Amphibians
Epidalea calamita	381	Amphibians	Amphibians
Pelobates cultripes	142	Amphibians	Amphibians
Pelophylax perezi	7	Amphibians	Amphibians
Pleurodeles waltl	20	Amphibians	Amphibians
Unidentified Amphibians	1037	Amphibians	Amphibians
Total Amphibians	1588		
Reptiles			
Coronella girondica	6	Snakes	Snakes
Hemorrhois hippocrepis	1	Snakes	Snakes
Macroprotodon brevis	4	Snakes	Snakes
Malpolon monspessulanus	39	Snakes	Snakes
Natrix maura	10	Snakes	Snakes
Rhinechis scalaris	39	Snakes	Snakes
Vipera latasti	8	Snakes	Snakes
Unidentified Snakes	22	Snakes	Snakes
Total Snakes	129		
Acanthodactylus erythrurus	20	Lizards	Lizards
Blanus cinereus	1	–	–
Chalcides bedriagai	2	–	–
Chalcides striatus	1	–	–
Chamaeleo chamaeleon	2	–	–
Podarcis carbonelli	19	Lizards	Lizards
Podarcis vaucheri	1	Lizards	Lizards
Psammodromus manuelae	79	Lizards	Lizards
Tarentola mauritanica	15	Lizards	Lizards
Timon lepidus	3	Lizards	Lizards
Unidentified Lizards	33	Lizards	Lizards
Total Lizards	170		
Birds			
Alectoris rufa	2	Resident	–
Apus pallidus	1	Nesting	–
Bubo bubo	1	Resident	–
Buteo buteo	2	Resident	–
Caprimulgus ruficollis	13	Nesting	–
Columba livia domestica	6	Resident	–
Cyanistes caeruleus	1	Resident	Small passerines
Cyanopica cooki	4	Resident	–
Emberiza calandra	4	Resident	Small passerines
Erithacus rubecula	27	Wintering	Small passerines
Ficedula hypoleuca	7	Migrant	Small passerines
Fringilla coelebs	2	Resident	Small passerines
Hirundo rustica	1	Nesting	–
Lanius senator	5	Nesting	–
Lophophanes cristatus	1	Resident	Small passerines
Lullula arborea	1	Resident	Small passerines
Muscicapa striata	1	Migrant	Small passerines
Oceanodroma leucorhoa	1	–	–
Parus major	1	Resident	Small passerines
Passer domesticus	4	Resident	Small passerines
Passer montanus	1	Resident	Small passerines
Phylloscopus collybita/ibericus	10	Migrant	Small passerines
Saxicola rubetra	2	Migrant	Small passerines
Saxicola rubicola	1	Resident	Small passerines
Serinus serinus	4	Resident	Small passerines
Strix aluco	2	Resident	–
Sylvia atricapilla	3	Migrant	Small passerines
Sylvia cantillans	2	Migrant	Small passerines
Sylvia melanocephala	6	Resident	Small passerines
Sylvia undata	8	Resident	Small passerines
Troglodytes troglodytes	1	Resident	Small passerines
Turdus philomelos	2	Wintering	–
Unidentified Small passerines	163	–	Small passerines
Total Birds	290		
Mammals			
Apodemus sylvaticus	5	Small mammals	Small mammals
Canis lupus familiaris	2	–	–
Crocidura russula	1	Small mammals	Small mammals
Eliomys quercinus	2	Small mammals	Small mammals
Erinaceus europaeus	17	–	–
Felis silvestris catus	2	–	–
Herpestes ichneumon	1	–	–
Lepus granatensis	4	–	–
Mus spretus	4	Small mammals	Small mammals
Oryctolagus cuniculus	17	–	–
Pipistrellus pipistrellus	1	–	–
Rattus rattus	2	Small mammals	Small mammals
Vulpes vulpes	5	–	–
Unidentified Mammals	9	–	–
Unidentified Small mammals	119	Small mammals	Small mammals
Total Mammals	191		

(woodland, scrubland or grassland) and *distance to the nearest water body*. The characterization of road sections by these variables was carried out using a geographic information system.

2.3. Data analysis

We calculated the correlation between candidate predictors in order to consider the potential effect of collinearity in life-history analysis (Appendix 1). *Abundance* strongly correlated with *size*, *food habits*, *territoriality* and *movement*. Therefore, we fitted a preliminary generalized linear model (GLM) using the whole species checklist. The response variable was the *species road-kill probability*, with a value of 1 for species found road-killed at least once in any of the roads and 0 for those that were not. The only predictor of the model was the *abundance*. The model had a binomial error distribution and logit link function (GLIMMIX procedure of SAS version 9.3; SAS Institute Inc., 2012). As the probability to detect road-killed rare species was much lower, all subsequent life-history analyses were done on a reduced dataset without rare species (both the road-killed and unaffected species). We fitted a separate GLM (binomial error distribution and logit link function) for every candidate life-history predictor: *size*, *breeding*, *activity*, *habitat preferences*, *food habits*, *territoriality*, *movement*, *speed* and *metabolic strategy*. The response variable was the *species road-kill probability*. We considered as plausible all models at $\Delta AIC < 2$ from the best model (Burnham et al., 2011). We calculated model support using Akaike weights (wAIC, ranging from 0 to 1, with larger numbers indicating greater support; Burnham and Anderson, 2002).

In the temporal analyses we followed a similar approach to evaluate the collinearity between factors, but we did not find relevant correlations (Appendix 2). For every temporal group we performed an AIC model selection (Burnham and Anderson, 2002) with generalized linear mixed models (GLMM). Our null hypothesis was based on the relevance of species phenology: the *number of road-kills per survey* (*i.e.* the survey of a given road in a given day) depends on a factor which can be considered as a proxy of the phenology of the group: the *photoperiod variation*. The further hypotheses also included a temporal predictor: *rainfall*, *temperature* or *seasonal traffic*. All the fitted models also included a methodological variable: the *time elapsed since the previous survey*. Finally, the full model included all the mentioned temporal factors. The *surveyed road* was included as a random factor. We used a negative binomial error distribution and a log link function using procedure GLIMMIX in SAS version 9.3.

In the spatial analyses, several of the candidate factors were strongly correlated (Appendix 3). As a consequence we removed some of them from the analyses. For every spatial group we performed an AIC model selection (Burnham and Anderson, 2002). Our null hypothesis was based on the relevance of species abundance: the *number of road-kills per road section* (50-m sampling plot) depends on two factors which are a proxy of abundance: *distance to the nearest water body* and *macro-habitat*. These two factors were correlated (Appendix 3) and for this reason we only included the distance to water in the spatial analysis. The further hypotheses also included a spatial predictor: *road width*, *traffic* or *speed* (traffic/speed hypotheses), presence/absence of *culverts*, *WCS* or *vertical signs* (mitigation measure hypotheses). For the spatial group of small passerines we did not implement the presence/absence of *culverts* and *WCS*. All the models also included the *surveyed road* as a random factor. We used a negative binomial error distribution and a log link function using procedure GLIMMIX in SAS version 9.3.

3. Results

We detected 2368 road-killed vertebrates and most (67%) were amphibians (1568 anurans and 20 urodeles; Table 1). We could identify only a fraction of the amphibians, mostly corresponding to *Epidalea calamita* (381 casualties) and *Pelobates cultripes* (142). We found 299 reptile casualties (12.6% of the total), including snakes (mainly *Malpolon monspessulanus* and *Rhinechis scalaris*) and lizards (mostly *Psammodromus manuelae*). Birds accounted for 12.2% of the casualties (290), covering a wide range of orders (*Erithacus rubecula* was the most frequent species.). Finally, we found 191 (8.1%) road-killed mammals (133 small mammals, mainly rodents).

In total we were able to identify 991 casualties as belonging to 66 different species (Table 1), representing 32% of our species checklist (Appendix 1). An important number of the road-killed species (16%) were globally classified at least as Near Threatened. Unidentified species were mainly amphibians, but also small mammals and small passerines (Table 1). The results of the preliminary GLM showed that *abundance* affected the *species road-kill probability*: both common and abundant species were at least four times more likely to be road-killed than rare species ($F = 9.13$; $p = 0.0002$; Fig. 2). The reduced dataset included only 148 common and abundant species, of which 60 were found as road-kills. The rest of the life-history models were run using this reduced subset. The only supported model included *metabolic strategy* and was almost five times better than the second ranked model (Table 2). Overall, ectotherm species were approximately twice as likely as endotherms to be found as road-kill victims (Fig. 2).

Table 2
Factors affecting *species road-kill probability*, model ranks by AIC weights (wAIC). ΔAIC is the difference of a given AIC value compared to the smallest AIC value. The only supported model (ΔAIC < 2) is shown in bold. AIC weights indicate the relative support of every model. Evidence ratio (ER) is the ratio of wAIC, comparing the best supported model with every competing one.

Model	AIC	ΔAIC	wAIC	Rank	ER
Thermal strategy	**189.8**	**0.0**	**0.78**	**1**	**1.0**
Movement type	192.8	3.1	0.17	2	4.7
Habitat preference	196.1	6.3	0.03	3	23.7
Offsprings	198.3	8.6	0.01	4	72.2
Body weight	199.8	10.0	0.00	5	154.4
Circadian activity	200.3	10.5	0.00	6	194.4
Territoriality	202.5	12.7	0.00	7	587.0
Feeding strategy	202.7	12.9	0.00	8	648.7
Speed	203.4	13.7	0.00	9	939.2

In the analysis of temporal patterns we considered 2156 road-kills (Table 1; Appendix 2 for more information on the temporal distribution of each temporal group). The best supported hypothesis was the phenology hypothesis for lizards, all birds and small mammals (Table 3). For these temporal groups the temporal variation of road-kills only depended on the *time elapsed since the previous survey* and the *photoperiod variation*. The only temporal groups with a best supported model including a climatic predictor were amphibians and snakes. The best supported hypothesis for both amphibians and snakes was the *temperature* hypothesis (Table 3): road-kills of amphibians decreased with high temperatures, but snakes showed the opposite pattern (Fig. 3). Wintering birds had a second supported model corresponding to the *rainfall* hypothesis (Table 3): their road-kills increased with high precipitations.

Finally, for the spatial analyses we considered 1617 road-kills (Table 1; Appendix 3 for more information on the spatial distribution of each spatial group). The abundance hypothesis was one of the best supported hypotheses for amphibians, snakes, lizards and small passerines (Table 4). Amphibians were more road-killed near *water* bodies; snakes, lizards and small passerines far from them. Mitigation measure hypotheses were always more supported than traffic/speed hypotheses (Table 4), but the effectiveness of such mitigation measures was contradictory. The presence of *culverts* decreased the number of road-killed snakes; whereas the presence of *WCS* decreased the number of road-killed lizards but at the same time increased the number of road-killed snakes and small mammals. For both snakes and small passerines the presence of *vertical signs* decreased the number of road-killed individuals (Fig. 4).

4. Discussion

Our results showed that several life-history, temporal and spatial factors were associated with road-kill patterns. Life-history analysis highlighted that abundant and ectotherm species were more likely to be road-killed. The temporal analysis showed that climatic predictors can contribute to determine group-specific road-kill seasonality, in our

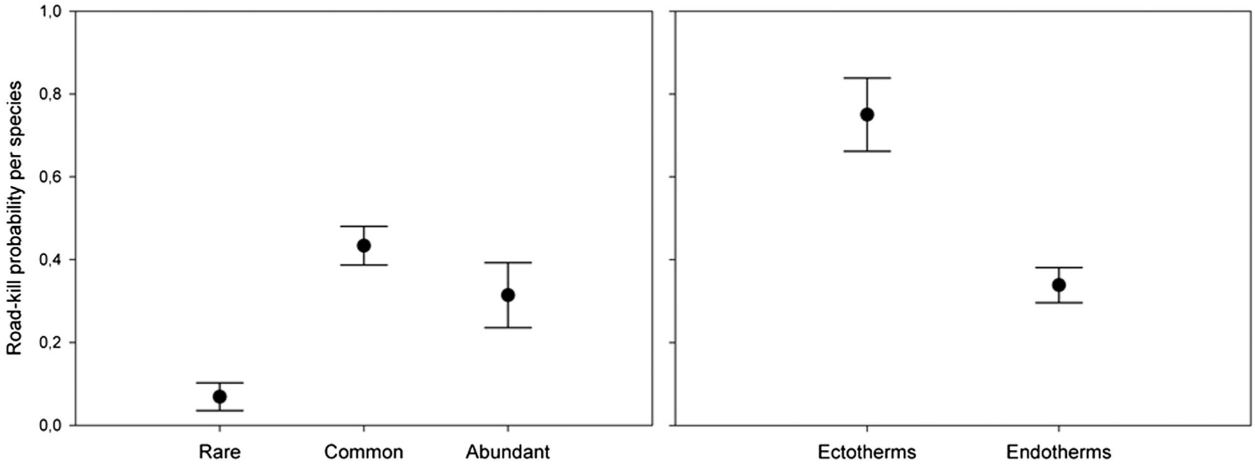

Fig. 2. Life-history factors and *species road-kill probability*. Probability (± standard error) of species to be found as road-kills as predicted by the preliminary model (on the left; whole dataset) and the best supported model (on the right; reduced dataset, with only common and abundant species). Left: species categorized by three coarse *abundance* categories (parameter estimates: $\beta = -0.8 \pm 0.4$; rare $= -1.8 \pm 0.6$, common $= 0.5 \pm 0.4$, abundant $= 0$). Right: species included within the abundant and common categories by their *metabolic strategy* ($\beta = 1.1 \pm 0.5$; endotherms $= -1.8 \pm 0.5$, ectotherms $= 0$).

Table 3
Factors affecting temporal distribution of road-kills. AIC values for every temporal hypothesis and group. The best supported models are shown in bold. Legend for abbreviations: t is *time since the last survey* and p is *photoperiod variation*; the predictors were R (*rainfall*), T (*temperature*) and ST (*seasonal traffic*). The complete group-specific tables with the values of ΔAIC, AIC weights and Model rank are shown in the Appendix 2.

Hypotheses	AIC							
	Amphibians	Snakes	Lizards	Resident birds	Nesting birds	Wintering birds	Migrant birds	Small mammals
Phenology								
$t + p$	781.4	837.0	**821.5**	**815.2**	**975.0**	**960.3**	**1070.4**	**746.8**
Climatic								
$t + p + R$	790.3	841.3	828.8	818.2	1044.2	**961.7**	1074.5	751.9
$t + p + T$	**752.0**	**781.8**	856.8	819.7	1106.8	990.6	1085.9	751.1
Seasonal traffic								
$t + p + ST$	777.1	850.6	830.2	831.4	1036.6	980.1	1080.3	761.8
Full								
$t + p + R + T + ST$	785.0	832.5	877.3	840.0	1112.4	1020.0	1102.1	770.0

case rainfall for wintering birds and temperature for both amphibians and snakes. The spatial analysis suggested a contradictory effect for some mitigation measures (WCS, culverts and road signs) for different groups of species. These results improve our understanding on some of the underlying mechanisms causing group-specific collisions in Mediterranean habitats.

In the life-history analysis we found that a coarse descriptor of species abundance correlated with other predictors, making difficult its inclusion in further analysis. According to the available bibliography (Ford and Fahrig, 2007; Møller et al., 2011), we expected that the probability of road-kill would be lower for rare species, and the preliminary analysis confirmed this hypothesis. The remaining analyses focusing only on common and abundant species showed that ectotherms (amphibians and reptiles) had a higher probability to be road-killed. This is probably because their metabolism causes slowness in amphibians (Hels and Buchwald, 2001; Puky, 2005) and basking behavior in reptiles (Ashley and Robinson, 1996; Tanner and Perry, 2007). Other reasons could be the relatively low environmental awareness and the behavioral freezing responses to threats (Andrews et al., 2006; Lima et al., 2015). On the other hand, ectotherms are intrinsically more abundant than endotherms (Currie and Fritz, 1993), and this correlation was possibly contributing to the life-history results. Nevertheless, our findings make clear that mitigation measures in Mediterranean habitats should focus on amphibians and reptiles, especially considering that amphibians are globally threatened (Blaustein and Wake, 1990; Stuart et al., 2004; also due to road impact: Rytwinski and Fahrig, 2012). Furthermore, we should consider that Doñana Natural Area is a biodiversity hotspot in which several Iberian endemic or vulnerable species are locally common amphibians and reptiles (*e.g. P. cultripes*, *P. manuelae*, *etc.*), and for this reason their conservation should be a priority. We recommend that drift fences should be extensively implemented to permanently reduce their road-kill numbers (Aresco, 2005; Puky, 2005); including along roads with low traffic where basking behavior is more frequent (Jones et al., 2008).

The findings of the temporal analysis supported other studies showing seasonal variations in road-kill probability for different temporal groups (Smith-Patten and Patten, 2008; Rodríguez-Morales et al., 2013). In most cases this variation mainly depended on species phenology, but we also found some associations between road-kill numbers and climatic predictors. This can be an important conservation tool because in Mediterranean environments the climatic predictors are quite unpredictable, in spite of which they can be used by managers to determine when to enforce temporary mitigation measures. Seasonal increases in abundance or activity can affect road-kill probability (Grilo et al., 2009; Lagos et al., 2012) and for this reason we expected than species phenology would be the main factor affecting the temporal variation of casualties. Temporal analyses confirmed this hypothesis for lizards, all birds and small mammals. As a consequence the best strategy to reduce the road-kill peaks for these temporal groups should be focused on group-specific phenology and based on the temporary management of traffic. Possible mitigation measures can be traffic-calmed zones or speed limitations (Jaarsma and Willems, 2002; Sullivan et al., 2004). Both of them should be implemented in road-kill hotspots during the group-specific seasonal increases of abundance or activity.

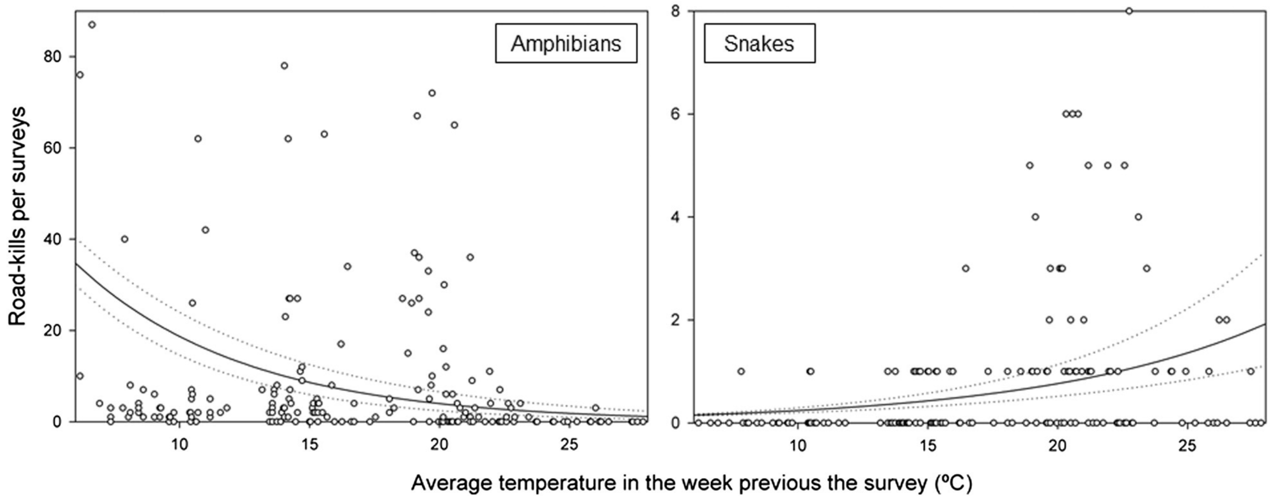

Fig. 3. Temporal road-kill patterns and *temperature*. The solid line represents the partial regression line of *road-kills per survey* on *temperature* (for amphibians and snakes). Dotted lines are the upper and lower 95% CI. White circles represent raw data.

Table 4
Factors affecting the spatial distribution of road-kills. AIC values for every temporal hypothesis and group. The best supported model is shown in bold. The complete group-specific tables with the values of ΔAIC, AIC weights and Model rank are shown in the Appendix 3.

Hypotheses	AIC				
	Amphibians	Snakes	Lizards	Small passerines	Small mammals
Abundance					
Water	**3923.2**	**5727.9**	**5678.6**	**5276.9**	5969.1
Wildlife road-crossing					
Water + Culvert	3928.9	**5727.1**	5712.9	–	5976.2
Water + Crossing structure	3928.1	**5728.9**	**5677.8**	–	**5963.5**
Water + Vertical signs	3930.0	**5728.2**	5732.4	**5276.9**	5968.3
Traffic/speed					
Water + Road width	3930.7	5737.3	5693.3	5286.3	5995.9
Water + Traffic	3942.6	5748.7	5703.3	5298.3	6006.9
Water + Speed	3936.9	5735.3	5741.3	5289.7	6025.8

In the Mediterranean region, this recommendation will be particularly important for *taxa* that have large seasonal fluctuations in abundance due to breeding or migration; such as lizards, all birds and small mammals (García et al., 2000; Román et al., 2006; Moreno and Rouco, 2013).

The climatic predictors affecting road-kill seasonality were rainfall for wintering birds and temperature for both amphibians and snakes. Wintering birds were more road-killed when precipitations were higher, possibly because rainfall may decrease visibility (Farmer and Brooks, 2012). Amphibians were almost not road-killed during the summer, because high temperatures typically drive them to aestivation in Mediterranean environments (Díaz-Paniagua et al., 2005; Gómez-Rodríguez et al., 2012). At the same time high temperatures typically stimulate the activity of snakes, increasing their road-kill probability (Ashley and Robinson, 1996; Meek, 2009). Both temperature and rainfall hypotheses also included photoperiod variation, which entails the relevance of species phenology also for amphibians and snakes; and again for wintering birds. For this reason any temporary mitigation measure focusing on amphibians, snakes and wintering birds should be implemented considering at the same time climatic predictors and group-specific phenology. More specifically, temporary mitigation measures targeting amphibians should be interrupted during the summer and applied at the beginning of the breeding migrations, the seasonal activity peak for this temporal group (Díaz-Paniagua et al., 2005; Semlitsch, 2008). Similarly, the actions focused on snakes should be implemented in warmer months and especially during the seasonal activity peak due to juvenile dispersal (Bonnet et al., 1999; Feriche et al., 2008). Finally, those temporary mitigation measures focused on wintering birds should be especially applied during rainy days of winter months.

We expected that the spatial distribution of road-kills would be mainly affected by species abundance and the spatial analysis confirmed this hypothesis showing that a proxy of species abundance in Mediterranean areas (*i.e.* the distance to the nearest water body) was the most relevant factor determining road-kill hotspots for amphibians, snakes, lizards and small passerines. In Mediterranean environments the mitigation measures focusing on amphibians should be implemented in the proximity of water bodies; contrarily to those actions aiming to reduce the road-kills of snakes, lizards and small passerines, which should be applied in drier areas. The hypotheses suggesting that mitigation measures would decrease the number of road-kills were partially rejected. Both drainage culverts and WCS showed a relatively low effectiveness in reducing the road-kills of small vertebrates. Our results suggested that these mitigation measures might act as ecological traps for some species (Orlowski, 2008; Baxter-Gilbert et al., 2015), because their locations often corresponded with natural corridors with a better micro-habitat than the surrounding matrix habitat. In our study area the WCS were designed for medium-sized mammals such as carnivores, and for this reason their drift fences were not effective for small vertebrates. Both culverts and WCS could be much improved with the addition of adequate drift fences. Further structures should be planned in correspondence to the group-specific areas of maximum road-kill risk.

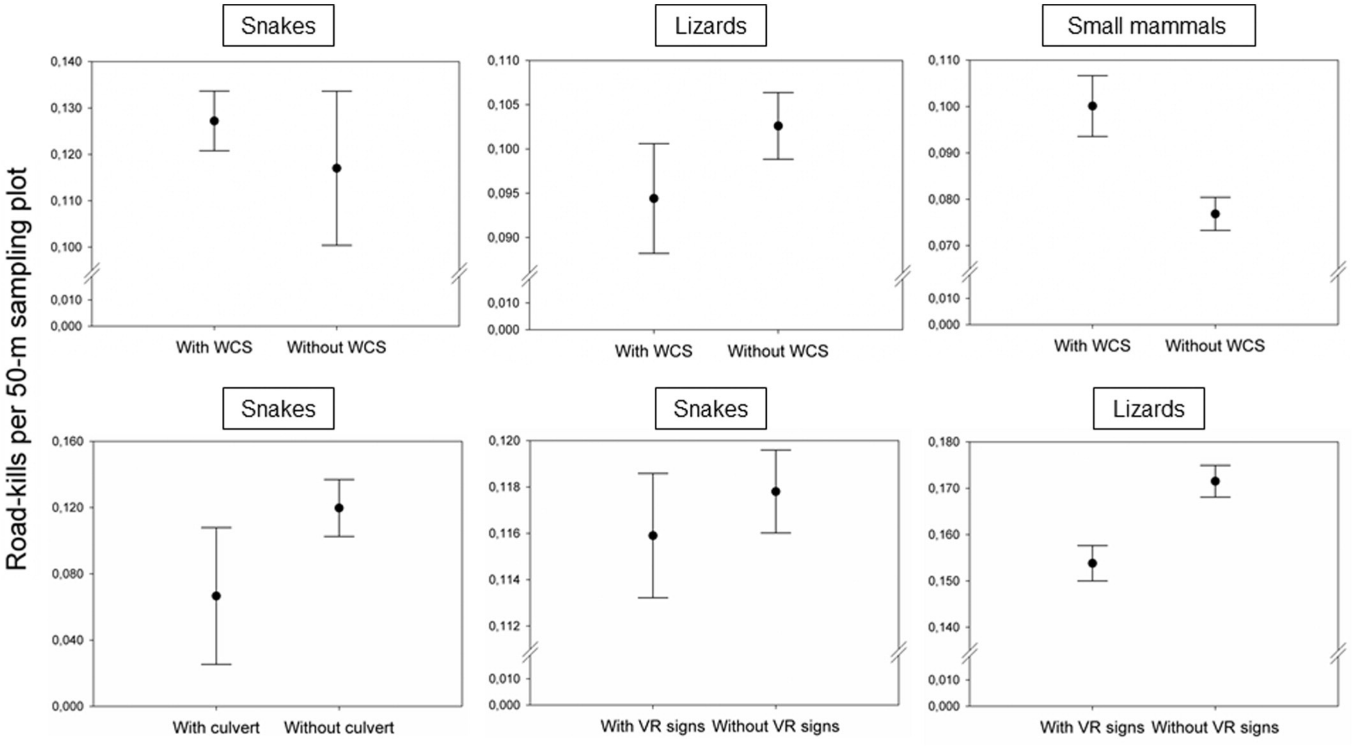

Fig. 4. Spatial road-kill patterns and wildlife road-crossing predictors. Relationship between the *number of road-kills* per 50-m sampling plot and presence/absence of wildlife road-crossing structure (*WCS*), *drainage culverts* and *vertical road signs* (VR signs).

Those road-kill hotspots should be also provided with vertical road signs, which seemed to be efficient in decreasing the number of road-killed individuals for snakes and small passerines. On the other hand, the hypotheses suggesting that the increase of traffic/speed would affect the number of road-kills were rejected. Nevertheless, we cannot state that traffic- and speed-related predictors did not affect road-kill numbers, because the lack of casualties might be consequence of local population decreases or a strong barrier effect imposed by a high traffic intensity (Jaeger et al., 2005; Hobday and Minstrell, 2008; van Langevelde et al., 2009). Unfortunately in the present study we could not discern between these alternative explanations; and we could not even determine the potential relevance of the correlated spatial predictor that we needed to remove from the analyses (for example the presence of shoulders, curves, *etc.*). The effects of these factors on the road-kill spatial distribution of the different species should be explored further.

Our results have relevant implications for the establishment of measures to mitigate road-kill impacts in our study area and also in other Mediterranean environments. Our spatial analysis suggests how to permanently decrease the road-kills of small vertebrates through the implementation of effective drift fences on already present WCS and culverts. Moreover we recommend the provision of further mitigation measures (*e.g.* WCS and road signs) in group-specific road-kill risk areas, such as the proximities of water bodies for amphibians. Whenever these mitigation measures could not be permanently applied, we also suggested temporary actions which can reduce the casualties during the seasonal road-kill peaks, for example traffic calmed zones and speed limitations. We also showed that managers of Mediterranean protected areas should focus on abundant and ectotherm species, many of them with conservation problems, as is the case of amphibians. Finally we would suggest to researchers and environmental managers to provide, whenever possible, more general approximations, performing studies aiming to investigate at the same time life-history, temporal and spatial factors affecting road-kill probability of whole animal communities. They should possibly focus on general predictors and underlying drivers of road-kill probability (*e.g.* species abundance and its temporal and spatial variation, climatic factors, *etc.*), always controlling for correlations between variables. Road ecology is an expanding discipline, and road-kill is its most investigated issue. Currently many researchers, managers and also nonprofessional environmental organizations are collecting data that should be used to improve our general understanding of the problem. We hope that this study contributes to the development of this discipline and to the conservation of threatened ecosystems.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.06.010.

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