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Carnivore Abundance near Motorways Related to Prey and Roadkills

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ABSTRACT Landscape disturbance by roads may increase abundance of prey in verges (i.e., strips of terrain adjacent to roadways) or create other features that can attract carnivores and expose them to a higher risk of mortality by vehicle collision. We studied a system that included European rabbits (*Oryctolagus cuniculus*) and their predators in central Spain near 3 motorways during 2011 and 2012. We analyzed carnivore and rabbit abundance and the potential effect of prey populations on carnivore roadkill. We estimated rabbit and carnivore abundance index by surveying scats in 1-km transects in the landscape, and calculated a roadkill index in motorway stretches parallel to the transects from a roadkill data obtained in

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a roadkill monitoring survey from 2007 to 2011. We analyzed carnivore response for the entire carnivore community and for 2 groups of species: the red fox, which is the most synanthropic carnivore in our study area, and the other carnivores. Fox abundance was higher near motorways compared to control sites, whereas the abundance of other species was related only to rabbit abundance. Furthermore, motorway stretches with higher carnivore abundance presented higher values of carnivore roadkills. Thus, motorways are a source of mortality for carnivores that should be managed carefully. The potential cascading effect of food resources near roads on carnivore mortality should be considered in management and food abundance near roads should be minimized in areas inhabited by carnivores of conservation concern.

KEY WORDS anthropogenic resources, human disturbance, *Oryctolagus cuniculus,* predator-prey dynamics, road ecology, *Vulpes vulpes*.

Wildlife populations respond to human disturbance of landscapes in multiple ways. Although some species avoid disturbance (McKinney 2002, van der Ree et al. 2005, Saito and Koike 2013), others profit from the new conditions and thrive in areas rich in anthropogenic resources (Fedriani et al. 2001, Kolowski and Holekamp 2008, Bino et al. 2010, Dellinger et al. 2013). Changes in habitat conditions also lead to alterations of the interspecific relationships in the ecosystem, including predator-prey relationships (Rodewald et al. 2011, Newsome et al. 2014). In areas with anthropogenic food, synanthropic predators may choose those resources over natural prey, resulting in high predator abundances with minimal effect on prey populations (Rodewald et al. 2011). Additionally, subsidized predators may change their preferred prey when anthropogenic food such as garbage is available, modifying trophic cascades (Newsome et al. 2014).

Roads are a common and widespread case of human disturbance that change landscape configuration and quality and modify habitat (Trombulak and Frissell 2000, Carr et al. 2002, Forman et al. 2003). Roads have negative to positive effects on wildlife. Negative effects include direct mortality from vehicles, habitat fragmentation, and habitat degradation, which can affect wild population persistence (Riley et al. 2006, Jackson and Fahrig 2011, van der Ree et al. 2015). Among the described positive effects, roads can provide new habitat in the strips of terrain next to the pavement (i.e., road verges). Some small mammals thrive in verges and reach dense populations (Bellamy et al. 2000, Rosa and Bissonette 2007). These small-mammal populations play the role of prey in the ecosystem and, in addition to other anthropogenic resources provided by roads (e.g., roadkills, garbage), can influence carnivore habitat use by attracting them close to roads (Mortelliti and Boitani 2008, Grilo et al. 2012). Animals living near roads are exposed to increased mortality risk by vehicle collision (Forman et al. 2003, van der Ree et al. 2015). Usually, prey species, such as the European rabbit (*Oryctolagus cuniculus*), have high reproductive rates that can compensate for this additional mortality. However, carnivores typically have lower reproductive rates and an increase in their mortality rates may negatively affect predator populations in the long term (Rytwinski and Fahrig 2012). Carnivores more tolerant to human disturbance, like the red fox (*Vulpes vulpes*), will approach roads more often (Ruiz-Capillas et al. 2013*a*), and thus, their mortality from vehicles is expected to be higher (Baker et al. 2004), which may affect the carnivore community by modifying the distribution or abundance of species. Thus, roads can act as traps for some carnivores, and only species that can avoid traffic will prosper in these environments (Jaeger et al. 2005, Rytwinski and Fahrig 2012).

In the Iberian Peninsula, some road verges sustain large populations of prey (e.g., mice, rabbits; Barrientos and Bolonio 2009, Sabino-Marques and Mira 2011, Ruiz-Capillas et al. 2013*b*), although prey abundance in verges may depend on surrounding habitat conditions (Planillo and Malo 2013). Rabbits are native to the Iberian Peninsula and a key prey species in Mediterranean ecosystems (Delibes-Mateos et al. 2008*a*); some carnivores select rabbits as prey when they are abundant (e.g., red foxes; Carvalho and Gomes 2001, Delibes-Mateos et al. 2008*b*), or during certain seasons (e.g., stone martens (*Martes foina*) in spring (Barrientos and Virgós 2006). Therefore, it is possible that in those areas were rabbit populations inhabit road verges they may attract carnivores and thus potentially create a cascading effect that could lead to increased carnivore mortality.

Our objective was to test the existence of this cascading effect. We focused on a community composed of rabbits, as the main prey, and several carnivore species in a typical Mediterranean landscape. We analyzed global carnivore response and red fox response to variability in rabbit abundance in the landscape, comparing motorway verges with control sites. We hypothesized that carnivores would favor areas near motorways because of prey abundance, resulting in more carnivores near motorways, and more carnivores killed by vehicles.

STUDY AREA

The study area was 60 × 45 km (2,700 km^2) in central Spain, in the provinces of Ávila and Segovia, centered on 40°46 N and 4°25 W (Fig. 1). The climate was Continental Mediterranean, characterized by cold winters ($\bar{x}$ temperature = 5º C), dry summers (17º C), and average annual precipitation of 408–573 mm (Ninyerola et al. 2005). This was a rural area, mainly devoted to cattle and extensive croplands for non-irrigated cereals, with a population density of 25.5 inhabitants/km^2. The landscape was modified by traditional human uses with patches of natural habitat spread throughout the area. Cattle pastures were typically characterized by the presence of open woodland (dehesas), and there were patches of natural vegetation between field crops and between grazed areas. Natural vegetation was dominated by sclerophyll shrubs, with Holm oak forests (*Quercus ilex*), and riparian forest along rivers. The study area included 3 areas of high conservation value included in the European Natura 2000 network, which covered >500 km^2. Wild carnivore species in our study area included

Iberian wolf (*Canis lupus signatus*), red fox, least weasel (*Mustela nivalis*), European polecat (*Mustela putorius*), American mink (*Neovison vison*), stone marten, Eurasian badger (*Meles meles*), European otter (*Lutra lutra*), common genet (*Genetta genetta*), and wildcat (*Felis silvestris*), being 3 listed as near threatened in the Spanish red list of International Union for Conservation of Nature (IUCN) (Iberian wolf, European polecat, and wildcat; Palomo et al. 2007). Feral cats and dogs were also common in the area. The study area included 3 motorways: AP-6, AP-51, and AP-61. Motorways AP-61 and AP-51 had medium traffic volumes (6,472 and 7,782 vehicles/day, respectively), and AP-6 had high traffic volume (28,684 vehicles/day). All 3 motorways were surrounded by a perimeter fence that excluded ungulates and humans but was permeable to other species.

METHODS

Data Collection

Our research protocols with animals were standard observational ones and they did not interfere with wild animals, thus we did not need any special permissions under European directive (UE Directive 2010/63/UE) or Spanish legislation (law 42/2007).

Rabbit and carnivore abundances.— To estimate species abundance, we established 36 linear transects within the study area, 18 along motorways and 18 in control zones (Fig. 1). We defined control zones as those with the same habitat structure and ≥4 km from motorways. We selected 4 km because home ranges of common carnivore species found in Spain range 2.5–5.8 km^2 (Rosalino et al. 2004, Santos-Reis et al. 2005, Rondinini et al. 2006), and thus it was unlikely that a single individual would move 4 km in linear distance. We sampled transects in similar habitats in motorway and control zones, controlling for similar structure in vegetation in both situations (i.e., for each motorway transect with shrub vegetation, there was a control transect with the same vegetation structure) to avoid a possible habitat effect. We double-checked transects for habitat similarity; first we inspected habitat characteristics from aerial photographs and then we assessed each transect in the field prior to to surveys.

Transects were 1 km long and located in rural dirt roads 1.5–2 m wide with sporadic traffic in both motorway and control zones, to assure scat detectability and to reduce potential detection bias across environments (Gompper et al. 2006). Motorway transects were always parallel to motorway verges using dirt roads that run along the perimeter fence, and therefore no more than 50 m from the verge itself, and they were distributed along the length of the motorway. The minimum distance between transects in the same motorway was 3 km. When motorway transects were <4 km apart, we distributed them at different sides of the motorway to minimize the possibilities of home ranges overlapping 2 transects (Rosalino et al. 2004, Santos-Reis et al. 2005, Rondinini et al. 2006).

We surveyed relative rabbit abundance in spring 2011 and 2012. To obtain a measure of rabbit abundance, we evenly distributed 10 plots of 0.5 m^2 along each transect and counted the rabbit pellets within the plots, avoiding latrines to prevent bias (Fernandez-De-Simon et al. 2011). We calculated the index value as the sum of all pellets counted in each transect.

We estimated a carnivore abundance index as the number of scats detected in each transect (Long et al. 2008). During 1 month in spring 2011 and 2012, the same 2 observers walked together along transects, one on each side, and recorded all carnivore scats. Scat density can be used to estimate carnivore densities over large spatial scales (Webbon et al. 2004), thus making it a good index to compare abundances. This index also served as a measure of carnivore activity; zones used more by carnivores for hunting will contain more scats (Piñeiro and Barja 2015). We performed surveys during spring to avoid summer high temperatures that cause rapid degradation of scats and growth of seasonal vegetation, and to avoid winter snow cover (Heinemeyer et al. 2008).

We assigned each scat to a species based on morphological characteristics based on previous field experience of the observers and the field guide of Blanco (1998). When the identification was not clear, or there was no consensus between the 2 observers, we classified the scat as unidentified carnivore.

Carnivore roadkills.— We estimated a carnivore roadkill index for the 1-km stretch of motorway closest to each motorway transect for the species detected in the abundance survey. We obtained data on carnivores killed by vehicles from a database of carnivore carcasses and a complementary monthly survey. The database was provided by the company responsible for the management of the motorways and it contained all the recorded casualties from 2007 to 2011 (Abertis Autopistas España S.A, Barcelona, Spain, unpublished data). As this database only included carcasses that needed to be removed to maintain good traffic conditions (Spanish law 8/1972), we conducted an additional survey once a month during 2010 and 2011 to complement the dataset with roadkilled individuals not detected by motorway workers. We conducted this survey by car, driving at low speed (30 km/h), with 1 driver and 1 observer recording the location and species of all the detected carcasses. Because carcasses have low detectability (Santos et al. 2011) and the number of carcasses in a single km are low, we computed the roadkill index as the sum of all the carnivore carcasses recorded from the database and the survey along the 5 years for analytical purposes.

Data Analyses

We analyzed our data as the global carnivore community response, and then we divided the global community into 2 groups based on expected behavior of the species and the results of our DNA analysis (see below). One group included the most synanthropic species, the red fox, and the other group included the rest of species, which were less associated to human resources (i.e., non-synanthropic species). The group of non-synanthropic species included mustelids (e.g., stone marten and badger), wildcats, and unidentified data. We opted to include unidentified data here because this is a heterogeneous group and there is a high probability that unidentified scats belong to these species because red fox scats were clearly detected (see below).

To assess the accuracy of scat identification, we conducted DNA analysis of a subsample of 40 fresh scats (Long et al. 2011), following a protocol specifically designed for carnivores of the Iberian Peninsula (Fernandes et al. 2008). In our subsample, the DNA results for red foxes were consistent with morphological identification (100% accuracy), but for stone martens, we detected some inconsistency with field identification, pointing to other mustelids and also foxes, with <50% accuracy at the species level; this is common for mustelids (Davison et al. 2002; Table S1, available online in Supporting Information). Therefore, we opted to analyze the fox data and group all the others to make results as reliable as possible.

Carnivore response to rabbit abundance.— We first analyzed differences in rabbit abundance index between motorway and control sites using generalized liner mixed models (GLMM) with a Poisson error structure and log link. Then, we analyzed changes in carnivore abundances related to the index of rabbit abundance and the transect (motorway or control site) also using GLMMs with Poisson error structure and log link. In both analyses, we included the identity of the transect and the year as random factors to avoid pseudoreplication and differences in numbers due to interannual variability, respectively.

For the carnivore GLMMs, we first tested the significance of the interaction between transects (next to motorway or control zone) and rabbit abundance using log-likelihood tests for nested models (Zuur et al. 2009). The interaction was not significant, thus we removed it from the model and we present the results of an additive model. We checked residuals and the dispersion parameter of the Poisson models for model fit (Zuur et al. 2013).

Relationship between rabbits, carnivores, and roadkills on motorways.— For this analysis, we focused only on the motorway transects, and we further evaluated if the abundance of rabbits had a cascading effect on carnivores, increasing their abundance and therefore their mortality by vehicles. Because we had only 1 value of roadkill index for each motorway stretch (see above), we computed the mean rabbit abundance and the sum of carnivore abundance index obtained during the 2 years of sampling for every transect to make the data comparable.

For the global carnivore community, we tested the cascading effect by path analyses, a modeling technique included in the more general term of structural equation modeling (SEM; Sokal and Rohlf 2012). Path analysis allows testing for linear relationships between variables, with the advantage of including indirect effects mediated by a third variable or mediator (Kline 2005, Hoyle 2012). In our case, the mediator variable was carnivore abundance, following the hypothesis that rabbit abundance affects carnivore mortality as a consequence of an increased carnivore abundance in motorway verges. We used the Satorra-Bentler robust estimators, recommended for small sample sizes, to account for non-normality of the variables (Kline 2005, Hoyle 2012). We confirmed the correct global adjustment of the SEM analysis by several recommended indices: Joreskog's goodness of fit index (GFI), root mean square error of approximation (RMSEA), and the Tucker–Lewis index (TLI) (Schermelleh-Engel et al. 2003, Garrido et al. 2005, Hoyle 2012).

For the analyses of the synanthropic and non-synanthropic species, the datasets were not large enough to obtain reliable results from the path analyses. Instead, we used a more conservative approach and tested the responses of abundance of each group (fox or other) to rabbit abundance and roadkill numbers to group abundance (only including roadkills of group species) using generalized linear models (GLMs) with a Poisson error structure and a log link. We checked model assumptions using the residuals (Zuur et al. 2009).

We used a threshold significance of $P > 0.05$. We conducted all analyses in R 3.3.3 (R Core Team 2017). We used lme4 package for GLMMs (Bates et al. 2015), and lavaan package for path analyses (Rosseel 2012). All the results are presented as mean ± standard error, unless otherwise indicated.

RESULTS

The mean rabbit abundance index was 148.06 ± 29.43 pellets (range = 0–597) in motorways and 52.78 ± 11.32 pellets (range = 0–303) in control transects. Although some motorway transects had the highest values of the index, the GLMM analysis did not reveal significant differences between control and motorway transects ($\beta = 0.49 \pm 0.56$, $P = 0.384$).

Carnivore Response to Rabbit Abundance and Transect Location

We found 868 carnivore scats: red fox (45%), mustelids (26.9%; 24% stone marten; 2.3% Eurasian badger; 0.6% least weasel), *Felis* spp. (wildcat and domestic cat; 3.5%), *Canis* spp. (Iberian wolf and domestic dog; 0.6%), and unidentified carnivores (24%). We did not detect scat of American mink, European otter, European polecat, or common genet. The distribution of the raw data in each transect type followed the same pattern for almost all the taxa, with higher mean values in motorways than in control sites (Fig. 2). Global carnivore abundance increased with rabbit abundance ($\beta = 0.103 \pm 0.044$, $P = 0.019$) and carnivore abundance was higher in motorway transects than control sites ($\beta = 0.400 \pm 0.175$, $P = 0.022$).

The red fox showed higher abundance in motorways ($\beta = 0.469 \pm 0.197$, $P = 0.017$) but no significant response to rabbit abundance ($P = 0.129$; Fig. 3). The non-synanthropic species showed the opposite response, with abundances positively related to rabbit abundance ($\beta = 0.119 \pm 0.044$, $P = 0.007$) but no differences in abundance due to the proximity of the motorway ($P = 0.084$; Fig. 3).

Cascading Effects: Rabbit Abundance, Carnivore Abundance, and Roadkills

In our 18 motorway stretches, 86 carnivore casualties were detected (57% red fox, 15% stone marten, 6% *Felis* spp., 20% *Canis* spp., and 2% unidentified carnivores). Among motorways, in the 6 km that were surveyed for this study, we found 13 roadkilled carnivores in AP-61, 28 roadkilled carnivores in AP-51, and 45 roadkilled carnivores in the high traffic motorway AP-6. In the associated carnivore transects in AP-61, AP-51 and AP-6, we found 118, 145, and 271 scats, respectively.

In the analyses for the global carnivore community, roadkills were positively and significantly associated with carnivore abundance ($\beta = 1.073 \pm 0.238$, $P < 0.001$), although the carnivore abundance regression on rabbit abundance was only marginally significant ($\beta = 0.311 \pm 0.169$, $P = 0.066$; Fig. 4A). In the analyses of the synanthropic and non-synanthropic species (Fig. 4B), the red fox showed a pattern similar to the global community, with no relation between rabbit abundance and fox abundance ($P > 0.05$), although there was a positive relation between fox abundance in verges and fox roadkills ($\beta = 0.052 \pm 0.022$, $P = 0.019$). The non-synanthropic species, however, showed a cascading effect of rabbit abundance in their roadkill rates. In the transects next to the motorway, there was a positive association between rabbit abundance index and abundance of these carnivores ($\beta = 0.062 \pm 0.031$, $P = 0.048$) and roadkill numbers increased with carnivore abundance ($\beta = 0.092 \pm 0.030$, $P = 0.002$).

DISCUSSION

At the landscape level, when comparing motorway verges to control sites of similar characteristics, we found 2 different responses. The most synanthropic carnivore, the red fox, was more abundant in motorway verges with no apparent relation to prey abundance. However, the rest of carnivores did not show preference for motorway verges, but their abundances were related to those of the prey. At a local scale and focusing only on motorway verges, higher abundances of carnivores in these areas are translated into higher roadkill numbers. For carnivores related closely to prey abundance, high prey abundance in verges creates a local cascading effect that leads to carnivore roadkills.

The increased abundance of the global carnivore community near motorways is probably due to higher fox abundance in these areas, as foxes comprised almost half of the data. The increased fox abundance is consistent with other studies that found similar patterns of abundance or activity within 1 km of the motorway (Ruiz-Capillas et al. 2013*a*). Our results confirm this pattern and extend it to the landscape because control sites were outside the home range of individuals using the motorway. Thus, the alteration created by the motorways seems to be enough to modify the distribution of this wild species in the landscape.

The higher fox abundance near motorways is not explained by rabbit abundance. The attraction of foxes to motorways may be due to a combination of various factors. The red fox is an opportunistic synanthropic species with an ability to exploit human food resources (Crooks 2002, Baker et al. 2007, Bino et al. 2010). With more frequent visits to the motorway verges, foxes can find waste and garbage to feed on, along with carrion provided by roadkills (Clevenger and Wierzchowski 2006). Additionally, even if prey abundance is not higher, some carnivores may prefer to hunt near motorways (James and Stuart-Smith 2000), because prey in disturbed areas may be less aware of the predators and less perceptive of the predation risk, thus making them easier to hunt (Barbosa and Castellanos 2005, Chan et al. 2010). Finally, apart from the population of rabbits, there may be other prey, like mice, living in the verges (Ascensão et al. 2012, Ruiz-Capillas et al. 2013*b*).

On the other hand, our group of non-synanthropic carnivores followed a different pattern. These carnivores neither selected nor avoided motorways. Rather, carnivore densities were related to rabbit abundance. Rabbits are a key prey species in Mediterranean ecosystems (Delibes-Mateos et al. 2008*a*), and thus, when rabbits are distributed across the landscape, carnivores that prey on them will follow rabbit distribution. In our study area, control sites had similar characteristics to motorway sites, including vegetation structure. In this situation, rabbits are not expected to present higher densities in motorway verges because they have more habitat at their disposal farther from roads (Planillo and Malo 2013). The similar rabbit densities in both motorway and control sites could explain the similar carnivore densities in both areas, with no apparent effect of the motorway.

When we focused on road surroundings, we found a strong relationship between carnivores and prey may, which may lead to a cascading effect that could be local (our study) or potentially extend over the landscape in other situations. In landscapes where rabbits are especially abundant near roads, carnivores may select those areas over more natural ones (Bautista et al. 2004, Barrientos and Bolonio 2009), and abundance of carnivores in verges is related to their roadkill numbers.

The non-synanthropic group was very heterogeneous and partially contaminated with fox data, as shown by DNA analysis, in which a majority of scat misidentifications belonged to fox and, probably, some unidentified scats (DNA results, above and Table S1 in online Supporting Information). This means that the prey response of the non-synanthropic carnivores group is probably stronger than the one detected because fox densities were not affected by prey.

Finally, the higher abundance of foxes near roads that we found could not be explained solely by the edge effect. Other studies have related the abundance of carnivores in verges to the edge effect created by motorways and the behavior of the species. Carnivores may use roads as home range boundaries and thus, visiting them often to mark and prevent other individuals entering their territory (Riley et al. 2006, Grilo et al. 2012). In our case, we carried out our survey in a modified landscape, with transects located between patches of different habitats in motorways and control sites. Therefore, edge effect is expected to be similar in both conditions. Additionally, carnivores may use the dirt roads used for transects in control sites as home range boundaries and mark them often (Güthlin et al. 2012).

A caveat to be considered in the interpretation of our results is the ability of scat counts to reflect actual difference in abundance among sites. Indirect abundance indices, such as sign surveys, may potentially provide biased estimates of population densities and they should be used carefully (Birk et al. 2004, Monterroso et al. 2013). One of the main issues is the misidentification of scats in the field (Davison et al. 2002, Harrington et al. 2010), which we controlled for by conducting DNA analysis to assess the accuracy of scat identification. We controlled for other potential sources of bias by choosing areas that were comparable in habitat characteristics, which can affect fecal persistence and scat detectability (Long et al. 2008, Monterroso et al. 2013). When those factors are taken into account in the design, the reliability of scat counts as abundance index have been demonstrated for several species, including red fox (Webbon et al. 2004), badger (Tuyttens et al. 2001), and wildcat (Lozano et al. 2013). In a similar way, pellet counts for rabbits are a good estimator of population abundance (Palomares 2001, Fernandez-De-Simon et al. 2011). Also, the strong relationship found between roadkills and scat counts provides evidence that the number of scats is positively related to the number of individuals. Thus, the number of scats found should show actual abundance differences between compared sites.

Our results highlight the response of carnivores to roads, either by direct selection of these features or mediated by prey abundance. Because resource availability is one of the main influences in carnivore habitat selection (Barbosa and Castellanos 2005, Boitani and Powell 2012), we recommend that any resource that may be selected by carnivores around roads should be carefully examined and minimized as much as possible, to prevent an increase in mortality rates in wild populations that may be caused by traffic. Although we have no data on population trends of carnivores in our study area, we would like to invoke the precautionary principle and we believe that any danger that increases mortality risk for carnivores should be considered carefully and studied in detail from a conservation point of view. Roadkills are among the main causes of human-induced mortality for several carnivore species, including foxes (Takeuchi and Koganezawa 1994, Snow et al. 2012), black bears (*Ursus americanus*; Brandenburg 1996), Iberian lynx (*Lynx pardinus*; Ferreras et al. 1992), panthers (*Puma concolor*; Maehr et al. 1991), and badgers (Clarke et al. 1998), and compromise the survival of populations and the success of reintroduction programs (Kramer-Schadt et al. 2004, Ceia-Hasse et al. 2017). Many studies show that the use of anthropogenic resources in disturbed areas by opportunistic carnivores, such as foxes, coyotes (*Canis latrans*), raccoons (*Procyon lotor*) or bears, usually is associated with increased mortality (Gosselink et al. 2007, Beckmann and Lackey 2008, Bateman and Fleming 2012, this study).

Although high abundance of a species may appear positive, if it is associated with high mortality rates, it may be indicative of a population sink (Battin 2004, Nielsen et al. 2006, Beckmann and Lackey 2008, Falcucci et al. 2009). Studies on long-term population effects are necessary to make informed management decisions that favor conservation objectives. Understanding wildlife responses to human-modified landscapes provides us with better knowledge of the communities and identifies which processes should be the focus of our conservation efforts.

MANAGEMENT IMPLICATIONS

When prey are abundant near motorways, carnivores increase their abundance in those areas. Higher abundances of carnivores were strongly related to higher mortality by vehicles. Therefore, the design and management of verges could be a key aspect for conservation of wild populations. When carnivore species are of conservation concern, the availability of any food resources in road verges should be minimized to avoid attraction of carnivores. A measure that could benefit many carnivores would be to avoid dense prey populations by making road verges unattractive to small-mammal species. Another measure is the implementation of better perimeter fences that are not permeable to mesopredators and that prevent carnivores to enter the road, combined with proper wildlife passages that avoid fragmentation.

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FIGURES

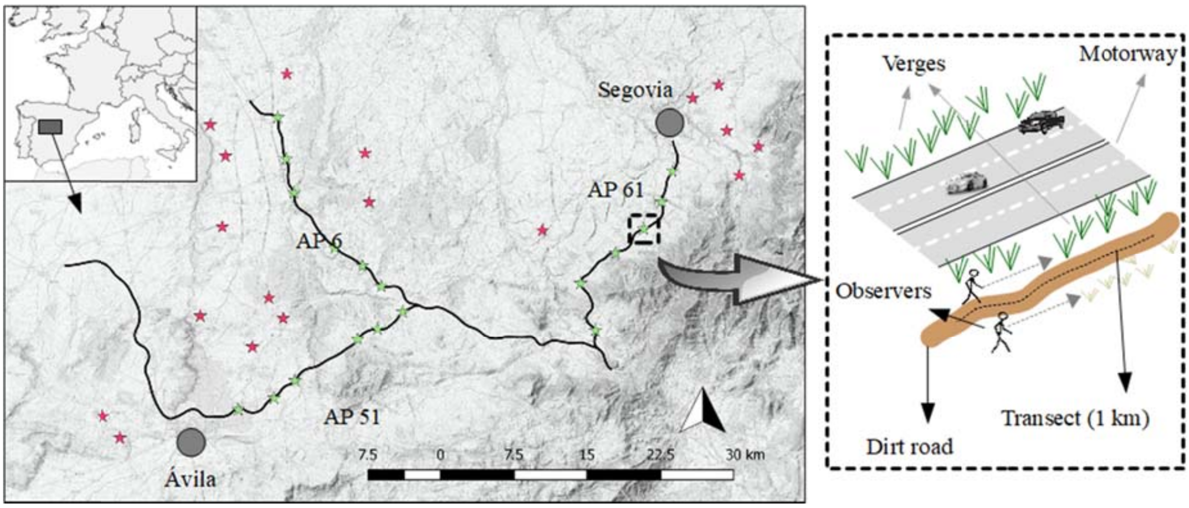

Figure 1. The location of the study area in Spain is highlighted in the small square at the top left. In the map, stars show the location of sampling transects for carnivore and rabbit surveys carried out in spring 2011 and 2012; green stars are motorway transects and red stars are control transects. Motorways are marked as black lines. In the right square there is a detailed scheme of a typical motorway transect, control transects being the same but without the motorway.

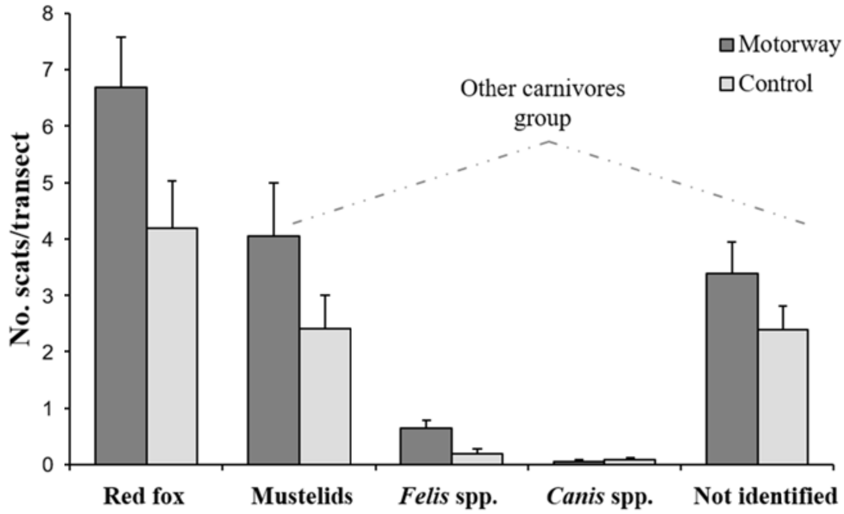

Figure 2. Carnivore scats detected for each taxon in motorway and control transects (mean + SE) in central Spain during spring 2011 and 2012.

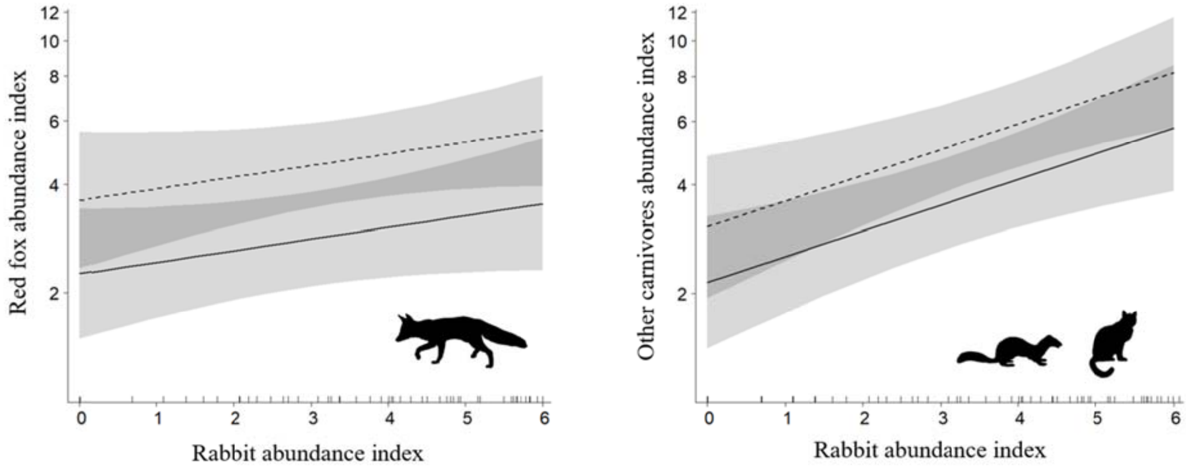

Figure 3. Fox response to rabbit abundance in motorway and control sites in central Spain, 2011-2012, with a significant effect of the location of the transect (left) and other carnivores (all carnivores but foxes) response to rabbit abundance in motorway and control sites, with significant effect of the rabbit abundance (right). Continuous lines represents control sites and dashed lines represents motorways. Shadowed areas represent the confidence intervals; the light grey area is the confidence interval of the model line in the center and the dark grey area represents the area where confidence intervals overlap.

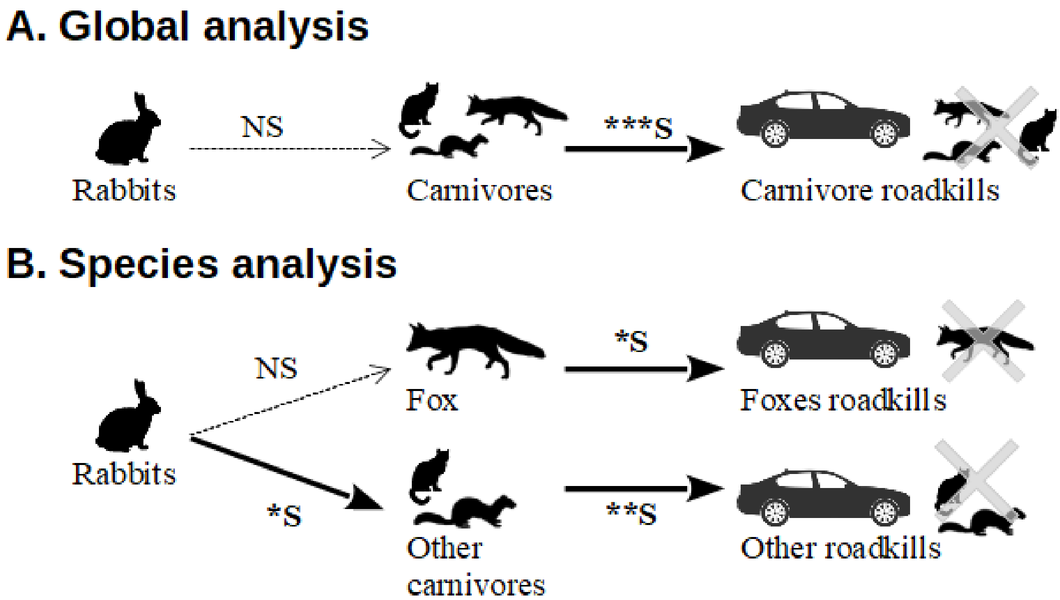

Figure 4. A) Path analysis for global data, showing a significant effect of carnivore abundance on carnivore roadkills, and non significant effect of rabbit abundance on total carnivore abundance. B) Analyses of the effect of rabbit abundance on foxes and other carnivores and carnivore abundance on their roadkill numbers. Data from central Spain; roadkill numbers were obtained from roadkill monitoring in 2007-2011. Abundances were estimated in 2011-2012. Each relationships is marked as NS (not significant) or S (significant; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Table 1. Carnivore species present in the study area with their conservation status in Spain.

English name	Scientific name	Family	IUCN-Spain conservation status
Iberian wolf	*Canis lupus signatus*	Canidae	Near Threatened
Red fox	*Vulpes vulpes*	Canidae	Least Concern
Least weasel	*Mustela nivalis*	Mustelidae	Least Concern
European polecat	*Mustela putorius*	Mustelidae	Near threatened
American mink	*Neovison vison*	Mustelidae	Least Concern (introduced)
Stone marten	*Martes foina*	Mustelidae	Least Concern
Eurasian badger	*Meles meles*	Mustelidae	Least Concern
European otter	*Lutra lutra*	Mustelidae	Least Concern
Common genet	*Genetta genetta*	Viverridae	Least Concern
Wild cat	*Felis silvestris*	Felidae	Near threatened
Dog	*Canis familiaris*	Canidae	Domestic / Feral
Cat	*Felis catus*	Felidae	Domestic / Feral

Summary of conclusions and management implications

Red fox, a synanthropic carnivore, selected motorways in the landscape in Spain, whereas non-synanthropic carnivores responded to prey abundance. When prey densities were high in motorway verges, carnivore densities increased, increasing the number of carnivores killed by vehicles. Minimizing food resources in motorway verges may prevent carnivore mortality from vehicles.