Biodivers Conserv (2009) 18:405–418
DOI 10.1007/s10531-008-9499-9

ORIGINAL PAPER

The presence of rabbits adjacent to roads increases polecat road mortality

R. Barrientos · L. Bolonio

Received: 17 December 2007 / Accepted: 26 September 2008 / Published online: 15 October 2008

Abstract Road mortality is an increasing problem for terrestrial vertebrate conservation due to the increase of both road numbers and vehicle flow. We hypothesize that the probability of a predator being killed on the road is related to the presence of its prey adjacent to the road, which is likely to be related to the use that these predators make of road verges. We aim to identify the features of specific stretches of road where road-kills of a predator (European polecat) occur in Mediterranean landscapes, including the presence of its main prey (European rabbit) and landscape and road features. We compared 85 100 m long stretches of road where at least one road-kill was recorded with 104 stretches without any road-kill in a dry agricultural landscape in central Spain. We used regression analysis to investigate the relationship between road-kill occurrence and the features in the 67% of the cases. Road-kill stretches were characterised by greater numbers of rabbit burrows in the road verges and by higher traffic flow and speed (i.e. higher speed limit, lower proportion of heavy vehicles, wider road and lower proportion of unbroken central lines). Road-kill stretches also had more metres built over bridges and lower densities of people. We validated our best model with a dataset (the 33% of the cases) not included in its development, which correctly classified 82% of road-kill stretches and 89% of non-road kill stretches. Our results highlight the need for taking into account food resource distribution when studying causes of animal road-kills.

R. Barrientos (✉)
Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas, CSIC, General Segura 1, 04001 Almeria, Spain
e-mail: barrientos@eeza.csic.es

L. Bolonio
Grupo Ornitológico Alcedo, Facultad de Biología, Universidad de Alcalá de Henares, N-II, km. 36.5, 28871 Alcala de Henares, Madrid, Spain
e-mail: luis.bolonio@terra.es

Keywords Carnivore conservation · *Mustela putorius* · *Oryctolagus cuniculus* · Resources distribution · Road verge · Traffic · Unbroken line

Abbreviations

AIC	Akaike information criterion
AICc	Corrected Akaike information criterion
IGN	The Spanish national geographic institute
PC	Principal component
PCA	Principal component analysis
UTM	Universal transverse mercator coordinate system

Introduction

Carnivores are commonly identified as species whose conservation is more difficult to guarantee due to their highly demanding habitat requirements (e.g. Ginsberg 2001). Present-day conservation strategies for carnivores focus on the integration of these species into multi-use landscapes dominated by people (Linnell et al. 2000; Iuell et al. 2003). Roads cause one of the most important anthropogenic impacts on wildlife communities and, as the cause of direct mortality, may reduce dispersal and reproductive or colonization events (reviewed in Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000; Forman et al. 2003). Even without road mortality, roads can cause barrier effects. For example in a study with another mustelid species, the badger (*Meles meles*), Clarke et al. (1998) found that high traffic loads may discourage badgers from attempting to cross major roads. Similar findings have also been found for other species (reviewed in Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000; Forman et al. 2003). However, roads can increase the foraging opportunities for predators through the availability of road-kill carrion (reviewed in Little et al. 2002). We hypothesize that prey availability in road verges can increase the fatality risk for predators. We tested this hypothesis with a study of the European polecat (*Mustela putorius* L.) and its main prey in several ecosystems, the European rabbit (*Oryctolagus cuniculus* L.).

The polecat is a small carnivore widely distributed in Europe where it remains in low densities throughout most of its range, particularly in the Mediterranean peninsulas (Mitchell-Jones et al. 1999; Marcelli et al. 2003; Virgós 2003; Virgós et al. 2007b). For several decades, the species has undergone a serious decline in population levels throughout the majority of its distribution. This decline has been caused by a combination of factors, some human related (i.e. hunting, road-kills), but competition with alien species, hybridization processes or low effective population sizes have also been implicated (Blandford 1987; Davison et al. 1999; Mitchell-Jones et al. 1999; Sidorovich 2000; Lodé et al. 2003). Recent status assessments in some parts of Europe have suggested that the polecat has declined or is at unfavourable conservation status (see Virgós et al. 2007b for the Iberian Peninsula). Consequently, it is currently listed on Annexe V of the EC Habitats and Species Directive and Appendix III of the Bern Convention. In Spain, the polecat was recently listed as “almost threatened” (Virgós et al. 2007b).

It has been suggested that uncultivated landscapes are important habitat resources for carnivores in the inhospitable agricultural ecosystems as they provide protection and connectivity among suitable habitats (Virgós 2001). The pattern of use of road verges by polecats is unclear as Blandford (1987) suggests that polecats make frequent use of this habitat, whereas Rondinini et al. (2006), contrary to their own prediction, found that road verges were used by polecats in proportion to their availability. Habitat use by polecats is dependent on habitat structure and food dispersion, visiting prey-rich habitat patches most frequently (Lodé 1994; Baghli et al. 2005; Zabala et al. 2005; Rondinini et al. 2006; Mestre et al. 2007). In agricultural landscapes, roadside vegetation is commonly more developed than surrounding fields as vegetation growth is promoted by water running off the road into the ditch (review in Forman et al. 2003). In addition, roadside vegetation is rarely harvested (Bellamy et al. 2000). Thus, if we assume that vegetation requirements of polecats could be met by roadside strips, the probability of road-kill, mediated by the use of roadsides by polecats, may depend on the presence of their prey. Rabbits, which commonly place their warrens in road ditches (authors, personal observation), are the main prey for polecats in several habitats, especially in Mediterranean ones (Roger 1991; Lodé 1997; Schröpfer et al. 2000).

Road mortality has been implicated as one of the major factors preventing the maintenance of healthy and stable populations of polecats in Mediterranean landscapes (Virgós et al. 2007b). In other geographic regions, where the ecology of the polecat is better known, road fatalities are also a major cause of polecat deaths (Blandford 1987; Birks 1997; Mitchell-Jones et al. 1999; Lodé 2003; Kristiansen et al. 2007). Despite these findings and that road-kills seem to be concentrated along certain stretches of road (Blandford 1987), no studies have analysed habitat and road-related variables at specific locations where road-kills occur. Road mortality patterns in small animals seem to be species-specific (Clevenger et al. 2003). However there is a general paucity of knowledge regarding the relationship between road features and small-animal fatalities (Ginsberg 2001). Traffic characteristics and road features play an important role in road-kills. For instance, the probability of road-kill mortality increases with both traffic volume and speed (Van Langevelde and Jaarsma 2004). However, some road effects such as barrier effects can adjust the level of mortality. For example Clarke et al. (1998) found that roads with high traffic loads have proportionately fewer badger road-kills due increased avoidance of these roads by the badgers. Unfortunately, this complex relationship is hard to capture without radio-tracking studies. Road width is another important feature, animals needing more time to cross wider roads, leading to a decrease in the probability of a successful crossing (Van Langevelde and Jaarsma 2004). This is particularly important for small animals (review in Forman et al. 2003). However, few of the studies that have focused on small vertebrates have analysed road-kill in detail at specific points where road-kills have occurred in order to develop predictive models of fatalities (but see Saeki and Macdonald 2004; Ramp et al. 2005, 2006).

The aim of our study was to identify the features of specific stretches where polecat road-kills occur and to provide the basis of a strategy to prevent this mortality. Specifically, we focused our research on three basic characteristics: (1) The presence of prey near the road. In our study area, rabbits make up the bulk (mean 43.6% year-round) of polecat diet by biomass (Cuesta 1994). Consequently, we expected road-kills to be associated with those stretches of road where rabbits were more abundant. (2) Roadside vegetation. Polecats are expected to make greater use of vegetated patches (Lodé 1994; Baghli et al. 2005; Zabala et al. 2005; Rondinini et al. 2006) and consequently the number of road-kills is expected to be positively associated with greater amounts of vegetation. (3) Road and traffic characteristics. We expected that stretches of road with higher speed limits and traffic volume would be linked with larger numbers of polecat road-kills (Van Langevelde and Jaarsma 2004).

Materials and methods

Study area and road kill survey

This study was carried out in the Tajo valley, Toledo province, central Spain, from August 2002 to July 2004. The Tajo basin ranges between 350 and 850 m in altitude. The climate is Mediterranean and during the study period annual rainfall averaged 340 mm. The average daily maximum temperature was 27.1°C (August) and the minimum 3.6°C (December). The dominant land cover is dry crops such as cereals, fallow and olive fields (altogether dry crops cover the 54.6%). The remaining land cover consists of irrigated crops (mainly maize fields) (2.1%), urban areas (10.1%) and non-cultivated land (33.2%) (dominated by scrubland composed of *Retama sphaerocarpa* and *Stipa tenacissima*). The study area was bounded to the North by motorway N–V (40°02′N, 04°26′W), by the city of Toledo (39°51′N, 04°01′W) to the East, by the Montes de Toledo mountain range (39°35′N, 04°37′W) to the South and by the roads CM-4015 and CM-4102 (39°48′N, 04°38′W) to the West. The extent of road development and traffic flow in the study area can be considered to be representative of that found in most of central Spain.

We surveyed polecat road-kills on all of the two-lane paved roads in the study area using a car. These roads total 246 km divided into two routes of 121 and 105 km. The number of surveys conducted was 41; two surveys per month except for 7 months when we could only carry out one survey. Thus, the total distance covered was greater than 10,000 km.

The survey was conducted by two observers. Whilst one drove at 40–50 km/h, the other looked for carcasses on the road surface. Polecats were often found in the middle of the road, although we cannot discount that some of the animals killed in the centre of the road were moved to the ditch at the side by motorists or just by the crash. To assess the degree to which we overlooked carcasses in the ditches, we randomly surveyed over 100 km of verges on foot, along all the road classes. We found only two polecat carcasses not detected by the previous vehicle survey. Despite surveys done by foot being more reliable, surveys were conducted by car as much larger distances could be covered. Furthermore, the probability of missing carcases in our car surveys was likely to be constant across the study area. All the carcases were removed from the road surface in order to avoid double counts. Undercounting of carcases due to removal by scavengers was likely to be negligible as the only scavenger common in the area is the magpie (*Pica pica*) which is not able to remove polecat carcasses. As such, we could monitor for months some carcasses at identifiable locations.

We divided the two sampling routes into 100 m stretches each delimited by two hectometre posts. To select random stretches for their inclusion in the dataset, we chose at random one stretch in every 20, discarding those with road-kills. Thus, if no polecat was found during any survey in a selected stretch, this was considered to be a "non-road-kill stretch" and it was included in the dataset. The stretches where we found any road-kill were considered "road-kill stretches". Although sampling was not paired, non-road-kill stretches were distributed along the study area in proportion to the total length of every road type. Overall, we randomly chose 104 non-road-kill stretches in order to compare their characteristics with those of the 85 stretches where at least one road-kill was recorded. Before constructed the model, we randomly divided the whole dataset into two, one made up of 126 cases (57 road-kill stretches and 69 without them) to use to develop the models. The second dataset was composed of 63 cases (28 road-kill stretches and 35 without them) and was used to validate the models.

Variables associated with road-kills

Landscape variables were assessed within a circular area based on the central point of the road section and extending 50 m along roadside on either side of the road. This scale was chosen as we started on the premise that rabbit presence is a key factor determining the use of road verges by polecats and therefore it will also affect the probability of polecats being killed on the road. The chosen scale for landscape variables matches the size of rabbit home ranges in Mediterranean habitats, which is about one hectare (Lombardi et al. 2007). The presence of fresh rabbit carcases can be another important factor attracting polecats on to roads (Birks and Kitchener 1999). As such, it is worth mentioning that rabbit carrion reached up to 1.2 carcases/km and survey on some stretches during our study (Authors, unpublished data). It is worth mentioning that the landscape composition is quite homogeneous at small scales as the area is dominated by extensive agriculture and non-cultivated lands and that no changes in agricultural use were detected while carrying out the study. This size of buffer zone also matched the 100 m measurement unit used for the road-related variables. Data obtained from a stretch of road where road works occurred during the study were excluded from the datasets. Following similar criteria to Ramp et al. (2005), variables were selected for inclusion in the models when they were known from literature to be related to animal fatalities, to be resources used by polecats or when they were management variables not specific to our study area (see Table 1 for variables studied and their definitions). Thus, variables such as dry fields, non-cultivated land or other land use types were incorporated in order to investigate the potential influence of landscape on polecat mortality through variable resource distribution effects (e.g. foraging, protection). The number of rabbit burrows and the distance from the road to the nearest burrow were used as measurements of the local abundance of rabbits. The study area is mainly deforested, probably leading to polecats to concentrate their movements in those patches with greater amounts of vegetation, especially riverbanks (Zabala et al. 2005; Rondinini et al. 2006; Mestre et al. 2007). To test for such a vegetation effect on road-kills, we included the percentage of woody vegetation cover and the distance to the nearest stream as model variables. The distance to the nearest house and town were used as proxies for human encroachment (i.e. greater presence of humans in the field, intensification of agricultural practices, alteration of ecosystems, pollution, etc.). Vehicle speed and traffic flow rate can affect the likelihood of collisions with animals (Malo et al. 2004; Van Langevelde and Jaarsma 2004; Seiler 2005), and we therefore included the speed limit, percentage of heavy vehicles, road width, percentage of unbroken line (where overtaking is forbidden) and traffic intensity as model variables. The lengths of sections of road with embankments, going over bridges and the distance to the nearest non-wildlife underpass (mainly culverts) were also included to control for the potential influence of structures which may funnel or facilitate animal movements at particular crossing points (Yanes et al. 1995; Malo et al. 2004). Finally, we included road class as a categorical factor, encompassing a range of road traits. This categorical variable consisted of first or second class roads, based on the autonomous govern classification of the two-lane paved roads. The characteristics of first class roads, measured in 63 random 100 m long stretches, were (mean $\pm$ SE): 10.2 $\pm$ 0.1 m for road width, 43.2 $\pm$ 4.6% unbroken line and a road surface of generally good quality. In contrast, second class roads, measured in 41 random stretches, were narrower (6.5 $\pm$ 0.2 m), had more stretches with bends (i.e. higher percent of unbroken line: 49.6 $\pm$ 6.6%) and had road surfaces of lower quality. We initially included variables that were likely to be correlated as an attempt to incorporate the best set of predictors in the models. However,

Table 1 The variables measured in each 100 m stretch used to study the factors that differentiate stretches with polecat road-kills from those without them

Variable	Definition
Landscape local-scale variables	
DRY	% Cover of dry crops within a radius of 50 m around both sides of the road
NON_CULTIV	% Cover of non cultivated lands within a radius of 50 m around both sides of the road
OTHER	% Cover of other land uses within a radius of 50 m around both sides of the road
WOODY	% Cover of woody plants in within a radius of 50 m around both sides of the road
M_BURROW	Distance (m) to the nearest rabbit burrow on any side of the road
N_BURROWS	Number of rabbit burrows within a radius of 50 m around both sides of the road
Landscape large-scale variables	
TOWN	Distance (m) to the nearest town
HOUSE	Distance (m) to the nearest isolated house on any side of the road
RIVER	Distance (m) to the nearest river
Road-related local-scale variables	
SPEED	Speed limit on the stretch of road
TRAFFIC	Monthly mean number of vehicles per day along the stretch
HEAVY	Mean % of heavy vehicles per day along the stretch
WIDTH	Road width (m)
PASS	Distance (m) to the nearest non-wildlife underpass
EMBANKMENT	Total metres of embankments of > 1 m height and > 60° slope on both sides of the 100 m stretch
BRIDGE	Length (m) of the 100 m stretch built over bridges.
UNBROK_LINE	% of the length of the 100 m stretch of the road where overtaking is forbidden.
CLASS	Categorical variable: 1 first, 0 second class regional road

where correlation between variables was found we excluded the one with the least explanatory power (see "Statistical analyses").

Altogether 14 quantitative local-scale variables (six landscape and eight road-related; see Table 1 for their measurement units) and one categorical variable were used. The quantitative variables were counted, measured or scored visually (percentage of vegetation coverage) and always by the same researcher (R.B.). Traffic data were obtained from Junta de Comunidades de Castilla-La Mancha and Diputación de Toledo. We used the monthly mean for traffic variables. Finally, the three landscape large-scale variables were measured using a 1:50,000 topographic map of Spain, IGN, using the coordinates Universal Transverse Mercator coordinate system (UTM) of the mid-point of a stretch as its location.

Statistical analyses

Quantitative differences between stretches with and without road-kills were evaluated using unpaired *t*-tests (e.g. Seiler 2005) and Bonferroni step-down correction (Holm 1979). Tests were calculated using STATISTICA 6.0 (Statsoft 2003).

We used a Factor Analysis with Principal Component Analysis (PCA) and the Varimax normalized factor rotation to build a correlation matrix to explore the degree of association among variables. For the subsequent model development, and in order to minimize multicollinearity (correlations >0.6) among independent variables, we only included the most highly correlated variable with each of the PC factors, discarding the remaining variables. Due to the strong associations of the variables selected according to PCA factor loadings, seven variables were removed before the model process: NON CULT, OTHER, WOODY, N_BURROWS, HEAVY, WIDTH and PASS (Appendix 1). We included road type (i.e. first or second class) as categorical factor in our models. Before starting the modelling process, we randomly set aside 33% of the data (i.e. 63 cases, of which 28 were road-kill stretches and 35 were without road-kills) to use them for model validation. Therefore model development used 67% of the data (i.e. 126 cases, of which 57 were road-kill stretches and 69 were without road-kills). We conducted a regression analysis utilising a binomial distribution (road-kill versus non-road-kill stretches) and logit link function. We used the best subsets procedure and the Akaike's information criterion (AIC) to identify the set of models best explaining the occurrence of road-kills in the 126 cases. We used this technique because it yields consistent results independent of the order in which variables are included in the model and allows models with different numbers of parameters to be directly compared with each other (Burnham and Anderson 2002). We used AIC values corrected for small sample size (i.e. AICc) as the ratio between the number of observations and estimator variables was under 40 (Burnham and Anderson 2002). The models were developed using STATISTICA 6.0 and the AIC values were corrected with Microsoft EXCEL 2003 (Microsoft) following Burnham and Anderson (2002). The models with the lowest AICc represent the best compromise between a maximal fit and a minimal number of explanatory variables (i.e. statistical parsimony). To evaluate the relative explanatory power of competing best models, we calculated the Akaike weights (ω_i). The evidence ratio was calculated to compare the Akaike weights of the best model and competing ones to determine to what extent one was better than another (Burnham and Anderson 2002). In order to estimate the relative importance of every variable included in any of the best models we calculated the sum of Akaike weights of the models where these variables were included (Burnham and Anderson 2002). The significance of variables included in the best model was assessed using the log-likelihood ratio test because it is the most suitable for small sample sizes (Moya-Laraño and Wise 2007). Model validation using data not used in the model development was carried out using simple logistic regression (e.g. Seiler 2005).

Results

Road-kill pattern

A total of 107 polecat road-kills were recorded in 85 stretches (2 stretches with 3 casualties, 18 with 2 and 65 with only 1) over a period of 24 months. Differences between road-kill and non-road-kill stretches based on *t*-tests are shown in Table 2.

Road-kill stretches had significantly more rabbit burrows being the nearest one at shorter distance. These stretches also had higher speed limits and traffic intensities, but had lower frequencies of heavy vehicles. Road sections with fatalities were significantly wider and had lower percentages of unbroken line (i.e. were straight). Road-kill stretches were also closer to streams and had lower percentages of other land uses (e.g. urban, irrigated crops).

The regression procedure with the best subset analysis provided a set of 13 models which could be considered as plausible models according to their AICc (i.e. the difference between their AICc and the lowest one was less than two; Burnham and Anderson 2002). The six best models are shown in Table 3. Our results do not give clear support for a single model amongst these six, indicated by the small differences in AICc values and the comparable values of Akaike weights (Table 3). Importantly, however, all the models included M_BURROW, BRIDGE, SPEED and UNBROK_LINE (i.e. $\Sigma\omega_i = 0.5994$). Less influential were TRAFFIC ($\Sigma\omega_i = 0.05262$), HOUSE ($\Sigma\omega_i = 0.5174$), TOWN ($\Sigma\omega_i = 0.2994$) and

Table 2 The results for the unpaired *t*-tests (mean ± SD) comparing the 17 variables quantifying habitat and road-related features between road-kill and non-road-kill stretches

Variable	Non-road-kill stretches	Road-kill stretches	Unpaired *t*-test	
	Mean ± SD	Mean ± SD	*t*-value	*P*-value
DRY	49.14 ± 3.69	50.97 ± 3.75	0.35	0.7305
NON_CULT	32.12 ± 3.24	42.39 ± 3.49	1.94	0.0535
OTHER	18.75 ± 3.27	6.71 ± 1.80	−3.06	0.0275
WOODY	10.54 ± 1.54	11.45 ± 2.24	0.34	0.7315
M_BURROW	22.07 ± 0.75	9.53 ± 0.92	−10.68	<0.0001
N_BURROWS	3.02 ± 0.69	27.69 ± 2.74	9.54	<0.0001
TOWN	2475.96 ± 205.72	2518.82 ± 158.18	0.16	0.8735
HOUSE	272.12 ± 27.38	315.88 ± 31.27	1.06	0.2921
RIVER	437.50 ± 45.02	284.70 ± 39.15	−2.50	0.0133
SPEED	92.98 ± 12.53	99.53 ± 2.13	4.76	<0.0001
TRAFFIC	2445.66 ± 204.05	3847.08 ± 264.74	4.26	<0.0001
HEAVY	13.76 ± 0.81	9.46 ± 0.44	−4.34	<0.0001
WIDTH	8.75 ± 0.20	10.17 ± 0.10	6.09	<0.0001
PASS	91.40 ± 2.51	84.40 ± 3.36	−1.70	0.0902
EMBANKMENT	10.77 ± 3.46	20.12 ± 5.33	1.52	0.1301
BRIDGE	0.64 ± 0.35	0.88 ± 0.50	0.42	0.1301
UNBROK_LINE	45.72 ± 3.80	30.59 ± 3.87	−2.77	0.0062

The table shows the *P*-values with Bonferroni step-down correction (Holm 1979). See Table 1 for variable codes

Table 3 The set of six models that best separated stretches with polecat road-kills from those without them

Model no.	Variables contained in the model	*K*	ΔAICc (Δ_i)	AICc weight (ω_i)	Evidence ratio
1	M_BURROW + HOUSE + TRAFFIC + BRIDGE + UNBROK_LINE + SPEED	6	0	0.1461	0.00
2	M_BURROW + TOWN + HOUSE + TRAFFIC + BRIDGE + UNBROK_LINE + SPEED	7	0.0418	0.1430	2.11
3	M_BURROW + TRAFFIC + BRIDGE + UNBROK_LINE + SPEED	5	1.1552	0.0820	78.18
4	M_BURROW + TOWN + HOUSE + RIVER + TRAFFIC + BRIDGE + UNBROK_LINE + SPEED	8	1.2021	0.0832	82.40
5	M_BURROW + TOWN + HOUSE + BRIDGE + UNBROK_LINE + SPEED	6	1.3809	0.0732	99.47
6	M_BURROW + HOUSE + RIVER + TRAFFIC + BRIDGE + UNBROK_LINE + SPEED	7	1.4174	0.0719	103.13

The ΔAICc is the difference in AICc values compared to the estimated best model (lowest AICc) what allows the ranking of models from an estimated best (top of the table) to the worst. AICc weight is the estimated probability that a model is the best model in the set. Evidence ratio indicates to what extent one model is better than another

RIVER ($\Sigma\omega_i = 0.0832$). We selected model no.1 (Table 4) as the best one because it represents the best compromise between a maximal fit and a minimal number of explanatory variables. The log-likelihood ratio test suggests that the most important variable associated with the occurrence of polecat road-kills was the presence of rabbit burrows close to the roadside.

Table 4 The best model after regression analysis with best subset procedure following AICc criterion including the variables that best separated road-kill stretches from non-road-kill ones

Parameter	Estimate	SE	Log likelihood-χ^2	*P*
CONSTANT	−9.787977	7.109625		
M_BURROW	−0.144964	0.028240	35.272	<0.001
HOUSE	0.001590	0.000920	3.155	0.076
TRAFFIC	0.000257	0.000122	4.926	0.026
BRIDGE	0.410774	0.235557	3.899	0.048
UNBROK_LINE	−0.018162	0.007623	6.305	0.012
SPEED	0.115488	0.072240	5.346	0.021

Model validation

Simple logistic regression analysis was used to validate the predictive capacity of our best model (Table 4). The use of the independent dataset showed that the model correctly predicted 82.1% of road-kill stretches and 88.6% of non-road-kill ones. Thus, our model succeeded in distinguishing between the occurrence and non-occurrence of polecat road-kills.

Discussion

Our results highlight the need for taking into account the distribution of food resources when studying animal road-kills. The presence or abundance of resources near roads may determine the use that animals make of roadsides and this, in turn, may affect their road-kill rates. In our polecat–rabbit system, we obtained a model where the main feature of stretches where road-kills were recorded was the presence of the polecat's main prey next to the road, measured as the distance of the nearest rabbit burrow to the roadside. Higher vehicle speeds (i.e. higher speed limits and smaller percentages of unbroken line) and higher traffic flows were also associated with road-kill stretches. Road-kill stretches also had greater lengths over bridges and were farther from the nearest house. Our best model had a high success rate in predicting polecat road-kill stretches using the independent data-set (82–89% of cases correctly classified).

Rabbits make up the bulk of polecat diet in many, mainly Mediterranean, regions (reviewed in Lodé 1997; see also Birks and Kitchener 1999; Virgós 2002). These lagomorphs are mainly hunted by polecats in their warrens (Cuesta 1994), although they can be consumed as carrion as well (Birks and Kitchener 1999). Thus, a significant cause of polecat road-kills must be their hunting movements among rabbit warrens on roadsides, although other causes not identified here (seeking mates, dispersal, territory marking, etc.) could also be important sources of polecat casualties (e.g., see Sleeman 1988 for a study on stoats). There are three potential reasons for rabbits to establish warrens along roadsides: (1) Both in cereal crops and sandy uncultivated areas, rabbits build their warrens between tree and shrub roots, seeking protection against warren collapse by using the roots as supporting structures (Palomares 2003; Gea-Izquierdo et al. 2005). However, human activities have eliminated roots from fields for agricultural reasons and other warren supporting/protecting structures, such as granite rocks or walls, are scarce in the study area (Gea-Izquierdo et al. 2005). Building warrens inside road embankments could be an adaptation to avoid their warrens collapsing by using the embankments as supporting structures. (2) Ploughing destroys rabbit warrens (Calvete et al. 2004). Consequently, rabbits avoid cultivated crops as areas to place their warrens and positively select non-ploughed ecotones (e.g. road verges) (Calvete et al. 2004; Gea-Izquierdo et al. 2005). (3) The rabbits are important prey for almost 30 predator species in the Iberian Peninsula but the activity of several predators decreases near roads, particularly in cultivated landscapes (Virgós 2001; Bautista et al. 2004), suggesting that road verges could act as safer breeding zones for rabbits. This effect could be reinforced by the absence of shooting near roads, which is forbidden by law.

Although scarce, stretches of road built over bridges were prone to be black spots. There are three potential explanations that we suggest for this: (1) streams are important ecotones selected by rabbits to place their warrens (Calvete et al. 2004) and stretches of road built over bridges could be visited preferentially by polecats during hunting (Zabala et al. 2005). (2) Although it was discarded in the pre-modelling process (see Appendix 1), woody coverage was positively related to the lengths of sections over bridges, probably because the occurrence of riparian woodlands is a dominant component of vegetation coverage in agricultural deforested areas. Utilisation of riparian vegetation is an essential part of polecat movements in the agricultural matrix due to the protection it provides (Zabala et al. 2005; Rondinini et al. 2006; Mestre et al. 2007). (3) Once a polecat is trapped on a stretch of road that is difficult to exit (e.g. on a bridge), the animal will move in an erratic way along the section dramatically increasing its chances of being run over.

The role of different habitat types in species survival in relation to landscape structure (suitable amounts of habitat, connectivity among patches or the geometry of patches) is a topic under continuous debate (Andrén 1994; Gutzwiller 2002). In agricultural landscapes, where most of the natural habitat has been transformed, the residual semi-natural vegetation along rivers or road verges is a key tool in the conservation biology of many species, including carnivores (Virgós 2001). If this kind of habitat is large enough, the effect of habitat loss or fragmentation can be minimized (Andrén 1994; Gutzwiller 2002). The non-agricultural habitat patches distributed across the agricultural matrix is capable of maintaining high levels of biodiversity because it can provide abundant food through the edge effect, allows animals to forage close to vegetation cover safe from humans or predators (Macdonald 1995) and maintains the connectivity among suitable patches (Andrén 1994; Gutzwiller 2002). In fact, some prey species inhabiting agricultural landscapes are settling in non-arable patches, such as road verges (e.g. Bellamy et al. 2000). Thus, the location of prey may become more predictable, and these patches will be visited more frequently by predators, leading to a greater number of road-kills of the predator as seems to be the case in our polecat–rabbit system.

Road-kills occur along those stretches of road that support higher traffic densities and where vehicles go faster as predicted the traffic flow theory (Van Langevelde and Jaarsma 2004). Road-kills are predicted in our study by higher speed limits, a lower density of heavy vehicles (i.e. allowing faster driving), wider roads and a lower amount of unbroken line (i.e. straight stretches). An animal crossing is successful if an acceptable gap in the traffic flow appears at the start of the crossing (Van Langevelde and Jaarsma 2004). Traffic speed determines traffic mortality because lower vehicle speeds increase the probability of a successful road crossing as they provide both the driver and the animal with a greater amount of time to react and avoid road-kill (Van Langevelde and Jaarsma 2004). The polecat is a small mammal. About 1 kg in weight and a body length of 50 cm (Blandford 1987). This is the reason why it is rarely included in the field-of-view whilst driving at high speed. Furthermore, polecats are often crepuscular or nocturnal (e.g. Marcelli et al. 2003), so are active on roads when visibility for drivers is lower. Finally, the particular morphology of polecats, with short legs and a long body (Blandford 1987), likely adaptations to hunting rabbits in their warrens (Cuesta 1994), means that this species requires more time to cross a road, decreasing its probability of a successful crossing, particularly on wider stretches (Van Langevelde and Jaarsma 2004).

Finally, the least significant predictor in the best model was the distance to the nearest isolated house, this being greater for the road-kill stretches The distance to the nearest town was also included in some of the best models, with a similar pattern. We interpret these results as human encroachment leading to a decrease in suitable habitat for polecats (Zabala et al. 2005).

One weakness of our model was that we did not know the density of live polecats in the areas studied and therefore could not quantify the effect of this variable on the incidence of road-kills. Several studies have found a positive relationship between population density and road-kills (e.g. Gehrt 2002; Seiler 2005; but see Klocker et al. 2006). However, our model correctly predicted 82% of road-kill stretches which suggests either that the road-kill pattern is density independent or that some of the variables that we measured were correlated with live polecat density, and thus we estimated polecat density indirectly. For example, it might be expected that polecat densities are higher in areas where its main prey, the rabbit, is more abundant. To estimate densities of live animals requires costly monitoring effort and would therefore not be feasible in most cases. The variables we measured are much easier and cheaper to obtain and the model developed was successful, and we therefore suggest that this model is a valuable tool for predicting polecat road-kills.

Management implications

The management measures we suggest must be easy and cheap to carry out as the road-kill stretches in this study represented only 3.8% of the total road network. First, the number of road-kills could be significantly reduced along stretches of road with high numbers of warrens in road embankments. This could be done by fencing off the road and connecting both sides with underpasses to permit the normal transit of both rabbits and their predators. Second, the establishment of rabbit warrens along the roadside could be managed. Artificial refuges are currently being used to reintroduce or maintain rabbit populations elsewhere (e.g. Gea-Izquierdo et al. 2005) as rabbits are declining in several areas (Virgós et al. 2007a). These artificial warrens could be used as part of a management strategy to dissuade rabbits from settling in road embankments, by placing the artificial warrens away from the roads. Even simple earth mounds can be used as a cheaper alternative to building artificial warrens, as they are commonly used by rabbits to build their own warrens (authors, personal observation). Third, traffic speed could be reduced along stretches of roads with high numbers of road-kills by the use of lower speed limits combined with the laying of speed bumps. This would be particularly necessary on straight stretches of road with high roadside rabbit warren densities. Lower vehicle speeds will certainly increase the successful crossing rate for this mustelid (Van Langevelde and Jaarsma 2004).

Acknowledgements We are very grateful to I. Cardiel, R. Jiménez, P.M. García, D. Martínez, O. Frías, J.A. Calvo, J.A. Lemus for their help in the field. We thank F. Valera, R. Václav, E. Virgós, J. Moya-Laraño, G. Hernández-Milián, J. Birks, D.P. Sleeman and an anonymous referee for their helpful suggestions. J. Moya-Laraño, Mark T. Bulling and B. Nicholls checked the English. Traffic data were provided by M. Vidal (Junta de Comunidades de Castilla-La Mancha), A. J. Cervantes and J. Cobas (Diputación de Toledo) and A. Oliver (TELVENT). The Dirección General del Medio Natural of Toledo Province (Junta de Comunidades de Castilla-La Mancha) partially supported our research by means of TO-01-03 and TO-01-04.

Appendix 1

The results of the principal component analysis run prior to the development of the models in order to investigate the multicollinearity among independent variables

Variable	PC1	PC2	PC3	PC4	PC5	PC6
DRY	0.421258	−0.132407	0.230408	−0.839526	−0.030065	−0.007502
NON_CULT	0.219066	0.230037	−0.097520	0.809347	0.067512	0.218732
OTHER	−0.820769	−0.107831	−0.182926	0.110852	−0.043183	−0.257860
WOODY	0.077028	0.633344	0.101267	0.369508	0.224009	−0.143506
M_BURROW	−0.242736	0.066876	0.115347	−0.127656	−0.071437	−0.805967
N_BURROWS	0.147825	0.027444	−0.132319	0.182981	0.218188	0.786171
TOWN	0.263878	−0.006824	0.377190	0.529965	−0.054079	0.212921
HOUSE	0.230201	−0.354476	0.494688	0.072375	0.239758	0.215083
RIVER	0.126340	−0.286418	0.083116	0.025225	0.384410	−0.539122
SPEED	0.854368	0.029600	−0.110758	0.169153	0.018011	0.078418
TRAFFIC	−0.161921	0.115909	−0.762606	0.150385	0.265780	0.115479
HEAVY	−0.085134	0.117805	0.647747	0.082747	−0.053125	−0.223346
WIDTH	0.431084	−0.088140	−0.617466	0.248435	−0.061471	0.129852
PASS	0.008378	−0.750472	0.007064	−0.033088	0.118274	−0.143836
EMBANKMENT	0.126225	0.086953	−0.269614	−0.031974	0.783474	0.109793
BRIDGE	0.043028	0.775742	−0.042387	0.075463	0.153974	0.017040
UNBROK_LINE	−0.443517	0.143221	0.132539	0.129783	0.563282	0.069696

References

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366. doi:10.2307/3545823

Baghli A, Walzberg C, Verhagen R (2005) Habitat use by the European polecat *Mustela putorius* at low density in a fragmented landscape. Wildl Biol 11:331–339. doi:10.2981/0909-6396(2005)11[331:HUBTEP]2.0.CO;2

Bautista LM, García JT, Calmaestra RG, Palacín C, Martín CA, Morales MB et al (2004) Effects of weekend road on the use of space by raptors. Conserv Biol 18:726–732. doi:10.1111/j.1523-1739.2004.00499.x

Bellamy PE, Shore RF, Ardeshir D, Treweek JR, Sparks TH (2000) Road verges as habitat for small mammals in Britain. Mammal Rev 30:131–139. doi:10.1046/j.1365-2907.2000.00061.x

Birks JDS (1997) A volunteer-based system for sampling variations in the abundance of polecats (*Mustela putorius*). J Zool (Lond) 243:857–863

Birks JDS, Kitchener AC (1999) The distribution and status of the polecat *Mustela putorius* in Britain in the 1990s. The Vincent Wildlife Trust, London

Blandford PRS (1987) Biology of the polecat *Mustela putorius*, a literature review. Mammal Rev 17:155–198. doi:10.1111/j.1365-2907.1987.tb00282.x

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York

Calvete C, Estrada R, Angulo E, Cabezas-Ruíz S (2004) Habitat factors related to wild rabbit conservation in an agricultural landscape. Land Ecol 19:531–542. doi:10.1023/B:LAND.0000036139.04466.06

Clarke GP, White PCL, Harris S (1998) Effects of roads on badger *Meles meles* populations in south-west England. Biol Conserv 86:117–124. doi:10.1016/S0006-3207(98)00018-4

Clevenger AP, Chruszcz B, Gunson KE (2003) Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. Biol Conserv 109:15–26. doi:10.1016/S0006-3207(02)00127-1

Cuesta M (1994) Bioecología de los mustélidos en los Montes de Toledo. Disseration, Universidad Complutense of Madrid

Davison A, Birks JDS, Griffiths HI, Kitchener AC, Biggins D, Butlin RK (1999) Hybridization and the phylogenetic relationship between polecats and domestics ferrets in Britain. Biol Conserv 87:155–161. doi:10.1016/S0006-3207(98)00067-6

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Evol Syst 29:207–231

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall DC, Dale VH et al (2003) Road ecology. Science and solutions. Island Press, Washington
Gea-Izquierdo G, Muñoz-Igualada J, San Miguel-Aynaz A (2005) Rabbit warren distribution in relation to pasture communities in Mediterranean habitats, consequences for management of rabbit populations. Wildl Res 32:723–731. doi:10.1071/WR04129
Gehrt SD (2002) Evaluation of spotlight and road-kill surveys as indicators of local raccoon abundance. Wildl Soc Bull 30:449–456
Ginsberg JR (2001) Setting priorities for carnivore conservation, what makes carnivores different? In: Gittleman JL, Funk SM, Macdonald D, Wayne RK (eds) Carnivore conservation. Cambridge University Press, Cambridge, pp 498–523
Gutzwiller KJ (ed) (2002) Applying landscape ecology in biological conservation. Springer, New York
Holm S (1979) A simple sequentially rejective Bonferroni test procedure. Scand J Stat 6:65–70
Iuell B, Bekker GJ, Cuperus R, Dufek J, Fry G, Hicks C et al (2003) Wildlife and traffic. A European handbook for identifying conflicts and designing solutions. KNNV Publishers, Delft
Klocker U, Croft DB, Ramp D (2006) Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. Wildl Res 33:5–15. doi:10.1071/WR04066
Kristiansen LV, Sunde P, Nachman G, Madsen AB (2007) Mortality and reproductive patterns of wild European polecats *Mustela putorius* in Denmark. Acta Theriol (Warsz) 52:871–878
Linnell JDC, Swenson JE, Andersen R (2000) Conservation of biodiversity in Scandinavian boreal forest, large carnivores as flagships, umbrellas, indicators, or keystones? Biodivers Conserv 9:857–868. doi:10.1023/A:1008969104618
Little SJ, Harcourt RG, Clevenger AP (2002) Do wildlife passages act as prey-traps? Biol Conserv 107:135–145. doi:10.1016/S0006-3207(02)00059-9
Lodé T (1994) Environmental factors influencing habitat exploitation by the polecat *Mustela putorius* in western France. J Zool (Lond) 234:75–88
Lodé T (1997) Trophic status and feeding habits of the European polecat *Mustela putorius* L. 1758. Mammal Rev 27:117–184. doi:10.1111/j.1365-2907.1997.tb00447.x
Lodé T (2003) Sexual dimorphism and trophic constraints: prey selection in the European polecat (*Mustela putorius*). Ecoscience 10:17–23
Lodé T, Pereboom V, Berzins R (2003) Implications of an individualistic lifestyle for species conservation: lessons from jealous beasts. C R Biol 326:S30–S36. doi:10.1016/S1631-0691(03)00024-6
Lombardi L, Fernández N, Moreno S (2007) Habitat use and spatial behaviour in the European rabbit in three Mediterranean environments. Basic Appl Ecol 8:453–463. doi:10.1016/j.baae.2006.09.004
Macdonald DW (1995) European mammals: evolution and behaviour. Harper Collins, Oxford
Malo JE, Suárez F, Díez A (2004) Can we mitigate animal-vehicle accidents using predictive models? J Appl Ecol 41:701–710. doi:10.1111/j.0021-8901.2004.00929.x
Marcelli M, Fusillo R, Boitani L (2003) Sexual segregation in the activity patterns of European polecats (*Mustela putorius*). J Zool (Lond) 261:249–255. doi:10.1017/S0952836903004151
Mestre FM, Ferreira JP, Mira A (2007) Modelling the distribution of the European polecat *Mustela putorius* in a Mediterranean agricultural landscape. Rev Ecol (Terre Vie) 62:35–47
Mitchell-Jones AJ, Amori G, Bogdanowicz W, Kryštufek B, Reijnders PJH, Spitzenberger F et al (1999) The atlas of European mammals. Academic Press, London
Moya-Laraño J, Wise DW (2007) Two simple strategies of analysis to increase the power of experiments with multiple response variables. Basic Appl Ecol 8:398–410. doi:10.1016/j.baae.2006.09.014
Palomares F (2003) Warren building by European rabbits (*Oryctolagus cuniculus*) in relation to cover availability in sandy area. J Zool (Lond) 259:63–67. doi:10.1017/S0952836902002960
Ramp D, Caldwell J, Edwards KA, Warton D, Croft DB (2005) Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. Biol Conserv 126:474–490. doi:10.1016/j.biocon.2005.07.001
Ramp D, Wilson VK, Croft DB (2006) Assessing the impacts of roads in peri-urban reserves: road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. Biol Conserv 129:348–359. doi:10.1016/j.biocon.2005.11.002
Roger M (1991) Food-habits and prey availability in the polecat *Mustela putorius*. Rev Ecol (Terre Vie) 46:245–261
Rondinini C, Ercoli V, Boitani L (2006) Habitat use and preference by polecats (*Mustela putorius* L.) in a Mediterranean agricultural landscape. J Zool (Lond) 269:213–219
Saeki M, Macdonald DW (2004) The effects of traffic in the raccon dog (*Nyctereutes procyonoides viverrinus*) and other mammals in Japan. Biol Conserv 118:559–571. doi:10.1016/j.biocon.2003.10.004

Schröpfer von R, Bodenstein C, Seebass C (2000) Der Räuber-Beute-Zusammenhang zwischen dem Iltis *Mustela putorius* L., 1785 und dem Wildkanichen *Oryctolagus cuniculus* (L., 1758). Z Jagdwiss 46:1–13. doi:10.1007/BF02240659

Seiler A (2005) Predicting locations of moose-vehicle collisions in Sweden. J Appl Ecol 42:371–382. doi:10.1111/j.1365-2664.2005.01013.x

Sidorovich VE (2000) The on-going decline of riparian mustelids (European mink, *Mustela lutreola*, polecat, *Mustela putorius*, and stoat, *Mustela erminea*) in eastern Europe: a review of the results to date and an hypothesis. In: Griffiths HI (ed) Mustelids in a modern world. Management and conservation aspects of small carnivore: human interactions. Backhuys Publishers, Leiden, pp 295–317

Sleeman DP (1988) Irish stoat road casualties. Ir Nat J 22:527–529

Spellerberg IF (1998) Ecological effects of roads and traffic, a literature review. Glob Ecol Biogeogr 7:317–333. doi:10.1046/j.1466-822x.1998.00308.x

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14:18–30. doi:10.1046/j.1523-1739.2000.99084.x

Van Langevelde F, Jaarsma CF (2004) Using traffic flow theory to model traffic mortality in mammals. Land Ecol 19:895–907. doi:10.1007/s10980-004-0464-z

Virgós E (2001) Relative value of riparian woodlands in landscapes with different forest cover for medium-sized Iberian carnivores. Biodivers Conserv 10:1039–1049. doi:10.1023/A:1016684428664

Virgós E (2002) *Mustela putorius*, Linneaus, 1758. In: Palomo LJ, Gisbert J (eds) Atlas de los Mamíferos Terrestres de España. Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid, pp 262–265

Virgós E (2003) Association of the polecat *Mustela putorius* in eastern Spain with montane pine forests. Oryx 37:484–487. doi:10.1017/S0030605303000863

Virgós E, Cabezas-Díaz S, Lozano J (2007a) Is the wild rabbit (*Oryctolagus cuniculus*) a threatened species in Spain? Sociological constrains in the conservation of species. Biodivers Conserv 16:3489–3504. doi:10.1007/s10531-006-9054-5

Virgós E, Cabezas-Díaz S, Lozano J (2007b) *Mustela putorius*, Linneaus, 1758. Ficha Libro Rojo. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid, pp 297–298

Yanes M, Velasco JM, Suárez F (1995) Permeability of roads and railways to vertebrates: the importance of culverts. Biol Conserv 71:217–222. doi:10.1016/0006-3207(94)00028-O

Zabala J, Zuberogoitia I, Martínez-Climent JA (2005) Site and landscape features ruling the habitat use and occupancy of the polecat (*Mustela putorius*) in a low density area, a multiscale approach. Eur J Wildl Res 51:157–162. doi:10.1007/s10344-005-0094-z