BIODIVERSITY RESEARCH

Can we explain regional abundance and road-kill patterns with variables derived from local-scale road-kill models? Evaluating transferability with the European polecat

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ABSTRACT

Aim We evaluated the transferability of variables previously found to have a significant effect on European polecat *Mustela putorius* road-kills at a local scale (i.e. 50 m around location points) when we extrapolate them to a large scale [Universal Transverse Mercator (UTM) 100 km^2] in a neighbouring area.

Location Andalusia, south Spain. We carried out our study in 821 of the 985 UTM 100 km^2 cells included in this region.

Methods The units of the different variables were adapted to the new scale. We used data from the Spanish Atlas survey to obtain the abundance of the different species and GIS data for the rest of the variables. We controlled the spatial autocorrelation by incorporating spatial filters obtained with Spatial Eigenvector Mapping into multiple regression analyses. We used AIC criteria and the best subset procedure to investigate the relationship between the selected variables and species abundance, and road-kill occurrence.

Results The best subset procedure provided two models that explained 40% of variation in polecat abundance and eleven models that explained around 25% of variation in road-kills. The main explanatory factor for polecat abundance was the abundance of other carnivores, whereas polecat abundance was the main factor for road-kills. In both cases, rabbit abundance was the second most important explanatory variable.

Main Conclusions Our findings highlight the possibility of partially explaining the abundance and road-kill patterns at a large scale based on significant variables from local-scale models. Mitigation measures to reduce polecat fatalities should combine actions at different scales. Routes that cross carnivore hotspots, including those of polecats, and areas with important populations of rabbits, should be avoided during road planning. When these routes are unavoidable, local-scale mitigation measures must be implemented.

Keywords

Atlas survey, road planning, road-related mortality, Spatial Eigenvector Mapping, spatial transferability, Universal Transverse Mercator grid.

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INTRODUCTION

Habitat fragmentation largely depends on landscape connectivity, that is, the degree to which the landscape facilitates or impedes the movement of organisms among patches (Taylor *et al.*, 1993). Roads are one of the most important fragmenting forces for several animal species, especially for those with high habitat requirements or limited dispersal (Sunquist & Sunquist, 2001). Roads can drive population fragmentation by simple barrier effects (i.e. without associated mortality), when high traffic loads may discourage animals from crossing them (e.g. Clarke *et al.*, 1998), as well as by road-kills, which lead to

population decline, but also ultimately cause population fragmentation because of a reduction in individual exchanges among subpopulations (Shepard *et al.*, 2008; Clark *et al.*, 2010; Simmons *et al.*, 2010). The ecology of carnivores makes them especially sensitive to road mortality (Forman *et al.*, 2003; Grilo *et al.*, 2009), and road casualties are a primary cause of human-related mortality for several species (e.g. Clarke *et al.*, 1998; Jones, 2000). Compared to other groups (e.g. their prey), carnivores cover larger foraging areas, dramatically increasing their probability of being killed on the road (Ginsberg, 2001). Moreover, from a population dynamics perspective, carnivores have low fecundity and density and are thus expected to be more intensely impacted by road mortalities (Ginsberg, 2001). In addition, the opportunistic use of locally abundant preys at road margins can increase the visitation rate to these areas by carnivores and, consequently, increase their road-kill risk (Barrientos & Bolonio, 2009).

Present-day conservation strategies for wildlife focus on the integration of animal species into multiuse landscapes dominated by people, and the measures to minimize infrastructure impacts must be necessarily taken (Linnell *et al.*, 2000; Iuell *et al.*, 2003). Most road-kill studies have been carried out at a local scale with highly variable buffer sizes (from 5 to 1000 m) around location points (Malo *et al.*, 2004; Seiler, 2005; Ramp *et al.*, 2006; Barrientos & Bolonio, 2009; Grilo *et al.*, 2009). On the contrary, studies on the impacts of roads on animal movements or population fragmentation are carried out at larger scales, typically on the scale of home range (Mladenoff *et al.*, 1995; Dyer *et al.*, 2002; Riley *et al.*, 2006), a scale seldom used in specific point road-kill studies (but see the study by Ramp *et al.*, 2005). Studies on animal movements employ radio-collared individuals to investigate the impact of roads on mortality and consequent population fragmentation (Mladenoff *et al.*, 1995; Dyer *et al.*, 2002; Riley *et al.*, 2006), an expensive method that is not always feasible. Thus, other research approaches should be employed when economic resources are limited.

As a model species, we used the European polecat (*Mustela putorius*), a species that undergoes large road-related losses elsewhere (Blandford, 1987), commonly during feeding activity (Barrientos & Bolonio, 2009). Previously (Barrientos & Bolonio, 2009), we found that three habitat and three road-related variables separated road-kill stretches (sections of road of 100 m long) from non-road-kill ones at a local scale (50 m radius around location points). The main variable characterizing road-kill stretches was the abundance of European rabbit (*Oryctolagus cuniculus*) burrows in the road verges, with traffic flow and speed being important as well (Barrientos & Bolonio, 2009). Road-kill stretches also had more metres of road built over bridges and lower densities of people (Barrientos & Bolonio, 2009). In the present study, we modelled the abundance of live polecats at a 100 km² spatial scale based on the three habitat variables found to have a significant effect on a local scale (main prey presence, human pressure and presence of potential habitat corridors), as well as the road-killed number at a 100-km² scale based on both habitat and road-related variables found to have a significant effect on a local scale (the above-mentioned plus traffic density and speed, and road quality).

Predicting species distribution (or forecasting ecological processes) is of fundamental importance for ecology and conservation (Zanini *et al.*, 2009). These distribution models are not only interested in biogeographical studies but are also valuable tools in conservation biology and species management (Miller, 1986; Carey & Brown, 1994; Godown & Peterson, 2000; Engler *et al.*, 2004). However, most published species distribution models have not been developed for a global scale or for the complete extent of a species' geographical range (Randin *et al.*, 2006). As a result, their applicability in predictions at other scales such as other areas (Thomas & Bovee, 1993; Fielding & Haworth, 1995; Glozier *et al.*, 1997; Ozesmi & Mitsch, 1997; Schröder & Richter, 1999; Kleyer, 2002), or other time periods (Schröder & Richter, 1999; Araújo *et al.*, 2005), is low (Randin *et al.*, 2006). This concept of geographical or temporal model cross-applicability was defined as 'transferability' (Randin *et al.*, 2006) and it is an important feature of these models, if they are used for projections in new areas (transferability in space) or for predictions of climate-change responses (transferability in time) (Fielding & Haworth, 1995). Testing model transferability could prove particularly powerful for complementing standard procedures of model evaluation (Randin *et al.*, 2006; but see the study by Maggini *et al.*, 2006).

In this study, we evaluate the explanatory capability of variables found to have a significant effect on road-kills at a local scale when extrapolating them to a large-scale framework, based on a Universal Transverse Mercator (UTM, 10 × 10 km; i.e. 100-km²) grid from a neighbouring region. The 100-km² grid is widely used in national atlas surveys (Donald & Fuller, 1998; Palomo *et al.*, 2007), with increasing importance in conservation biogeography and population ecology studies (e.g. Virgós, 2003; Virkkala *et al.*, 2005; González-Taboada *et al.*, 2007; Moreno-Rueda & Pizarro, 2007; Reino *et al.*, 2009). It generates the most accurate resolution for the study of road impact at regional or national scales (e.g. Jędrzejewski *et al.*, 2008). We expect that (i) cells with higher prey availability present both higher density of the target predator species and higher number of predator road-kills. In the study region, rabbit makes up the bulk of the polecat diet (Virgós, 2007), and the relationship between carnivore presence and the presence of their preys has been recently demonstrated at a large scale in the study region (Moreno-Rueda & Pizarro, 2010); (ii) the abundance of target species is an important explanatory factor of road-kills, as the more abundant one species is, the greater its road-kill probability (e.g. Gehrt, 2002; Mysterud, 2004; Seiler, 2005; Roger & Ramp, 2009); (iii) we expect that road network development increases road-kills, as landscapes with more and better roads, with more traffic volume and traffic speed, are more dangerous for the species that inhabit them (e.g. Saeki & Macdonald, 2004; Ramp *et al.*, 2006; Barrientos & Bolonio, 2009); and (iv) we expect a moderate transferability of local-based variables when explaining

regional scale models because both the scales and the training and the testing regions differ. Even more importantly, it is difficult to find variables that exactly mirror those used at other scales; for instance, it is complicated to transfer some traffic traits (e.g. speed limit or traffic volume) from a local to a regional scale.

METHODS

Study species and study area

The European polecat is a small carnivore distributed across Europe, where it usually maintains low densities (Mitchell-Jones *et al.*, 1999; Virgós, 2007). Several processes, such as human-related factors (hunting, road casualties), competition with alien species or hybridization processes with domestic lineages, have led this species to a population decline in several regions (Blandford, 1987; Davison *et al.*, 1999; Mitchell-Jones *et al.*, 1999; Sidorovich, 2000; Lodé, 2003). In the Iberian Peninsula, where it was recently listed as threatened (Portugal) or almost threatened (Spain), the reduction of its main prey (the European rabbit), hybridization processes with ferrets, poisoning, habitat loss and road-kills have been cited as factors threatening their populations (Virgós *et al.*, 2007). In this region, it has been recently demonstrated that the presence of rabbit burrows on road embankments increases polecat road mortality (Barrientos & Bolonio, 2009), as this is the polecat's main prey in this and in other regions (Lodé, 1997; Santos *et al.*, 2009).

In the Iberian Peninsula, the polecat has a patchy distribution (Virgós, 2007). Central Spain, the training region (Barrientos & Bolonio, 2009), is one of the areas in which

the species is more abundant, being less common in Andalusia (Virgós, 2007; Fig. 1), the area selected as the testing region. Andalusia is a region that covers more than 87,000 km^2 in the southernmost part of mainland Spain (Fig. 1). The region presents two important mountain ranges: Sierra Morena, along the northern limit of the region, and the Betic system, mainly in the eastern and south-eastern part of the region. The most important plain is the Guadalquivir Valley, located between the two mountain ranges. Its climate is Mediterranean, with mild winters and severe summer droughts. Mean annual temperature ranges from 9.8°C to 19.4°C (Font, 2000). Annual rainfalls, which are markedly heterogeneous between years, as is typical in Mediterranean habitats, are more abundant in certain mountains (up to 1800 mm) and very low (170 mm) in the subarid south-east. Half of the Andalusian land area is cultivated, mainly by olive groves and cereals, with the other half covered mainly by shrubland, pine and oak forests.

Cell and variable selection

We used the number of polecats and road-kills per 100 km^2 cell as response variables. This cell size represents 40–280 times the home range of the European polecat (Baghli *et al.*, 2005; Rondinini *et al.*, 2006). These data have been obtained from the Spanish National Atlas survey and were kindly supplied by the Spanish Society for the Conservation and Study of Mammals (Sociedad Española para la Conservación y Estudio de los Mamíferos, SECEM). Taking into account that the polecat is protected by Spanish law (Virgós *et al.*, 2007), the vast majority of death records were road-kill specimens, and in the few cases in which the cause of death was unknown, it was assumed that they had been killed on the road (L.J. Palomo,
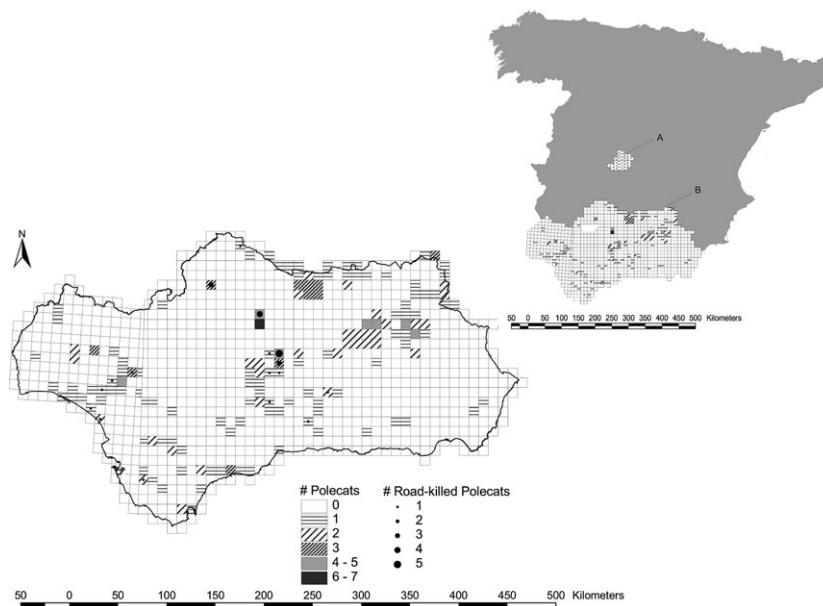

Figure 1 Study area within the Iberian Peninsula. In the upper right map, Barrientos & Bolonio's (2009) study region (a) and ours (b) are shown. In the bottom map, we show the cells where polecats (all records) and road-killed polecats were recorded.

pers. com.). The region of Andalusia contains 985 100 km² UTM cells, although not all of them are the same size, as coastal or border cells are often smaller. For that reason, we selected those cells larger than 80 km², that is, 821 cells (i.e. 83% of cells, 93% of total surface). Thus, cell area was held as constant as possible and was not included explicitly in the analysis. Note that hereafter cell size is taken as 100 km². With this correction, we lost 10% of the polecat records and 3% of road-kills from the original Atlas data. However, we believe these precautions to be necessary to homogenize Atlas data. Indeed, zeros from very small cells (for instance, originally there were 37 cells smaller than 10 km²) are likely due to false absences, and we wanted to avoid them, as they can impair transferability (Zanini et al., 2009).

The use of data from atlas, in which many observers not following clearly defined methodological standards or employing similar sampling efforts participate, could lead to strong biases in macroecological studies (e.g. grid cells with denser human populations or more attractive habitats could be more intensively sampled; see the studies by Luck et al., 2004; Ferrer et al., 2006). Thus, we tried to find a variable that could be used as a surrogate of sampling effort. For that reason, we used the number of other carnivore observations (excluding the polecat, which was the single carnivore in only two out of 821 cells) in the database to control for the sampling effort. This guild includes 10 species (totalling 7,522 observations in Andalusia), with very different degrees of 'conspicuousness', including from those species easy to detect (e.g. red fox Vulpes vulpes) to cryptic species (e.g. weasel Mustela nivalis). As we thought that this is a suitable group to control for, we included the variable 'OTHER CARNIV' (i.e. number of other carnivores per 100 km² cell) in the model selection and multimodel inference after log-transforming it. We included in the analyses only the transformed variable here as well as in the rest of cases. The use of other carnivore records as a surrogate variable of sampling effort could be conservative, as it also reflects those areas richer in carnivores, independent of sampling. We discarded the use of the number of observers per square to control for sampling effort bias because data from the Atlas were not collected with standardized effort; that is, not all the participants employed the same amount of time to prospect their squares. Furthermore, occasional observations are also included in Atlas data. Thus, we are confident that the use of 'OTHER CARNIV' can better control for this effort biases, as better sampled squares accumulate more cites both from polecat and from other carnivores. Moreover, testing 'OTHER CARNIV' as an additional explanatory variable (rather than as an offset variable) allows us to evaluate polecat as a bioindicator for the rest of carnivores in the Mediterranean region.

In a previous study on polecat road-kills, Barrientos & Bolonio (2009) modelled the variables that best separated road-kill road stretches from non-road-kill ones. However, they based their conclusions on local-scale data (i.e. 50 m radius around location points). In the present study, we rescaled these variables to 100 km² cells, a scale widely used in national atlas surveys (see the study by Palomo et al., 2007 for

Spanish mammal Atlas). The use of different scales implies that different units of the explanatory variables must be used (Table 1). Thus, whereas the presence of rabbits close to the road is the most important variable at the local scale, for the 100-km² scale, we used the number of rabbit observations (log-transformed) per cell based on the Spanish Atlas, defined as 'RABBIT'. As polecat road-kills were related to the distance to the nearest house at the local scale, we included the number of rural buildings per 100 km² cell, defined as 'HOUSE'. The metres of road built over bridges were rescaled to the length of rivers per cell, defined as 'RIVER'. The abundance of polecats was log-transformed before the analysis.

In addition to the three above-mentioned habitat-related variables, for the modelling of road-kills, we rescaled the three road-related ones that were found to be important at the local scale (Barrientos & Bolonio, 2009). Data on traffic flow per cell are not available; however, we assume that traffic is related to the human population density. We used the surface area occupied by population nuclei as a surrogate of human population density per cell and defined it as 'TOWN'. Despite the fact that this variable can be related to road categories, at least in our study region, road building is sometimes a policy decision, and it happens that good roads are built in areas with

Table 1 Variables at the local scale that best separated road-kill stretches from non-road-kill ones, from the study by Barrientos & Bolonio (2009), and those variables rescaled for the present study. Range values are included in brackets.

Variable at local (50 m radius) scale	Variable at regional (100 km²) scale
Distance (m) to the nearest rabbit burrow on either side of the road [1–26]	'RABBIT': Number (n) of rabbit observations per cell based on the Spanish Atlas [1–17]
Distance (m) to the nearest isolated house on either side of the road [0–1950]	'HOUSE': Number (n) of rural buildings per cell [0–19]
Length (m) of the 100-m stretch built over bridges [0–40]	'RIVER': Length (m) of rivers per cell [1381–99,917]
Monthly mean number (n) of vehicles per day along the stretch [480–12,205]	'TOWN': Surface (m²) taken up by towns per cell [0–33,753,544]
Percentage of the length of the stretch of the road where overtaking is forbidden [0–100]	'ROAD 1ST': Length (m) of regional roads of first order per cell [0–32,112] 'ROAD 2ND': Length (m) of regional roads of second order per cell [0–69,933]
Speed limit (km h⁻¹) on the stretch of road [50–100]	'ROAD 1ST': Length (m) of regional roads of first order per cell [0–32,112] 'ROAD 2ND': Length (m) of regional roads of second order per cell [0–69,933]

low human density (and thus, low traffic volume). Thus, in an attempt to evaluate traffic volume itself, we included the human density as its surrogate, as we expect that the higher the human density is, the higher the traffic volume. We used a statistical approach that allows the initial inclusion of likely correlated variables as the less influential will ultimately be discarded in the modelling procedure. The percentage of the length of the road where overtaking is forbidden and the speed limit on the stretch were surrogated by the length of regional roads of first ('ROAD 1ST') and second ('ROAD 2ND') order as these road classes differ in their characteristics, including the percentage of unbroken lines and speed limits (Barrientos & Bolonio, 2009). We also included the number of polecat observations per cell ('MP ABUND') after log-transforming it to evaluate the importance of polecat abundance as an explanatory factor of polecat road-kills. Finally, we also included in this modelling process the number of observations of other carnivores ('OTHER CARNIV').

Statistical analyses

We explored multicollinearity among variables by using a PCA, with the varimax normalized factor rotation, to build a correlation matrix to explore the degree of association among the three (in polecat presence models) and seven (in polecat road-kill models) explanatory variables. For the subsequent model development, and to minimize multicollinearity among independent variables, we should include the most highly (> 0.7) correlated variable with each of the PC factors, discarding the remaining highly correlated variables. However, using this criterion, we found that no variable should be discarded before model development (only one variable, if any, presented correlation > 0.7 with every PC factor, data not shown), and we thus proceeded with all the variables in our analyses.

The observed values of polecat abundance and road-kills can be influenced, at any given grid cell, by their values at surrounding ones, because of contagious biotic (e.g. reproduction, migration) or abiotic (for instance, in the Iberian Peninsula, the European polecat reaches higher densities in Mediterranean habitats from central Spain, Virgós, 2007; where rabbits are especially abundant because of soil traits) processes (Legendre, 1993). In these cases, because the value at any cell can be at least partially predicted by the values of neighbouring cells, we must control for spatial autocorrelation (Legendre, 1993; Rangel et al., 2006). As controlling spatial autocorrelation helps to increase the variance explained by our models, we used the routine implemented in the program Spatial Analysis in Macroecology (SAM, version 4, Rangel et al., 2010) based on Gaussian models in a spatially explicit framework. Despite the fact that, formally, it should be tested with Poisson models, both distributions converge when sample size is large, as it is in our case (n = 821), based on the central limit theorem. We controlled spatial autocorrelation by incorporating spatial filters obtained with Spatial Eigenvector Mapping (SEVM) into multiple regression analysis (Diniz-

Filho & Bini, 2005; Diniz-Filho et al., 2008). The basic idea is to extract eigenvectors from distance data among spatial units (i.e. cells in the 100 km^2 grid), and use these eigenvectors, which describe the spatial structure of the region under study at different scales, as additional explanatory factors of the response variables (polecat abundance or road-kills). With this procedure any remaining spatial structure in regression residuals would be taken into account, and so these models would not be affected by spatial autocorrelation (Diniz-Filho & Bini, 2005; Diniz-Filho et al., 2008). We used geographical coordinates (latitude and longitude) of the central points of each cell covering Andalusia to calculate the distances, and the maximum distance was truncated under minimum spanning tree criterion (Rangel et al., 2010). We selected the eigenvectors that minimized residual spatial autocorrelation (Griffith, 2003), and, consequently, we avoided an excess of variables in the multiple regression as we used only filters that contain important parts of the geometry of the region in the analysis (Diniz-Filho & Bini, 2005).

Following Diniz-Filho et al. (2008), we included the eigenvectors obtained with SEVM as the variables present in all models to take into account the spatial autocorrelation in the residuals. The explanatory factors were the m variables, which are those for which all possible 2m–1 combinations are used to find the model with the smallest AIC value. Resultant models were ranked together using the second-order information criterion (AICc), and the Akaike weight of each model (ω_m) was estimated. The model with the lowest AICc represents the best compromise between a maximal fit and a minimal number of explanatory variables (i.e. statistical parsimony). Those models with an AICc difference lower than two when compared with the lowest one were considered as plausible models (Burnham & Anderson, 2002). 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 & Anderson, 2002). To estimate the relative importance of every variable included in any of the best models, we calculated the relative sum of Akaike weights of the models where these variables were included (Burnham & Anderson, 2002). We also investigated whether arbitrary factors (so-called 'red herrings'; Lennon, 2000; Diniz-Filho et al., 2005) could be biasing our results by repeating the analyses without spatial filters. We proceeded with partial regressions as implemented in SAM to assess the percentage of variation in the response variable explained by every explanatory variable. The Moran's I coefficient was also calculated with SAM.

RESULTS

We carried out our analyses on 821 cells, with polecats found alive in 130 of them (212 records) and road-killed in 17 (28 records). Controlling spatial autocorrelation helped to explain more variance in both model sets (data not shown); thus, we can reject the generation of 'red herrings' in our analyses.

Polecat abundance based on environmental variables

Geographic variation in polecat abundance in Andalusia was strongly autocorrelated at short distances, showing a monotonic decrease in Moran's I coefficient across distances (Fig. 2). The SEVM selected 38 spatial filters to control for this autocorrelation, which were included in the regression procedure. The best subset procedure provided two models, which could be considered as similarly plausible according to their AICc (i.e. the difference between their AICc was less than 2, Table 2). Both models explained around 40% of variation in polecat abundance. Among the variables, the highest weight was for OTHER CARNIV as it was included in both models ($\Sigma \omega_i = 1.000$), whereas RABBIT was less influential ($\Sigma \omega_i = 0.462$), as it was included only in the second model. Both OTHER CARNIV and RABBIT were positively related with the response variable (Fig. 3). Partial regressions showed that whereas OTHER CARNIV explained 14.6% (40.0% when combined with spatial filters) of the variance, RABBIT explained 7.1% (38.2% together with spatial filters).

Polecat road-kills based both on environmental and road-related variables

Geographic variation in polecat road-kills was also autocorrelated at short distances, showing a monotonic decrease in Moran's I coefficient across distances (Fig. 4). The SEVM selected 13 spatial filters to control for this autocorrelation. The best subset analysis provided eleven models, which could be considered as similarly plausible (Table 3). All models explained around 25% of variation in polecat road-kills. Among the variables, the highest weights were for MP ABUND and RABBIT as they were included in all models ($\Sigma \omega_i = 1.000$). These two variables were positively related

with polecat fatalities (Fig. 5). Less important were OTHER CARNIV ($\Sigma \omega_i = 0.868$), RIVER ($\Sigma \omega_i = 0.730$), HOUSE ($\Sigma \omega_i = 0.420$), 2ND ROAD ($\Sigma \omega_i = 0.248$) and 1ST ROAD ($\Sigma \omega_i = 0.132$). Partial regressions showed that MP ABUND was the variable that explained more variance (10.7% alone, 24.4% together with spatial filters), followed by RABBIT (3.9% alone, 15.6% when combined with spatial filters), whereas OTHER CARNIV explained only 1.4% (15.0% together with filters). The rest of the variables explained less than 2% when assessed alone.

DISCUSSION

Our results show that it is possible to partially explain polecat abundance and road-kill patterns at a large-scale based on variables from models developed with local-scale data, although most of the variance remains unexplained, and thus, our findings must be taken with caution. Despite using a different scale to that used in a previous study on polecat road-kills (Barrientos & Bolonio, 2009), our approach could be considered as a validation of its findings. This evaluation of transferability adds additional interest to the present study, as there is a recognized need for spatial models to confirm their generality with independent data (Vaughan & Ormerod, 2005), including those on road-kills (Gunson et al., 2011).

In the polecat abundance models, the most important variable was the abundance of other carnivores, followed by the abundance of rabbits. In the road-kill models, polecat abundance was the most important explanatory factor, again followed by rabbit abundance. These three variables could be affected by sampling effort in the original data from the Atlas. In fact, it could be argued that those cells with more observations (live polecats, other carnivores or rabbits) could
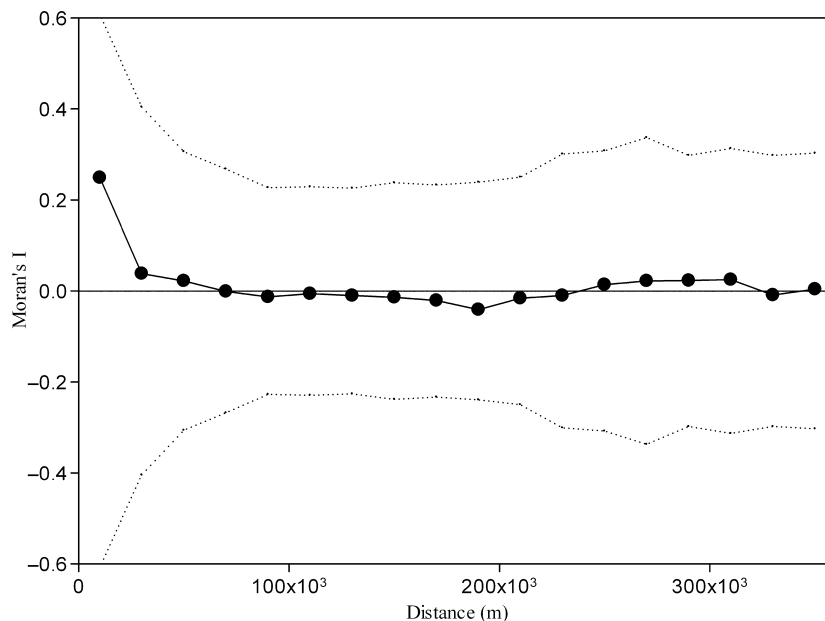

Figure 2 Moran's I values for the residuals of the polecat abundance model. Dotted lines mark the maximum Moran's I.

Table 2 The two models that best defined the abundance of live polecats. The R^2 is the percentage of variation in the polecat abundance explained by the full model (including spatial filters), and K is the number of environmental variables contained in every model. The ΔAICc is the difference in AICc values compared with the estimated best model (lowest AICc) that allows the ranking of models from an estimated best (top of the table) to 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.

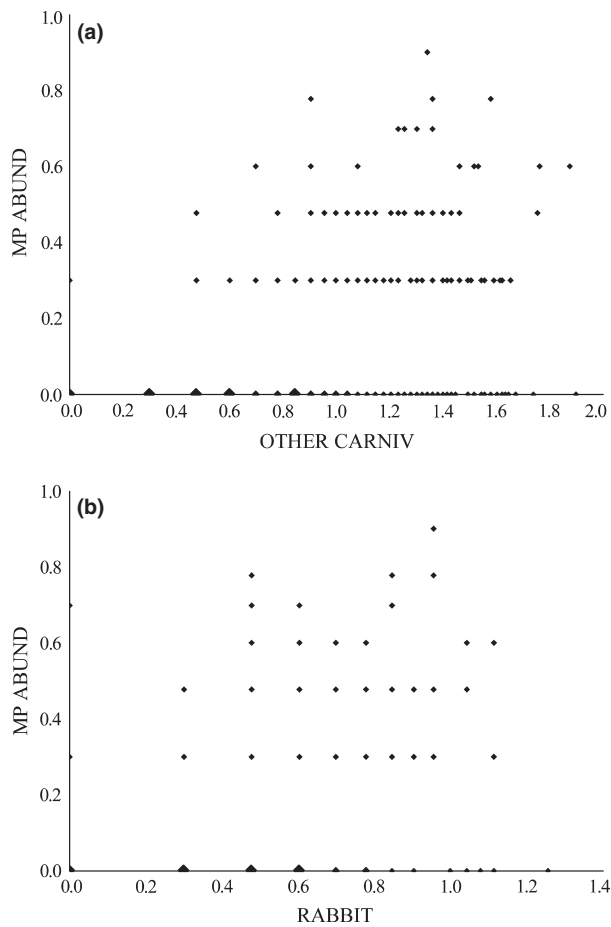| Model no.	Environmental variables contained in the model	R^2	K	ΔAICc (Δ_i)	AICc weight (ω_i)	Evidence ratio
1	OTHER CARNIV	0.400	1	0.000	0.300	0.00
2	RABBIT + OTHER CARNIV	0.401	2	0.305	0.258	16.47

Figure 3 Relationship between the OTHER CARNIV (abundance of other carnivores, 3a) and RABBIT (abundance of rabbits, 3b) variables with MP ABUND (polecat abundance). All the variables were log-transformed. The mark ◆ represents ≤ 20 cells, ◆ 20–50 cells and ◆ > 50 cells.

have been better sampled during the Atlas survey (Luck *et al.*, 2004; Ferrer *et al.*, 2006). If this is the case, a positive relationship between human density and the number of observations of live polecats, other carnivores and rabbits would be expected. However, the surface area occupied by population nuclei, used as a surrogate of human density, explains only 0.02, 0.7 and 3.3 of their respective variances (simple regression, data not shown), thus allowing us to reject such a bias. Nevertheless, it is difficult to disentangle the causes of such large-scale patterns as the possible underlying mechanisms may be correlated (e.g. Loreau *et al.*, 2001). Some non-mutually exclusive factors could account for the observed patterns: (i) one of the potential factors driving species richness is environmental heterogeneity (reviewed by Tews *et al.*, 2004). Environmental heterogeneity, commonly expressed as habitat or land use diversity, or topographical variability, may facilitate the existence of more niches and thus, the presence of more carnivore species, including the polecat, in certain cells (Moreno-Rueda & Pizarro, 2007, 2010). (ii) The presence of higher diversity of preys in some cells may favour carnivore species coexistence (Ray & Sunquist, 2001; Moreno-Rueda & Pizarro, 2010). Despite polecats predating mainly on rabbits in our study region (reviewed by Lodé, 1997; Santos *et al.*, 2009), the presence of complementary preys could increase their density. (iii) Several studies highlight the existing relationship between species richness and productivity (reviewed by Waide *et al.*, 1999), which could lead to carnivore hotspots in our study region (see Table 6 in the study by Moreno-Rueda & Pizarro, 2007). Consequently, polecat could be considered as a bioindicator in the Mediterranean region, the edge of the species' range, as it is only present in those cells richer in other carnivores. This finding mirrors those obtained in other studies in this region, where the polecat was one of the scarcest species within the carnivore pool (Pita *et al.*, 2009; Sobrino *et al.*, 2009), with heterogeneous habitats being important for the presence of polecats (Mestre *et al.*, 2007).

As expected, the presence of live polecats is the main variable explaining road-kills. Despite the fact that several variables can modulate fatalities, it becomes apparent that those areas where the target species reach higher densities (or, alternatively, those well-connected habitats, e.g. Grilo *et al.*, 2011) are also those where more road-kills occur. This seems to be true when corresponding confounding factors are controlled. For instance, Fahrig *et al.* (1995) found that despite there being an effect of date, time and traffic intensity on the proportion of frogs and toads found dead compared with those found alive, this ratio was constant when comparing two Canadian regions, with the number of absolute road-kills higher in the region with higher abundance of live amphibians. Similarly, Mysterud (2004) found that an increase in annual harvest (as a surrogate of population size) of red deer *Cervus elaphus* led to an increase in the number of car-killed deer only when excluding the year effect. In Sweden, moose *Alces alces* road-kills were most likely to occur on unfenced roads with intermediate traffic volumes and intermediate speed limits, and in hunting districts where moose harvesting was elevated (Seiler, 2005). Roger & Ramp (2009)
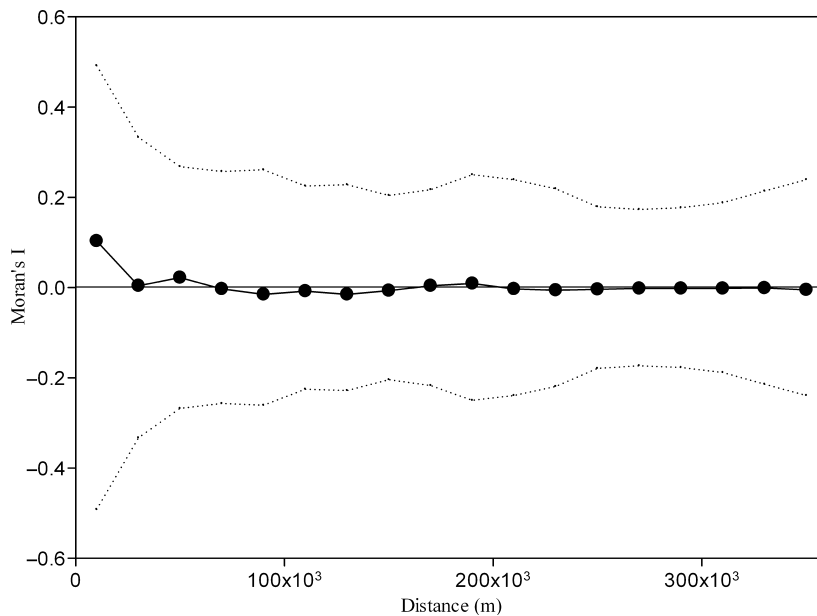
Figure 4 Moran's *I* values for the residuals of the polecat road-kill model. Dotted lines mark the maximum Moran's *I*.

Table 3 The eleven models that best defined the polecat road-kills. The R^2 is the percentage of variation in the polecat road-kills explained by the full model (including spatial filters), and K is the number of environmental variables contained in every model. The ΔAICc is the difference in AICc values compared with the estimated best model (lowest AICc) that allows the ranking of models from an estimated best (top of the table) to 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.

Model no.	Environmental variables contained in the model	R^2	K	ΔAICc (Δ_i)	AICc weight (ω_i)	Evidence ratio
1	MP ABUND + RABBIT + RIVER + OTHER CARNIV	0.254	4	0.000	0.058	0.00
2	MP ABUND + RABBIT + HOUSE + RIVER + OTHER CARNIV	0.255	5	0.351	0.048	19.18
3	MP ABUND + RABBIT + OTHER CARNIV	0.251	3	0.583	0.043	33.84
4	MP ABUND + RABBIT + RIVER +ROAD 2ND + OTHER CARNIV	0.255	5	0.768	0.039	46.81
5	MP ABUND + RABBIT + HOUSE + OTHER CARNIV	0.253	4	1.151	0.032	77.80
6	MP ABUND + RABBIT + HOUSE + RIVER + ROAD 2ND + OTHER CARNIV	0.256	6	1.425	0.028	103.91
7	MP ABUND + RABBIT + RIVER + ROAD 1ST + OTHER CARNIV	0.254	5	1.629	0.026	125.80
8	MP ABUND + RABBIT + ROAD 2ND + OTHER CARNIV	0.252	4	1.637	0.025	126.71
9	MP ABUND + RABBIT + HOUSE + RIVER	0.252	4	1.641	0.025	127.16
10	MP ABUND + RABBIT + RIVER	0.250	3	1.777	0.024	143.15
11	MP ABUND + RABBIT + HOUSE + RIVER + ROAD 1ST + OTHER CARNIV	0.256	6	1.880	0.023	156.00

used the distance to the nearest burrow to the road to reflect environments where common wombat *Vombatus ursinus* density is likely to be higher and found that this predictor is related with the probability of fatality. It is worth noting that some authors suggest that long periods of negative impact on target species (i.e. road-related losses over population viability threshold) may lead to population decline in those areas (Fahrig *et al.*, 1995; Roger & Ramp, 2009). Nevertheless, this evidence is not so strong in other cases where mortality rates are also high. For instance, road traffic is believed to kill around half of all adult and post-emergence badger cubs in Britain, while population trends show a notable increase (ca. 25%). Surpris-

ingly, in our study, road development (i.e. the amount of road kilometres per square) was only relatively important in explaining road-kills at a large scale. Our results mirror those from other studies that have found that other road traits like visibility, surrogated as sinuosity (Grilo *et al.*, 2011), or roadside vegetation coverage (Seiler, 2005), can be more important in explaining road-kill patterns than the simple amount of road.

Rabbits are the main prey of polecats in many regions, especially in Mediterranean habitats (Lodé, 1997; Santos *et al.*, 2009). These lagomorphs are commonly hunted by polecats in their warrens (Cuesta, 1994), although they can be consumed as carrion as well (Birks & Kitchener, 1999). However, on a
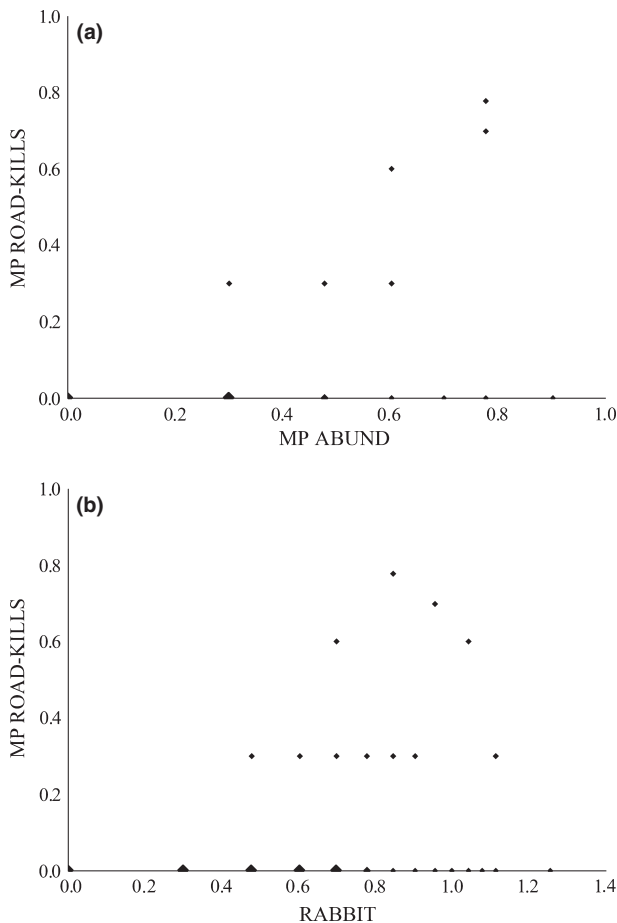
Figure 5 Relationship between the MP ABUND (polecat abundance, 5a) and RABBIT (rabbit abundance, 5b) variables with MP ROAD-KILLS (polecat road-kills). All the variables were log-transformed. The mark ◆ represents ≤ 20 cells, ◆20–50 cells and ◆> 50 cells.

consuming and require field work, which was beyond the scope of our study design based on atlas data.

Road-kill models were less accurate than abundance models, despite including specific variables related to road-kills. We based our models on such explanatory variables previously found to be important for explaining casualties at a local scale (Barrientos & Bolonio, 2009), some of them (human population density, riparian habitat cover) also found to be key variables in Mediterranean polecat habitat selection studies (Virgós, 2003; Rondinini *et al.*, 2006; Mestre *et al.*, 2007). However, whereas we did not study other factors found to be important in these works, like pine forest cover or altitude (Virgós, 2003), habitat variables have been related with road fatalities elsewhere (e.g. Clevenger *et al.*, 2003; Malo *et al.*, 2004; Saeki & Macdonald, 2004; Seiler, 2005). The inclusion of other variables could, perhaps, have increased the explained variance in road-kill models. Nevertheless, this possibility falls outside of a spatial transferability design, the basic idea of our paper, as we based our large-scale models on explanatory variables previously found to be significant at a local scale (Barrientos & Bolonio, 2009). We could not include as independent explanatory variables other road-related traits like traffic volume or speed because it is very difficult, and likely unreliable, to obtain a single value per cell when working with 100 km^2 cells. Instead, we used surrogate variables, i.e. the length of different road classes per cell. This fact could have limited the detection of road-kill patterns at large scales as it is difficult to find variables that exactly mirror those used at different scales. Furthermore, other explanations like differences in the ranges of values for the employed variables, as is expected a larger range in the larger region (i.e. in Andalusia, our testing region), could be influential as well. Indeed, from a transferability perspective, a model with variables that cover the same or a wider range in the training region is more likely to give accurate predictions in the testing region than the reverse (Randin *et al.*, 2006). An important issue in geographical transferability is that one cannot extrapolate beyond the range found in the training region (Van Horne, 2002). Differences in land-uses could reduce the transferability (McAlpine *et al.*, 2008), as in our study the training region is dominated by dry crops and uncultivated lands (Barrientos & Bolonio, 2009), while crops, scrubland and forests in different proportions cover most of Andalusia. The type of variables, the design of non-random sampling and false absences may also lead to invalid inference and may impair transferability (see the study by Zanini *et al.*, 2009 for more details). Our study is the first analysing the polecat road-kill pattern at a large scale, and it is possible that the numerous complex interactions common in casualties are likely to result in lower explained variance. The low number of cells with road-kill records compared to those with live polecats (17 vs. 130) could have influenced our results as well. The use of presence/absence data or larger cell sizes (e.g. 50 × 50 km or larger) could help to prevent such limitations. However, data resolution at those scales may not be appropriate for detecting road-kill patterns or the use of their findings in road planning.

local scale, rabbit abundance on road embankments seems to be a better explanatory variable of road-kills (Barrientos & Bolonio, 2009) than it is at a larger scale. Thus, other causes linked with territoriality, such as dispersal, seeking mates, territory marking or fluctuations in food availability (Davies *et al.*, 1987; Sleeman, 1988; Saeki & Macdonald, 2004; Langen *et al.*, 2009), could also be important sources of casualties at a large scale. Nevertheless, rabbit abundance is indirectly related to these factors, as it is also an important variable in explaining polecat abundance, as we show in our first model. It is possible that we could have obtained higher explanatory power by using a more precise rabbit abundance index. The one we used was employed because it was similar to the index used to evaluate polecat abundance in our meta-data. Other landscape-level studies have sampled rabbits by means of several methods, for instance 1-km-long transects (Virgós *et al.*, 2003), 1.5- to 3-hour surveys (Virgós & Travaini, 2005), 4-km-long transects combined with hunting statistics (Ferreira *et al.*, 2010) or comparing several methods (Fernandez-de-Simon *et al.*, 2011). However, all of these techniques are expensive and time-

Implications for road planning

To our knowledge, this is the first study that attempts to infer road-kill patterns at different scales and our findings could be useful in guiding future studies. Conclusions from the present study should be combined with those from local-scale studies (Barrientos & Bolonio, 2009) to minimize road-related mortality in the target species. Thus, a mitigation strategy to reduce polecat fatalities must be undertaken by means of two main steps. First, by using a 100-km^2 cell grid, those cells with higher polecat (or, alternatively, other carnivore) and rabbit densities should be located. Routes that do not cross these cells are preferred. Second, if alternative routes are not available, mitigating measures must be carried out at a local scale. These must be centred in those stretches of road with high numbers of rabbit warrens on road embankments (see the study by Barrientos & Bolonio, 2009). We are confident that this approach using different scales is useful not only to minimize polecat road-kills but also for any species that undergoes high levels of road fatalities.

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