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ORIGINAL PAPER

Response of carnivores to existing highway culverts and underpasses: implications for road planning and mitigation

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Abstract Roads with high traffic volumes are a source of animal mortality, can disrupt normal animal movements and dispersal, and may represent a potentially serious threat to wildlife population stability and viability. Retrofitting existing structures built for other purposes (e.g., drainage culverts or small below-grade access roads) to facilitate wildlife crossing by animals and to reduce mortality may be expensive if modifications to the existing structures themselves were involved. However, the environmental context surrounding these structures may influence the willingness of animals to cross, and management of some of these attributes may enhance the attractiveness of these structures. Culverts and underpasses are two common structures along roads in Portugal. We quantified the response of small and medium-sized carnivores to the presence of both types of existing passages by determining: (1) frequency of use; (2) whether use differed by type of passage, and if so; (3) by examining if associated environmental attributes might explain the differences observed. We surveyed 57 different passages along 252 km of highway with a total sampling effort of 2,330 passage trap-days. The mean passage rate for carnivores combined was 0.7 complete passages per crossing structure per day. Crossings by weasel, polecat, otter, and wildcat were infrequent or absent. Red fox, badger, genet and Egyptian mongoose used the crossing structures regularly and without obvious preference; stone marten preferred underpasses. Regression analyses showed the frequency of use by carnivores varied with structural, landscape, road-related features, and human disturbance with 17 of 26 (65%) attributes being significant. Larger passages with vegetation close to the passage entrances, favorable habitat in the surrounding area, and low disturbance by humans were important key features to regular use by the guild of species studied. Mitigation planning in areas with ecological significance for carnivores will be beneficial. Structural attributes and human disturbances are more difficult or expensive to change,

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even though related significantly to crossing use. Management of vegetation at passage entrances and restricting human use near passages in carnivore suitable areas may substantially improve crossing attractiveness for the guild of carnivore species.

Keywords Carnivores · Conservation · Habitat connectivity · Non-wildlife passages · Road design

Introduction

Increasing road density has emerged recently as a major conservation issue (Noss et al. 1996; Trombulak and Frissel 2000; Forman et al. 2003). Wide roads with high traffic volumes represent a serious threat to wildlife by introducing an additional source of mortality (Forman and Alexander 1998; Gerlach and Musolf 2000; Trombulak and Frissel 2000; Iuell et al. 2003; Epps et al. 2005). Furthermore, roads can disrupt animal movement and dispersal, creating effective barriers and resulting in the loss of landscape connectivity. Highways, in particular, often are avoided by wildlife as a consequence of increasing urbanization (Ruediger 1998; Hlaváč and Anděl 2002; Whittington et al. 2005). In some mammalian carnivores there is evidence of vulnerability to road network expansions (Ferreras et al. 1992; Haas 2000; Cain et al. 2003; Percy 2003; Kramer-Schadt et al. 2004) because of their relatively large ranges and low densities (Sunquist and Sunquist 2001). Some carnivores face threats of extinction in some regions. For example, Van der Zee et al. (1992) explicitly linked badger population declines in the Netherlands during the late 1980s to high road density; Thiel (1985) found that wolves disappeared when road densities exceeded 0.6 km km^{-2}. According to Chruszcz et al. (2003), in Banff National Park, Canada, grizzly bears were found closer to roads with low traffic volumes. In Spain, road density impacted fox and stone marten movements (Blanco 1988; Lopéz-Martin et al. 1997) resulting in home range changes. Similarly, Whittington et al. (2004) reported that roads increased the tortuosity of wolf movement pathways in areas of high road density. Given these data, it is clear that barrier effects in particular, have emerged as a significant threat to the viability of some carnivore populations world-wide. Thus, an opportunity to minimize barrier effects includes the adaptation of existing transportation infrastructures to facilitate passage and restore large-scale habitat connectivity.

Passages designed specifically to increase road permeability have been constructed for some groups of vertebrates (Foster and Humphrey 1995; Keller and Pfister 1997; Clevenger and Waltho 2000) but they are not common in Portugal. However, because existing structures built for other purposes (e.g., drainage culverts, and below-grade local access roads) are numerous and may often coincide with preferential crossing locations, they have received increasing attention as potential valuable alternatives to mitigate barrier effects (Hunt et al. 1987; Yanes et al. 1995; Rodriguez et al. 1996; Clevenger et al. 2001; Cain et al. 2003; Mata et al. 2005). The use of existing passages by carnivores is relatively well-described (Foster and Humphrey 1995; Clevenger et al. 2001; Gloyne and Clevenger 2001; Cain et al. 2003; Dodd et al. 2004; Clevenger and Waltho 2005). There is evidence that carnivores do not cross highways at random, but rather focus their crossing activity in locations that vary with passage characteristics, road-related attributes, surrounding habitat characteristics, and human disturbance levels (Barnum 2003; Rodriquez et al. 1997; Clevenger and Waltho 2000; Mata et al. 2005). Therefore, managing the habitat surrounding in existing crossing structures may well be a cost effective way of increasing their use (Iuell et al. 2003).

In the Mediterranean region, a world biodiversity hotspot (Myers et al. 2000), some studies have investigated the role of existing structures and their importance in restoring landscape permeability for some small and medium-sized carnivores (Yanes et al. 1995; Rosell et al. 1997; Rodriguez et al. 1997; Mata et al. 2005; Ascensão and Mira 2007). However, there is little consensus on whether the type of passage significantly influences crossing rates. Rosell et al. (1997) found no significant differences related to size of passage; Mata et al. (2005) reported that most carnivores in Spain (except weasels) preferred larger structures; Yanes et al. (1995) and Ascensão and Mira (2007) found some carnivore species used smaller culverts regularly. To examine the importance of passage size on restoring carnivore habitat connectivity, we collected quantitative data on the response of small and medium-sized carnivores to the most common existing structures along selected highways in Portugal: culverts and underpasses. Culverts are small-sized circular or rectangular tubes that allow for water flow from surrounding drainages, whereas underpasses are larger passages usually built for passage by farm vehicles. We first sought to determine how often carnivores used crossing structures. Second, we were interested in whether differences in passage use were related to structure size, or to measurable environmental variables associated with each structure. We expected a regular use of existing passages by carnivores but different crossing rates for each type of passage. Specifically, we predicted that both fossorial (fox and badger) and ground-dwelling (mongoose) species would use the culverts more often whereas arboreal (stone marten and genet) species would use the larger underpasses. Additionally, we expected that cover would explain some of the variance in passages use.

Study area and methods

Study area

The study was conducted along 252 km of two highways (A2—94 km and A6—158 km) in Alentejo province, southern Portugal between March and September 2004. Both highways are four-lane roads and are bordered on both sides by unburied livestock exclusion fences (1.5 m high, 10 cm mesh size). Between 1998 and 2001, reconstructed stretches of both highways were opened to traffic. Currently A2 and A6 have an average daily traffic volume of ~13,000 and ~6,000 vehicles/day, respectively. The densities of the different crossing structures were similar for both highways and averaged: 1.22 circular culverts/km (1 × 1 and 1.5 × 1.5 m), 0.34 box culverts/km (2 × 2, 3 × 3, 4 × 4 and 5 × 5 m), and 0.47 underpasses/km (5 m height and 8 m width). Mean distance between crossing structures was ~390 m, and ranged from 5 to 1,566 m.

The study area was characterized by its vast plains, with elevations ranging from ~200 to 500 m, and by its Mediterranean climate. The region was originally covered by woodlands and scrublands, but has been modified by human activity for centuries, and especially since the 1930s. The resulting landscape is highly fragmented, with about half of the area occupied by cropland. The remaining area is dominated by cork oak (*Quercus suber*) woods in the west and holm oak (*Quercus ilex*) woods in the east. Primary human activities include cork extraction, livestock, agriculture, and hunting. Three Natura 2000 sites (Sado, Cabrela, and Monfurado) are located in the province. Human population density is ~43 inhabitants km^{-2} (INE 2002) and the road network density averages 0.25 km km^{-2}, about half of the mean national road network density of 0.49 km km^{-2} (IgeoE 1999).

The carnivore community in the study area is diverse and comprised of nine species (Santos-Reis and Petrucci-Fonseca 1999): fox (*Vulpes vulpes*), weasel (*Mustela nivalis*), polecat (*Mustela putorius*), stone marten (*Martes foina*), badger (*Meles meles*), otter (*Lutra lutra*), genet (*Genetta genetta*), Egyptian mongoose (*Herpestes ichneumon*) and wildcat (*Felis silvestris*). The wildcat is legally classified as threatened (Vulnerable), while the polecat is classified as Data Deficient (Cabral et al. 2005). The otter, although classed as Least Concern in Portugal (Cabral et al. 2005) is of conservation concern in Europe (Near Threatened, IUCN 2006).

Crossing structures and monitoring

A sample of 57 crossing structures was selected for monitoring of carnivore use along the A2 and A6 highways (Fig. 1), and included two structural designs: (1) 44 circular culverts (1 and 1.5 m of diameter) and 13 underpasses (5 m high, 8 m wide). On average, the minimum distance between crossings selected for this study was 2 km (roughly equivalent to the average diameter of carnivore home range, as documented by Palomares and Delibes 1994; Rosalino et al. 2004; Santos-Reis et al. 2004; Rondinini et al. 2006) in order to minimize the effects of spatial autocorrelation and help insure independence of observations (Guisan and Zimmermann 2000).

Field work took place during the driest period of the year when passages were least likely to be flooded. We used marble dust to detect tracks during 20 consecutive days in spring and 20 days in summer, 2004. A dust plot 1 m wide and 3–10 mm deep was put on the ground at both ends of each culvert and in the middle of the underpass, checked every 5 days, and carnivore tracks identified (Lawrence and Brown 1973; Blanco 1998; Piñero 2002). On average, we checked each crossing eight times during the monitoring periods. Adverse weather conditions and livestock and human activities occasionally prevented clear identification of tracks, hence we only recorded data when a correct assessment of

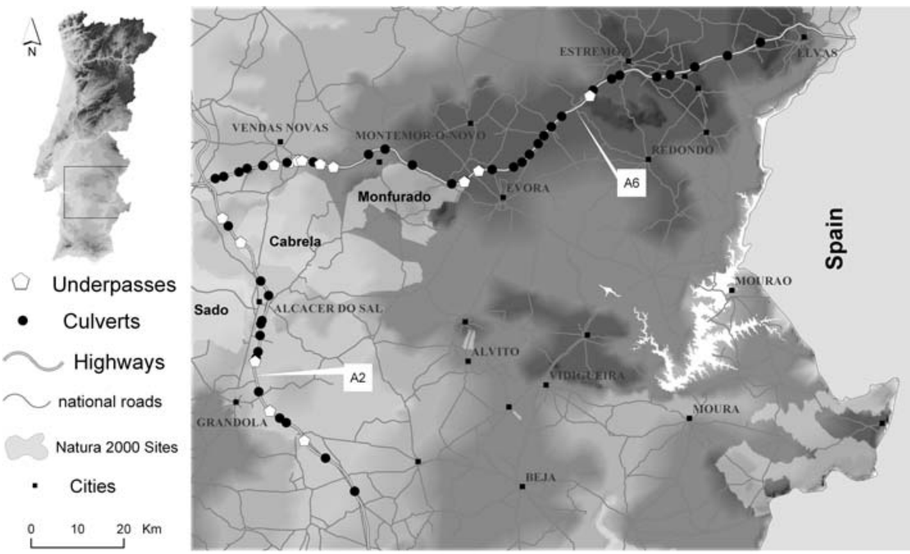

Fig. 1 Study area and passages location along the A2 and A6 highways

animal sign was possible. Each record included species ID, number of tracks, and whether the tracks completely or partially crossed through the passage). In selected passages, infra-red digital Camtrack® cameras were used at both entrances to validate track identifications.

Data analysis

To calculate the crossing rate, we summed the number of times a given species used the passage (complete passage) and divided by the number of operative days the passage was sampled for each season. We also quantified partial passage, which occurred when the tracks were not found in both passage entrances in the same direction and infra-red cameras detect enter and exit of the same species in a short period of time.

In general, crossing rates tended to be higher in spring than in other seasons, with significant differences between spring and summer (Wilcoxon test, $P < 0.05$), hence for the analysis, we compared the mean crossing rates between the two seasons.

To evaluate the effect of passage size on number of crossings, we removed the confounding effects of the surrounding landscape by using two approaches: (1) we analyzed 26 crossing structures (13 circular culverts plus 13 underpasses) placed along both highways; and (2) we compared six paired culverts and underpasses. Mann–Whitney *U*-tests ($P < 0.05$) were conducted to test for significant differences in use of passages based on size and Wilcoxon signed rank tests for differences in use for six paired passages.

To assess the influence of environmental variables on passage use, we used all sampled crossing structures ($n = 57$); each was characterized according to 32 independent variables (Table 1). Structural variables included crossing structure dimensions: width, height, and an openness ratio (Yanes et al. 1995), distance from highway to passage, and year of construction. Landscape attributes at a micro-scale included percentage of five land use types measured within a 500 m radius of the crossing structure: urban, intensive agriculture, extensive agriculture, oak woodlands, and production forest (*Pinus* spp.; *Eucalyptus* spp.). In order to evaluate the influence of landscape variables on the passages use, we also estimated the proportion of the five habitat cover types mentioned above within a circle with a radius equivalent to the carnivores' home range around each passage. We used the home range size of 300 ha for stone marten, genet and mongoose data (see Palomares and Delibes 1991, 1993; Santos-Reis et al. 2004), and 500 ha for fox and badgers (see Rosalino et al. 2004). Distances from passage to the nearest forest cover, as well as the proportion and average height of shrubs within 10 m were also measured. In order to evaluate the role of streams and associated vegetation, streams were characterized by width, direction, and distance to the highway. Road-related attributes included: number of additional existing structures in a 1,000 m buffer around each passage, distance to the next nearest crossing structure, and average distance from each structure to the nearest two structures. Human disturbance attributes included 2004 daily average traffic volume (BRISA, unpublished data), intensity of human activity, minimum distance to other roads and average distance to urban areas.

Because of the proportional nature of the response variable (species crossing rates), we assumed that errors followed a binomial distribution (Zuur et al. 2007). Therefore, generalized linear models with a logarithmic function were fitted to the data to investigate the influence of environmental attributes near passages on species crossing rates (Faraway 2004). Only variables that yielded significant results ($P < 0.10$) for species-specific crossing rates in the bivariate regression analysis were used as predictors for subsequent

Table 1 Names, definitions, mode and range of values of variables used in the analysis

Variables	Definition	Mode	Range values
Structural			
Width	Crossing structure width (m)	1	1–9
Height	Crossing structure height (m)	1	1–6.2
Openness	Crossing structure openness (= width × length/height)	0.03	0.03–1.33
Landscape			
Urban_500 m	Urban within 500 m radius (%)	0	0–10
Intensive agriculture_500 m	Intensive agriculture within 500 m radius (%)	0	0–50
Extensive agriculture_500 m	Extensive agriculture within 500 m radius (%)	0	0–100
Oak woodland_500 m	Oak woodland within 500 m radius (%)	0	0–100
Production forest_500 m	Production forest within 500 m radius (%)	0	0–20
Urban_hr	Urban within home range area[a] (%)	0	0–7
Intensive agriculture_hr	Intensive agriculture within home range area[a] (%)	0	0–100
Extensive agriculture_hr	Extensive agriculture within home range area[a] (%)	0	0–95
Oak woodland_hr	Oak woodland within home range area[a] (%)	0	0–98
Production forest_hr	Production forest within home range area[a] (%)	0	0–7
% Shrub cover_500 m	Shrub cover measured within 500 m radius (%)	0	0–100
Distance to forest cover	Minimum distance from the passage to forest cover (m)	0	0–2,000
Density of vegetation at the entrance	0 = absent; 1 = sparse; 2 = dense	0	0–2
Height vegetation	Average height of vegetation within 10 m of both entrances (m)	0	0–1.25
Stream width	Stream width (m)	0	0–8
Distance to streams	Distance to streams (m)	2,000	0–2,000
Stream direction	0 = absent; 1 = parallel, 2 = perpendicular	0	0–2
Type of riparian vegetation	0 = absent, 1 = shrubs, 2 = gallery	0	0–2
Structure of riparian vegetation	0 = absent, 1 = open, 2 = closed	0	0–2
Road-related			
Highway—passage distance	Distance from the passage entrance to highway edge (m)	7	1–21
Year of construction	Year of construction of the highway (year)	1998	1995–2001
Distance to the nearest passage	Distance to the nearest crossing structure (m)	100	1–580
Distance to the two nearest passages	Average distance to the nearest crossing structure at both sides of the passage (m)	250	75–875
Number passages	Number passages in within 1,000 m radius from the passage	6	1–12

Table 1 continued

Variables	Definition	Mode	Range values
Human disturbance			
Traffic volume	Mean 2004 average daily traffic volume (no vehicles/day)	9,404	3,000–18,000
Human use	0 = absent; 1 = irregular; 2 = regular	0	0–2
Distance to roads	Minimum distance to linear infra structures (other roads) (m)	349	109–519
Distance to cities	Average distance to cities within 1,000 m radius (m)	250	0–4,031
Road density_hr	Sum of road length within home range area[a] (m)	2,514	2,247–8,591

[a] 300 ha for stone marten, genet and mongoose and 500 ha for fox and badger

multiple regression analysis. We applied a stepwise selection procedure to retain significant variables and their interactions. Suitable transformations on the dependent and independent variables were conducted to reduce the effect of outliers (Chaterjee and Price 1991). In addition, we constructed a correlation matrix and excluded correlated variables to minimize multicollinearity. All statistical analyses were conducted using the Brodgar 2.5.1 (Zuur et al. 2007) and SPSS 14 v. (SPSS 2003) software programs.

Results

Which species used the crossings?

Eight carnivore species used the crossing structures over 2,330 trap-days: red fox, weasel, polecat, stone marten, badger, otter, genet, and Egyptian mongoose. Although present in the study area (Pinto and Fernandes 2001; Fernandes 2004), no wildcats were recorded. A total of 1,940 carnivore tracks were recorded; 1,649 (85%) were complete passages. The average crossing rate was 0.7 complete passages per structure per day (Table 2). Egyptian mongoose (28%) and badger (27%) crossed most frequently, followed by fox (18%), stone marten (12%), genet (12%) and otter (2%). Weasels ($n = 2$) and polecats ($n = 1$) crossed least frequently. The average number of species detected at a crossing structure was 3.32 ($SD = 1.17$). Absence of wildcat records and the small number of weasel, polecat, and otter records precluded statistical analysis. We focused on complete crossings by the five species that used the passages the most (red fox, stone marten, badger, genet, and Egyptian mongoose).

Did passage size make a difference?

Even though there was a tendency to use the larger underpasses (Fig. 2), only stone marten showed a statistically significant preference ($U = 40.5, 0.01 < P < 0.05$). When use of paired culverts and underpasses was conducted, we found similar results: selection was random except for stone marten, which preferred underpasses ($Z = -1.782, 0.01 < P < 0.05$).

Table 2 Movements through crossing structures expressed in number of tracks per day

Type[a]	Fox		Weasel		Polecat		Stone marten		Badger		Otter		Genet		Mongoose	
	CP	PP	CP	PP	CP	PP	CP	PP	CP	PP	CP	PP	CP	PP	CP	PP
Spring	0.085	0.014	0.000	0.001	0.001	0.000	0.117	0.028	0.212	0.025	0.013	0.001	0.104	0.021	0.188	0.060
Summer	0.151	0.015	0.000	0.000	0.001	0.000	0.053	0.017	0.162	0.015	0.013	0.003	0.065	0.006	0.207	0.043

[a] CP, complete passage; PP, partial passage

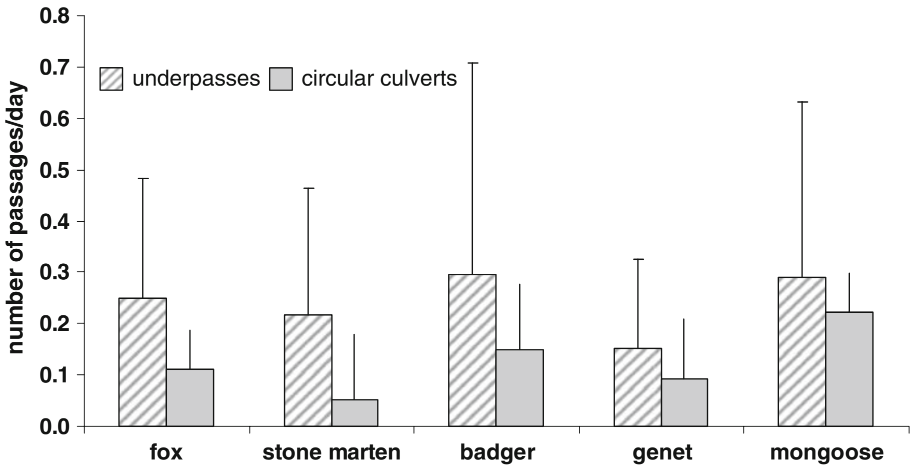

Fig. 2 Mean crossing rates for the culverts and underpasses and standard deviation respectively ($n = 26$)

Table 3 Deviance explained with their slope (± slope value) and level of significance and numbers (1–9) indicating variable importance rank for each species

Variables	Fox		Stone marten		Badger		Genet		Mongoose	
Structural										
Width	+0.09**	1	+0.22**	1	+0.100**	5	+0.06*	5	ns	
Height	+0.08**	2	+0.18**	2	+0.080**	7	+0.04*	6	ns	
Openness	+0.07**	3	+0.16**	4	0.060**	9	+0.06*	5	ns	
Landscape										
Extensive agriculture_500 m	ns		0.08**	6	−0.18**	1	−0.09*	2	ns	
Oak woodland_500 m	+0.08**	2	+0.17**	3	+0.11**	4	+0.07**	4	+0.04*	5
% Shrub cover_500 m	ns		ns		ns		ns		+0.07**	4
Intensive agriculture_hr	ns		−0.17*	3	ns		ns		ns	
Oak woodland_hr	ns		0.12*	5	0.07*	8	ns		ns	
Distance to forest cover	ns		−0.08**	7	−0.17**	2	−0.06*	5	ns	
Height of vegetation	+0.07**	3	ns		ns		ns		+0.14**	1
Stream direction	ns		ns		+0.04*	10	ns		+0.11**	2
Type of riparian vegetation	ns		ns		+0.09**	6	ns		+0.07**	4
Structure of riparian vegetation	ns		ns		ns		ns		+0.07**	4
Road-related										
Distance to the nearest passage	ns		−0.09**	6	ns		ns		−0.08**	3
Highway—passage distance	ns		+0.08*	7	ns		ns		ns	
Human disturbance										
Traffic volume	ns		ns		+0.06**	8	ns		ns	
Human use	ns		ns		−0.08**	7	−0.08*	3	ns	
Distance to roads	+0.07**	3	+0.06**	8	+0.12**	3	+0.10**	1	ns	
Distance to cities	ns		ns		+0.04*	10	ns		ns	
Road density_hr	ns		ns		ns		−0.09*			

ns—not significant; * $0.05 > P < 0.10$; ** $0.00 > P < 0.05$

What environmental variables influenced passage use?

Regression analyses showed that the frequency of use by carnivores varied with structural, landscape, road-related features, and human disturbance variables (Table 3); 19 of 32 (59%) attributes were significant. Structural attributes (width, height, and openness) had high explanatory power; with the exception of mongoose, carnivores were less likely to use smaller passages. Landscape attributes also influenced crossing rate. All carnivores tended to use passages within oak woodland areas. High vegetation height at crossing entrances was important for fox and mongoose; distance to forest cover was important for all carnivores. Mongoose crossings were correlated with stream direction, as well as the type and structure of riparian vegetation. Stone marten and mongoose passage use was negatively correlated with distance to the next nearest existing structure. Intensive agriculture and forest production, density of vegetation at the entrance, stream width, and distance to streams, as well as road related descriptors such as the number of passages in a 1,000 m buffer and year of highway construction, were not significantly related to crossing use.

Five species-specific models were developed (Table 4). The proportion of variance (R^2) explained by the models developed for each carnivore had values that ranged from 0.15 to 0.40, suggesting other unmeasured variables were responsible for crossing behavior. Some structural attributes, habitat features, road-related attributes, and human disturbance were

Table 4 Variables retained in the stepwise regression model for each carnivore species, coefficients (B), standard error, significances, *P*-value (*t* test) and deviance explained (D)

Species	Variables	B	Std Error	*P*-value	D
Fox[a]	(Constant)	−2.03	0.037	0.000	0.146
	Oak woodland_500 m	0.01	0.004	0.010	
	Height vegetation	0.09	0.04	0.030	
Stone marten[a]	(Constant)	−3.04	0.501	0.000	0.311
	Width (1)	0.09	0.430	0.040	
	Width (2)	1.2	0.380	0.002	
	Oak woodland_500 m	0.01	0.005	0.010	
Badger[a]	(Constant)	−2.61	0.640	0.001	0.395
	Oak woodland_500 m	0.01	0.003	0.010	
	Distance to roads	0.00	0.001	0.003	
	Cover distance	−0.31	0.120	0.010	
	Type of riparian vegetation (1)	0.78	0.260	0.005	
	Type of riparian vegetation (2)	0.16	0.300	0.590	
Genet[a]	(Constant)	−3.11	0.770	0.000	0.245
	Distance to roads	0.01	0.001	0.010	
	Oak woodland_500 m	0.00	0.004	0.010	
	Human use (1)	−0.69	0.330	0.040	
	Human use (2)	−0.83	0.450	0.070	
Mongoose[a]	(Constant)	−1.20	0.230	0.000	0.195
	% Shrub cover_500 m	0.01	0.003	0.008	
	Stream direction (1)	0.26	0.320	0.410	
	Stream direction (2)	0.90	0.290	0.003	

[a] The data used for these species were square root transformed

important model components for carnivores, although their influence varied by species. Except for mongoose, the presence of oak woodland forest was the most important variable in the models. Distance to other roads was positively related to badger and genet crossing rates, whereas human use was negatively correlated with genet crossings. Passage width was a predictor of stone marten crossings. Vegetation height and % shrub cover helped to explain fox and mongoose crossing rates, respectively.

Discussion

The most common habitat-generalists (fox, stone marten, badger, genet and mongoose) used large and small passages regularly, but specific attributes influenced species differently in determining the effectiveness of a passage. Our findings suggest that structure size is important especially for the arboreal stone marten which preferred larger passages. In general, crossing rates were two times higher in passages 1.5 m wide or larger. These results differ from those reported by Rodriguez et al. (1997) who did not find any preference or avoidance by fox or wildcat; however, their passages ranged from 1.2 to 3.5 m while our passages ranged from 1 to 8 m, suggesting a threshold response.

In general, larger passages with vegetation close to the passage entrances, favorable habitat in the surroundings, and low disturbance by humans were important key attributes. The presence of vegetation >0.5 m high at the passages entrances was associated with higher fox, stone marten, and mongoose crossing rates. When the proportion of oak woodland forest cover was >75%, we found higher values of crossing rates for all carnivores. Both features contributed to masking passage structure and provide greater protection and security for animals. Human disturbances in the vicinity of passages limited their use (Clevenger and Waltho 2000; Ng et al. 2004; Ascensão and Mira 2007). We observed a significant increase in fox, stone marten, badger, and genet crossing rates when distance to other roads was 500 m or greater. Where we found absence of human activity, the crossing rates doubled for badger and genet. When the distance to urban centers was greater than 2,000 m, badger crossing rates increased significantly. We documented that when stream flow passed through a passage, mongoose crossing rates were two times higher than when the stream paralleled the crossing. Streams with riparian vegetation provide travel corridors providing shelter and food, and anti-predator cover (Simberloff and Cox 1987; Hobbs 1992; Palomares and Delibes 1993; Virgós 2001), and influence the moving pattern of the mongoose, a largely diurnal species that avoids open areas (Palomares and Delibes 1991).

Both culverts and underpasses play an important role in maintaining landscape connectivity for carnivores in general, but the existing structures appear to be selectively permeable. Species-specific habitat preferences contribute to the observed differences in permeability and may act cumulatively. Otters, polecats and wildcats are habitat specialists. Otters are water-obligate (Beja 1992), and because we specifically chose the driest season to avoid water in the passages, their lower frequency of crossing does not reflect their high abundance in Portugal (Trindade et al. 1998; Cabral et al. 2005). Polecats, although not strictly water dependent, show a high association with aquatic environments (Lode 1994; Zabala et al. 2005) for the higher availability and diversity of prey (e.g., amphibians and crayfish). For wildcats, as forest-dependent and highly persecuted species (Fernandes 2004), the need for undisturbed old growth forest patches may not apply to the road-related environments, at least at the scale of analysis of this study. Weasels, on the contrary, do not show strict habitat preference (King 1975; Santos-Reis 1989; Blanco

1998; Klemola et al. 1999) but are rodent-specialists and this largely influences their demography with populations showing strong fluctuations that in some cases may lead to almost local extinctions (Santos-Reis 1989). The 2 year drought preceding and during the study was the driest period during the last 75 years and influenced plant productivity and rodent numbers, and weasel populations were very low. Regardless, weasels avoid open areas and use linear corridors such as stone walls or vegetation strips (King 1975); structures not normally present in the passages.

The variability found on passages use frequency was also related to differences in population densities. The occurrence of a particular species in the vicinity of a passage and fluctuations in its local abundance and activity patterns may explain the large amount of crossing rate variance (Yanes et al. 1995; Rodriguez et al. 1996; Clevenger et al. 2001; Hlaváč and Anděl 2002). Rodriguez et al. (1997) found that for foxes and wildcats the variance explained by passage attributes was much lower (0.06–0.16) than that explained by patterns of the species abundance (0.23–0.53). Undoubtedly, shelter and food resources exert an important role. We found an increase in crossing rates in oak woodland where relative abundances were higher.

Overall, our results indicate that culverts and underpasses facilitate the crossing of highways by carnivores. These structures appear to be important for landscape connectivity. To increase the likelihood of passage use by the carnivores guild we suggest some guidelines for highway managers: (1) promote the construction of large passages; (2) prioritize mitigative measures in areas with ecological significance for carnivores, e.g., forested areas of natural woods and where streams associated with riparian vegetation run through or close to the passages; (3) plant vegetation at passage entrances to guide animals towards the existing structure; (4) restrict human use of passages and (5) maintenance of natural vegetation structure inside the passage (soil, logs, rocks, woody debris) will help encourage use by more sensitive species (weasel and polecat) to artificial structures.

An integrated approach using combined mitigation measures should reduce the impact of roads. Additional work on other methodologies that account for seasonal and yearly variations as well as effective monitoring to evaluate the effectiveness of these measures will be beneficial. Further information is needed to clarify the relationship between species density and crossing rates.

Less common species are important components of the ecosystem and their inclusion will be important. Consideration of adequate gene flow and connected populations will enable decisions regarding the effectiveness of passages and the restoration and maintenance of basic ecological processes and functions.

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