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Research article

Impact of culvert flooding on carnivore crossings

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ABSTRACT

Along many roads worldwide, drainage culverts are the only structures wildlife can safely use to cross. However, culverts inundate and can become unavailable to terrestrial fauna during rainy periods. We conducted a field study over wet and dry seasons in southern Portugal to assess the effect of culvert flooding on crossings by medium-sized carnivores. We set up track stations inside 30 culverts along intermediate-level traffic roads to evaluate complete crossings (n = 1211) and used mixed-effects models to quantify the effects. Carnivores were more likely to cross and crossed more frequently if the culvert had a natural dry pathway at the time of the crossing. Carnivores were also more likely to cross culverts with streams running through them. Moreover, culverts with flowing streams during the wet season were still more likely to be crossed during the dry season when the streams were dry. The significance of the difference in crossing rates between wet and dry seasons was species-specific. Our study reveals that flowing water and dry pathways jointly contribute to promoting crossings by this carnivore community. Culverts including streams may act as a continuation of riparian corridors, being incorporated into carnivores' movement routes. Our results lend empirical support to recommendations advising the implementation of dry pathways to provide crossing paths. Interventions to offset the transient impacts of water flooding in new or existing culverts can be a cost-effective solution promoting connectivity across roads allowing movement of individuals.

1. Introduction

Although roads increase habitat fragmentation, act as barriers to movement, and kill many animals (Grilo et al., 2015), much effort has been made to mitigate these effects. It is becoming increasingly common to include technically sound structures allowing safe animal road-crossings, especially along roads and highways (Clevenger and Waltho, 2000, 2005; Forman et al., 2003). Because fully adequate wildlife crossing structures are expensive (Ascensão and Mira, 2007; Glista et al., 2009), safe road-crossings commonly rely exclusively on drainage culverts designed for water flow (Delgado et al., 2018). Regrettably, these culverts inundate repeatedly becoming unavailable to most terrestrial fauna during rainy periods (Liu and Zhao, 2003; Grilo et al., 2010).

Culverts are primarily engineered to allow rainwater runoff and stream flow under the road and prevent flooding (Liu and Zhao, 2003). Culvert dimensions may be determined for an estimated return period of the maximal discharge (e.g., 50 years between occurrences) based on local climatological and hydrological characteristics (Schall et al., 2012). Notwithstanding, different groups of vertebrates regularly use drainage culverts worldwide (Dodd et al., 2004; Ng et al., 2004; Crook et al., 2013), including in Mediterranean areas (Yanes et al., 1995; Rodriguez et al., 1996; Clevenger et al., 2001; Mata et al., 2005), such as in southern Portugal (Ascensão and Mira, 2007; Grilo et al., 2008; Serronha et al., 2013; Villalva et al., 2013). Different species can show species-specific preferences for how the culvert is designed (Martinig and Bélanger-Smith, 2016).

Given their large home-ranges, low population densities, low reproductive rates, and dispersal needs, carnivores are particularly vulnerable to road impacts (Grilo et al., 2015). Carnivores forage and disperse across roads throughout their territory, increasing the likelihood of road encounters and car collisions (James and Stuart-Smith, 2000; Clevenger and Wierzchowski, 2006). Among medium-sized carnivores, the European badger (*Meles meles*) is a well-documented species in which 10–40% of mortality events in some populations may be due to roadkill deaths (van der Zee et al., 1992; Aaris-Sørensen, 1995; Clarke et al., 1998; Revilla et al., 2001). In southern Portugal, Grilo et al. (2009) estimate an annual roadkill rate of about 47 medium-sized carnivores/100 km/year along 314 km of national roads. Noticeably, animal deaths may diminish on roads with implemented mitigation

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measures (Clevenger, 1999; Barrueto et al., 2014), although there is still a lack of empirical evidence on how the recurring inundations impact animal crossings in wildlife passages.

Few studies evaluate the effect of water flooding on wildlife crossings through drainage culverts. Serronha et al. (2013) found most carnivore species tend to avoid culverts with a water depth higher than 3 cm and with an increasing percentage of ground covered with water (herein referred to as water cover). In southern Portugal, Villalva et al. (2013) installed 50-cm dry ledges to promote carnivores' crossings and found red foxes and badgers avoid culverts with ledges. Previous studies show culvert openness (*sensu* Reed and Ward, 1985) and vegetation near the entrances as being among the most important factors influencing culvert crossings by carnivores (Rodriguez et al., 1996; Ascensão and Mira, 2007; Grilo et al., 2008, 2015; Villalva et al., 2013). Also, other factors may exert important roles on carnivore crossings. For example, extensive farm fencing (Mata et al., 2005) too close to culverts' entrance may hinder access. Conversely, one may expect widespread roadside guardrails (Malo et al., 2004) to hamper access to the road, leading approaching animals to cross through the nearest culvert. In a broader spatial context, larger distances between culverts can be positively correlated with animal crossing rates (Smith, 2003; Clevenger and Waltho, 2005).

We conducted a field study covering the wet and dry seasons in southern Portugal to assess the effect of water inundation among factors influencing the crossing of drainage culverts by medium-sized carnivore mammals. Along three intermediate-level traffic roads, we set up track stations inside 30 culverts to evaluate carnivore crossings. We were interested in the effects of flooding on overall and species-specific responses. Our analyses considered two distinct datasets (wet and dry seasons) and sought to answer the following three questions: (i) Does water-related variables (pathway dry width, water cover, and water depth at crossing time) explain differences in the probability of crossings over the wet season? (ii) are water-related variables correlated with crossing rates?, and (iii) are crossing rates similar between the wet and dry seasons? We hypothesized that carnivores would be less likely to cross and cross less often if the culvert had more water (narrower dry width and greater water cover and depth), possibly leading to higher crossing rates during the dry season. Conversely, water flooding would have positive effects on crossings by semi-aquatic species such as the Eurasian otter (*Lutra lutra*).

2. Materials and methods

2.1. Study area and study design

Our study was conducted from 11 March to 6 May 2016 (wet season) and from 1 to 14 August 2016 (dry season) along three national roads (asphalt paved; two-lanes) in the Alentejo region of southern Portugal (Fig. 1). The local climate is Mediterranean with cold, wet winters (mean annual precipitation is 620 mm) and hot, dry summers with temperatures exceeding 40 °C (range: 7 to 43 °C). Typically, the wet season in the Euro-Mediterranean region goes from November to early March but in 2016 the main rainfall in Alentejo lasted from early March to late May (see IPMA, 2016), a time window mostly captured by our wet sampling season. Local total precipitation during the wet and dry sampling seasons was 131 and 0 mm, respectively. The landscape had undulating relief with altitudes ranging from 200 to 400 m asl and was dominated by cork oak (*Quercus suber*) and holm oak (*Quercus rotundifolia*) stands managed by an agro-forestry system called *montado* (*dehesa* in Spain), pastures, and a few olive groves. Specifically, the land cover 1500 m from our culverts was generally homogeneous, dominated (> 70% of the 1500 m buffer area) by pastures (n = 15 culverts) or *montados* (n = 15). The population density in the study area was 23 inhabitants/km^2 (INE, 2015).

The three road stretches, EN114, EN4, and EN18 (27.3, 56.9 and 43.2 km in length) were located in the Évora district and had traffic

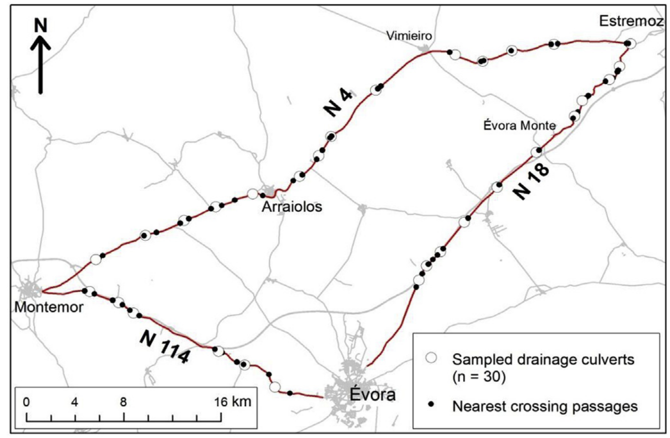

Fig. 1. The 30 drainage culverts sampled in southern Portugal, and their nearest passages. N4, N18, N114 = National roads.

ranging from 3000 to 10000 vehicles / day. These roads had high levels of carnivore mortality (Santos et al., 2011a). Two European Natura 2000 network Sites nearby – Monfurado and Cabrela – contribute to a high carnivore richness in the area. Carnivore species in the study area included Egyptian mongoose (*Herpestes ichneumon*), Common genet (*Genetta genetta*), Eurasian otter, European badger, Stone marten (*Martes foina*), European polecat (*Mustela putorius*), Weasel (*Mustela nivalis*), and Red fox (*Vulpes vulpes*).

To select culverts for both wet and dry sampling seasons, we first censused all the road crossing passages – driving at ~10–20 km/h. We geo-referenced 307 crossing passages, including culverts, bridges, viaducts, and underpasses for human and livestock use. We then haphazardly selected 30 drainage culverts (Fig. 1) spaced 2 km apart on average (1.5 km minimum), which was ~800 m longer than the maximum radius of the home range of the carnivore species in the area, ensuring the temporally independence of crossings between culvert samplings (Guisan and Zimmermann, 2000; Grilo et al., 2008). The selected culverts included 22 box, four circular, and four arch culverts. No perched culverts were present. They were made of concrete and generally had an irregular floor substrate with soil and sediments. Their sizes were small to medium in height (mean = 1.5 m ± 0.1 SE), width (2.1 m ± 0.3 SE), and length (19.4 m ± 1.1 SE). From road asphalt to culvert entrance, mean distance was 4.4 m (± 0.6 SE) and the slope was steep (ratio of vertical drop per horizontal distance = 44.4% ± 2.3 SE). The mean vegetation height at 10 m outside of the entrances was 75.7 cm (± 3.7 SE) on 18 July 2016.

2.2. Assessing carnivore crossings through culverts

To assess carnivore crossings, we mounted track stations inside the 30 drainage culverts. To record carnivore tracks, we used marble dust covering two boards (width = 60 cm; height = 0.3 cm; length = same as culvert width), both placed transversely inside the culvert, usually at 1.0–2.5 m distance from each entrance. To minimize dust contact with the floor moisture, we nailed rectangular wood cuboids (10 × 3 × 3 cm) on the underside of each board raising it 3 cm above ground (Fig. S1, Supporting information). We did this for every board over both the wet and dry sampling seasons. Whenever the culvert was inundated (over the wet sampling season), we further raised the boards up to a maximum of 10 cm using roof tiles and stone blocks. If there was no place with a water depth less than 10 cm to mount the boards, we temporarily removed them and did not record tracks over that flooding period. To enhance animals' habituation, the boards were left mounted inside the culverts for four consecutive days prior to the beginning of both wet and dry sampling seasons.

We covered each board with 0.3–0.5 cm marble dust smoothed with

Table 1
Names, definitions and range for the 8 attributes used in the analysis of the surveyed drainage culverts (n = 30) in Alentejo, Portugal.

Variable	Description	Range
Dry width	Average of three dry widths inside the culvert as measured (m) at both entrances and at the midpoint of the culvert tunnel having the shortest dry transverse width (Fig. S3, Supporting information).	0.00–5.53
Water depth	Average of the water depths measured (cm) at the same points as dry width.	0.00–33.30
Water cover	Visually estimated percentage of the culvert's ground covered with water.	0–100
Fence distance	Distance (m) class from the culvert entrances to a perpendicular farm fence (barbed wire fences usually with mesh size ≤ 15 cm): 0 = no fence, 1 = fence present at > 5 m, 2 = fence within 5 m distance.	
Guardrail	Presence of a guardrail on the road verge: 0 = none, 1 = single rail, 2 = double rail (Fig. S4, Supporting information).	
Stream	Persistence of a stream (yes/no) running inside the culvert over the entire wet sampling season.	
Grass cover	Visually estimated percentages of grasses 10 m from both culvert entrances.	0–100
Distance to the nearest passage	Distance (km) to the nearest crossing passage (culvert, bridge, viaduct, underpass for livestock).	0.03–1.61

a steel trowel. Marble dust is a scentless and persistent material that allows high-quality tracks (Yanes et al., 1995). Overall, our raised track stations with marble dust handled very well and provided accurate results despite the humid environment. To reduce inter-observer variability, one trained person only identified carnivore species onsite, or upon photographic record in a few cases. Whenever there were identification doubts between two carnivore species, the track was recorded as non-identified. If we felt the uncertainty could have arisen from confusion with domestic animals (cats, dogs), the record was discarded.

In the wet season, each culvert was sampled every two days (Mateus et al., 2011) for 29 operative days (i.e., days when tracks were recorded without water and/or wind damage). In one case, for logistic limitations, the sampling visit to all culverts took place three days after the previous visit. In the dry season, each culvert was sampled every day for 14 operative days. Hence, each culvert was sampled 14 times over the wet season, plus 14 times over the dry season. At each sampling date, we recorded the tracks/trails per species on each board and the movement direction. When having tracks/trails from the same species on one board, only clearly separated trails were considered as different records. At each sampling date, the marble dust was smoothed or replaced in order to prevent recount in the subsequent sampling date. The records were then converted to number of culvert crossings per species.

We analyzed complete carnivore crossings only, not visits to explore the interior of the culvert (see Martinig and Bélanger-Smith, 2016). We considered a carnivore to have visited but not crossed the culvert when there were tracks in both directions on one of the two boards. We assigned complete crossings to most of the other trail combinations (Fig. S2, Supporting information). We considered two complete crossings in the particular situation of two-directions on one board plus one direction in the other board. We took into consideration the possibility that carnivores may jump over track stations (van Vuurde and van der Grift, 2005; Costa, 2014).

2.3. Validating crossing assessment

Others have demonstrated using cost-benefit analyzes that track stations with marble dust can be more appropriate than video-surveillance in detecting drainage culvert crossings by our carnivore species in Alentejo (Mateus et al., 2011). In this study, to further confirm the adequacy of our track stations as compared to the widely used camera trapping method (Meek et al., 2016), a subset of the 30 culverts (20 during the wet and 12 during the dry seasons) was surveyed concurrently with infrared cameras. We used 14 Reconyx™ HC600 Hyperfire (Holmen, WI, USA) and six Bushnell® Trophy HD Aggressor (Kansas City, MO, USA) cameras since both devices allowed for continuous monitoring with minimal maintenance. They recorded two pictures per trigger with 5 s delay. We visited them during each sampling visit to replace SD cards and NiMH batteries as necessary.

We installed one tested camera trap device 2 m from one of the culvert entrances (Rowcliffe et al., 2011). In six cases, because the device field of view did not cover the entire culvert tunnel, two devices were installed, one per entrance. Over the wet and dry sampling seasons, all camera sensors operated continuously (taking photographs when motion-activated) one day before the boards were assembled to allow for habituation and five days prior to the beginning of track samplings. This period enabled us to assess the initial disturbance of our track stations on the species behavior. We used both methods simultaneously thereafter to determine the number of events in which they agreed (the two methods recorded at least one crossing or both recorded zero crossings) or performed differently (at least one crossing was recorded by one method and not by the other). An event was a period of time between consecutive track sampling visits. When analyzing the photographic records, we recorded complete crossings only, i.e., when an animal entered and was not seen turning back through the same entrance within 2 min (Serronha et al., 2013).

2.4. Other data collection

During each track sampling visit to a drainage culvert, we derived the mean number of complete crossings/day (hereafter crossing rate) by carnivore species and we collected variables that could possibly explain that response. The culverts were repeatedly flooded during the wet sampling season and were all dry during the dry sampling season. Thus, variables reflecting the water level inside the culvert were collected over the wet season only. Water-related variables and the remaining attributes are summarized in Table 1. Openness for each culvert was also calculated as its cross-section area divided by the culvert tunnel length (Reed and Ward, 1985). Following exploratory analysis, water cover was later simplified using the Jenks Natural Breaks classification method (Jenks, 1967) to determine the best arrangement of the percentage values into four classes: 0 = 0, 2 =]0,27], 3 =]27,57], and 4 =]57,100].

2.5. Statistical analyses

2.5.1. Wet season

To assess the effect of water-related variables and covariates (fence distance, guardrail, stream, grass cover, distance to the nearest passage) on carnivore crossings, we analyzed the wet season dataset alone. Each variable was expressed per species in each sampling date to a culvert. Because data records were nested by culvert, we used mixed-effects models with culvert as the random factor to explore relationships between carnivore crossings and explanatory variables. Openness was significantly correlated with dry width (Spearman correlation; $r_s = 0.7$, $P < 0.001$). We gave priority to using the latter when building the models because it was one of our water-related variables of interest. The other explanatory variables were not collinear ($r_s < 0.4$) and therefore could be included together in our mixed-effects models.

To determine if any of the water-related variables or covariates explained differences in the probability of crossing, we used the presence of carnivore species as a binary response variable (0 = not present; 1 = present). We conducted logistic generalized mixed models (GLMM) with a logit link using the *lme4* package in R (Bates et al., 2011). We built a logistic GLMM for the probability of crossing by all species combined and then built species-specific models.

To determine if any of the water-related variables or covariates explained crossing rates, we used the number of complete crossings / day / culvert (omitting records with zero crossings) as the response variable. In this case, we log(x)-transformed the response variable and conducted linear mixed-effects models (LMM) using the identity link in the *nlme* package in R to fit LMM (Pinheiro et al., 2011). We opted for just one LMM for all carnivore species combined as data were insufficient for modeling species-specific crossing rates. In both GLMM and LMM for all species combined, to account for the variance associated with species, we considered adding carnivore species as a random factor. However, a likelihood ratio test suggested adding species to random effects was a significant improvement in the GLMM ($L = 262.30$, $P < 0.001$) but not in the LMM ($L = 3.10$, $P = 0.099$), so we only included species to random effects of the GLMM.

Each minimal adequate (final) GLMM or LMM was arrived at by fitting the full model followed by backward elimination of non-significant ($P > 0.05$) explanatory variables one at a time and then applying an *F*-test of the likelihood ratios for the nested models (Zuur et al., 2009). We evaluated model adequacy by checking for normal distribution of residuals, plotting residuals vs fitted values and explanatory variables, and we evaluated model fit by the marginal R^2 (proportion of variance explained by the fixed effects; Nakagawa and Schielzeth, 2013). Spatial autocorrelation in the models' residuals was analyzed with Mantel tests (Legendre and Fortin, 1989). To evaluate model predictive performance, we applied a leave-one-out cross-validation procedure to each final model. Through this procedure, one observation at a time was left out, the model was fit using the remaining data, and the left out observation was predicted. Lastly, as predictive metrics, we calculated the Area Under the ROC curve (AUC) for each GLMM (*AUC* command in *cvAUC* package in R; LeDell et al., 2014) and the Root Mean Square Error (RMSE) for the LMM (*rmse* command, *hydroGOF*; Zambrano-Bigiarini, 2017). We performed all statistical analysis using R version 3.3.3 (R Development Core R Core Team, 2017).

2.5.2. Dry season and comparison between wet and dry seasons

To evaluate whether crossing rates were similar between the wet and dry seasons, we conducted LMM (one model per species and one for all species combined), in which season was the explanatory variable and culvert was the random factor. We also included species as random factor in the LMM for all species combined to account for the significant variance associated with it ($L = 1180.64$, $P < 0.001$). We further assessed whether the presence of a flowing stream during the wet season and a subsequently dry stream in the same culverts during the dry season would be influential in carnivore crossings through these culverts. To explore this relationship between crossings and stream only (no other predictors tested), we used separate logistic GLMM, each predicting the probability of crossing over the dry season for individual species and then for all species combined. In the latter case, we included species as random factor to account for the significant variance associated with it ($L = 205.37$, $P < 0.001$).

3. Results

We recorded a total of 1211 complete carnivore crossings through the 30 drainage culverts (Table 2), including 794 crossings over the 29 operative days of the wet sampling season (mean 0.96 ± 0.17 SE crossings / day) and 417 crossings over the 14 operative days of the dry sampling season (1.01 ± 0.21).

3.1. Crossing assessment reliability

When analyzing camera records (Fig. S5, Supporting information), we seldom saw behavioral responses likely to cause biases into our track crossing samples. In the first three days, some individuals did reacted to the track stations, smelling repeatedly or retreating from them. The amount of these behaviors was however residual from the fourth day on when track samples were collected. We never noticed jumps over the track stations.

Overall, we confirmed the adequacy of our track stations in recording drainage culvert crossings by these carnivore species as compared to infrared cameras. Indeed, in 99% of 466 events (sampling periods using both methods, lasting on average 1.61 ± 0.03 SE days), track stations performed better (54% events in which track stations recorded at least one crossing that was not detected by the camera trap) or similarly (45% agreement). Only in five events we recorded at least one crossing using cameras that was not detected by the track station with marble dust.

3.2. Wet season

3.2.1. Crossing probability for all species

In the wet season, the overall probability of crossing (Table 3, Fig. 2A–C) significantly (Type-II Wald chi-square: $\chi^2 = 3.89$, df = 1, $P = 0.040$; Fox and Weisberg, 2011) increased with dry width (a natural dry pathway through the culvert at the time of crossing). For example, the probability of crossing increased by 11% from 0.5 to 1.0 m dry width (Fig. 2). The presence of a stream (i.e., water flowing through the culvert during the wet season) significantly increased the probability of crossing by 2.5 times over the dry season ($\chi^2 = 5.16$, df = 1, $P = 0.022$). On the contrary, the probability of crossing significantly decreased with greater grass cover outside the culvert ($\chi^2 = 5.17$, df = 1, $P = 0.021$). Other variables were not deemed significant predictors of probability of crossing of all species combined. The model did not show spatial autocorrelation in its residuals (Moran's $I = -0.006$, $P = 0.990$). AUC reached 0.89, indicating covariates considered in this model could accurately predict crossing probability.

3.2.2. Crossing probability for each species

For Egyptian mongoose, the probability of crossing (Table 3; Fig. 2D and E) significantly ($\chi^2 = 4.93$, df = 1, $P = 0.026$) increased with dry width (e.g., 26% increase from 0.5 to 1.0 m dry width). The effect of water cover was also significant ($\chi^2 = 18.83$, df = 3, $P < 0.001$), having been the probability of crossing five times as much in culverts with intermediate wetness (27–57% water cover) as in dry ones (water cover = 0%). For European badger, the probability of crossing (Table 3; Fig. 2F and G) significantly ($\chi^2 = 5.01$, df = 1, $P = 0.025$) increased with dry width (e.g., 40% increase from 0.5 to 1.0 m dry width). Moreover, badger crossings were significantly more likely to occur with the presence of a farm fence within 5 m ($\chi^2 = 12.13$, df = 2, $P = 0.002$). For Common genet, the probability of crossing (Table 3; Fig. 2H) significantly ($\chi^2 = 5.88$, df = 1, $P = 0.015$) increased with dry width (e.g., 16% increase from 0.5 to 1.0 m dry width). For Eurasian otter, the presence of a stream significantly ($\chi^2 = 11.55$, df = 1, $P < 0.001$) increased the probability of crossing by 65 times compared to culverts without a stream (Table 3; Fig. 2I).

No other variables were found to be significant for each species probability of crossing. There was no significant spatial autocorrelation for the Egyptian mongoose (Moran's $I = -0.03$, $P = 0.886$), European badger ($I = -0.03$, $P = 0.936$), Common genet ($I = -0.002$, $P = 0.714$), or Eurasian otter ($I = -0.05$, $P = 0.990$) probabilities of crossing. Models had good to excellent predictive performances (AUC range = 0.77–0.90). Due to insufficient sample size, we excluded Stone marten and Red fox from our species-specific analyses.

Table 2
Summary values and significance level in the mixed-effects models testing for differences in the medium-sized carnivore crossing rates between the wet and dry seasons. O. d. = operative days. Crossings from non-identified species during the wet (15% of total) and the dry (5% of total) seasons are not shown. *** ≤ 0.001; ** ≤ 0.01; * ≤ 0.05; NS ≥ 0.05.

	Species						
	Egyptian mongoose	European badger	Common genet	Eurasian otter	Stone marten	Red fox	All species combined
Wet sampling season							
Crossings/day	0.26	0.22	0.18	0.09	0.03	0.01	0.96
Total (29 o. d.)	234 (29%)	187 (24%)	150 (19%)	76 (10%)	25 (3%)	5 (< 1%)	794
Dry sampling season							
Crossings/day	0.45	0.17	0.11	0.10	0.05	0.05	1.01
Total (14 o. d.)	188 (45%)	71 (17%)	47 (11%)	42 (10%)	21 (5%)	20 (5%)	417
Significance	**	*	***	NS	NS	***	NS

3.2.3. Crossing rate for all species

Whenever a culvert was crossed by at least one carnivore species, the number of crossings per day (Table 4; Fig. 3) significantly (χ^2 = 4.20, df = 1, P = 0.044) increased with dry width at the time of crossing (e.g., 5% increase from 0.5 to 1.0 m dry width). The presence of a stream during the wet season significantly increased the crossing rate by 44% compared to culverts without a stream (χ^2 = 6.54, df = 1, P = 0.016). Crossing rate significantly (χ^2 = 4.58, P = 0.033) increased with distance to the nearest passage (e.g., 22% increase from 0.5 to 1.0 km distance). Also, a significantly greater crossing rate was likely to occur when the road had a double guardrail (χ^2 = 8.30, P = 0.007). No other variable was found to have a significant effect on the crossing rate of all species combined. There was no significant spatial autocorrelation in the model residuals (Moran's I = −0.07, P = 0.998). RMSE reached 0.45, indicating a fair model prediction error.

3.3. Dry season and comparison between wet and dry seasons

Contrary to expectations, the crossing rate for all species combined did not change significantly from the wet to the dry sampling season (Table 2). However, that number did significantly increase in the dry season by 73% for Egyptian mongoose and by 400% in Red fox, although fox crossings were still few (5% of total). Conversely, the crossing rate significantly decreased by 23% for European badger and by 39% for Common genet.

Interestingly, culverts with flowing streams throughout the wet season were still more likely to be crossed by all carnivore species combined over the dry season when they were fully dried-up (Table 5). Species-specific models revealed the significance of the single effect of stream on increasing the crossing probabilities for Egyptian mongoose, Common genet, or Stone marten over the dry season.

Table 3
Fixed part of the optimal logistic mixed-effects models predicting the probability of crossing through a drainage culvert over the wet season by medium-sized carnivores. SE = standard error; CI = effect size confidence intervals.

Variable	Estimate	SE	*z*	2.5% CI	97.5% CI	*P*
All species combined	**(marginal R^2 = 0.16, conditional R^2 = 0.51; *AUC* = 0.89)**					
intercept	−2.012	0.547	−3.68	−3.105	−0.939	< 0.001
stream (yes)	0.661	0.326	2.22	0.021	1.314	0.022
dry width	0.216	0.112	2.02	0.060	0.437	0.040
grass cover	−0.017	0.008	−2.28	−0.033	−0.002	0.021
Egyptian mongoose	**(marginal R^2 = 0.24, conditional R^2 = 0.50; *AUC* = 0.82)**					
intercept	−2.908	0.553	−5.25	−4.096	−1.843	< 0.001
water cover [0,27%]	0.159	0.509	0.31	−0.883	1.135	0.754
[27,57%]	2.382	0.564	4.22	1.322	3.565	< 0.001
[57,100%]	1.290	0.691	1.87	−0.118	2.658	0.062
dry width	0.558	0.251	2.22	0.0319	1.055	0.026
European badger	**(marginal R^2 = 0.23, conditional R^2 = 0.59; *AUC* = 0.86)**					
intercept	−2.745	0.626	−4.38	−4.199	−1.633	< 0.001
farm fence (< 5 m)	2.372	0.690	3.44	1.048	3.910	< 0.001
(> 5 m)	0.373	0.646	0.58	−0.980	1.718	0.564
dry width	0.739	0.330	2.24	0.127	1.480	0.025
Common genet	**(marginal R^2 = 0.14, conditional R^2 = 0.28; *AUC* = 0.77)**					
intercept	−1.834	0.288	−6.35	−2.467	−1.293	< 0.001
dry width	0.361	0.148	2.43	0.067	0.675	0.015
Eurasian otter	**(marginal R^2 = 0.37, conditional R2 = 0.71; *AUC* = 0.90)**					
intercept	−5.924	1.144	−5.18	−9.163	−4.192	< 0.001
stream (yes)	4.365	1.284	3.40	2.251	7.885	< 0.001

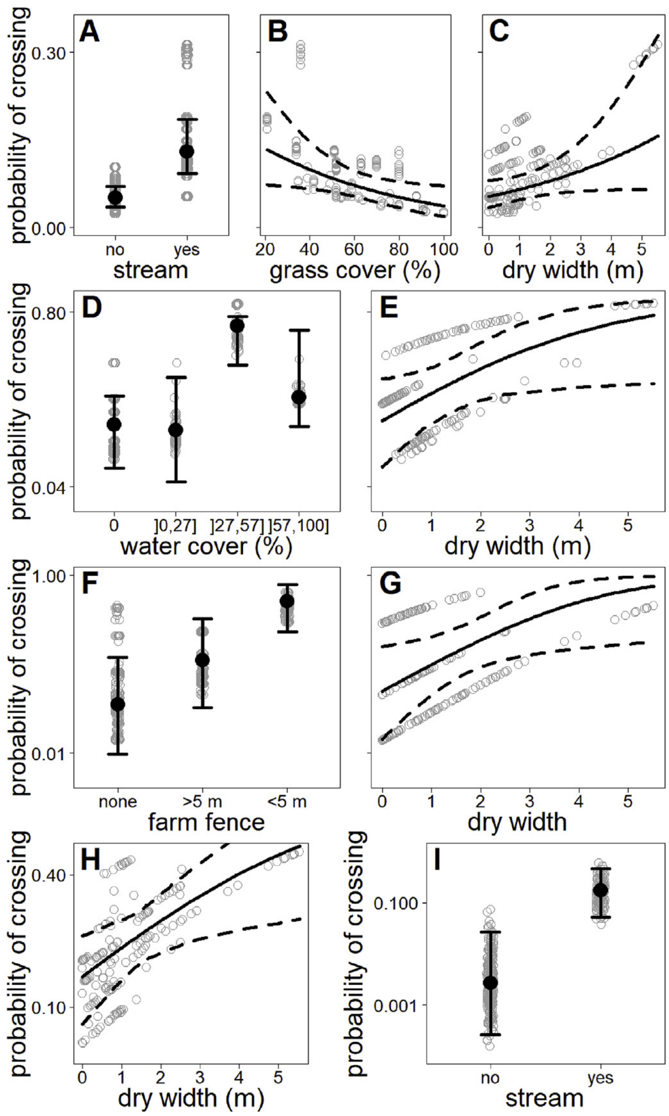

Fig. 2. Mean (± 95% CI from 1000 bootstrap replicates) fitted values for the optimal logistic mixed-effects models predicting the probability of crossing through drainage culverts over the wet season by all carnivore species (A–C), Egyptian mongoose (D–E), European badger (F–G), Common genet (H), and Eurasian otter (I). Grey circles are predicted values.

4. Discussion

The success of drainage culvert to offset the impacts of water flooding will depend on understanding how water-related factors in addition to other driving features determine usage by wildlife. However, little progress has been made on this topic. An exception is Serronha et al. (2013), pointing out to lower crossing rates through culverts with water depths greater than 3 cm. Our study determined that even partial water flooding had the potential to significantly affect the crossing success by medium-sized carnivores. However, contrary to our expectations for most species, our outcome suggested that medium-sized Euro-Mediterranean carnivores did not necessarily prefer dry culverts. When not completely flooded, culverts were still used for successful crossings by all carnivore species.

4.1. How does water in drainage culverts affect crossings by carnivores?

The presence of a dry pathway through the culvert at the time of crossing was crucial to increase both the probability and the frequency of successful crossings by the carnivore species assessed. An exception was the Eurasian otter, well adapted to freshwater environments. This corroborates previous work suggesting otters are more likely to use culverts having more than 70% water cover and 50 cm water depth (Serronha et al., 2013). For the remaining species, our results lend empirical support to recommendations advising the implementation of dry ledges or ledge-like structures in culverts (Cain et al., 2003; Glista et al., 2009; Clevenger and Huijser, 2011). This implementation should likely be done in culverts of smaller openness first, as culverts with greater openness in our dataset tended to have wider dry pathways already. In line with Villalva et al. (2013) emphasizing the importance of dry ledges for Stone marten and Common genet, our results highlight the major influence of a dry pathway to augment the probability of crossings by Common genet as this was the only significant factor for this species. Although little empirical evidence exists, a common recommendation for a dry ledge width is a minimum of 50 cm (MAAMA, 2015). From our model prediction, enlarging the dry width from 0.5 m up to 1 or 2 m increased the probability of crossing by ~11% and ~35%, respectively. In general, our results demonstrated an increase in a dry pathway led to a marked augment in probability and in frequency of successful carnivore crossings. This knowledge meets the call for empirical evidence to support ledge design, in particular for carnivore species (Villalva et al., 2013).

Our general expectation that dry culverts would be more likely to be crossed and would be crossed more often was not corroborated. Noticeably, flowing water inside a culvert during the wet season actually influenced positively both these responses by all species combined, not only as expected for otters (Philcox et al., 1999). Carnivores are known for having an association with riparian ecosystems, as these can function as movement and dispersal corridors or as sources of food and water resources (Santos et al., 2011b; Grilo et al., 2016; Delgado et al., 2018). We suggest culverts embedding streams may act as a continuation of these corridors, possibly being incorporated into carnivores' movement routes.

Only for Egyptian mongoose was water cover a main driver of the probability of crossing. Although we were expecting dry culverts to be favored by this species, interestingly, intermediate values of water cover favored mongoose probability of crossing. However, it is noteworthy that this factor adds to the positive effect of a dry pathway through the culvert. Both these results conveyed a preference for culverts with some water but not fully flooded. In line with this trend,

Table 4
Fixed part of the optimal linear mixed-effects model predicting the number of crossings/day through a drainage culvert over the wet season by medium-sized carnivores. SE = standard error; CI = effect size confidence intervals.

Variable	marginal R^2 = 0.25, conditional R^2 = 0.42; *RMSE* = 0.45					
	Estimate	SE	*t*	2.5% CI	97.5% CI	*P*
intercept	−0.535	0.121	−4.40	−0.760	−0.309	< 0.001
stream (yes)	0.363	0.142	2.56	0.098	0.626	0.016
guardrail (double)	0.396	0.137	2.88	0.141	0.649	0.007
distance to nearest passage	0.402	0.187	2.14	0.050	0.752	0.033
dry width	0.091	0.051	1.99	0.003	0.189	0.044

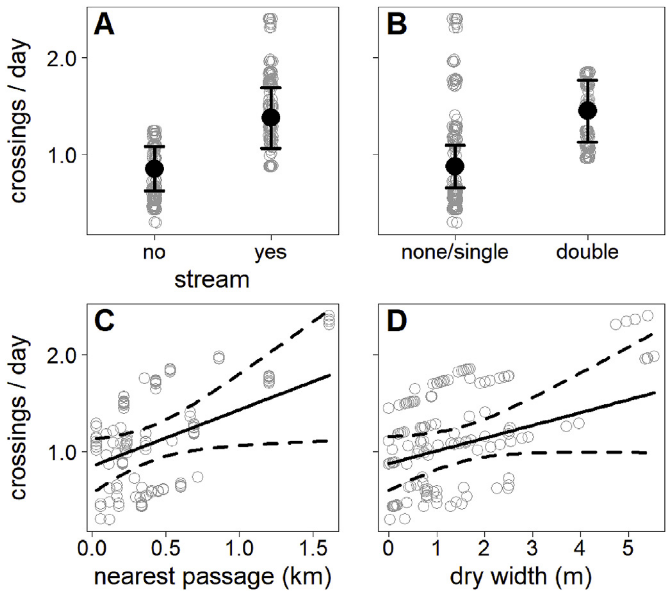

Fig. 3. Mean (± 95% CI from 1000 bootstrap replicates) fitted values for the optimal linear mixed-effects model predicting crossing rate through a drainage culvert over the wet season by all carnivore species. Grey circles are predicted values.

Table 5
Summary of the fixed parts of separate logistic mixed-effects models predicting the effect of stream only (flowing through the culvert during the wet season) on the probability of crossing through fully dried-up culverts over the dry season by medium-sized carnivores. Models concern each species and all species combined. SE = standard error; CI = effect size confidence intervals.

Species	Estimate	SE	*z*	2.5% CI	97.5% CI	*P*
Egyptian mongoose	1.940	0.586	3.31	0.800	3.220	< 0.001
European badger	0.370	0.987	0.38	−1.805	2.401	0.707
Common genet	1.850	0.773	2.39	0.348	3.719	0.017
Eurasian otter	6.427	4.048	1.59	−1.507	14.361	0.112
Stone marten	1.122	0.487	2.30	0.160	2.130	0.021
Red fox	0.058	0.655	0.09	−1.422	1.466	0.929
All species combined	1.4412	0.403	3.57	0.650	2.288	< 0.001

Grilo et al. (2008) document Egyptian mongoose crossing rates up to two times greater when water flows through a culvert than when a stream parallels the crossing structure.

4.2. Crossing drivers other than flooding

As expected, distance to the nearest passage did influence the crossing rates in each culvert. Indeed, we would anticipate a higher usage of culverts having fewer passages nearby and lower usage otherwise (Clevenger and Waltho, 2005) and our results for crossing rates supported this trend. Plus, different percentages of grass cover outside culverts could also exaggerate differences in culvert discovery, i.e., the arrival of an animal at the culvert entrance (Martinig and Bélanger-Smith, 2016), favoring culverts with less grasses. The presence of herbaceous vegetation which averaged ~76 cm high may have hindered the discovery of the culvert. However, once discovered, the vegetation could contribute to masking the passage structure, reducing reluctance to approach and cross (Rodriguez et al., 1997) or provide protection from predators (Grilo et al., 2008). Other studies found grass at entrances promote carnivore crossing rates (Rodriguez et al., 1996, 1997; Ascensão and Mira, 2007; Grilo et al., 2008), although these studies do not distinguish between visits and complete crossings.

Although we expected the opposite pattern, crossing probability seems to increase with farm fencing at short distance from culvert entrance (< 5 m) for the European badger. However, it is noteworthy that cattle farm fences were not carnivore-proof fences, having a large mesh size (≤15 cm) with soil excavations in many sites (e.g., rabbit excavations). Our result may indicate a guidance role of the farm fence, i.e., badgers may have been conducted along the wire fence to the culvert entrance, thus facilitating its discovery. Ascensão and Mira (2007) found numerous carnivore tracks along these fences and suggest a similar guidance role. More studies may provide further information to address this apparent paradox in the future (but see Bélanger-Smith, 2015).

Interestingly, the crossing rate was also higher once the road had a double guardrail. This brings novelty to the literature since only one study addresses the importance of guardrails. Malo et al. (2004), suggest that the presence of a guardrail acts to prevent collisions. We suggest double guardrails may act as barriers for medium-sized carnivores approaching the road, further guiding them toward the nearest culvert entrance.

5. Conclusions

We show partial flooding has a marked effect on carnivore crossings through culverts but it does not necessarily imply fewer crossings, even when these structures incorporate streams. On the contrary, our findings suggest an important role of streams, likely leading carnivores foraging and dispersing along the riparian corridor into the culvert entrance. However, it is paramount to note that a dry band through the culvert tunnel is required to provide a natural pathway for most of these animals.

For a culvert to benefit the majority of carnivore species surveyed here, our results clearly suggest the inclusion of dry bands to provide a crossing pathway. Furthermore, our data show that dry pathways and flowing water (the primary reason for culverts) jointly contribute to promoting crossings in this carnivore community. Clearly, practitioners should not ignore dry ledges in culverts incorporating streams. Also, although some vegetation near the culvert entrance may reduce animal reluctance to approach the structure, our results suggest that vegetation cutting might be beneficial to promoting greater probabilities of crossing. In addition, according to our data, distance between culverts seems to be of relevance for culvert crossing rates. Available recommendations for wildlife passages suggest roughly one structure within an individual's home range (e.g., every 900–1200 m for our medium-sized carnivores), adjusting locations to known dispersion routes (Clevenger et al., 2001; Smith, 2003; Ascensão and Mira, 2007). In general, interventions in extant drainage culverts to accommodate wildlife may be a cost-effective solution when funds are limited. Such interventions should promote connectivity across roads allowing movement of individuals and gene flow among carnivore populations.

Authors' contributions

Conceived the study: AM PGV. Designed the experiment: PGV. Performed the experiment: JC PGV JB. Analyzed the data: PGV. Wrote the paper: PGV JC AM JB.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2018.10.108.

References

Aaris-Sørensen, J., 1995. Road-kills of badgers (*Meles meles*) in Denmark. Ann. Zool. Fenn. 32, 31–36.
Ascensão, F., Mira, A., 2007. Factors affecting culvert use by vertebrates along two stretches of road in southern Portugal. Ecol. Res. 22, 57–66.
Barrueto, M., Ford, A.T., Clevenger, A.P., 2014. Anthropogenic effects on activity patterns of wildlife at crossing structures. Ecosphere 5, 19.
Bates, D., Maechler, M., Bolker, B., 2011. lme4: Linear Mixed-effects Models Using S4 Classes. R Statistical Package. Version 0.999375-42. R Project for Statistical Computing, Vienna, Austria.
Bélanger-Smith, K., 2015. Evaluating the Effects of Wildlife Exclusion Fencing on Road Mortality for Medium-sized and Small Mammals along Quebec's Route 175. M.Sc. Thesis. Concordia University.
Cain, A.T., Tuovila, V.R., Hewitt, D.G., Tewes, M.E., 2003. Effects of a highway and mitigation projects on bobcats in Southern Texas. Biol. Conserv. 114, 189–197.
Clarke, G.P., White, P.C.L., Harris, S., 1998. Effects of roads on badger *Meles meles* populations in south-west England. Biol. Conserv. 86, 117–124.
Clevenger, A.P., 1999. Trans-Canada Highway Research Project. Publication and summary data, Banff, Alberta October 1999.
Clevenger, A.P., Chruszcz, B., Gunson, K.E., 2001. Drainage culverts as habitat linkages and factors affecting passage by mammals. J. Appl. Ecol. 38, 1340–1349.
Clevenger, A.P., Huijser, M.P., 2011. Wildlife Crossing Structure Handbook: Design and Evaluation in North America (No. FHWA-CFL/TD-11-003).
Clevenger, A.P., Waltho, N., 2000. Factors influencing the effectiveness of wildlife underpasses in Banff national Park, Alberta, Canada. Conserv. Biol. 14, 47–56.
Clevenger, A.P., Waltho, N., 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. Biol. Conserv. 121, 453–464.
Clevenger, A.P., Wierzchowski, J., 2006. Maintaining and restoring connectivity in landscapes fragmented by roads. In: In: Crook, K., Sanjayan, M. (Eds.), Conservation Biology, vol. 14. Cambridge University Press, pp. 502–535.
Costa, P., 2014. Wildlife Monitoring Program for the Southern Railway Line. Progress Report. University of Évora (in Portuguese). http://www.isa.ulisboa.pt/inbio/theoeco/projects/PMF_REFER_Relatorio2014(Nov14).pdf, Accessed date: 15 September 2018.
Crook, N., Cairns, S.C., Vernes, K., 2013. Bare-nosed wombats (*Vombatus ursinus*) use drainage culverts to cross roads. Aust. Mammal. 35, 23–29.
Delgado, J.D., Morelli, F., Arroyo, N.L., Durán, J., Rodríguez, A., Rosal, A., Palenzuela, M.d.V., Rodríguez, J.D.G.P., 2018. Is vertebrate mortality correlated to potential permeability by underpasses along low-traffic roads? J. Environ. Manag. 221, 53–62.
Dodd, C.K., Barichivich, W.J., Smith, L.L., 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily travelled highway in Florida. Biol. Conserv. 118, 619–631.
Forman, R.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.
Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, second ed. Sage, Thousand Oaks CA. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion, Accessed date: 15 September 2018.
Glista, D.J., DeVault, T.L., DeWoody, J.A., 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landsc. Urban Plann. 91, 1–7.
Grilo, C., Bissonette, J.A., Santos-Reis, M., 2008. Response of carnivores to existing highway culverts and underpasses: implications for road planning and mitigation. Biodivers. Conserv. 17, 1685–1699.
Grilo, C., Bissonette, J.A., Santos-Reis, M., 2009. Spatial–temporal patterns in Mediterranean carnivore road casualties: consequences for mitigation. Biol. Conserv. 142, 301–313.
Grilo, C., Bissonette, J.A., Cramer, P.C., 2010. Mitigation measures to reduce impacts on biodiversity. In: Jones, S.R. (Ed.), Highways: Construction, Management, and Maintenance. Nova Science Publishers, Inc., Hauppauge, NY 11788978-1-61728-862-3, .
Grilo, C., Smith, D.J., Klar, N., 2015. Carnivores: struggling for survival in roaded landscapes. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology, first ed. John Wiley & Sons, Ltd.
Grilo, F., Ferreira, E., Alcobia, S., Simões, L., Santos-Reis, M., 2016. Do fine-scale factors shape the use of riparian galleries by carnivores in a Mediterranean agro-forested environment? International Journal of Environmental & Agriculture Research 2 2454–1850.
Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Model. 135, 147–186.
INE (National Institute of Statistics), 2015. Statistical Yearbook of the Alentejo Region. INE, Lisbon (in Portuguese).
IPMA (Portuguese Institute of the Sea and the Atmosphere), 2016. Seasonal Climatological Bulletin – Spring 2016. ISSN 2183-1084. (in Portuguese).
James, A.R.C., Stuart-Smith, A.K., 2000. Distribution of caribou and wolves in relation to linear corridors. J. Wildl. Manag. 64, 154–159.
Jenks, G.F., 1967. The data model concept in statistical mapping. Int. Yearb. Cartogr. 7, 186–190.
LeDell, E., Petersen, M., van der Laan, M., 2014. cvAUC: Cross-validated Area under the ROC Curve Confidence Intervals. R Package Version 1.1.0. https://CRAN.R-project.org/package=cvAUC.
Legendre, P., Fortin, M.J., 1989. Spatial pattern and ecological analysis. Vegetatio 80, 107–138.
Liu, R., Zhao, D., 2003. Evaluation of Best Management Practices for Mitigating Impacts of Highways on Stream and Wildlife Ecology. First Progress Report. Auburn University.
Malo, J.E., Suárez, F., Diez, A., 2004. Can we mitigate animal–vehicle accidents using predictive models? J. Appl. Ecol. 41, 701–710.
Martinig, A.R., Bélanger-Smith, K., 2016. Factors influencing the discovery and use of wildlife passages for small fauna. J. Appl. Ecol. 53, 825–836.
Mata, C., Hervás, I., Herranz, J., Suárez, F., Malo, J., 2005. Complementary use by vertebrates of crossing structures along a fenced Spanish motorway. Biol. Conserv. 124, 397–405.
MAAMA (Ministry of Agriculture, Food and Environment), 2015. Technical Requirements for the Design of Wildlife Passages and Perimeter Fencing. MAMA, Madrid (in Spanish).
Mateus, A.R.A., Grilo, C., Santos-Reis, M., 2011. Surveying drainage culvert use by carnivores: sampling design and cost-benefit analyzes of track-pads vs. video-surveillance methods. Environ. Monit. Assess. 181, 101–109.
Meek, P., Ballard, G., Fleming, P., Falzon, G., 2016. Are we getting the full picture? Animal responses to camera traps and implications for predator studies. Ecology and Evolution 3216–3225.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4, 133–142.
Ng, S.J., Dole, J.W., Sauvajot, R.M., Riley, S.P., Valone, T.J., 2004. Use of highway undercrossings by wildlife in southern California. Biol. Conserv. 115, 499–507.
Philcox, C.K., Grogan, A.L., Macdonald, D.W., 1999. Patterns of otter *Lutra lutra* road mortality in Britain. J. Appl. Ecol. 36, 748–761.
Pinheiro, J., Bates, D., Debroy, S., Sarkar, D.R., Development Core Team, 2011. Nlme: Linear and Non Linear Mixed Effects Models. R Statistical Package. Version 3.1-102. R Project for Scientific Computing, Vienna, Austria.
R Core Team, 2017. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org.
Reed, D.F., Ward, A.L., 1985. Efficacity of methods advocated to reduce deer-vehicle accidents: research and rationale in the USA. Routes et Faune Sauvage. Service d'Etudes Techniques de Routes et Autoroutes, Bagneaux, France, pp. 285–293.
Revilla, E., Palomares, F., Delibes, M., 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana national Park. Conserv. Biol. 15, 148–158.
Rodriguez, A., Crema, G., Delibes, M., 1996. Use of non-wildlife passages across a high speed railway by terrestrial vertebrates. J. Appl. Ecol. 33, 1527–1540.
Rodriguez, A., Crema, G., Delibes, M., 1997. Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway. Ecography 20, 287–294.
Rowcliffe, J., Carbone, C., Jansen, P.A., Kays, R., Kranstauber, B., 2011. Quantifying the sensitivity of camera traps: an adapted distance sampling approach. Methods in Ecology and Evolution 2, 464–476.
Santos, S.M., Carvalho, F., Mira, A., 2011a. How long do the Dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. PloS One. https://doi.org/10.1371/journal.pone.0025383. e25383.
Santos, M.J., Matos, H.M., Palomares, F., Santos-Reis, M., 2011b. Factors affecting mammalian carnivore use of riparian ecosystems in Mediterranean climates. J. Mammal. 92, 1060–1069.
Serronha, A.M., Mateus, A.R.A., Eaton, F., Santos-Reis, M., Grilo, C., 2013. Towards effective culvert design: monitoring seasonal use and behavior by Mediterranean mesocarnivores. Environ. Monit. Assess. 185, 6235–6246.
Schall, J.D., Thompson, P.L., Zerges, S.M., Kilgore, R.T., Morris, J.L., 2012. Hydraulic Design of Highway Culverts. Publication No. FHWA-hif-12-026. Federal Highway Administration, U.S. Department of Transportation.
Smith, D.J., 2003. Monitoring Wildlife Use and Determining Standards for Culvert Design. Final Report. Contract No. BC354-34. Florida Department of Transportation, Tallahassee, FL.
van der Zee, F.F., Wiertz, J., Ter Braak, C.J.F., van Apeldoorn, R.C., Vink, J., 1992. Landscape change as a possible cause of the badger *Meles meles* L. decline in The Netherlands. Biol. Conserv. 61, 17–22.
van Vuurde, M.R., van der Grift, E.A., 2005. The effects of landscape attributes on the use of small wildlife underpasses by weasel (*Mustela nivalis*) and stoat (*Mustela erminea*). Lutra 48, 91–108.
Villalva, P., Reto, D., Santos-Reis, M., Revilla, E., Grilo, C., 2013. Do dry ledges reduce the barrier effect of roads? Ecol. Eng. 57, 143–148.
Yanes, M., Velasco, J.M., Suárez, F., 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biol. Conserv. 71, 217–222.
Zambrano-Bigiarini, M., 2017. hydroGOF: Goodness-of-fit Functions for Comparison of Simulated and Observed Hydrological Time Series. R Package Version 0.3-10. https://doi.org/10.5281/zenodo.840087. http://hzambran.github.io/hydroGOF/, Accessed date: 15 September 2018.
Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.