Understanding the mechanisms behind road effects:

linking occurrence with road mortality in owls

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Short title - Linking occurrence with road mortality in owls

Abstract

Several studies suggest that species mortality rates are positively related with local population abundances. Because owls have shown both high road mortality rates and road avoidance behaviors, we hypothesize that road-kill likelihood is not always directly linked to their occurrence. In this study, we examine the relationship between the likelihood of species occurrence in the vicinity of major roads and the road-kill risk for barn owls *Tyto alba*, tawny owls *Strix aluco* and little owls *Athene noctua*. Specifically, we address: 1) the role of road-related features on spatial patterns of species' occurrence and road-kills; 2) the composition of road-kills and their distribution throughout the year; and 3) the relationship between species' occurrence likelihood and mortality risk. Our findings show that changes in movement patterns is probably the main behavioural mechanism that threatens owls in roaded landscapes. The high mortality risk of barn owls in autumn and winter seasons, after the peak of dispersal period, provides support for the hypotheses of expanding movements due to lack of food. However, mortality due to high occurrence likelihood seems to also explain tawny owl response toward roads. The high occurrence likelihood of little owls combined with low mortality rate also suggests avoidance of road crossings. Although, it is clear that within species there is variation according to age and territory-holding status, closely related species have different sensitivities to roads as a function of their varying food preferences. We believe that linking species distribution with mortality risk may be more effective in focus conservation efforts. Therefore, we suggest measures should be applied to reduce prey availability close to roads and in road verges. This is particularly important for barn owls, for which foraging in the vicinity of roads during the cold season is especially risky.

Keywords: road-kills; distribution; dispersal; barrier effect; road avoidance; *Tyto alba*; *Strix aluco*; *Athene noctua*.

Introduction

Roads represent a major barrier to daily and dispersal movements for many species due to road avoidance and an important source of mortality (e.g. Riley *et al.*, 2006; McGregor *et al.*, 2008; Gunson *et al.*, 2011). In many cases, road avoidance responses are primarily due to traffic disturbance (e.g. noise and light illumination, Berthinussen & Altringham, 2011). Road mortality can depress population abundance if wildlife-vehicle collisions add a substantial toll to background mortality rates, reducing gene flow by eliminating either dispersing and/or breeding individuals (Jackson & Fahrig, 2011). These effects can lead to reduced population sizes and increases in genetic drift and inbreeding, therefore affecting population viability (Clark *et al.*, 2010).

Recent studies highlight the importance of habitat quality and connectivity next to roads in determining the impact of road mortality suggesting the existence of a positive relationship between local population abundances and high mortality rates (Roger & Ramp, 2009; Barrientos & Miranda, 2011; Grilo *et al.*, 2011). These results support a rule of thumb indicating that road mitigation measures should be placed in areas with high species abundance and richness, such as protected areas (e.g. Clevenger *et al.*, 2002; Cox & Underwood, 2011; Roger *et al.*, 2012). Nevertheless, other areas of overall lower habitat quality can be relevant, for example, during dispersal, acting as movement corridors, which can be of crucial importance to ensure individual survival and population persistence.

The patterns of response towards growing road networks are complex and species-specific, particularly when high road mortality rates and road avoidance behavior occur simultaneously. Owls in general suffer high mortality rates (Boves & Belthoff, 2012; Guinard *et al.*, 2012), with some studies showing that they tend to avoid the proximity of roads with high traffic intensity (Grilo *et al.*, 2012; Hindmarch *et al.*, 2012; Silva *et al.*, 2012). Nevertheless, there is also evidence that road mortality contributed for depleting barn owl populations in rural England during the past century (ca. 40% reduction, Ramsden, 2003). Similarly, little owl decline in several regions of Europe is mostly attributed to vehicle collisions (Fajardo *et al.*, 1998; Le Gouar *et al.*, 2011). Therefore, in order to explain road-kill patterns, approaches based on the relationship between road-kill rates and habitat

71 surrounding roads i.e. occurrence likelihood, need to be complemented with the simultaneous
72 evaluation of the role of other biological and road-related features.

73 We suggest four hypotheses not necessarily mutually exclusive to explain the patterns of road
74 mortality and their relationship with species occurrence (Figure 1). I) Individuals do not respond to
75 roads, hence the higher the occurrence likelihood, the higher is the mortality rate. This has been the
76 main reason to explain mortality rates for a great majority of species. II) Road-kills occur when
77 individuals increase the range of their movements, for example due to dispersal or in periods of
78 reduced food availability: a pattern of high mortality may occur even in areas of low occurrence
79 likelihood due to dispersal of inexperienced sub-adults or to individuals that are attracted to road
80 verges when food abundance decreases elsewhere. III) Individuals avoid roads, generating a pattern of
81 low mortality associated with a low occurrence in the vicinity of roads. IV) Individuals avoid crossing
82 roads, with the presence in the vicinity of roads being associated to low mortality rates. These
83 hypotheses have been often used in isolation when investigating the impact of roads. We may need a
84 combination of those hypotheses to better understand the main patterns of road mortality.

85 In this study, we examine the relationship between occurrence patterns in the vicinity of major roads
86 and mortality risk for three common owl species (barn owls *Tyto alba*, tawny owls *Strix aluco* and
87 little owls *Athene noctua*) in order to understand the mechanisms underlying the patterns of population
88 responses towards roads. Specifically, we address: 1) the role of road-related features on spatial
89 patterns of both species' occurrence and road-kills; 2) the composition of road-kills (age and sex) and
90 their distribution throughout the year; and 3) the relationship between species' occurrence likelihood
91 and mortality risk. With the outcome of the analysis, we evaluate which hypotheses are more
92 applicable to the three owl species to provide further information on the mechanisms that underline
93 their vulnerability to roads and therefore where effective road mitigation measures should be placed.

94 **Methods**

95 **Study area**

96 This study was conducted on major roads in the Alentejo province (southern Portugal): two highways,
97 (total 116 km), and six national roads (total 314km) (Figure 2). Both highways have four-lanes, a 7 m
98 wide median strip, livestock exclusion fencing on both sides and a speed limit of 120 km/h. National
99 roads have mainly two-lanes with speed limit of 100 km/h, without median strip, and only in some
100 segments we found livestock exclusion fencing. Annual average daily traffic (AADT) at night (6pm to
101 6am) ranges from 400 to 2161 vehicles in the six national roads, and from 3011 to 5536 vehicles in the
102 highway sections, both showing a peak in traffic intensity in summer. This region is characterized by
103 its vast plains, with elevations ranging from 200 m to 500 m a.s.l. The climate is Mediterranean and
104 the landscape is dominated by a cropland matrix (44% of the study area), cork oak woodlands (39%),
105 an agro-silvo-pastoral mix that includes both cork and holm oaks, followed by conifer and eucalyptus
106 plantations (8%) and orchard patches/olive yards (7%). Average human population density (excluding
107 the two major cities, Évora and Beja) is 21 inhabitants/km² (source: INE, 2002). Mean road density is
108 0.27 km/km², where 8% are highways.

109 **Data collection and explanatory variables**

110 We searched for road-kills twice a month in the national roads between July 2003 and February 2009
111 (Figure 2) (see also Silva *et al.*, 2008; Gomes *et al.*, 2009). One observer drove along the roadside in
112 both directions at low speed (~30 kmh⁻¹) searching the road and its verge for owl casualties. For each
113 observed casualty we identified the species, date and geographic coordinates using a global
114 positioning system. When possible, sex and age were identified.

115 We determined the presence of owl species by broadcasting adult calls with a portable radio over 27
116 nights between November 2007 and January 2008 in 122 sites selected randomly at several distances
117 from major roads (Figure 2) to identify territorial individuals (those with a potential breeding status).
118 Broadcasting surveys were conducted 30 min after sunset using three consecutive calls for each

species. Each call comprised periods of three minutes of broadcasting with recorded calls (10 calls/min) and we remained silent for 10 min between each species' call. To assure constant detection probability, three potential factors that may influence detection were accounted in the survey: traffic intensity, coexisting species, and weather conditions. We confirmed in previous tests that detectability of calls at 400m from major roads was not affected by traffic noise and therefore broadcasting sites were set at least at that distance to minimize interference. To minimize the influence of competitor species, calls were performed following the sequence little owl, barn owl and tawny owl. In order to ensure the sound travelled all directions the player was slowly rotated 360° during the broadcast. Surveys were conducted under good weather, without rain or wind (Lengagne & Slater, 2002; O'Donnell, 2004). Sites were separated from each other at by at least 3000 m to minimize detection of the same individuals.

We characterized the broadcasting stations and road segments regarding road- and landscape-features (Table 1). For broadcasting stations we defined variables in a buffer of 400 m radius. We segmented the major roads in sections of the average diameter for each of the species' home-ranges (Martinez & Zuberogoitia, 2004; Van Nieuwenhuyse *et al.*, 2008; Neves, 2009) and 10 m width. In this way, we obtained 101 road segments of 3000 m for barn owls, 443 road segments of 700 m for tawny owls and 619 road segments of 500 m for little owls. Annual average daily traffic (2005) was provided by Estradas de Portugal S.A. and BRISA Autoestradas de Portugal S.A. Road layers were obtained from BRISA (highways) and Instituto Geográfico do Exército (IgeoE) (national roads). Curves were defined as a turn up to 135° from the previous direction. A land use map was prepared using COS'90 land cover (a vectorial map produced by photo interpretation of 1990s aerial photographs; source: IGP) and georeferenced 1998 SPOT imagery with a spatial resolution of 20m (IgeoE). We aggregated the land use data into four classifications: forest (cork oak woodlands, coniferous and eucalyptus plantations), extensive agriculture (croplands), intensive agriculture (vineyards and olive plantations) and urban areas and estimate the area they occupy in each broadcasting site and road segment. Streams were

144 obtained through Google Earth (30 October 2006 image 2010 IGP/DGRF Europe Technologies, Tele
145 Atlas). We then generated layers with distance to major roads, curves, urban areas and streams with a
146 resolution of 20 m. We computed all GIS using ArcGis 9.3 (ESRI, 2009).

147 **Statistical analyses**

148 We evaluated the factors affecting the probability of species occurrence in the vicinity of roads using
149 Generalized Linear Models (GLM) with binomial distribution using species presence/absence as a
150 response variable and the road and landscape features as predictors. We designed candidate models
151 using three sets of models assuming that: 1) road type/structure and traffic affect owls occurrence; 2)
152 owls are more likely to occur in suitable habitat independently of roads and 3) both road- and
153 landscape features explain owls occurrence (defined with the variables included in the best models
154 obtained from the previous two sets). Models were ranked according to Akaike's Information
155 Criterion (AIC, Burnham and Anderson, 2002). We started with no variables in the model (null model)
156 and sequentially added variables one at a time according to the lowest AIC. Traffic was assessed for
157 its linearity by comparing the performance of the linear term with its quadratic counterpart. To prevent
158 collinearity, we avoided entering in the same model variables with a Pearson coefficient >0.5 . We
159 considered the best model as the one with the lowest AIC. The accuracy of the best model was
160 examined through the ability to correctly classify presences and absences (CC), the calculation of the
161 area under the ROC curve (AUC) and the prediction error through 6-fold cross-validation (CV).

162

163 Road-kill temporal patterns were assessed by calculating the percentage of the total number of road
164 kills for each month between January 2004 and December 2008 and compared with the phenology of
165 each of the species (egg laying, birth, feeding young and dispersal period - movements away from
166 their natal areas).

167

168 We analyzed the spatial distribution of road-kills by modeling the road- and landscape- related
169 features that may explain the occurrence of road-kills using the same procedure as in the occurrence
170 species likelihood. We designed candidate models using three sets of models assuming that: 1) traffic
171 and distance to curves influence the location of road casualties; 2) road-kills are more likely to occur
172 in suitable habitat independently of road features and 3) both road- and landscape features explain
173 owls road mortality (variables from the best models obtained from the previous two sets of models).
174
175 We then assigned each of 122 broadcast sites with information on the probability of owl presence to
176 the nearest segment of road with information on road-kill probability and added the distance between
177 the site and the road segment. Afterwards, we evaluated the relationship between occurrence and road-
178 kills likelihood controlling for the distance between the broadcasting site and the road segment using
179 beta regression (betareg package in R 2.15.2, Cribari-Neto & Zeileis, 2010 using R Development Core
180 team 2012). We run two sets of candidate models: 1) presence probability explains road-kill
181 probability and 2) road-kill probability is better explained by occurrence probability controlled by
182 distance to the road. We selected the model with the lowest AIC. All models and plots were performed
183 using R (R Development Core team 2012).
184

185 **Results**

186 **Effect of roads on owl presence**

187 A total of 59 barn owls, 227 tawny owls and 115 little owls were detected during the broadcasting
188 survey mainly through calls. Several times we observed barn owls (n=19) and just one observation
189 was made for tawny and for little owl. On average ($\pm$ SD), owls presences occurred at further distances
190 (1591 ± 960 m) than absences (1097 ± 826 m, Table 2; Figure 3). Best models show that distance to major
191 roads is the main factor explaining owl distribution but the strength varied among species (all final
192 models had a fair accuracy and prediction ability, Table 2). Barn owl seems to be the species more

193 sensitive to the presence of major roads, while both tawny owl and little owl seem to stand the
194 proximity of roads within their suitable habitat (Figure 3).

195 **Factors affecting owl road mortality**

196 We found a total of 1024 owl carcasses. The apparent mortality rate, which is a minimum estimate,
197 was 35 barn owls/year/100km, 21 tawny owls/year/100km, 14 little owls/year/100km. Over the road
198 survey period, no substantial changes in land use or traffic were detected, thus we assume similar
199 mortality and occurrence likelihood.

200 We collected 61 barn and 54 tawny owls in good condition to determine age (in the case of little owls
201 we cannot tell them apart). The majority of records were sub-adults for both barn (67%) and tawny
202 owls (76%). Adult barn owl casualties occurred over the year with a peak in November, while the
203 number of road-kill sub-adults increased from May to January. Adult tawny owls occurred mainly
204 between March and May whereas the pattern of sub-adults was irregular with a peak in November.
205 Among the 51 barn owls that we were able to determine sex, 68% were females. Overall, we found a
206 higher incidence of road-kills in certain periods of the year: mainly between November and January
207 for barn owls and from July to September for both tawny and little owls (Figure 4).

208 In total, we found 68 road segments with presence of barn owl casualties and 34 segments with no
209 casualties. In the case of tawny owls, we found 135 segments with presence of casualties, selecting
210 other 135 segments at random to perform the analyses. Little owl casualties occurred in 144 segments,
211 again selecting the same number of random segments without casualties between the available ones.
212 Besides the variables related with habitat quality for each species, barn owl and tawny owl road-kill
213 likelihood increases as traffic volume increases. However, the influence of traffic on road mortality
214 model is significant only for barn owl (Table 2). The mortality of little owls was only associated with
215 the habitat quality for the species (Table 2).

216 **Relationship between road mortality risk and occurrence likelihood**

We found a significant negative relationship between risk of mortality and occurrence likelihood for barn owls and little owls (Table 2; Figure 5). This relationship is expressed in different ways: a high barn owl mortality risk was associated with areas of low occurrence probability, while low little owl mortality risk was related with high a probability of occurrence in the road vicinity. In contrast, as the probability of tawny owl presence increased, the risk of mortality also increased. Distance to the road showed some influence to explain the relationship between mortality risk and occurrence likelihood for barn owl and tawny owl (Table 4, Figure 5). Medium and high mortality risk is associated with low barn owl occurrence in the vicinity of roads. The same pattern seems to occur for tawny owls but it is not as evident as for barn owls.

Discussion

To our knowledge, this study is one of the first linking species road mortality risk with occurrence likelihood to understand the mechanisms underlying the effects of roads on wildlife. Our findings show that mixed responses can be expected even within groups of similar species such as owls, emphasizing that distinct mechanisms determining species-specific mortality risk are at play. In the case of barn owls, our results support the hypothesis on the increase in the range of their movements in explaining their responses to roads: 1) lower occurrence probability in the vicinity of major roads; 2) most victims were sub-adults; 3) high mortality during late autumn and winter; 4) road-killed individuals seemed to ignore traffic; and 5) low occurrence probability of individuals in road vicinity is not related with a lower mortality risk. Interestingly, a different pattern was found for tawny owls. Both increase in the range of movements hypothesis and the hypothesis linking mortality on roads to the occurrence of individuals are supported by our findings: 1) tawny owls can occur in the vicinity of major roads; 2) sub-adults are also the majority of road casualties; 3) peak in mortality occurred during the dispersal period; 4) individuals seem to ignore traffic; and 5) there is a positive relationship between tawny owl mortality risk and occurrence likelihood, wherever there is adequate habitat. Finally, little owls fall more within the road crossing avoidance hypothesis, together with the increase

in the range of movements hypothesis. This is supported by the high mortality rates during the dispersal period, although the lack of data on the age of carcasses prevented assessing which age class is more affected. Apparently, this species ignores both road structure and traffic intensity since distance from roads seems to have no influence on occurrence likelihood in suitable habitat and mortality is not explained by traffic volume. Nevertheless, they seem to avoid crossing roads because mortality rate is low when the occurrence likelihood is high.

Although, it is clear that within species there is variation according to age and territory-holding status, closely related species have different sensitivities to roads. This raises the question of how biological features and the behavior of individuals influences species responses towards roads.

Common to the three owl species, increasing the range of their movements increases the likelihood of facing roads, which, results in a higher risk of mortality. The higher number of road-killed sub-adults which may reflect the age structure of the population together with a higher incidence of mortality when inexperienced sub-adults move away from natal areas, suggest that dispersal seems to play an important role in explaining mortality mainly for tawny and little owls. In fact, owls can disperse long distances from their natal site (14.5 km and 8.3 km for tawny and little owls, respectively, Paradis *et al.*, 1998), which lead them to move to unknown areas and are more likely to stay in poor-quality habitat after prolonged dispersal durations (Burgess *et al.*, 2012).

In contrast, for barn owls the incidence of mortality occur mainly in autumn and winter, after the dispersal of sub-adults, suggesting that the diet type may play a major role on their vulnerability to roads than dispersal itself. Being ground-prey dependent with a narrower range of prey than other owl species, barn owls may have to expand their hunting area to fulfill their energetic needs of the upcoming reproductive season, which corresponds to a dramatic reduction of prey abundance (Taylor *et al.* 1994). Indeed, Ascensão *et al.* (2012) found high prey availability in highway verges with cattle exclusion fences and a previous study show that barn owls tend to move towards road verges with herbaceous cover where small mammals are abundant (Grilo *et al.* 2012). Our results clearly show that

267 barn owls may become more tolerant to roads and traffic when prey is scarce (see Massemin *et al.*,
268 1996), making verges to function as attractive sinks or habitat traps (Newton 1998, Grilo *et al.* 2012).
269
270 We also found differences in owl tolerance to road presence and traffic. Barn owls were most unlikely
271 to persist in the vicinity of major roads (Hindmarch *et al.*, 2012), although the existing mortality
272 outside the dispersal period suggest that all species can settle in its vicinity with nesting sites close to
273 roads as observed in a previous study (Grilo *et al.*, 2012). It is generally agreed that vocal activity is
274 crucial to communicate with their mates, defend their territories and signal its occupancy, which, may
275 vary among species (Zuberogitia *et al.*, 2007). Indeed, traffic noise can limit the detection of other
276 individuals, making it more difficult for birds to establish and maintain territories as well as attracting
277 mates (Parris *et al.*, 2008). Studies comparing site fidelity, vocal activity and sense of hearing among
278 species are missing and may help to understand which biological processes are related with different
279 responses to roads. In the future, a better knowledge on the relationship between traffic noise and the
280 species acoustic behavior and owl's detection during surveys will help to understand the role of road
281 disturbance on these species. Finally, the low flight height of hunting barn owls may increase the risk
282 of collision with vehicles, thereby promoting a regular loss of individuals in the vicinity of major roads
283 (Grilo *et al.*, 2012, Reijnen & Foppen, 2006). This phenomenon may disturb the population dynamics
284 by constantly creating unoccupied areas that are more likely to be settled by dispersers, therefore
285 acting as sinks at the population level and reducing the overall occurrence likelihood in the vicinity of
286 roads.

287
288 We believe that linking species distribution with mortality risk may be more effective in focusing
289 conservation efforts. Our findings highlight three different aspects of species vulnerability towards
290 roads: food preferences seem to be critical for barn owls; tawny owls seem to ignore roads and traffic;
291 little owls ignore traffic but the actual presence of a road seems to inhibit road crossings. Therefore,

we suggest measures should be applied to reduce prey availability close to roads and road verges. In particular for barn owls, road verge management should manage grazing areas in order to reduce prey availability and hence the probability of barn owl presence (Ascensão et al., 2012). We also call for the evaluation of the effectiveness of regularly mowing of road verges in order to diminish the prey abundance and therefore, its attractiveness. Finally, the feasibility of increasing the height of earth berms or other barriers to induce higher flights and promote safer road crossings in areas of high mortality should also be evaluated (Grilo *et al.*, 2012).

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400

401 Figure 1 – Conceptual model on the different individual responses (hypotheses I to IV) to explain the spatial
402 match between the road-kills and occurrence likelihood.

403

404 Figure 2 – Study area with broadcast sites and major roads surveyed.

405

406

407 Figure 3 – Occurrence likelihood in relation to distance to roads - graphs showing the fitted values (solid
408 line) obtained by the GLM applied on the barn owl, tawny owl and little owl presence/absence data. Tawny
409 owls: black line - no extensive agriculture; grey line - 100% extensive agriculture; little owls: black line - no
410 forest; grey line - 100% forest. Dots are observed data.

411

412 Figure 4 – Percentage of road-kills for each month observed over five years (January 2004-December 2008)
413 for each species and species life-history traits (double arrows): egg laying (solid line), birth (dash line),

414 feeding young (dash dot line), peak of dispersal (round dot line) and late dispersal/pre-breeding (grey solid
415 line) (Catry *et al.*, 2010).

416
417 Figure 5– Road-kill likelihood vs. occurrence likelihood accordingly to distance to nearest road (m) (n=122).
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