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ORIGINAL ARTICLE

Road effects on species abundance and population trend: a case study on tawny owl

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Abstract

Urbanization and its inherent road network are one of the major movements that impulse landscape and biodiversity change, and its effects have yet to be fully understood. Few works focus on the effect of this urbanization on abundance and population trend of a certain species, as this study does, using the tawny owl (*Strix aluco*) as our case study. Although the tawny owl is not threatened at European or global scale, it is often found roadkilled. We studied the effects of different road types on tawny owl abundance in southern Portugal, from 2005 to 2016. In woodlands far from roads, we found high tawny owl abundance, a stable population trend, and low variation in site occupancy. On the contrary, main roads disrupted habitat quality for tawny owls—limiting their abundance and site occupancy and leading to a negative population trend due to disturbance and/or mortality. Secondary roads did not severely disrupt habitat quality, allowing initial occupation and relatively high densities, yet they may act as ecological traps, revealing instability in occupation along the breeding season and a negative population trend. Tawny owl individuals may settle near secondary roads while waiting for a vacant space in woodlands far from roads (the prime high-quality habitats). To avoid the negative effects of roads on tawny owl populations, mitigation efforts should be applied to both main and secondary roads.

Keywords Road impacts · Population dynamics · *Strix aluco* · Main roads · Secondary roads

Introduction

The road network resulting from increasing urbanization impacts animal populations directly and indirectly. The most visible effect includes both wounding and mortality of a large number and diversity of animals (Coffin 2007; Karlson et al. 2014). Other negative effects of roads may include habitat fragmentation that often generates edge and barrier effects (Ascensão and Mira 2006; Borda-de-Água et al. 2011; Lesbarrères and Fahrig 2012; Grilo et al. 2014); pollution, including chemicals, light, and noise (which may decrease breeding success; Reijnen and Foppen 2006); facilitated human access; and heightened invasion attempts by exotic species (Coffin 2007; Planillo et al. 2015).

Many studies conducted on roads demonstrate the impact they have on bird populations, which live near or somehow interact with these infrastructures (Rheindt 2003). These impacts are generally more noticeable around roads with a greater traffic volume, and many studies appoint noise pollution as the possible principal cause for a negative reaction from birds (Summers et al. 2011; McClure et al. 2013; Fröhlich and Ciach 2018). Due to the diminished capacity for receiving and interpreting conspecific calls, and reduced perception of potential predators, noise pollution seems a plausible hypothesis; nevertheless, there are many other factors that could potentially justify the aversion of some birds to roadside areas (Summers et al. 2011). Studies performed on the effects of roads on birds often focused on mortality rates and the location of mortality "hotspots" (Erritzoe et al. 2003). As

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secondary roads generally have a lower top speed limit than main roads like highways and large national roads, and have a lower traffic volume, the main and secondary roads should have differing effects on birds (Reijnen and Foppen 2006).

Vehicle collision affects some bird species and populations more than others, of which owls (Strigiformes) have been known to be particularly susceptible (Erritzoe et al. 2003; Hell et al. 2005; Boves and Belthoff 2012; Kambourova-Ivanova et al. 2012). In addition, the construction of roads leads to fragmentation, dividing large areas into smaller patches, often leading to the segregation and disappearance of owl species from the area (Redpath 1995). Visual signal reception, on which nocturnal birds rely in part (e.g., Lourenço et al. 2013), may be hindered due to the artificial lighting that roads create from dusk until dawn. Indirect effects to owls may vary, dependent on the road itself and the surrounding landscape. High tree or bush density in the vicinity of roads may limit the spread of light, noise, and chemical pollution, whereas in open landscape, these effects should travel further (Reijnen and Foppen 2006). The effect this has on owl species should rely also on their own biological needs and behavior (Planillo et al. 2015; Van Der Ree et al. 2015). Habitats near main roads may be of inferior quality for owls (Šušmelj 2011; Hindmarch et al. 2012; Silva et al. 2012; Grilo et al. 2014), and therefore attract immature individuals or floaters that wish to avoid territorial disputes (Campioni et al. 2012). In turn, territories in suitable habitat further from main roads, generally, represent high-quality habitats and should be occupied by individuals with higher social rank (Sergio and Newton 2003; Newton 2007). Low-quality territories may also represent “sinks,” if population replenishment is too slow to balance out the number of fatalities. However, these territories may still be maintained, if there is a “source” habitat that sustains it, as individuals disperse from the high-density (source) area (Pulliam 1988). These sinks may be ecological traps, as individuals can find food and shelter in often conspecific-free areas, all while not perceiving the risk associated with vehicles.

Tawny owls (*Strix aluco*) are a common mesopredator species in Portugal and throughout much of Europe (Hagemeijer and Blair 1997; Lourenço et al. 2015). While there are peak periods when tawny owls announce their territory possession spontaneously (Zuberogoitia et al. 2019), they will generally defend it throughout the year when provoked (Redpath 1994). Territories located in habitats with high density of suitable forest reveal more frequent spontaneous calls, possibly due to a higher density of “neighbor” owls (Redpath 1994; Lourenço et al. 2013). Most vocal activity is carried out near the border of the home range (Burgos and Zuberogoitia 2018). Tawny owls are typically sit-and-wait predators, using perches (electrical poles, trees, fences) to survey for prey (Mikkola 1983; Galeotti 2001). This hunting tactic may augment risk of vehicle-animal collision if these structures are located near roads (Gomes et al. 2009). Even though habitat fragmentation may affect tawny owls, they seem to tolerate some degree of fragmentation, if the surrounding habitat is not completely deprived of trees or of other structures that may serve as a perch (Redpath 1995). That said, they do require a minimum small wooded patch of habitat to breed, and often other areas where they may be detected (e.g. urban areas) are used mostly for foraging (Ranazzi et al. 2000).

This study brings a new look on the effects of roads, over various years, using the population dynamics of tawny owls from southern Portugal as a case study. Moreover, the effect of different road types, distinguishing between main and secondary roads, has seldom been addressed. We wish to determine if the locations near to roads present a lower abundance and a more negative population trend in relation to those locations far from roads, and if the locations near roads have more noticeable variation in intra and inter-year tawny owl abundance. The temporal scale in this study is near long term, as it extends over the period of a decade, which allows estimation of a possible population trend.

To realize the abovementioned ideas, five objectives were set: (1) determine the effect of two road types on the population abundance of the tawny owl, using information collected during the breeding period of 2015/2016; (2) estimate the population trend of the tawny owl in the period of 2005 to 2016 and its variation according to road type; (3) determine the effect of roads on the inter-year variation of tawny owl abundance (2005–2016); (4) determine the effect of roads on the intra-year variation of tawny owl abundance (2015/2016); (5) compare individual aggressiveness as potential indicator of the social status of tawny owl individuals near and far from main roads, which can provide indication of the quality of the habitats near roads.

Materials and methods

Study area

The main study area (586 km^2; Fig. 1) is located in southern Portugal, confined by Montemor-o-Novo, Évora, and Arraiolos. In winter 2015/2016, we also censused in an extended study area (1694 km^2), comprised between Vendas Novas (to the west), Elvas (to the east), Ponte de Sor (to the north), and Moura (to the south).

The study areas boast a Mediterranean climate, with warm and dry summers, and mild winters, with between 500 and 800 mm of mean annual precipitation (Atlas Digital do Ambiente – Agência Portuguesa do Ambiente, https://sniamb.apambiente.pt/?language=pt-pt). The terrain is characterized by an undulating relief, where *montado* (an agro-silvo-pastoral system typical to the Iberian Peninsula) of cork (*Quercus suber*) and holm oak (*Quercus rotundifolia*)

Fig. 1 The main (**a**) and extended (**b**) study areas, located in southern Portugal

are dominant (close to 50% of the area), mixed in with a large portion of agricultural lands. Less common are olive tree plantations, orchards, vineyards, plantations of *Eucalyptus* spp. and maritime pine (*Pinus pinaster*), areas of intensive agriculture, and urban expanses (Silva et al. 2012; Santos et al. 2013). The main study area is traversed by various types of roads: (1) main roads, like the AE6 highway (25 km), and national roads with high traffic density (57 km); (2) secondary roads, with moderate to low traffic (61 km); (3) dirt roads, unpaved roads which give access to agricultural areas and estates (Silva et al. 2012; Santos et al. 2013). Road type was defined according to criteria used by Silva et al. (2012): main roads consisted of highways and highly used national roads with between 400 and 1700 vehicles passing every 8 h; secondary roads consisted of municipal roads and less-used national roads, with generally less than 170 vehicles passing within 8 h (official traffic volume information for 2005; Estradas de Portugal).

We studied the effects of road type on tawny owl abundance in the extended study area, while the long-term population trend, inter- and intra-year site occupancy, and individual aggressiveness were carried out in the main study area.

Tawny owl abundance

The long-term monitoring was carried out in the main study area, where we performed the same set of 65 sampling points in 2005, 2007, 2009, 2011, and 2016, from March to May (one visit to each sampling point per year). In the beginning of the breeding season 2015/2016 (November 2015–February 2016), we enlarged the monitoring to the extended study area. Here, we used the same methodology as previously to perform 511 different sampling points, visited only once. The 65 sampling points visited once in the period March–May 2016 had been also visited in the beginning of that breeding season during the sampling carried out from November 2015 to February 2016, allowing a comparison of the abundance from the beginning to the end of the reproduction (i.e., intra-year variation).

During sampling points, we broadcast the male’s hoot to increase the probability of detection of tawny owl territories (Zuberogoitia et al. 2010; Worthington-Hill and Conway 2017; Vrezec and Bertoncelj 2018). Each sampling point consisted in a playback period of 1 min 30 s, followed by a period of 10 min to listen to responses. For every individual, we recorded direction, distance, and sex, in order to estimate the number of tawny owl territories. The sampling points were chosen for an even-as-possible coverage and so that, whenever possible, a minimum of 1500 m was left between them. The sampling points were performed in the period beginning 15 min after sunset and ending 3 to 4 h later, on nights with favorable meteorological conditions, avoiding days of heavy rainfall or strong winds.

Tawny owl aggressiveness

To gather some evidence on the social status of the individuals that occupy sites near and far from main roads (and inherently the quality of these sites), we compared the aggressive behavior of individuals towards a simulated territorial intrusion

(Appleby et al. 2008), performed during capture attempts carried out near main roads (less than 500 m) and attempts off-road (farther than 1km from main and secondary roads). We expected that less aggressive individuals would be of lower social status, such as floaters and immatures (Martínez and Zuberogoitia 2003; Sergio and Newton 2003; Newton 2007; Penteriani and Delgado 2012). During the breeding season of 2015/2016, we made one capture attempt in each territory, 10 near main roads and seven far from roads in the core area of known occupied territories. We used mist-nets for capturing individuals, luring them with a tawny owl dummy and the playback of male and female tawny owls duetting (Zuberogoitia et al. 2019). Each capture attempt lasted a maximum of 30 min (with continuous playback) and ended immediately if the individual was captured in the mist-net. Four behavioral response types were considered (adapted from Lourenço et al. 2011): (1) close-range attack (intensive vocal displays, diving flights with or without contact with the dummy, and capture), (2) approach but no attack (individuals vocalized close to the playback but without diving flights, and without capture), (3) response but no approach (individuals vocalized but always further than 100 m from the playback), and (4) no response (individuals did not vocalize and were not observed). All captures were carried out under permits from Portuguese legal authorities (Instituto da Conservação da Natureza e das Florestas; No. 227/2015; 230/2016).

Data analysis

We analyzed the following parameters as response variables: (1) tawny owl abundance—number of territories at each sampling point for the breeding season 2015/2016; (2) tawny owl abundance—number of territories at each sampling point for the period 2005–2016; (3) inter-year variation of abundance—coefficient of variation of the number of territories for the period 2005–2016; (4) intra-year variation of abundance—difference in the number of territories in each sampling point between the beginning and the end of the breeding season 2015/2016; (5) behavioral response of territorial individuals (four response types). As explanatory variables we considered: (1) road type (road nearest to the point: main road, secondary road, or dirt road); (2) proportion of woodland (proportion of woodland within a 1-km radius of the listening point, using the COS 2007 classification level 2—Carta de Ocupação do Solo 2007 (scale 1:25000); Direção-Geral do Território, Portugal); (3) month (only for the breeding season 2015/2016), and (4) year (only for the population trend analysis). All variables were initially checked for normality and heterogeneity through histograms and boxplots. When response variables were counts, we used a Poisson distribution.

We used a multi-model inference approach for all response variables, comparing a set of competing models and performing a model averaging process (Burnham and Anderson 2002). When using more than one explanatory variable, all model combinations were performed, and models were compared by their AICc (Burnham and Anderson 2002). The null model was included in the comparisons as a measure of model fitness. The set of best competing models was considered to be those models with ΔAICc < 2.0 (Burnham and Anderson 2002). Model fit was assessed using diagnostic plots, adjusted R^2, and correlation between fitted and observed values.

To analyze the potential effects of road type on tawny owl abundance during the breeding season 2015/2016, the number of tawny owl territories in each point count ($n = 511$ points) was used as response variable (generalized linear model with a Poisson distribution for count data—GLM Poisson), while the three explanatory variables were road type, proportion of woodland, and month.

The effect of road type on tawny owl population trend was estimated using generalized estimating equation models (GEE with Poisson distribution) using the collective data of 2005, 2007, 2009, 2011, and 2016. These models account for the spatial dependence (repeated points) by including a vector that identifies clusters (sampling points), and we used an auto-regressive correlation structure (ar1; Halekoh et al. 2006). The model included tawny owl abundance (number of breeding pairs) as the response variable and road type, year, and the interaction between these two as explanatory variables. The nested models were then compared using the ANOVA method—Wald test statistic (Halekoh et al. 2006).

To detect the effect of road type on inter-year variation of the abundance (2005 to 2016), we used the coefficient of variation of tawny owl territories as response variable in linear models. Only road type was used as explanatory variable.

To detect the effect of road type on intra-year variation of the abundance during the breeding season 2015/2016, we used linear models with the explanatory variable road type and proportion of woodland.

Differences in the behavioral response of territorial individuals were analyzed through a chi-squared test, with significance set at $p < 0.05$.

All statistical analyses were performed in the software R, version 3.4.3 (R Core Team 2017), with the packages MuMIn (Barton 2016), gplots (Warnes et al. 2016), and geepack (Halekoh et al. 2006).

Results

Effects of road type on tawny owl abundance

The set of best models explaining tawny owl abundance included the variables road type, proportion of woodland, and month. The best model contained the three variables and had a probability of 58% of being the best model among the candidate models ($w = 0.58$), while the second model, consisting of the variables road type and proportion of woodland, held the probability of 42% of being the best model (Online Resource 1 in ESM_1).

The variables road type and proportion of woodland both held a higher relative importance of 1, when compared to the variable month, with a relative importance of 0.58 (Table 1).

Tawny owl abundance was lowest near main roads, but there was no evident difference between dirt and secondary roads (Fig. 2). More tawny owl territories were detected during listening points with higher proportion of woodland (Fig. 3).

Effects of road type on tawny owl population trend

The model comparison (ANOVA method–Wald test statistic; M0–M1: X2 = 5.24, $p = 0.022$; M1–M2: X2 = 17, $p < 0.001$; M2–M3: X2 = 9.65, $p = 0.008$) showed that the best GEE model included the variables road type, year, and their interaction (Table 2).

A negative trend was more noticeable near main roads and secondary roads, although abundance near main roads was generally lower than near secondary roads. Far from main and secondary roads, the population trend of tawny owls showed a slight increase over the 10-year period (Fig. 4).

Inter-year variation of abundance

The linear model with the road factor as explanatory of the coefficient of variation of tawny owl abundance had an AICc difference of 9.19 compared with the null model ($w = 0.99$; $R^2 = 0.21$). The coefficient of variation of the abundance was highest for main road type (Fig. 5; Table 3). This parameter, which gives a relative amount of variation, suggests that main roads showed greater variation (i.e., instability) in tawny owl abundance along the years, especially compared to areas far from roads.

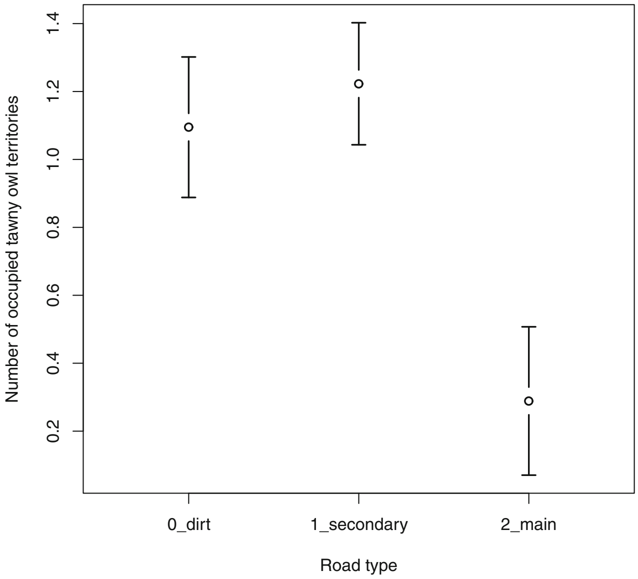


Fig. 2 Tawny owl abundance (number of occupied territories) according to road type (main, secondary, and dirt roads). Plot of means with 95% confidence intervals

Intra-year variation of abundance

The two best candidate models included the variables road type and proportion of woodland (Online Resource 2 in ESM_1). Relative variable importance was greatest for the variable road type (0.99), followed by the proportion of woodland (0.67; Table 4).

The intra-year variation of tawny owl abundance was next to null for main and dirt roads (i.e., no considerable change in the number of occupied territories between the beginning and end of the breeding season), whereas secondary roads experienced a negative variation (i.e., losing territories between the beginning and the end of the breeding season when compared to dirt roads; Fig. 6). To a lesser extent, intra-year variation also seemed to be influenced by the proportion of woodland, with a greater potential for a decrease in the number of territories in areas with a larger proportion of woodland.

Table 1 Conditional model average results and relative variable importance, resulting from the analysis of the effects on tawny owl abundance during 2015/16 (SE standard error, adjusted SE adjusted standard error, *z* z value,). November (Nov) is the reference category for the variable month. Dirt roads is the reference category for the variable road type

Variable	Estimate	SE	Adjusted SE	z	*P* value	Relative variable importance
Intercept	− 0.6509	0.2082	0.2088	3.117	0.0018	
Month (Nov/Dec)	− 0.1244	0.1441	0.1446	0.860	0.39	0.58
Month (Nov/Jan)	0.0725	0.1303	0.1307	0.555	0.58	
Month (Nov/Feb)	− 0.2917	0.1576	0.1582	1.844	0.065	
Road type (dirt road: main road)	− 1.1829	0.2912	0.2922	4.049	< 0.001	1.00
Road type (dirt road: secondary road)	0.1595	0.1060	0.1064	1.500	0.13	
Proportion of woodland	0.8432	0.1804	0.1810	4.658	< 0.001	1.00

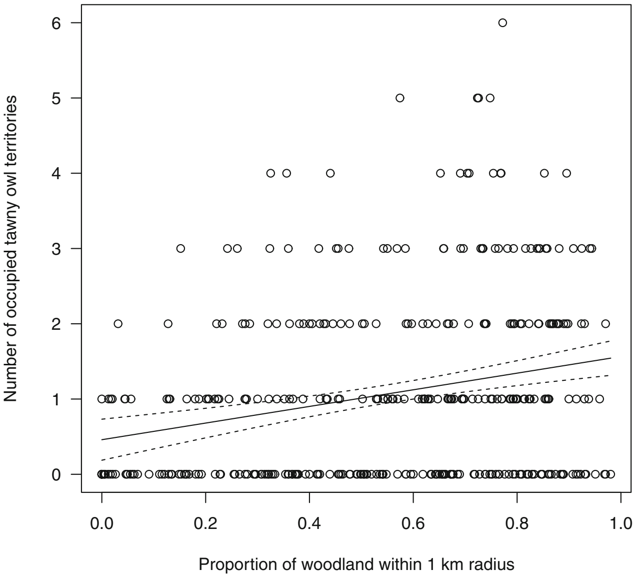


Fig. 3 Relationship between tawny owl abundance (number of occupied territories) and the proportion of woodland. Plot with the GLM regression line with 95% confidence intervals

Tawny owl aggressiveness

The behavioral response of tawny owl individuals to a territorial intrusion showed marked differences near main roads and near dirt roads (chi-squared = 14.248, df = 3, $p = 0.0026$).

Overall, simulated territorial intrusions near main roads mostly yielded an absence of response (70%), whereas near dirt roads, territorial intrusions mostly resulted in the attack of the territorial individual on the owl dummy (71.4%; Fig. 7).

Discussion

Besides the well-known effect of increased mortality that owls suffer when living near main roads, the evidence gathered in this case study suggests that different road types can have different disturbance effects on tawny owl populations, by reducing or making abundance more unstable. The different effects caused by main and secondary roads have both a temporal and spatial expression, and these aspects have rarely been considered in literature.

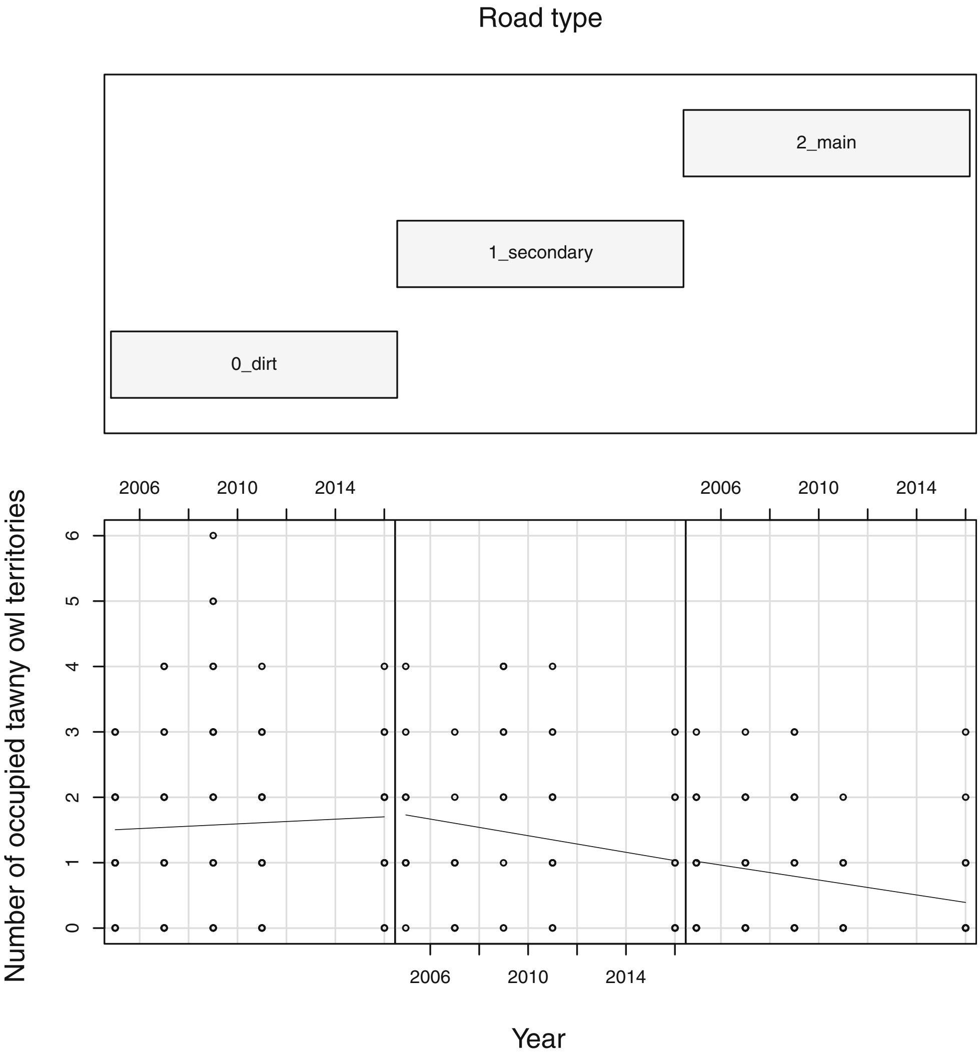
After accounting for the effect of habitat type (i.e., the known preference of tawny owls for woodlands compared to open areas), tawny owl abundance was much lower near main roads, most likely associated with increased mortality or avoidance due to various types of disturbances (e.g., light, noise) that create territories of low quality. Accordingly, compared to other sites, there should be a lower number of attempted establishments in territories near main roads, resulting in a lower abundance. However, the difference in tawny owl abundance between secondary and dirt roads was minimal, potentially due to the lower traffic volume on secondary roads being enough to make any disturbance effects tolerable for tawny owls, especially if competition is lower or there is a decent food availability that makes up for it. Within the matrix of suitable habitat (i.e., mature holm or cork oak woodlands), sites far from the main and secondary roads ("dirt roads" in our study) generally represent the best option to establish a territory, as there is minimal disturbance caused by vehicles, often a good supply of food, and high-quality habitat.

The 5-year population trend estimates for the tawny owl in Portugal (2010–2014) were slightly positive (Lourenço et al. 2015), while the most recent trend (9 years) estimate is undetermined but suggests an overall slight decrease (GTAN-SPEA 2019). The interpretation of the 10-year trend calculated in the overall study area was not straightforward, considering that the population trend varied according to road type, being slightly positive for dirt roads, but negative for both secondary and main roads. This reveals that although tawny owl abundance did not seem adversely affected by secondary roads when considering only a single spatial analysis, this road type seems to affect abundance at a temporal scale. Apparently, not only main roads adversely affect tawny owl population and act as a population sink but the negative effects may also extend to some secondary roads. It is assumed that main roads are where most collisions with vehicles happen, as besides a larger traffic volume and speed, also larger vehicles such as trucks are a lot more common (Erritzoe et al. 2003; Silva et al. 2012; Grilo et al. 2014). Even so, the lower volume of traffic on secondary roads may lull birds into a false sense of security, and they may pass more often over the road while hunting, for example. Although mean speed of vehicles is

Table 2 Best model results (GEE Poisson; model comparison by ANOVA method) for the analysis of the effects on tawny owl population trend from 2005 to 2016 (*SE* standard error,). Dirt roads are the reference category for the variable road type.

Variable	Estimate	SE	Wald	*P* value
Intercept	− 21.44	31.27	0.47	0.49
Year	0.011	0.016	0.49	0.48
Road type (dirt road: main road)	151.06	58.04	6.77	0.009
Road type (dirt road: secondary road)	175.47	78.91	4.94	0.026
Road type (dirt road: main road) × year	− 0.075	0.029	6.77	0.009
Road type (dirt road: secondary road) × year	− 0.088	0.039	4.98	0.026

Fig. 4 Tawny owl population trend during 2005–2016 for each road type (regression line on the number of occupied tawny owl territories per point)



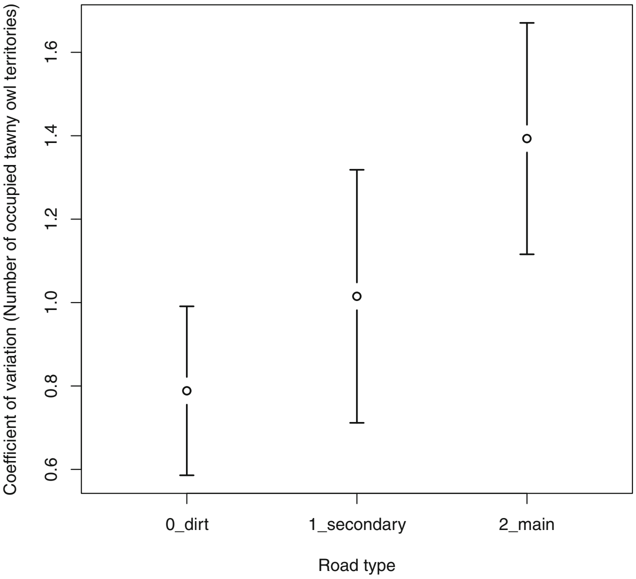


Fig. 5 Effect of road type on the coefficient of variation of the number of occupied tawny owl territories for the period 2005–2016. Plot of means with 95% confidence intervals

lower on secondary roads, vehicles can still travel at speeds fast enough that, combined with the stun factor of headlights, seems to be enough to cause a fair amount of collisions (Santos et al. 2013). Thus, our results suggest that secondary roads may act as an ecological trap. So, secondary roads may be perceived as potentially good habitats (compared to main roads) but still present considerable risk of mortality.

The negative population trend registered on both types of roads may have also been determined by changes in road management policies. Fire-prevention policies have been remodeled after 2005, a year when there was an inordinate quantity of wildfires across the country (around 50% more than average; Instituto da Conservação da Natureza e das Florestas 2017). Since then, roadside vegetation has been cut more regularly. This new practice may have influenced the attractiveness of road verges to prey in dry Mediterranean habitats (e.g., small mammals; Sabino-Marques and Mira 2011), and food availability will have fallen, making establishment of a tawny owl territory near the roads even more unlikely over the years.

Table 3 Linear model output of the effect of road type on the coefficient of variation of tawny owl abundance (*SE* standard error, *z* z value). Dirt roads are the reference category for the variable road type

Variable	Estimate	SE	z	*P* value
Intercept	0.7885	0.1025	7.691	< 0.001
Road type (dirt road: main road)	0.6047	0.1578	3.833	< 0.001
Road type (dirt road: secondary road)	0.2265	0.1824	1.242	0.22

Low inter-year variation in tawny owl abundance can be interpreted as an indicator of stability in territory occupancy. Inter-year variation was highest for main roads, which could have resulted from high territory turnover every year due to roadkills or desertion; however, this calls for future confirmation. This adds to the general expectation that areas near roads should be occupied mainly by lower socially ranked individuals, such as floaters and immatures (Penteriani 2003; Newton 2007; Penteriani et al. 2011).

On the other hand, the largest intra-year variation in the number of tawny owl territories per site was found for secondary roads, suggesting a higher instability within the breeding season, especially when compared with sites far from roads. Sites near secondary roads, being of higher quality than sites near main roads (more disturbed), may potentially have a wider range of territories along the years and within the same year, which can result in a greater variation associated with territory abandonment. In turn, sites near main roads generally will not surpass one territory within or between years, due to a low number of attempted and successful establishments. On the contrary, territories near dirt roads should be of higher quality and will most likely be disputed, every year and within the year, by socially dominant individuals, maintaining a constantly higher abundance.

High-quality territories (i.e. with lower disturbance from roads) should be occupied preferably by socially dominant individuals, more willing to defend their territories from conspecific intruders (Appleby and Redpath 1997; Sergio and Newton 2003; Newton 2007; Penteriani and Delgado 2012; Sergio et al. 2017). Socially dominant individuals in good habitats should display more aggressive responses to territorial intrusions simulated using playbacks of a conspecific breeding pair. Low-quality territories (i.e., those near main roads and thus with higher disturbance) should probably be occupied by individuals with lower social rank (immatures or floaters), which should be less territorial and therefore less likely to engage intruders aggressively (Newton 2007), choosing instead to return call from afar or have no reaction, as the territory, to them, should not be worth a fight. The presence of some tawny owl males near main roads may have been the result of a temporary establishment without a female correspondence. Single males may not be so inclined to defend a territory, especially considering we used a simulated intrusion by a male and a female.

The proportion of native oak woodlands along the road type has a considerable effect on tawny owl abundance. Considering proportion of woodland to be an

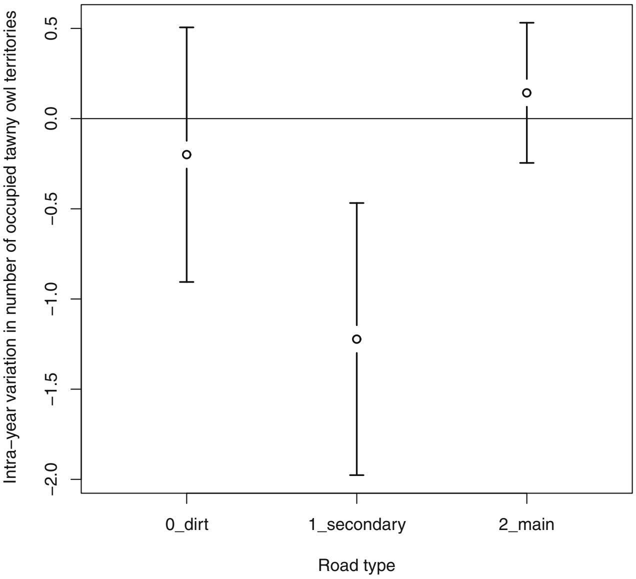


Fig. 6 Intra-year variation in the number of occupied tawny owl territories (2015/2016) according to the road type (regression line with 95% confidence intervals)

Table 4 Conditional average results and relative variable importance resulting from the multi-model inference analysis of the effects of road type on intra-year variation of abundance during the season 2015/2016 (*SE* standard error, *Adjusted SE* adjusted standard error, *z* z value)

Variable	Estimate	SE	Adjusted SE	z	*P* value	Relative variable importance
Intercept	0.50	0.80	0.81	0.62	0.54	
Road type (dirt road: main road)	− 0.028	0.77	0.78	0.035	0.97	0.99
Road type (dirt road: secondary road)	− 1.004	0.68	0.69	1.45	0.15	
Proportion of woodland	− 1.12	0.72	0.74	1.51	0.13	0.67
Road type (dirt road: main road) x proportion of woodland	1.50	1.45	1.48	1.02	0.31	0.15
Road type (dirt road: secondary road) × proportion of woodland	− 0.57	1.43	1.46	0.39	0.70	

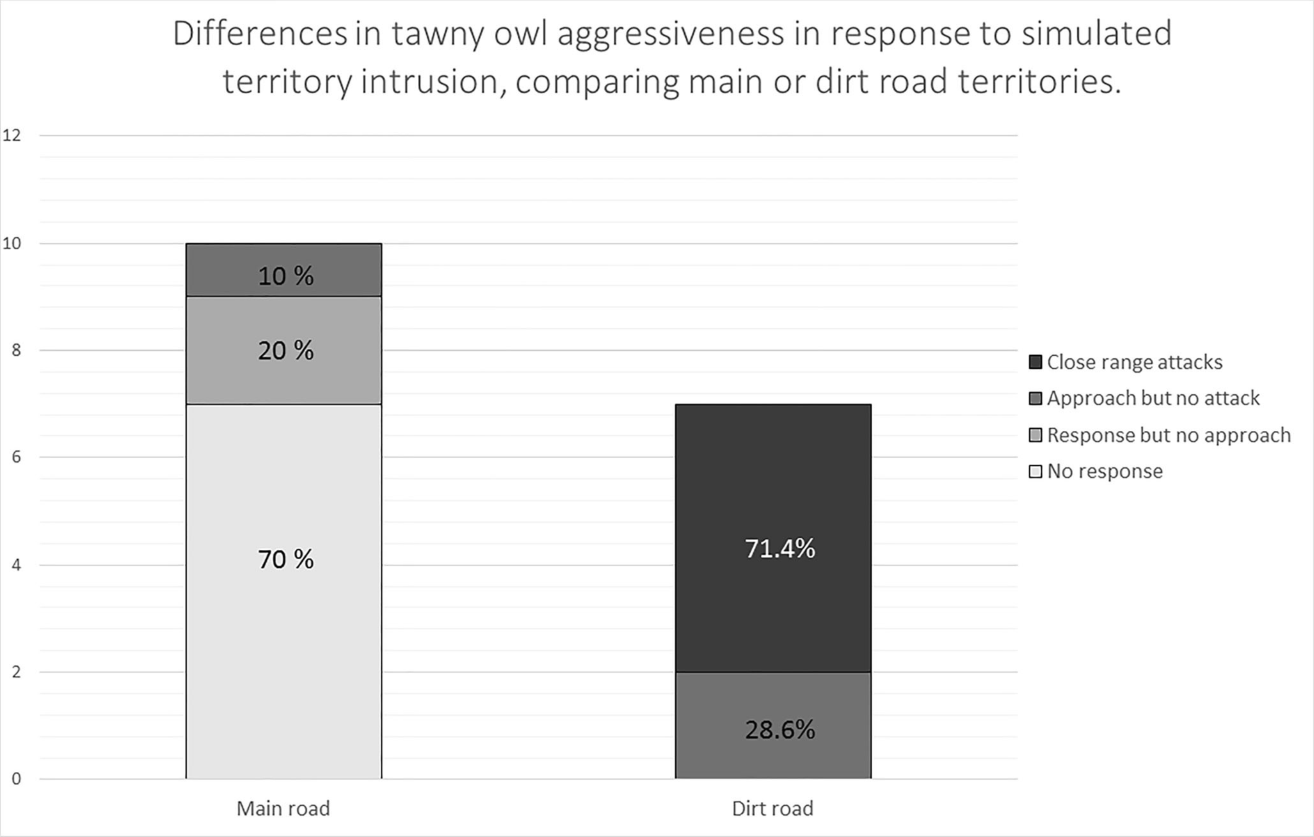


Fig. 7 Behavioral response of tawny owl individuals to simulated territorial intrusions using an owl dummy and call playback

appropriate proxy of the most suitable habitat for tawny owls (Redpath 1995; Lourenço et al. 2013; Santos et al. 2013), a higher fragmentation of the landscape (and lower proportion of woodland) should result in lower tawny owl abundance. This woodland fragmentation will be intensified not only by large patches of agricultural land, which represents a less suitable environment for tawny owls due to low tree density, but also by main roads (namely four-lane highways).In summary, woodland areas near main roads are well-known "bad habitats" for tawny owls, with increased mortality, disturbance, and fragmentation effects. As observed in our study, woodlands near main roads can be sink habitats, with low abundance, high instability, and negative population trends. Woodland areas near secondary roads can potentially be "ecological traps" for tawny owls, attracting individuals that cannot establish in the best- quality habitats far from roads. This leads to high abundance, but high instability (especially with loss of territories along the breeding season), resulting in a negative population trend. Finally, woodland areas far from roads are comparatively the "good habitats" for tawny owls, holding high abundance and stability, contributing to a stable or slightly positive population trend. As such, conservation measures directed at mitigating direct and indirect effects of roads on owls (e.g., mortality, disturbance, barrier effects), should consider that not only the main roads should be targeted, as the negative effects associated to some secondary roads could be creating a strong impact on populations, parallel to the impacts of main roads.

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