



Policy analysis

Sensory pollutants have negative but different effects on nestbox occupancy and breeding performance of a nocturnal raptor across Europe[☆]

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ABSTRACT

Anthropogenic noise and artificial light at night (ALAN) are expanding globally, acting as pervasive sensory pollutants that can disrupt wildlife behaviour and reproduction. While most research has focused on diurnal species, the effects of these pollutants on the ecological response of nocturnal predators remain poorly understood. Using data from nine European countries, we investigated the effects of traffic noise, ALAN, and road proximity on nestbox occupancy and reproduction in the Tawny Owl (*Strix aluco*), a nocturnal raptor widespread across Europe. Traffic noise consistently reduced both nestbox occupancy and reproductive success regardless of road proximity. ALAN also impaired occupancy and reproduction, but its negative effect on reproduction changed based on the proximity to roads. Interestingly, the negative effect of ALAN was stronger in sites further from roads, but it attenuated in their proximity, where owls' hatching success and brood size moderately improved. This finding suggests that near roads, where prey abundance and availability are also generally high, owls may either find the prey regardless of ALAN or they may exploit it to facilitate hunting and brood

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provisioning. However, vicinity to roads might enhance mortality by vehicle collisions, which represents one of the greatest threats for the conservation of owls. Our findings highlight that anthropogenic noise and the co-occurrence between ALAN and roads can affect settlement decisions and breeding performance in nocturnal raptors, with potential consequences across the food chain. Mitigating anthropogenic noise and promoting nighttime-lighting systems that minimize owls' presence close to roads will represent valuable actions to improve their conservation.

1. Introduction

Urbanisation is a pervasive form of environmental change, which modifies natural landscapes and is projected to strongly increase by 2030 (Seto et al., 2012). The ecological effects of urbanisation extend beyond city boundaries (Hoffmann et al., 2023), for example through the expansion of road networks, and the associated emission of noise and light pollution (Buxton et al., 2017; Cox et al., 2020). Anthropogenic noise and artificial light at night (ALAN) have been receiving growing attention due to their association with changes in species environmental perception and behaviour, and are thereby referred to as sensory pollutants (Shannon et al., 2016; Gaston et al., 2017; Falcón et al., 2020). Importantly, these pollutants can influence habitat selection and reproduction (Shannon et al., 2016; Kleist et al., 2017; Falcón et al., 2020), and such effects have been documented across several taxa, including vertebrates (e.g. birds and mammals, Halfwerk et al., 2011; Bunkley and Barber, 2015) and invertebrates (e.g. insects, Bowen et al., 2020; Boyes et al., 2021). Many studies have shown a decrease in reproductive fitness as a result of the exposure to sensory pollution (Halfwerk et al., 2011; May et al., 2019; Senzaki et al., 2020a). Furthermore, sensory pollutants interfere with biotic interactions such as intra-specific communication and predator-prey dynamics (Siemers and Schaub, 2011; Dittmer et al., 2021a; Janza et al., 2024), which can disrupt ecosystem functioning and thereby have conservation implications (Dominoni et al., 2020).

Raptors play a vital role for ecosystem functioning, for example by enhancing biodiversity in the sites where they occur and breed (Sergio et al., 2005). Therefore, changes in raptor distribution, abundance and reproductive outputs could indicate declines in biodiversity and ecosystem health (Natsukawa et al., 2021; Natsukawa and Sergio, 2022). While urbanisation can benefit raptors by increasing nesting opportunities and reducing competition for resources (Kettel et al., 2018), it also poses significant threats, including habitat loss and mortality due to road collision and poisoning (Hager, 2009; McClure et al., 2018; Šálek et al., 2019; Panter et al., 2022). Despite the global expansion of anthropogenic noise and artificial light (Buxton et al., 2017; Kyba et al., 2023), their impacts on raptor ecology remain poorly explored (McClure et al., 2018, 2022), yet it may have important implications for conservation given the raptors' role as indicators of biodiversity and ecosystem health (Burgas et al., 2014; Senzaki et al., 2015).

The response of nocturnal raptors (i.e. owls) to these sensory pollutants is particularly interesting, as many owl species are adapted to hunt in low-light conditions by hearing (Konishi, 1973; Martin, 1986). Most owls are territorial predators for whom territory establishment is essential for successful breeding, which strongly depends on prey availability (Southern and Lowe, 1968; Southern, 1970). Previous studies have revealed that anthropogenic noise impairs owls' ability to detect and catch prey (Mason et al., 2016; Senzaki et al., 2016), which might explain why owls avoid noise-polluted environments (Fröhlich and Ciach, 2019). The avoidance of such environments might also be due to the possible adverse effect of noise on owl communication, since noise forces territorial birds to vocalize louder and at higher pitches, thus causing higher energetic costs of communication (Brumm, 2004). Similarly, some studies suggest that owls also avoid areas with high ALAN levels (Marín-Gómez et al., 2020; Hanmer et al., 2021). However, ALAN can also be exploited by owls to catch prey attracted to artificial

lights (e.g. nocturnal insects and small birds) (Rodríguez et al., 2021). This suggests that the relationship between ALAN and owls might depend on their foraging habits and prey-ALAN interaction. Additionally, owls can exploit roads and areas in their vicinity as suitable grounds for hunting and foraging (de Bruijn, 1994; Hager, 2009; Grilo et al., 2014). Artificial lights along roads contribute to attraction of prey (Rodríguez et al., 2021) and high perch availability near roads (e.g. light and signposts, fences, tree belts) may facilitate raptor hunting (Meunier et al., 2000), including owls that hunt with a sit-and-wait strategy (e.g. Tawny Owls *Strix aluco*, Southern, 1954). For these reasons, nest sites near roads might be selected by owls for nesting and breeding, although this could increase roadkill risk and might turn them into ecological traps (Hager, 2009; Silva et al., 2019; van der Horst et al., 2019).

As an all-year sedentary and territorial nocturnal predator that typically hunts by hearing, the Tawny Owl is an excellent model species to study ecological responses to sensory pollutants (Weaving et al., 2016). Tawny Owls are widespread across Europe (Cramp, 1985) and primarily breed in woodlands by nesting in tree cavities (Yatsiuk and Wesolowski, 2020). However, they also readily use nestboxes, which can sustain populations in areas lacking natural cavities (Karell et al., 2009). Tawny Owls display foraging plasticity and environmental adaptability (Grzędzicka et al., 2013), allowing them to nest also in urban and open environments (e.g. croplands and grasslands), which are often included within their home ranges as long as tree patches are available (Redpath, 1995; Sunde and Bølstad, 2004). Here, we use the Tawny Owl as a model species to test the effects of traffic noise, ALAN and road proximity on nestbox occupancy and breeding performance. We predicted the following:

- (i) Nestbox occupancy
 - a) Lower occupancy in sites near roads with high levels of traffic noise. Perch availability and high small mammal abundance in habitats near roads (Meunier et al., 1999a; Bellamy et al., 2000; Hill et al., 2021) could make these areas ideal hunting grounds (de Bruijn, 1994; Zorn, 1998; Meunier et al., 2000; Grilo et al., 2014), and therefore attractive for nesting. However, since previous studies have shown road avoidance by owls due to traffic volume (including the Tawny Owl, Silva et al., 2012), we expected owls to not occupy sites near roads with high levels of traffic noise.
 - b) Higher occupancy in sites closer to roads with high levels of ALAN but low levels of noise. Owls might exploit artificial lights in roadside habitats to enhance hunting success, making these areas attractive for nesting. Some small mammals, such as voles and mice (key prey for Tawny Owls, Southern, 1970), may increase their space use under ALAN (Hoffmann et al., 2018, 2019). Moreover, since Tawny Owls also prey on other animals (e.g. birds, amphibians, Grzędzicka et al., 2013), ALAN might help them catch alternative prey more effectively, such as birds or nocturnal insects (Canário et al., 2012; Rodríguez et al., 2021).
- (ii) Breeding performance
 - a) A decrease in clutch size, hatching success and brood size with increasing traffic noise. Since noise lowers owl prey detection (Mason et al., 2016; Senzaki et al., 2016), fewer prey items are expected to be caught and delivered by male owls – which provide food

throughout most of the breeding period (Southern, 1970) – to sustain incubating females and the offspring. A previous study in the USA showed that noise is indeed associated with a decrease in clutch size across birds (Senzaki et al., 2020a).

- b) An increase in clutch size, hatching success and brood size in sites near roads with high levels of ALAN. In such environments owls might exploit artificial lights to increase hunting success (Rodríguez et al., 2021), thereby improving reproductive outcomes.

2. Materials and methods

2.1. Data collection

We use data on 6285 breeding attempts collected from 17 study sites across nine European countries, which encompassed a mixture of urban, wooded and open land environments (Fig. 1). The assemblage of data

from multiple countries allowed us to account for regional variation in the breeding performance of Tawny Owls, which can vary due to climatic conditions and small mammal availability (Karell et al., 2009; Ratajc et al., 2023). For this study, we used long-term data from 1800 nestboxes monitored between 2011 and 2023. However, not all nestboxes were monitored consistently each year during this period (see Appendix A1 for details on number of sites and nestboxes in each country).

2.2. Nestbox occupancy and breeding performance data

We defined nestbox occupancy as the presence or absence of breeding Tawny Owls in the nestboxes during the field survey (1 = occupied; 0 = not occupied). A nestbox was considered occupied if a clutch or a brood was found (Rumbutis et al., 2017). For successfully occupied nestboxes ($n = 6285$), we evaluated three traits to assess breeding performance, representing key stages of the owl breeding



Fig. 1. Geographical distribution of the study sites ($n = 17$) across the nine European countries (SCO: Scotland; NOR: Norway; SWE: Sweden; FIN: Finland; LTU: Lithuania; CZE: Czech Republic; SLO: Slovenia; CHE: Switzerland; FRA: France) where the Tawny Owl nestboxes were surveyed to collect occupancy and breeding performance data. On the top left corner, an example of purpose-built Tawny Owl nestbox is shown. The satellite map was obtained from the Google Satellite layer available from the *QuickMapService* plugin in QGIS v 3.32 (Quantum GIS Development Team, 2023).

cycle:

- (i) Clutch size: number of eggs laid ($n = 1876$)
- (ii) Hatching success: proportion of eggs within the clutch that hatched ($n = 1839$)
- (iii) Brood size: number of chicks recorded in the nestbox at the time of ringing (when chicks were approximately 2–3 weeks old). Mortality among nestlings typically occurs earlier, within one and ten days after hatching (Hirons, 1985; Sasvári et al., 2004). Therefore, brood size at this stage of chick rearing is an effective proxy for the number of fledglings ($n = 2000$).

Sample size for brood size is higher than clutch size since on several occasions the nestboxes were checked only during the chick rearing period, and the number of eggs laid is therefore unknown. To minimize potential bias, we excluded observations where nestboxes were occupied by other species or where predation events occurred ($n = 365$). This information was available for most countries ($n = 5$) included in the study.

2.3. Environmental and anthropogenic variables

We computed environmental variables within a 500 m radius around each nestbox, reflecting the average Tawny Owl home range size (Redpath, 1995; Sunde and Bølstad, 2004). Since our data came from study sites located in different countries, we relied on globally available and open-source datasets to ensure methodological consistency at a large scale across countries.

We calculated the proportion of urban, wooded and open landcover using annual data from ESA Sentinel-2 Land Use/Land Cover Time Series (Esri and Impact Observatory; <https://livingatlas.arcgis.com/landcoverexplorer>). For each nestbox, we determined the total number of pixels for each landcover within the 500 m radius and converted these counts into proportions (see Appendix A2a for detailed description of these landcover types). Since Sentinel-2 data has been available only since 2017, we applied 2017 landcover values to our nestbox data collected before that year. Given that landcover values slightly changed from 2017 to 2023 within the 500 m radius around the nestboxes (ca. 1 % overall in each country; Appendix A2b), we assumed no substantial changes between 2011 and 2016 for the purpose of our study.

For road proximity, we obtained road data from Open Street Map (OSM) (<https://www.geofabrik.de>) and calculated the distance between each nestbox and the nearest vehicular road. Therefore, we considered only motorways, primary, secondary, tertiary and residential road types, which are most impactful for owls in terms of vehicle collisions and traffic noise (Hager, 2009; Hanmer and Robinson, 2021).

We used the QGIS plugin *opeNoise Map* (Arpa Piemonte; <https://plugins.qgis.org/plugins/opeNoise>, v.2.2) to estimate the average traffic noise levels within the 500 m buffer. This plugin allowed to calculate the levels of noise in a bidimensional space around the nestboxes, generated by road sources (i.e. the road types used for road proximity) at receiver points and buildings (Morelli et al., 2023). For this purpose, we based the levels of noise for each road source on the noise levels modelled by Staab et al. (2022), who used the same OSM road sources to generate noise profiles for each road type. We used OSM building sources as an input for noise reduction and diffraction (Morelli et al., 2023) (see Appendix A3a for further details on the use of the plugin). To test the reliability of the noise levels calculated with the QGIS plugin, we obtained noise data at a sample of nestbox locations in Scotland ($n = 40$), via on ground measurements at sunset (Sound Level Meter, Extech Instruments HD600). We then used Pearson's $|r|$ correlation coefficient to relate the plugin-generated noise levels with on-ground measurements. Pearson's $|r|$ revealed positive and significant correlation ($r = 0.74$, $p < 0.001$) between plugin and ground noise levels, indicating the reliability of the plugin-generated noise levels (see Appendix A3b for further details).

We estimated ALAN using NASA's Black Marble nighttime lights product, which derives from Visible and Infrared Imaging Suite (VIIRS) data (Jurij Stare, <https://www.lightpollutionmap.info>, v.3.0.3 – VIIRS-NASA's VIIRS/NPP Lunar BRDF-Adjusted Nighttime Lights Yearly). This data is lunar BRDF-corrected (i.e. bidirectional reflectance distribution function, Román et al., 2018), which minimizes the effects of confounding environmental sources and biases (e.g. moonlight, clouds, atmospheric effects), thus resulting in only ALAN-related contributions (Román et al., 2018; Ditmer et al., 2021b; Huang et al., 2023). VIIRS started providing annual data from 2012 and it has been widely used to examine the effects of ALAN on wildlife, including at the landscape level (Ciach and Fröhlich, 2019; Senzaki et al., 2020a; Ditmer et al., 2021b). For each nestbox, we calculated the average annual light pollution intensity within the 500 m radius. For the missing 2011 light data, we applied 2012 light data to our nestbox data collected in that year.

We used packages *sf* (Pebesma, 2018) and *terra* (Hijmans, 2024) within R (R Core Team, 2023, v. 4.2.2) to compute data for landcover, light pollution and road proximity. Traffic noise calculations were conducted with the *opeNoise Map* plugin in QGIS (Quantum GIS Development Team, 2023, v. 3.32).

2.4. Data analysis

We conducted statistical analyses using R (R Core Team, 2023, v. 4.2.2) and we used a mixed modelling approach to examine the effects of landcover (i.e. wooded, urban and open environment), ALAN, traffic noise and road proximity on each response variable. Before modelling, these explanatory variables were centred (mean = 0) and scaled (SD = 1) to improve comparison between regression coefficients (Schielzeth, 2010). Moreover, we assessed collinearity between explanatory variables using the Variance Inflation Factor (VIF) to prevent overfitting (Kosicki, 2020), with a VIF > 5 indicating collinearity issues (James et al., 2014). Since the urban environment landcover showed a VIF > 5, this predictor was excluded it from the analysis.

We then fitted Generalized Additive Mixed Models (GAMMs) with Binomial error distribution to assess the effects of predictors on nestbox occupancy and hatching success. To model clutch and brood size, we fitted GAMMs with Poisson error distribution. GAMMs were fitted using the *mgcv* package (Wood, 2001). Landcover, road proximity, traffic noise and ALAN were specified as fixed effects. Since we were interested in investigating the interactive effects between road proximity (i.e. distance between nestbox and nearest road), traffic noise and ALAN, we included the three-way interaction term 'Road proximity*Traffic noise*ALAN', and all nested two-way interactions. Random effects included 'year' to account for temporal dependence and differences in survey effort (Jørgensen et al., 2016; Koivula et al., 2018) and 'nestbox ID' to account for repeated measures from the same nestboxes. Moreover, we also included latitude and longitude as random effects to account for spatial autocorrelation (Boakye et al., 2023; Mazziotta et al., 2024). GAMMs are widely used to account for the presence of spatial structure in the data (Hanzelka et al., 2019), and they allowed us to include the joint effects of latitude and longitude with a tensor product smooth with Gaussian basis (Boakye et al., 2023; Mazziotta et al., 2024). This enabled to investigate Tawny Owl response to the anthropogenic variables of our interest while accounting for geographical variations, which can influence occupancy and reproductive patterns (Brambilla et al., 2020; Ratajc et al., 2023).

For each response variable, we then conducted model comparison between full models (i.e. inclusive of all interaction terms) and reduced models (Appendix A4). Since in our study we were specifically interested in the interactive effects between road proximity, noise and ALAN, we selected the best models using a stepwise approach, based on the sequential removal of non-significant interactions (Whittingham et al., 2006). Therefore, starting from the full model, we sequentially removed one non-significant interaction at a time, while we retained significant interactions ($p < 0.05$) if these were found (see Appendix A4 for the

order of reduced models). We excluded non-significant interactions also to reduce model complexity based on the parsimony principle (Johnson and Omland, 2004; Coelho et al., 2019). If no interactions were significant, the best models contained only the main effects. The habitat variables (wooded and open environment) were included in all models to account for any influence of habitat. Finally, we assessed the best models by testing whether any spatial pattern persisted in the residuals using Moran's I test from the DHARMA package (Hartig, 2022), where a $p < 0.05$ would indicate persistent spatial dependence. For binomial GAMMs, we also checked model performance using Receiver Operating Characteristic (ROC) curves, from which we calculated the Areas Under the Curves (AUC). Large areas between 0.7 and 0.9 under ROC curves would indicate high model performance (Manel et al., 2001). For Poisson GAMMs, we also checked for overdispersion and underdispersion to ensure the validity of the models by using the package performance (Lüdtke et al., 2021). Although the package provides the dispersion ratio, it formally tests only for overdispersion. A dispersion ratio between 0.75 and 1.4 usually indicates absence of under/overdispersion (Senzaki et al., 2020b). If under/overdispersion was detected, we verified the consistency of the results by fitting the models with a quasi-Poisson distribution (Kerr et al., 2024).

3. Results

Overall nestbox occupancy rate was approximately 36 % ($n = 6285$ breeding attempts across the study period). Among occupied nestboxes, Tawny Owls laid an average of $3.1 \text{ eggs} \pm 1.4 \text{ SD}$, with a hatching rate of approximately 78 %. The average brood size was $2.3 \pm 1.6 \text{ SD}$. Country-specific breeding estimates are provided in Appendix A1.

We found that both traffic noise and ALAN negatively affected Tawny Owl nestbox occupancy, regardless of road proximity (traffic noise: $\beta = -0.13 \pm 0.06$, $z = -2.30$, $p = 0.02$; Table 1; Fig. 2; ALAN: $\beta = -0.15 \pm 0.07$, $z = -2.07$, $p = 0.04$; Table 1; Fig. 2). Model comparison showed no significant interactions between road proximity, noise and ALAN (Appendix A5). The best model therefore contained only the main effects.

For clutch size, there was no statistically significant effect of any of the habitat or anthropogenic factors we considered, or interactions between them. However, there was some evidence of a weak negative effect of traffic noise on the number of eggs laid (Table 2a, Appendix A5).

We found that both noise and ALAN negatively affected hatching success and brood size, but the effect of ALAN changed based on the proximity to roads (Fig. 3). For both response variables, model comparison showed a significant interaction effect between road proximity and ALAN (Appendix A5). The best models thus showed lower hatching success and brood size were recorded in sites further from roads with high levels of ALAN, but not in illuminated areas close to roads (hatching success: $\beta = -0.17 \pm 0.07$, $z = -2.59$, $p = 0.009$; brood size: $\beta = -0.06 \pm 0.03$, $z = -2.32$, $p = 0.02$; Table 2b-c; Fig. 3). Both breeding parameters also decreased with increase in traffic noise (hatching success: $\beta = -0.14 \pm 0.07$, $z = -2.17$, $p = 0.03$; brood size: $\beta = -0.06 \pm 0.02$, $z = -2.89$, $p = 0.004$; Table 2b-c; Fig. 3).

Table 1

Results of the best GAMM related to Tawny Owl nestbox occupancy ($n = 6285$). Column headings indicate the variable estimate (β), standard error (SE), z-value (z), number of the effective degrees of freedom (edf), reference degree of freedom (Ref.df) and p-value (p).

Model term	β	SE	z	edf	Ref.df	p
(Intercept)	-0.765	0.085	-9.008			<0.001
Wooded environment	-0.089	0.057	-1.546			0.122
Open environment	0.028	0.058	0.488			0.625
Road proximity	-0.029	0.052	-0.561			0.575
ALAN	-0.145	0.070	-2.066			0.038
Traffic noise	-0.131	0.057	-2.303			0.021
Nestbox ID				408.59	905.00	<0.001
Year				9.55	12.00	<0.001
Longitude*Latitude				17.26	18.56	<0.001

We found no evidence of spatial dependence in any of the best models' residuals ($p > 0.05$). Binomial GAMMs also showed high performance (nestbox occupancy: AUC = 0.87; hatching success: AUC = 0.83; Appendix A6a). Overdispersion was not detected in Poisson GAMMs (clutch size: dispersion ratio = 0.56; brood size: dispersion ratio = 0.88). Underdispersion was moderate in the Poisson clutch size model. However, the equivalent quasi-Poisson model that accounted for underdispersion did not reveal different results (Appendix A6b).

4. Discussion

In our study, we found negative effects of sensory pollutants on Tawny Owl nestbox occupancy and breeding performance across Europe. Traffic noise impaired both nestbox occupancy and breeding performance regardless of proximity to roads. Similarly, ALAN negatively affected both traits, but its effect on hatching success and brood size diminished in areas closer to roads.

4.1. Traffic noise and ALAN reduce nestbox occupancy

As predicted, we found a negative relationship between nestbox occupancy and traffic noise, which remained consistent regardless of road proximity. This finding supports previous research showing detrimental effects of noise on bird abundance, distribution (Francis et al., 2009; Chen and Koprowski, 2015; Fröhlich and Ciach, 2018, 2019) and also audibility (Poprach and Machar, 2019), which may affect owls' ability to hear and locate the prey. Sites with high levels of noise pollution are thus likely to be avoided by acoustic-oriented animals for nesting. Our result indicate that noise affects the nest site selection process for Tawny Owls, in addition to other factors identified in previous research, such as prey availability (Southern, 1970), mature and broadleaf forest availability (Rumbutis et al., 2017; Hanmer et al., 2021), climatic conditions (Brambilla et al., 2020) and interspecific competition (Vrezec and Tome, 2004; Sergio et al., 2007).

ALAN did also affect nestbox occupancy, suggesting that this factor is involved in the nest site selection process. However, contrary to our prediction, ALAN did not increase occupancy, neither in areas closer to roads. This result may be explained by the role of ALAN in enhancing visibility and predation risk. Since the exposure to ALAN increases the risk of predation by nocturnal predators (Falcón et al., 2020; Sanders et al., 2021), nestboxes located in highly lit areas may have been unattractive to Tawny Owls, as nesting in such locations could make them (including their offspring) more visible and vulnerable to other night-active predators, such as bigger owls (e.g. Eagle Owl *Bubo bubo*, Sergio and Hiraldo, 2008) and Pine Martens (*Martes martes*), which often access owls' nest sites and take their eggs and nestlings (Overskaug et al., 1999; Sonerud, 2022). Higher predation risk at the nest due to ALAN has also been recorded in other nocturnal birds (e.g. nightjar species, Adams et al., 2024). Therefore, it is plausible to think that the expansion of light pollution through the nocturnal landscape may influence owl settlement decisions, supporting previous evidence showing a negative relationship between owl occupancy and light-polluted areas based on acoustic

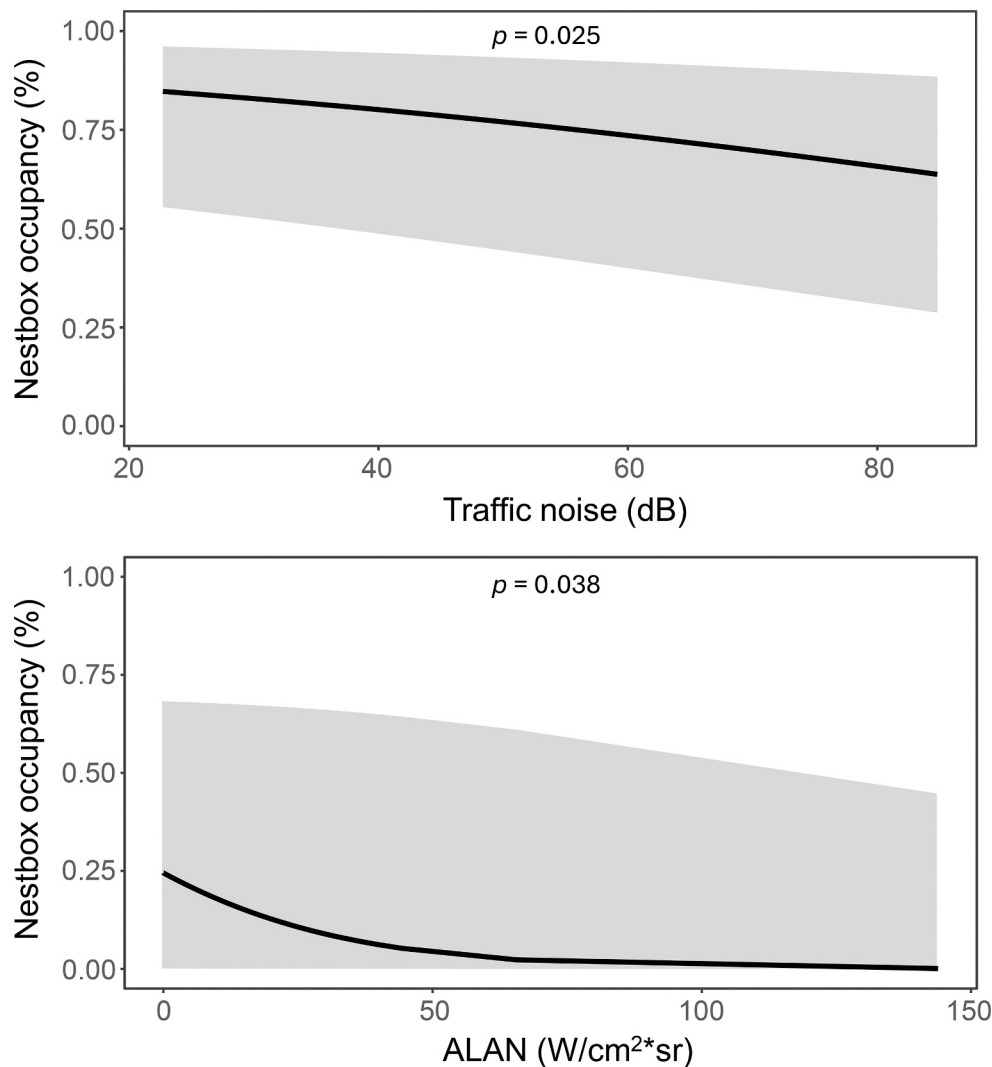


Fig. 2. Traffic noise and ALAN reduce Tawny Owl nestbox occupancy. The black lines represent the slope of the regression based on the predictions of the best model, and the grey areas represents the 95 % confidence intervals. The p -values from the model result (Table 1) showing the statistical significance ($p < 0.05$) are also indicated.

surveys at night (Hanmer et al., 2021).

We also acknowledge that in regions where multiple owl species coexist, competition with conspecifics or other owl species might also influence settlement patterns and nestbox occupancy (Morosinotto et al., 2017; Ratajc et al., 2022). For example, in central and southern Europe, Tawny Owl nestbox occupancy decreases at higher elevations since Tawny Owls are outcompeted by Ural Owls (*Strix uralensis*) in the regions where the two species coexist (Vrezec and Tome, 2004).

4.2. Both traffic noise and ALAN affect breeding performance, but in different ways

As predicted, traffic noise negatively impacted hatching success and brood size, regardless of the distance from roads. This finding supports evidence that anthropogenic noise, including traffic noise, is detrimental to wildlife reproduction (Halfwerk et al., 2011; Schroeder et al., 2012; Shannon et al., 2016) and suggests that noise can impair owls' hunting ability not only along roads. Previous experimental studies have shown that noise reduces owls' ability to detect and catch prey, with these impairing effects extending beyond 120 m from roads (Mason et al., 2016; Senzaki et al., 2016). Together with these past experiments, our results suggest that owls breeding in noisy environments may experience reduced hunting success, which in turn could lead to fewer prey

deliveries to nests and ultimately smaller broods. We also found a decrease in hatching success in response to traffic noise. This result aligns with previous findings by Kleist et al. (2018) and Williams et al. (2021), who reported lower hatching rates in birds exposed to anthropogenic noise. Lower hatching success has been linked to alterations in hormone (maternal corticosterone) levels and incubation behaviour in response to noise exposure, which can increase stress during this breeding stage (Kleist et al., 2018). Noise might also affect owls' stress levels and incubation behaviour, for example by influencing how tightly incubating owls sit on their eggs, thereby hatching success (Williams et al., 2021). Interestingly, although we found evidence for a weak relationship between noise and clutch size, our results indicate the lack of a significant negative effect of noise, which was however observed in other avian species (Senzaki et al., 2020a). This suggests that the most detrimental effects of noise on breeding success of Tawny Owls emerge after egg-laying. Adult male Tawny Owls start providing food to adult females already in the pre-laying stage, allowing them to accumulate enough reserves of fat and protein necessary for laying eggs (Hirons, 1985). While food provisioning might be enough at this stage to achieve the energetic investment in egg formation, it might not be after the egg-laying stage, when males must provide more prey items to sustain both the female and the offspring (Southern, 1970). It is possible that the increasing food demand is harder to meet in noisy environments due to

Table 2

Results of the best GAMMs related to Tawny Owl breeding performance: (a) clutch size ($n = 1876$), (b) hatching success ($n = 1839$) and (c) brood size ($n = 2000$). Column headings indicate the variable estimate (β), standard error (SE), z-value (z), number of the effective degrees of freedom (edf), reference degrees of freedom (Ref.df) and p-value (p).

Model term	β	SE	z	edf	Ref.df	p
a: Clutch size						
(Intercept)	1.113	0.013	83.054			<0.001
Wooded environment	0.012	0.016	1.056			0.291
Open environment	0.021	0.018	1.182			0.237
Road proximity	-0.006	0.014	-0.456			0.648
ALAN	0.016	0.014	1.104			0.269
Traffic noise	-0.027	0.015	-1.823			0.068
Nestbox ID				<0.1	566.00	1.00
Year				<0.1	1.00	0.53
Longitude*Latitude				7.36	8.17	<0.001
b: Hatching success						
(Intercept)	1.134	0.065	17.568			<0.001
Wooded environment	0.026	0.064	0.404			0.686
Open environment	0.103	0.069	1.482			0.138
Road proximity	0.009	0.062	0.161			0.872
ALAN	-0.161	0.062	-2.605			0.009
Traffic noise	-0.142	0.066	-2.165			0.030
Road proximity*ALAN	-0.173	0.067	-2.587			0.009
Nestbox ID				279.53	545.00	<0.001
Year				3.71	12.00	0.091
Longitude*Latitude				5.51	5.83	<0.001
c: Brood size						
(Intercept)	0.792	0.036	21.854			<0.001
Wooded environment	0.012	0.020	0.596			0.551
Open environment	0.027	0.021	1.303			0.192
Road proximity	-0.009	0.018	-0.515			0.607
ALAN	-0.044	0.024	-1.854			0.064
Traffic noise	-0.056	0.019	-2.891			0.004
Road proximity*ALAN	-0.058	0.025	-2.317			0.020
Nestbox ID				116.73	561.00	<0.001
Year				9.68	12.00	<0.001
Longitude*Latitude				3.00	3.00	<0.001

the impairing effect of noise on hunting behaviour (Mason et al., 2016; Senzaki et al., 2016). However, we acknowledge that data on prey abundance was not available for this study, so we could not quantify how much prey (and which prey type) owls captured in highly noisy environments. Also, similar to territories closer to roads (van der Horst et al., 2019), territories in noisy habitats might be suboptimal and thus occupied by young and unexperienced owls outcompeted from optimal territories (i.e. less noisy) by older conspecific competitors.

Our results indicate that ALAN can also affect the breeding success of Tawny Owls. Similar to noise, ALAN negatively impacted hatching success and brood size, although this negative effect diminished with road proximity. In fact, nearer to roads ALAN did not impair breeding performance. This finding suggests that the negative effect of ALAN on breeding performance attenuates near roads, where Tawny Owls may increase hunting success which, in turn, enhances breeding performance. Conversely, illuminated areas further away from roads were associated with a lower breeding output. The negative effect of ALAN can be explained by the fact that the exposure to ALAN might increase the visibility of the owls to their prey, thus impairing hunting efficiency and, as a consequence, breeding success. Such inefficiency may be linked to higher vigilance of small mammals when exposed to artificial light (Zhang et al., 2020), which may allow them to detect predators before a hunting strike. As suggested in previous studies on the distribution of forest owls, including Tawny Owls, (Marín-Gómez et al., 2020; Hanmer et al., 2021; Orlando and Chamberlain, 2023), the negative effect of ALAN is likely to be indirect, and generated by altered predator-prey interactions due to the presence of light. Nevertheless, this pattern

might change across different habitats, such as habitats near roads.

Based on our results, the negative effect of ALAN seems to be compensated by the vicinity to roads, which may create unique environments where owls can either find prey regardless of ALAN, or they might exploit it more easily due to higher prey availability and good hunting opportunities. In fact, habitats near roads host high levels of species richness and abundance (e.g. mice, voles, shrews, Bellamy et al., 2000; Ascensao et al., 2012; Hill et al., 2021; birds, Depalma et al., 2022), and are suggested to be attractive hunting grounds for raptors (Meunier et al., 2000; Dean and Milton, 2003; Planillo et al., 2015), including owls (Martínez et al., 1998; Hager, 2009; Grilo et al., 2014). For example, rodent abundance in herbaceous road verges has been shown to attract both Barn Owls and Tawny Owls (Grilo et al., 2012; Silva et al., 2019). Similar to moonlight (Clarke, 1983), owls might take advantage of ALAN in such habitats to increase prey detectability and catchability at night (Rodríguez et al., 2021). The abundance of small mammals in roadside habitats is mainly due to the wide use of these habitats as important refuges and foraging sites (Bellamy et al., 2000; Ascensao et al., 2012; Ruiz-Capillas et al., 2013; Hill et al., 2021), and some rodents have also been observed to increase space use and foraging behaviour in response to artificial light (Hoffmann et al., 2018; Zhang et al., 2020), thus increasing predation risk. Moreover, owls exploit ALAN to catch alternative prey, such as nocturnal insects drawn to artificial lights near roads (e.g. Burrowing Owl *Athene cunicularia*, Rodríguez et al., 2021) and birds (Canário et al., 2012), which use tree belts and hedgerows near roads for breeding and foraging (Munguira and Thomas, 1992; Meunier et al., 1999b; Morelli et al., 2014; Depalma

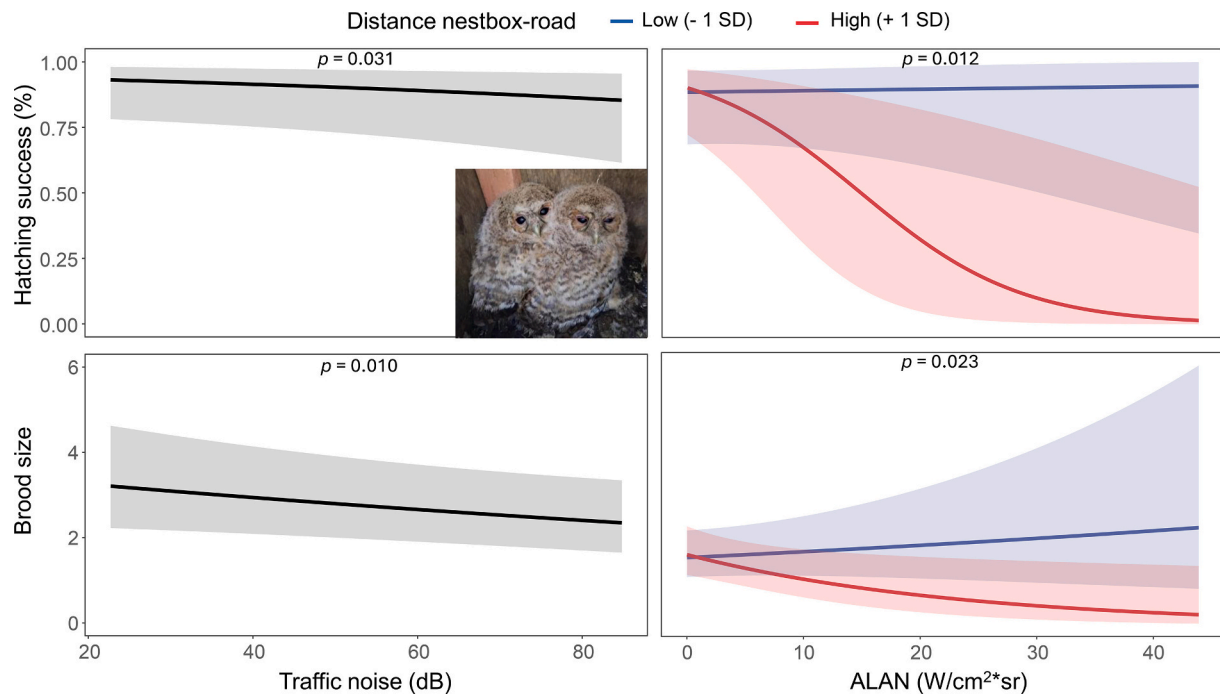


Fig. 3. Sensory pollutants affect Tawny Owl hatching success and brood size, but the effect of ALAN changes with road proximity. The depicted lines represent the regression lines based on the predictions of the best models, with 95 % confidence intervals. For the distance nestbox-road, low/high (± 1 SD) indicate a value that is one standard deviation above and below the mean value of the variable. The p -values from the model results (Table 2) showing the statistical significance ($p < 0.05$) are also indicated. The top-left panel illustrates a couple of young Tawny Owls in a nestbox almost ready to fledge.

et al., 2022). Plausibly, owls may use ALAN to catch diurnal passerines more easily, since they extend foraging and singing activities to the nighttime due to ALAN-induced altered activity rhythms (Kempenaers et al., 2010), becoming easier targets for nocturnal predators. Birds are often included in the diet of Tawny Owls (Grzędzicka et al., 2013), particularly in urban settings where the levels of light pollution are higher. The use of artificial lights by predators to catch birds has been recorded even in diurnal raptors (e.g. Peregrine Falcons *Falco peregrinus*, DeCandido and Allen, 2006), which are not adapted to hunt at night but may find in nighttime lighting an opportunity to increase hunting success (DeCandido and Allen, 2006). Furthermore, traffic noise can make prey near roads less perceptible of predation risk, thus making them easier to catch (Chan et al., 2010). However, since anthropogenic noise impairs also owl ability to detect the prey (Mason et al., 2016; Senzaki et al., 2016), owls may be expected to either select only quiet roadside habitats or illuminated ones regardless of noise. For the latter scenario, owls might hunt relying on their sight rather than their hearing. In this regard, a recent experimental study showed that Tawny Owls can rely on visual cues to find the prey when they are exposed to ALAN and noise separately (Passarotto et al., 2025). Interestingly, when owls were simultaneously exposed to both stressors, ALAN antagonistically affected noise by enhancing prey location by hearing rather than sight, likely because light provides a clearer and better view of the surroundings and helps owls to find the prey by hearing more efficiently (Passarotto et al., 2025). However, in our study we did not find evidence to support the preference for illuminated areas near roads regardless of noise, as we did not find a significant result from the interaction between noise, ALAN and road proximity. To better explore the interplay between these three factors, further research is needed, which could integrate prey abundance data in roadside habitats with data from GPS-tracked owls in a range of noisy and lit environments where roads are present to provide insights into how noise and ALAN affect the selection of hunting areas.

4.3. Implications for owl conservation

Our findings indicate the existence of a moderate but positive relationship between proximity to illuminated areas near roads and owl reproductive performance. However, proximity to roads may have severe consequences on the survival of owls. The use of roads and areas in their proximity can affect population stability due to the detrimental effects of vehicle collisions (Hager, 2009; Šálek et al., 2019), which often target adult breeding individuals and also juveniles during the dispersal phase, when road-related deaths are particularly common (Hanmer and Robinson, 2021). Silva et al. (2019) also showed that mice abundance along road verges explains roadkill events in owls (including Tawny Owls), indicating that habitats near roads may act as ecological traps (van der Horst et al., 2019). Therefore, to improve owl conservation, further road management actions should be explored to make these specific habitats more predator-friendly. For example, some measures could limit the abundance of small mammals along road verges (Ascensao et al., 2012; Grilo et al., 2012, 2014) and make wider roadside habitats to reduce the chances of exposing the owls to vehicles (Meunier et al., 2000). Importantly, we highlight the need to reduce noise pollution. Mitigation measures like noise barriers (e.g. natural barriers such as tree rows and wooded patches, Fröhlich and Ciach, 2018) may be beneficial in areas where owls occur and breed, for example in urban parks and natural reserves that are intersected or surrounded by roads. Additionally, strategies to reduce traffic noise in such areas should be considered. Measures such as lowering speed limits, promoting electric vehicles, or controlling traffic volume through temporal restrictions may help to protect natural soundscapes and enhance both human well-being and biodiversity conservation (Felappi et al., 2024). Limiting anthropogenic noise to preserve the conservation value of natural and urban habitats where owls are present can indeed benefit species at lower trophic levels too, since the presence of owls (Sergio et al., 2005), like other raptors (Natsukawa et al., 2021), is associated with species richness and higher biodiversity value (Sergio et al., 2005; Natsukawa and Sergio, 2022). Finally, as light pollution is expected to increase globally

in the future (Kyba et al., 2017, 2023), wildlife-friendly lighting systems are required to mitigate the impact of ALAN on the nighttime environment (Gaston et al., 2023). In the context of nocturnal owls, minimizing the spread of unnecessary ALAN across the landscape may be beneficial for settlement decisions. Also, it may prevent prey-predator interactions along road networks, which might expose owls to higher risks of vehicle collisions. Evaluating appropriate wildlife-friendly ALAN spectra, intensity, shielding and night-timing (Gaston et al., 2012) to prevent these species interactions will have important conservation implications aimed at preventing ecological traps near roads.

4.4. Conclusions

We showed that sensory pollutants have negative but different effects on nestbox occupancy and breeding performance in a nocturnal acoustic predator commonly found in Europe. Noise consistently impaired both occupancy and breeding performance regardless of road proximity, highlighting the importance to account for noise exposure in conservation planning beyond the immediate vicinity of roads. ALAN also impaired both traits, but its negative effect on reproduction changed based on road proximity, and it decreased in areas nearer roads, where hatching success and brood size were moderately higher. Importantly, we suggest that higher breeding performance in sites nearer to roads may be a consequence of owls either finding the prey regardless of ALAN, or exploiting it to hunt in these areas where prey availability is higher. Future studies should aim at testing this hypothesis and determine whether illuminated areas near roads function as ecological traps for owls, which could have significant implications for raptor conservation.

CRedit authorship contribution statement

Giuseppe Orlando: Writing – review & editing, Writing – original draft, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Luca Nelli:** Writing – review & editing, Writing – original draft, Supervision, Software, Methodology, Conceptualization. **Paul Baker:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Patrik Karel:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Al Vrezec:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Rimgaudas Treinys:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Gian Luigi Bucciolini:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Karel Poprach:** Writing – review & editing, Writing – original draft, Resources, Investigation. **David Anderson:** Resources, Investigation. **Katy Anderson:** Resources, Investigation. **Hugues Baudvin:** Resources, Investigation. **Gérard Olivier:** Resources, Investigation. **Deivis Dementavičius:** Resources, Investigation. **Peter Ericsson:** Resources, Investigation. **Lars-Ove Nilsson:** Resources, Investigation. **Ingar J. Øien:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Saulius Rumbutis:** Resources, Investigation. **Dani Studler:** Resources, Investigation. **Laurent Vallotton:** Writing – review & editing, Writing – original draft, Resources, Investigation. **Maria I. Bogdanova:** Writing – review & editing, Writing – original draft, Supervision, Conceptualization. **Davide M. Dominoni:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Ethical statement

In each country, all applicable international, national and institutional guidelines regarding the handling and care of wild animals were followed carefully. Tawny Owls were always captured, handled, and ringed with appropriate permits and ringing licenses.

Declaration of competing interest

The authors declare that they have no competing or financial interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111533>.

Data availability

Data and R code supporting the results of this study are freely available at: <https://github.com/beppe96/owls-ecology.git>.

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