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# Does artificial light interfere with the activity of nocturnal mammals? An experimental study using road underpasses

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ABSTRACT

The emission of artificial light at night (ALAN) generates a light pollution. The impacts on fauna, flora and ecosystems have been increasingly studied in recent decades. However, mammals - except bats or rodents - remain under-studied, particularly in terms of space use. Here, we implemented a three-year in-situ before–during–after exposure protocol to assess the effect of artificial light at night at five underpasses of a motorway in a French regional natural park. Using camera traps, we recorded movements of medium-sized wild mammals and collected data on 12 species, especially European badger *Meles meles*, red fox *Vulpes vulpes* and martens (*Martes martes* and *M. foina*). Our results showed that lighting significantly decreased the probability to cross the underpasses for European badger in spring and autumn and for red fox in spring, while there was no significant effect of lighting for martens. Lighting also reduced crossing speed for badgers. We can conclude that, for some medium-sized wild mammals, ALAN triggers an avoidance behaviour that prevents them from crossing lit underpasses during certain seasons. This suggests that ALAN can act as a nightscape fragmentation, which is in line with previous studies on other taxa - as bats, insects, amphibians or eels. This additional barrier effect confirms the value of dark infrastructure; i.e. ecological network policies to preserve dark habitat patches and dark corridors.

## 1. Background

For several decades, the emission of artificial light at night (ALAN) has spread worldwide, generating global light pollution (Falchi et al., 2016). This phenomenon affects all biomes (Bennie et al., 2015) and concerns both urban, rural and even inhabited areas (Aguilera and González, 2023; Khanduri et al., 2023). In recent years, the increasing use of light-emitting diodes (LED) has further amplified the process (Gaston and Sánchez De Miguel, 2022). ALAN can take different forms - such as sky glow or glare - and depends on time, colour and intensity of light (Kocifaj et al., 2023). ALAN is one of the sensory pollutants along with anthropogenic noise and odors (Halfwerk and Slabbekoorn, 2015). Light pollution can cause a very wide range of adverse effects on many living organisms - e.g. birds (La Sorte et al., 2022), anurans (Touzot et al., 2019), mammals (Shier et al., 2020), fishes (Nelson et al., 2022), insects (Levy et al., 2024), and at different levels of life - e.g. at gene (Hui et al., 2023), community (Davies et al., 2012), ecosystem (Knop et al., 2017) or landscape levels (Camacho et al., 2021). For example, ALAN may decrease species diversity and abundances, being associated with a shift in the abundance of trophic groups in arthropod communities (Brown et al., 2023). It can disturb interspecific relationships, even between plants and animals (Cieraad et al., 2023). It may alter life-history traits (e.g. growth, survival, fecundity, mobility) (Sanders et al., 2021) and have impacts on physiology (melatonin production) (Yang et al., 2024).

Research on the impacts of ALAN on fauna, flora and ecosystems has grown significantly over the last 30 years and the current knowledge concerns a wide range of taxa and outcomes (e.g. (Brayley et al., 2022;

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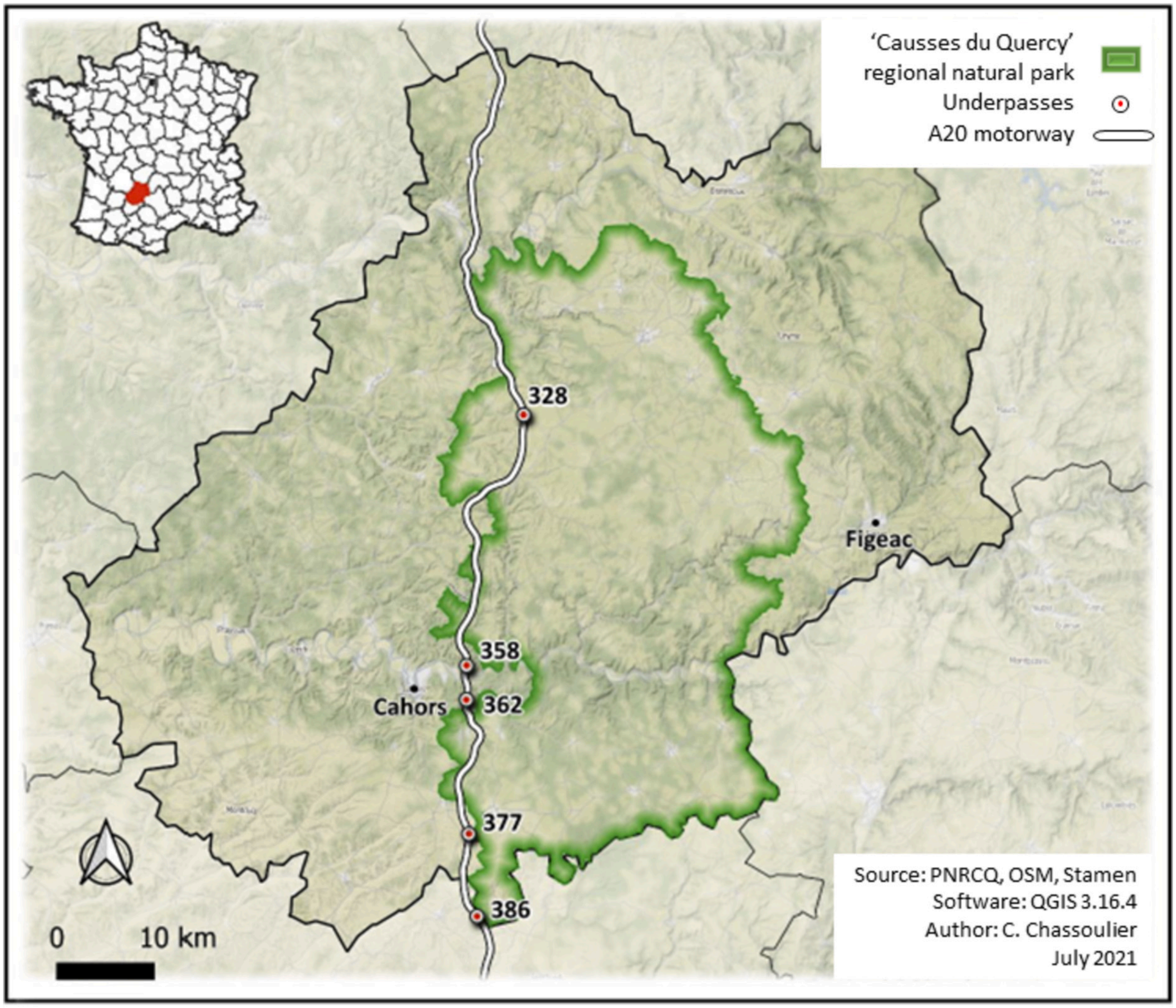
Jägerbrand and Spoelstra, 2023)). However, terrestrial mammals - such as ungulates and carnivores - seem to remain relatively understudied compared to bats, birds, amphibians, fish or insects (Pérez Vega et al., 2022). This is particularly surprising as 3624 species of terrestrial mammals worldwide are known to have experienced an increase in average light intensity across their range, while significant decreases were reported for only 41 species (Duffy et al., 2015). ALAN is also identified as a global source of range fragmentation for terrestrial mammals across the United States (Ditmer et al., 2021). In a meta-analysis on the impacts of ALAN on living organisms, the authors focussed on rodents and birds as these were the two most documented groups (Sanders et al., 2021). Indeed, many studies on mammals deal with small terrestrial mammals, particularly rodents (e.g. Zollner and Lima, 1999; Bird et al., 2004; Zhang et al., 2020). Bats have also been the target of several studies in recent years (Dzul-Cauich and Munguía-Rosas, 2022; Voigt et al., 2021). This may be partly explained by the fact that bats have recently benefited from a strong evolution of monitoring techniques (e.g. ultrasound recording, infrared thermal imaging (Kunz and Parsons, 2009) and the possibility of automatically assigning species from acoustic signatures (Barré et al., 2019). On the other hand, studies of large and medium-sized mammals are more difficult to conduct because they are time-consuming (Ford et al., 2009) and involve heavy and expensive monitoring (Goodyear, 1989).

Few studies show that ALAN is likely to have adverse effects on space use (Laguna et al., 2022) or feeding activity (Brieger et al., 2017). Two studies highlighted that light pollution is negatively correlated with the occurrence of European roe deer *Capreolus capreolus* (Ciach and Fröhlich, 2019) and wild boar *Sus scrofa* (Ciach et al., 2022). Studies on movements are even rarer while movement is a key factor in feeding, reproduction or the search for favourable habitats (Finnerty et al., 2022).

ALAN can have detrimental effects on animal behaviour, particularly regarding movements, which can affect many activities such as feeding or reproduction (Sordello, 2024). Hence, we focused our study on the movements of some terrestrial wild mammals exposed to artificial lighting. To investigate potential barrier effects of ALAN on several species, we recorded their behaviour when reaching underpasses of a French motorway. We used artificial lighting of the entrances of underpasses to simulate the possible aversion of mammals to a source of artificial light that may index a broader response to ALAN. We hypothesized that (1) lighting reduces the probability of underpasses being used by terrestrial wild mammals, (2) the crossing speed of terrestrial wild mammals that do use the underpasses increases, so as to minimize the time spent in a stressful environment, and (3) any impact of lighting on movements of terrestrial wild mammals would disappear after light removal. We carried out a before–during–after exposure protocol, over a three-full-year study in order to test the possible influence of seasons on animal behaviour.



Source: PNRCQ, OSM, Stamen
Software: QGIS 3.16.4
Author: C. Chassoulier
July 2021

**Fig. 1.** Location of the five underpasses studied along the A20 motorway in the 'Causses du Quercy' regional natural park, France.

## 2. Material & Methods

### 2.1. Study area

The study was conducted in the ‘Causses du Quercy’ regional natural park, situated in the Lot department, SW France (Fig. 1). This park covers 185,000 ha with a sparsely but uniformly populated rural setting (17.5 inhabitants/km$^2$).

Most of this territory is made of natural and agricultural lands (95 %), covered by pubescent oak (*Quercus pubescens*) forests, dry grasslands and juniper heaths, the Lot and Célé valleys adding some humid habitats. Calcareous plateaus are followed by wooded hills, valleys and cliffs, all of which contribute to the region’s UNESCO-recognized geological heritage. These landscapes extend to an average altitude of 135 m above sea level.

This park is renowned for the quality of its nocturnal environment, being one of the areas where darkness is the most preserved in France (ONB, 2021). In 2012, the park engaged a first work of considering ALAN in the identification of ecological networks (Granier, 2012). This work highlighted knowledge gaps about the impact of ALAN on the movement of certain groups of species. In 2016, a first experimental protocol based on forest sites was undertaken to study the impact of artificial lighting on the movements of nocturnal terrestrial mammals. Few data were collected even if they provided exploratory results (Drouglazet, 2016). We therefore decided to develop a second protocol based on cement underpasses that allow wildlife flow under the motorway (A20) bordering the park. This configuration gave us the opportunity to improve our knowledge of the effects of ALAN on the movements of several species of terrestrial mammals known to be present in the park, and likely to use these subways during their life cycle.

The most relevant sites of the studied territory were selected for the present study; i.e. unlit underpasses with quite similar length, height and structure and previously known to be visited by numerous mammal individuals (Figs. 1, 2, Table 1). The process for selecting the study sites was as follows. A first selection of 76 potential sites was made by cross-referencing various criteria (covered passage of sufficient size, minimum human traffic, no works planned, etc.). This initial phase resulted in the selection of 17 sites. Data on animal use from the Lot hunting federation reduced this pool to 9 sites. These 9 sites were monitored by camera trap over a one-month period to confirm their use by wildlife. Within this pool 5 sites were finally selected because the other four sites were not visited.

### 2.2. Experimental design and monitoring

The study targeted all terrestrial wild mammals likely to be detected crossing the underpasses by camera trapping, and subsequently identified. We therefore excluded small mammals (such as weasel, hedgehog, shrews, small rodents, etc.) and bats, too small to be systematically recorded and/or identified based on camera pictures. We used infrared camera traps (Reconyx Hyperfire SC 950) triggered by movement for taking photographs since videos consume much more battery power and saturate storage cards much more quickly. Camera traps were placed on each side of the five underpasses located in different environments (e.g. grassland, forest, with/without watercourse, Table 1). Light treatment was produced using a LED spotlight installed inside each underpass (Fig. 3). LEDs were chosen for this study because they are the most widely installed outdoor lighting technology in the world today. We used a LED 12/24 V, which spectral composition corresponds to LEDs that are very frequently installed in outdoor lighting (white cool LEDs). The light source was powered by a lithium battery connected to a solar panel and it was installed near the western entrance of the underpass pointing towards the ground and in the direction of the opposite side. Equipment and all settings were standardized among sites and for the two sides of each site. Additional file 1 - Appendix A provides details of the installation, characteristics and settings of the camera and artificial light source. Field monitoring was performed by staff of the Lot hunting federation (i.e. collecting photographs at each underpass). After an acclimation phase, the monitoring was performed during three years to allow a full comparison before and after the exposition to ALAN:

- Acclimation period (November 2017–May 2018 inclusive, 6 months): designed to allow wildlife to get used to the presence of the study device without any lighting;
- Off1 period (June 2018 inclusive - May 2019 inclusive, 1 year): lighting was turned off;
- On period (June 2019 inclusive - May 2020 inclusive, 1 year): lighting was turned on at night;
- Off2 period (June 2020 inclusive - May 2021 inclusive, 1 year): lighting was turned off.

### 2.3. Data extraction from the photographs

We used MapView (v.3.7.2.2) to collect different pieces of information from the photographs: underpass identifier, study period (Off1, On, Off2), date and moon phase (such information was included on the photographs by the camera), species identity and animal behaviour regarding underpass use. We identified 4 possible behaviours, all corresponding to one sighting: crossing (animal seen on both sides), probable crossing (animal seen on one side only), turning back, or unknown (unclear behaviour). When several individuals of a species were visible together in the same photograph, only one sighting was coded when they performed the same behaviour, or several sightings were coded

**Fig. 2.** Overview of the western (top line) and eastern (bottom line) openings of each of the five underpasses studied in the ‘Causses du Quercy’ regional natural park, France. The figures refer to site ID (see Table 1).

**Table 1**
Characteristics (length, height and altitude in meters) of the five underpasses studied in the 'Causses du Quercy' regional natural park, France, and number of sightings for the three taxa with the largest number of sightings over the three-year study period the percentages detail the proportion of sightings in the different habitats in relation to the total of sightings for each species). Martens: *Martes martes* and *M. foina (grouped here as Martes* spp.*)*. One sighting corresponds to one of the four expected behaviours, i.e. either a confirmed crossing, a probable crossing, a turning back, or an 'unclear' behaviour (unknown).

| Site ID | Length | Height | Altitude | Environment | *Meles meles* | *Vulpes vulpes* | Martes spp. |
|---|---|---|---|---|---|---|---|
| 328 | 45 | 1.5 | 327 | Grassland | 808 (24 %) | 98 (7 %) | 74 (6 %) |
| 358 | 40 | 1.5 | 184 | Rocks, grassland, facing a deciduous forest | 336 (10 %) | 177 (13 %) | 193 (16 %) |
| 362 | 45 | 1.9 | 132 | Rocks, grassland, shrubs, temporary watercourse | 695 (21 %) | 671 (49 %) | 152 (13 %) |
| 377 | 35 | 1.9 | 241 | Grassland with some trees | 1334 (39 %) | 230 (17 %) | 235 (19 %) |
| 386 | 82 | 1.5–2 | 171 | Trees, watercourse | 214 (6 %) | 194 (14 %) | 560 (46 %) |
| | | | | Total | 3387 | 1370 | 1214 |

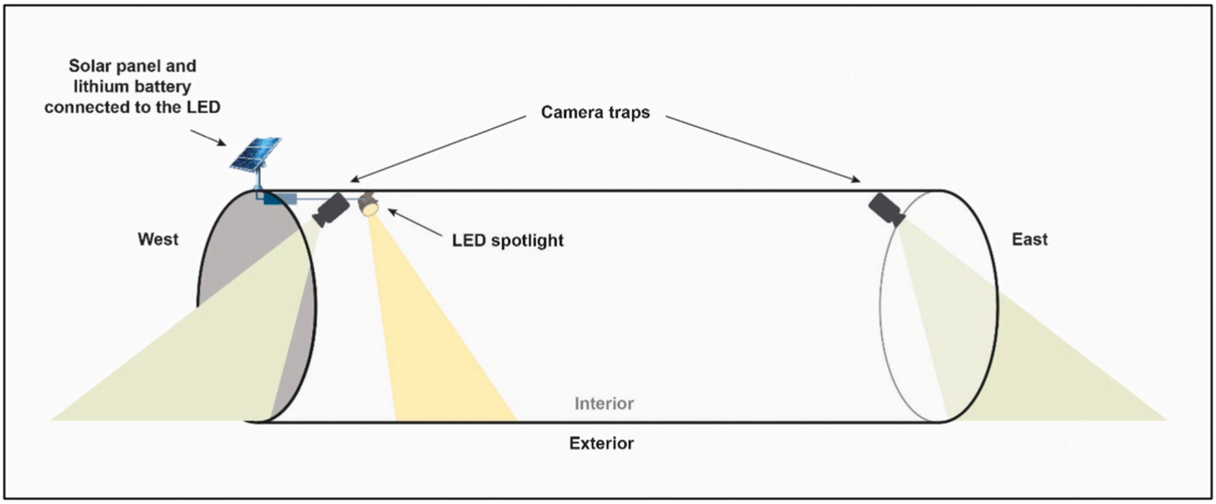


**Fig. 3.** Camera trapping device implemented at each underpass studied in the 'Causses du Quercy' regional natural park, France. Cameras were positioned on each side of each underpass, facing the ground at an angle of around 30–40°. The artificial light source was installed inside the underpasses, near the western entrance of each underpass, pointing towards the ground and in the direction of the opposite entrance. Equipment (camera and LED) and all settings were standardized among sites and for the two sides of each site. See Additional File 1 - Appendix A for more details about characteristics and settings of the material.

when they displayed different behaviours (one per each type of behaviour). When a crossing behaviour was recorded, the duration of the crossing was also calculated when possible (time length between the photographs taken on each side of the underpass), and then the crossing speed as the ratio of the duration of crossing to the length of the underpass. Based on the date, sunrise (when top edge of the sun appears on the horizon) and sunset (when top edge of the sun disappears below the horizon, evening civil twilight starts) times were calculated at 44.64° latitude and 1.56° longitude using the suncalc R package (Thieurmel and Elmarhraoui, 2022). The difference between sunrise and sunset times was used to calculate night length (as 24 h minus day length). These sunrise and sunset times were also used to define four seasons centred on solstices and equinoxes: summer from May 4th to August 7th, autumn from August 8th to November 7th, winter from November 8th to February 1st, and spring from February 2nd to May 3rd.

### 2.4. Statistical analyses

We modelled the probability of an animal to cross the underpass (confirmed crossings only) as a function of predictors using a binomial generalised linear mixed model. This response variable was calculated at the individual level: for each animal detected at an underpass, the variable was assigned a value of 1 if the animal crossed (crossing), or 0 if the animal did not cross (probable crossing, turning back, unknown). We chose to model the probability of crossing rather than the number of sightings or of crossings because of the potential confounding effect of variations in population densities among years, which might have confounded the effect of the treatment period. The full model included as fixed effects: night length (continuous, in hours, as a control of the duration of the sampling period), moon phase (factor with 8 levels: new moon; waxing crescent; first quarter; waxing gibbous; full moon; waning gibbous; last quarter; waning crescent; for testing the potential moderating effect of the moon extra source of light), season (factor with four levels: summer; autumn; winter; spring), treatment period (factor with three levels: Off1; On; Off2), and the interaction between treatment period and season. The length of the night was used to control the fact that the length of the sampling period differs according to the length of the night (longer night in winter, shorter in summer). The wildlife crossing structure (site factor with five levels) was specified as a random effect on the intercept to consider the dependency among observations at the same site. The five sites showed strong differences in sighting numbers (Table 1).

We modelled the crossing speed (in m/s) of the animals crossing the structure as a function of predictors using a linear mixed model. The crossing speed was log-transformed to improve the normality of the distribution and model fitting. The full model included as fixed effects: season (factor with four levels: summer; autumn; winter; spring), treatment period (factor with three levels: Off1; On; Off2), and the interaction between treatment period and season. Unlike the binomial model, we were unable to include moonlight phase in this model, which would have made the model over-parameterised, given the small amount of data about crossing speeds. The wildlife crossing structure (site factor with five levels) was specified as a random effect on the intercept to consider the dependency among observations in the same site.

Only events recorded at night were kept in the analyses, limited to the three taxa with a large number of sightings, namely European badger (*Meles meles*), red fox (*Vulpes vulpes*) and martens *Martes* spp. (*Martes*

*martes* and *Martes foina* could not be distinguished in the photographs). A model was fitted for each taxon separately.

All analyses were performed using the R software version 4.2.1 (R Core Team, 2022). The binomial generalised linear mixed models and the linear mixed models were fitted using the lme4 R package (Bates et al., 2015). Best models were selected using the dredge() function in the MuMIn R package (Bartoń, 2022). The model with the lowest second-order Akaike information criterion (AIC, i.e. AIC for small samples) was chosen, if the difference with the second model with the lowest AICc was at least 2. To interpret the results for categorical variables in the final model, pairwise comparisons tests were performed using the emmeans R package (Lenth, 2022). Residuals of the models were checked for potential deviation from expected distribution, from uniformity, and potential over- or under-dispersion using the DHARMa R package (Hartig, 2022). DHARMa creates, through a simulation-based approach, readily interpretable residuals for generalised linear (mixed) models that are standardized to values between 0 and 1, and that can be interpreted as intuitively as residuals for the linear model.

For the binomial generalised linear mixed models, multicollinearity between model predictors was checked by computing the variance inflation factor (VIF) using the performance R package (Lüdecke et al., 2021). Treatment and moon phase showed a VIF between 1.02 and 1.11 while night length and season showed a VIF between 4.88 and 5.75 (see Additional File 1 - Appendix B for full details), which was considered as an acceptable low or moderate multicollinearity according to the literature (James et al., 2013; Kutner, 2005; Montgomery et al., 2012). As a result, all predictors were kept before model selection. Multicollinearity between model predictors was also checked for crossing speed model and all variables showed acceptable VIFs between 1.05 and 1.10 (see Additional File 1 - Appendix B for full details).

## 3. Results

A total of 12 species of wild mammals were detected by the camera traps: European badger, red fox, European pine marten *Martes martes,* beech marten *Martes foina,* Eurasian otter *Lutra lutra,* European polecat *Mustela putorius,* common genet *Genetta genetta,* European roe deer *Capreolus capreolus,* wild boar *Sus scrofa,* European rabbit *Oryctolagus cuniculus,* European hare *Lepus europaeus,* and nutria *Myocastor coypus* (Table 2). The most frequency recorded species at the five sites were: European badger (3387 sightings), red fox (1370 sightings) and martens (1214 sightings). The pattern was similar for the number of crossings. The other species were recorded far less frequently, with a number of sightings between 202 for nutria and 5 for European rabbit.

### 3.1. Species general activity patterns

The three taxa targeted for analyses exhibited a similar activity pattern (Fig. 4). Activity started mainly after sunset and stopped often after sunrise, in particular in foxes and martens. European badger and martens were active one hour after nightfall whatever the season; red foxes were similarly active except in winter, when their nocturnal activity started as soon with nightfall.

**Table 2**
Number of sightings (all behaviours, i.e. crossing, probable crossing, turning back, unknown) and crossings per taxon from the photographs taken at the five underpasses studied in the 'Causses du Quercy' regional natural park, France, during the three-year study period. The two species *Martes martes* and *Martes foina* were grouped together because they could not be distinguished in the photographs.

| Taxa | Sightings | Crossings |
|---|---|---|
| European badger *Meles meles* | 3387 | 2120 |
| Red fox *Vulpes vulpes* | 1370 | 443 |
| Martens *Martes* spp. | 1214 | 355 |
| Nutria *Myocastor coypus* | 202 | 65 |
| Wild boar *Sus scrofa* | 141 | 87 |
| European hare *Lepus europaeus* | 79 | 10 |
| European roe deer *Capreolus capreolus* | 55 | 5 |
| Eurasian otter *Lutra lutra* | 27 | 3 |
| Common genet *Genetta genetta* | 26 | 5 |
| European polecat *Mustela putorius* | 23 | 1 |
| European rabbit *Oryctolagus cuniculus* | 5 | 2 |

### 3.2. Effect of underpass lighting on crossing probabilities

The final model selected for European badger crossing probabilities included night length and the interaction between treatment period and season (see model selection in Additional file 1 - Appendix C). The probability for a badger to cross the underpasses significantly increased with night length (Table 3a). During the Off1 and Off2 periods, crossing probabilities were significantly lower in autumn and winter than in summer and spring (Table 2a, Fig. 5a). Within each season, the crossing probabilities during the Off1 and Off2 periods were not significantly different. During the On period, crossing probabilities were significantly lower in autumn than in summer, but there was no significant difference among the other pairs of seasons. The lighting (On period) significantly reduced the crossing probabilities in autumn and spring, but not in summer and winter (Fig. 5a).

Likewise, the final model selected for red fox crossing probabilities included night length and the interaction between treatment and season. The probability for a red fox to cross the underpasses however significantly decreased when night length increased (Table 3b). During the three treatment periods, crossing probabilities did not vary according to seasons (Table 2b, Fig. 5b). The lighting (On period) significantly reduced crossing probabilities only in spring (Fig. 5b). During the Off1 and Off2 periods the crossing probabilities were not significantly different within each season.

The final model selected for martens crossing probabilities included only night length and season. The probability for martens to cross the underpasses slightly increased with night length but the effect was not statistically significant (Table 3c). Likewise, crossing probabilities were slightly lower in autumn than in the other seasons but no pairwise differences between seasons were statistically significant (see Additional File 1 - Appendix D - Fig. 5c).

The analysis of model residuals did not reveal any fitting problem for European badger, whereas a slight deviation from expected distribution and uniformity was observed for red fox and martens (see Additional File 1 - Appendix E - Fig. S1-S3). This was likely due to the imbalanced number of observations among sites (Table 1). The proportion of variance explained by the fixed effects was also very low for these two taxa (6.5 % and 0.8 % for red fox and martens, respectively) compared to European badger (14.9 %, Table 3).

### 3.3. Effect of underpass lighting on crossing speed

Descriptive data on the crossing speed of each species are provided in Table 4. The final model selected for European badger crossing speed included treatment and season (Table 5) (see model selection in Additional file 1 - Appendix C). The analysis of model residuals revealed that the model did not perfectly fit the data, with a slight deviation from expected distribution and uniformity (see Additional File 1 - Appendix E - Fig. S4). The model revealed that the crossing speed of European badgers was significantly lower in autumn (and to a lesser extent in winter) than in the other seasons (Fig. 6a), and that lighting significantly reduced the crossing speed (Fig. 6b). There was no significant difference in crossing speed between the Off1 and Off2 periods.

None of the fixed predictors were included in the final model for the crossing speed of red fox or martens (i.e. the null model was the "best" model, 433 and 353 data for red fox and martens, respectively). Lightning therefore did not significantly impact the crossing speed of red fox and martens.

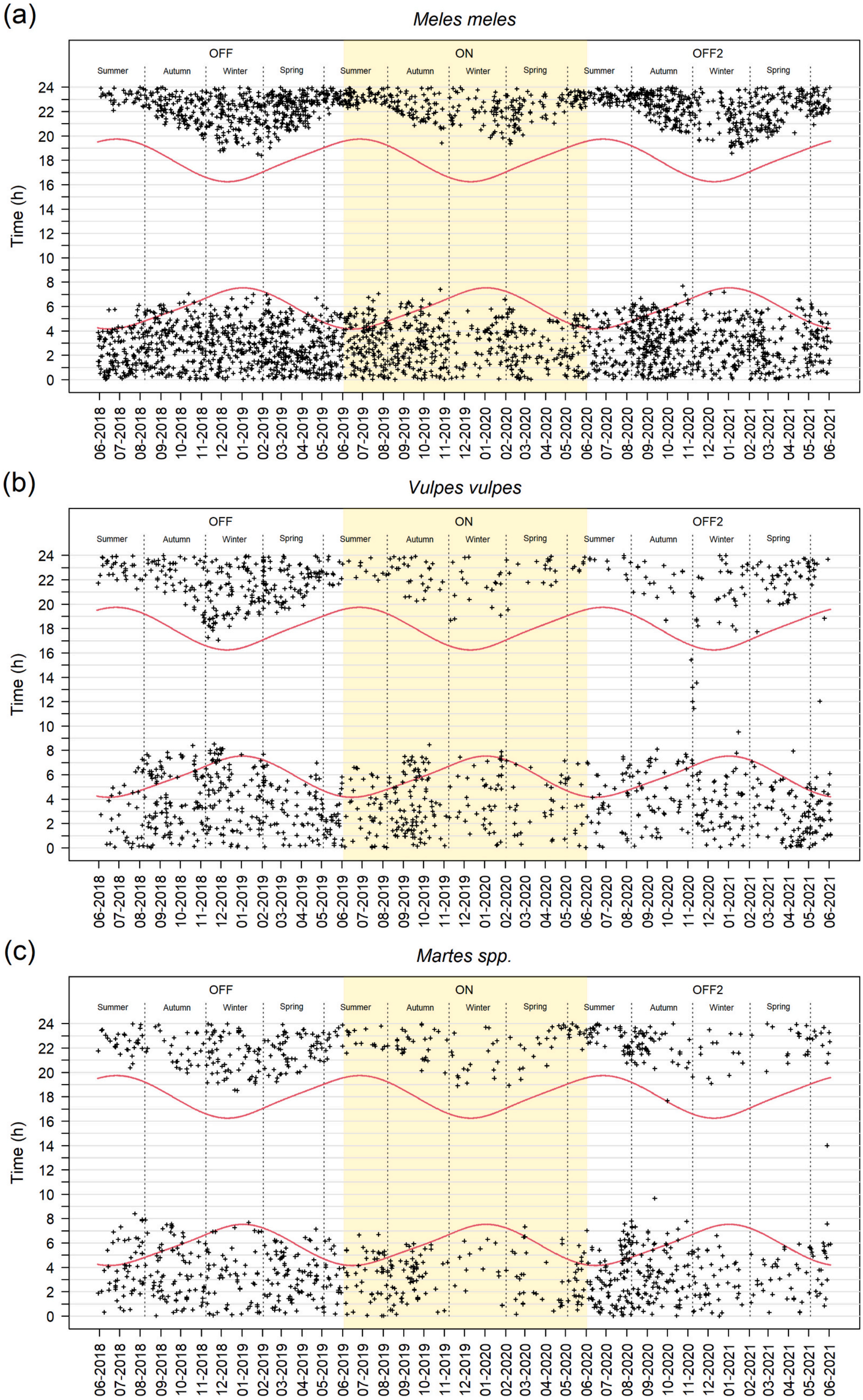


**Fig. 4.** Temporal distribution of all sightings per taxon from the photographs taken at the five underpasses studied in the 'Causses du Quercy' regional natural park, France, according to date and daytime during the three-year period. In (c), the two species *Martes martes* and *Martes foina* were grouped together as *Martes* spp. because they could not be distinguished in the photographs. Sightings are indicated by black dots. The red lines indicate the sunrise and sunset times used to define night. The vertical dotted lines point out the seasons. The lighted period (On) is highlighted in yellow. Exact UTC (0) was used. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**
Model estimates of parameters for crossing probabilities of (a) European badger, (b) red fox, and (c) martens, at the five underpasses studied in the 'Causses du Quercy' regional natural park, France. The marginal $R^2$ is only the variance of fixed effects, while conditional $R^2$ is the variance of both fixed and random effects.

| | Estimate | Std. Error | z value | P-value |
|---|---|---|---|---|
| (a) *Meles meles* | | | | |
| 3387 observations; variance of the random effect = 0.2708; marginal $R^2$ = 0.149; conditional $R^2$ = 0.213 | | | | |
| Intercept | −3.360 | 0.437 | −7.689 | < 0.001 |
| Night length | 0.403 | 0.040 | 10.173 | < 0.001 |
| Treatment_On | −0.505 | 0.176 | −2.868 | 0.004 |
| Treatment_Off2 | −0.469 | 0.182 | −2.572 | 0.010 |
| Season_Autumn | −1.100 | 0.208 | −5.301 | < 0.001 |
| Season_Winter | −1.041 | 0.301 | −3.457 | 0.001 |
| Season_Spring | −0.127 | 0.206 | −0.617 | 0.537 |
| Treatment_On: Season_Autumn | −0.169 | 0.253 | −0.666 | 0.505 |
| Treatment_Off2: Season_Autumn | 0.660 | 0.240 | 2.739 | 0.006 |
| Treatment_On: Season_Winter | 0.294 | 0.317 | 0.926 | 0.355 |
| Treatment_Off2: Season_Winter | 0.087 | 0.278 | 0.313 | 0.754 |
| Treatment_On: Season_Spring | −0.461 | 0.271 | −1.698 | 0.089 |
| Treatment_Off2: Season_Spring | 0.222 | 0.267 | 0.830 | 0.406 |
| (b) *Vulpes vulpes* | | | | |
| 1370 observations; variance of the random effect = 0.5139; marginal $R^2$ = 0.065; conditional $R^2$ = 0.191. | | | | |
| Intercept | 1.30169 | 0.68570 | 1.898 | 0.057651 |
| Night length | −0.21992 | 0.06375 | −3.449 | 0.000562 |
| Treatment_On | −0.55953 | 0.32842 | −1.704 | 0.088438 |
| Treatment_Off2 | −0.47151 | 0.30618 | −1.540 | 0.123564 |
| Season_Autumn | −0.17954 | 0.33869 | −0.530 | 0.596041 |
| Season_Winter | 0.28450 | 0.45482 | 0.626 | 0.531628 |
| Season_Spring | 0.39394 | 0.33086 | 1.191 | 0.233789 |
| Treatment_On: Season_Autumn | 0.32063 | 0.43989 | 0.729 | 0.466076 |
| Treatment_Off2: Season_Autumn | 0.44831 | 0.46770 | 0.959 | 0.337796 |
| Treatment_On: Season_Winter | 0.88181 | 0.49170 | 1.793 | 0.072911 |
| Treatment_Off2: Season_Winter | 0.78748 | 0.41720 | 1.888 | 0.059085 |
| Treatment_On: Season_Spring | −1.25548 | 0.60952 | −2.060 | 0.039418 |
| Treatment_Off2: Season_Spring | 0.80711 | 0.39893 | 2.023 | 0.043056 |
| (c) *Martes* spp. | | | | |
| 1214 observations; variance of the random effect = 0.1702; marginal $R^2$ = 0.008; conditional $R^2$ = 0.056. | | | | |
| Intercept | −1.03783 | 0.65524 | −1.584 | 0.113 |
| Night length | 0.02122 | 0.06875 | 0.309 | 0.758 |
| Season_Autumn | −0.14904 | 0.24488 | −0.609 | 0.543 |
| Season_Winter | 0.15738 | 0.44322 | 0.355 | 0.723 |
| Season_Spring | 0.21398 | 0.27121 | 0.789 | 0.430 |

## 4. Discussion

Our results reveal that artificial light at night significantly decreased the probability to cross underpasses, during autumn and spring for European badgers and during spring for red foxes. However, there was no significant effect of lighting for martens, leading to a partial confirmation of our first hypothesis. We also recorded that European badger reduced its crossing speed in lit underpasses during all seasons while crossing speed did not change according to light treatment for other species; all these results contradict our second hypothesis. Finally, no difference in crossing probability or in crossing speed between the Off1 and Off2 periods for all seasons was recorded for our three studied taxa, which validates our third hypothesis that the impact of lighting can disappear after light removal.

### *4.1. Limitations of the study design*

A first limitation of our study concerns the lack of control sites. This is the result of a compromise to optimise the experimental protocol with a limited number of sites. Indeed, the process of selecting potential sites within the regional natural park led us to identify only 5 valid underpasses. We therefore preferred to use these 5 sites as spatial replicates rather than splitting this pool into two samples (treated vs. control) which would have reduced the robustness of the results.

Our experimental study design is based on a temporal comparison: five treated sites simultaneously experienced three periods through a before-during-after exposure protocol. Such temporal comparison is very common in ecology; in particular such protocols are very often used, in-situ or ex-situ, to assess the effects of artificial light on various animal taxa (Bolliger et al., 2020; May et al., 2017; Riley et al., 2012) including mammals (Finch et al., 2020; Hoffmann et al., 2019; Laguna et al., 2022; Rotics et al., 2011). A systematic map on light pollution and birds based on 490 publications revealed that $\sim$40 % of studies had no comparator (whether temporal or spatial) and only 4 % were based on a before-after-control-impact protocol (Adams et al., 2021).

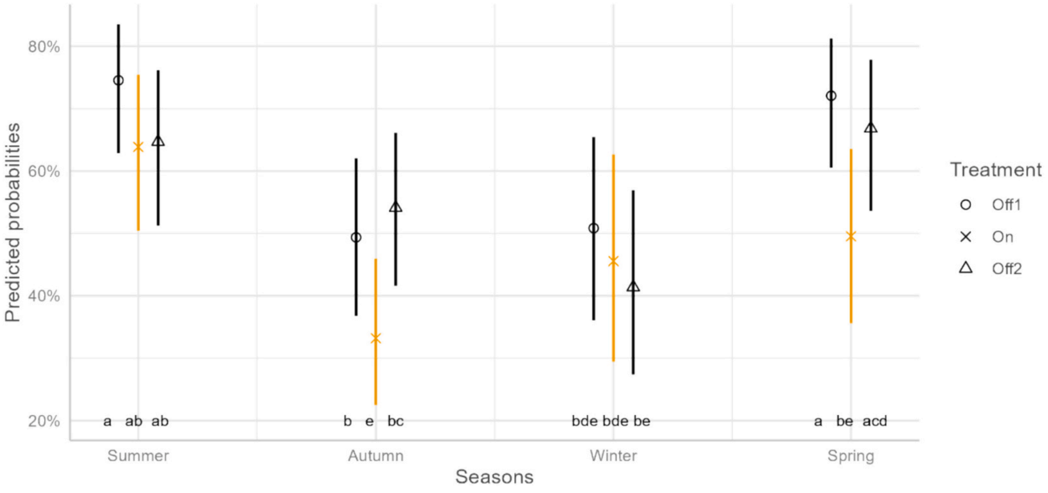
By considering both a 'before' and an 'after' period (double time comparison) we were able to check in the 'after' period whether any changes in animal behaviour observed in the 'during' period compared with the 'before' one were indeed due to exposure and to observe any resilience of the animals after the light treatment. As each period lasted a full year, we were able to test a possible habituation of animals to exposure and variations due to seasons, which alternating short periods of light and darkness would not have allowed. Finally, a spatial control may be a weak control when the effect of a sensory disturbance is being studied. Indeed, a high individual variability may be expected, as it is the case for noise pollution (Harding et al., 2019), which limits the interest of a distant control site with different individuals. By applying a before/after to the same site, we increased the odds that identical individuals - with their own sensitivity to ALAN - used the underpass throughout the three periods.

The lack of data on population dynamics of the three taxa in the study area impeded us to directly analyse the number of crossings of each species. Indeed, fewer crossings during the 'during' period could be linked either to the artificial light treatment or a lower density of individuals that year. Having hunting data around the underpasses could have helped to limit this bias. However, to overcome this lack, we addressed in this study the influence of artificial light on the behaviour of animals arriving at the wildlife crossing using the ratio of animals crossing/not crossing as outcome, which is independent to population dynamics. This was the relevant outcome for our study, which did not aim at checking whether the underpasses enable the population to function optimally but at acquiring fundamental knowledge about the influence of artificial light, the crossing structure being merely a pretext for the feasibility of the experimental protocol.

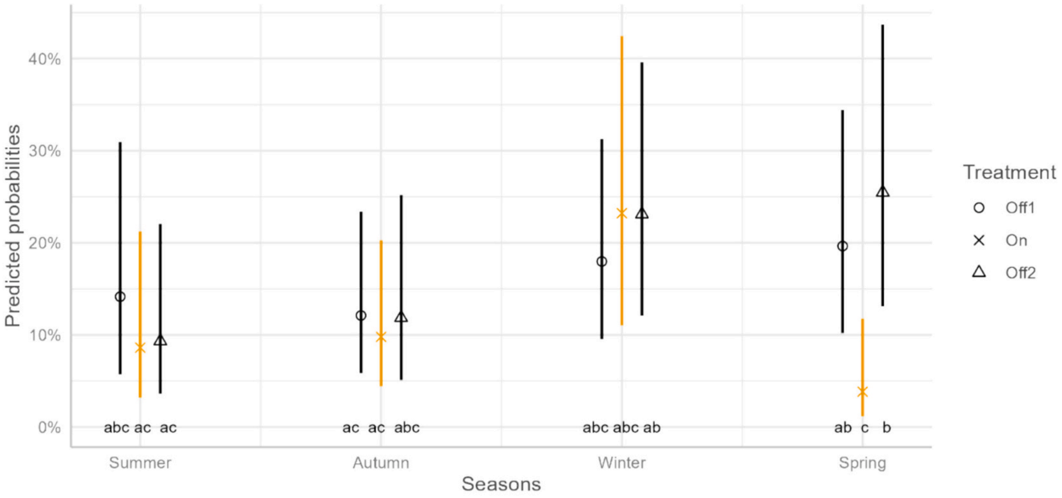
At last, we are aware that videos can provide more information than images to analyse animal mobility. However, photos are much quicker to process than videos (the viewing time of a video for a human is much longer, and we had not planned to use AI for this study). Moreover, taking videos consumes much more battery power and saturates storage cards much more quickly. For all these reasons, we made the decision to store images, which remain a relevant medium for analysing the passage of individuals (thanks to the use of two cameras on the opposite sides of the passage) and are often used in wildlife crossing monitoring.

### *4.2. ALAN is a barrier for certain wild mammal species depending on seasons*

Our study stresses that illuminating wildlife underpasses can make them less functional for some terrestrial mammals. Since such structures may be the only way to connect two patches of habitat separated by a transport infrastructure such as a motorway, we can assume that ALAN is likely to create a barrier for terrestrial mammals. Hence, our results confirm the need to address intangible pollution in conservation planning (Dominoni et al., 2020; Elmer et al., 2021). However, the effects of lighting depended on seasons (spring and autumn for European badger and spring for red fox). Since the lighting of the underpasses began in summer in our experiment and that effect was detected in spring (i.e. end of the phase), we can exclude a potential habituation by the animals *(a) Meles meles*



*(b) Vulpes vulpes*



*(c) Martes*

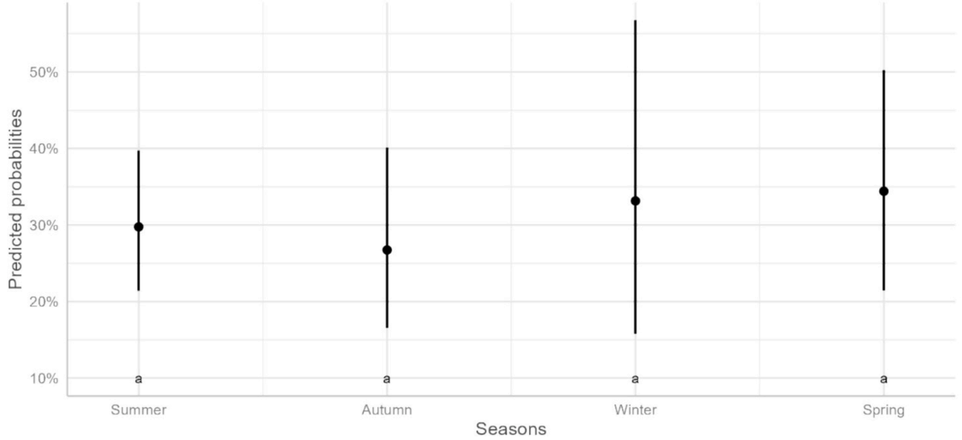


**Fig. 5.** Probability to cross the five underpasses studied in the 'Causses du Quercy' regional natural park, France, by treatment period and/or season as predicted by the model for (a) European badger, (b) red fox, and (c) martens, with 95 % confidence intervals (adjusted for night length = 11.01, 14.12 and 8.44 h in (a), (b) and (c), respectively). In (c), predicted probabilities are for all treatments combined. Letters indicate statistically significant differences between pairs of means (see Additional File 1 - Appendix D for full results of pairwise comparison tests). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 4**
Descriptive data on the crossing speed (m/s) of each species at the five underpasses studied in the ‘Causses du Quercy’ regional natural park, France.

| Taxa | Min | Max | Median | Mean |
|---|---|---|---|---|
| European badger<br>*Meles meles* | 0.083 | 7.500 | 1.029 | 1.140 |
| Red fox<br>*Vulpes vulpes* | 0.197 | 5.625 | 1.286 | 1.259 |
| Martens<br>*Martes* spp. | 0.159 | 4.824 | 1.242 | 1.258 |

**Table 5**
Model estimates of parameters for European badger crossing speed at the five underpasses studied in the ‘Causses du Quercy’ regional natural park, France.

| | Estimate | Std. Error | t value |
|---|---|---|---|
| 2077 observations; variance of the random effect = 0.048; marginal $R^2$ = 0.047; conditional $R^2$ = 0.25 | | | |
| Intercept | 0.04800 | 0.10211 | 0.470 |
| Treatment_On | -0.17849 | 0.02543 | -7.019 |
| Treatment_Off2 | -0.04111 | 0.02174 | -1.891 |
| Season_Autumn | -0.14801 | 0.02989 | -4.952 |
| Season_Winter | -0.03300 | 0.02943 | -1.121 |
| Season_Spring | 0.06355 | 0.02847 | 2.232 |

to explain this seasonal (spring) effect. For both European badger and red fox, spring is the season of parturition and lactation which means that females are less mobile and do not stray far from their burrows (Do Linh San, 2006; Meia, 2016). Otherwise, Cresswell and Harris (1988) showed that moonlight was consistently the most important variable in explaining badger activity during spring: reduction of nocturnal range size and delay of emergence time (Cresswell and Harris, 1988).

Very few studies have focused as we have on wildlife crossings to assess the impacts of ALAN on mammals, which limits available comparisons. However, these comparable studies also showed that illuminating wildlife underpasses (and overpasses) reduces their use (Bhardwaj et al., 2020; Bliss-Ketchum et al., 2016). More generally, the effects of light pollution on the wild mammal species recorded in our study have been little investigated in-situ. ALAN effect on red fox was studied once in-situ to our knowledge, showing that lighting may affect fox activity depending on the light source: fulltime lighting increased activity while motion-detector spotlight slightly decreased it (Hall and Fleming, 2021). Furthermore, red fox is known to exhibit night activity in towns, which means that some individuals may adapt to artificial lighting (Doncaster and Macdonald, 1997). Finally, although strict comparisons with our results are limited, they are in line with the few existing in-situ studies assessing the global effects of ALAN on the movement of wild mammals (Beier, 1995; Drouglazet, 2016) - mainly bats (Azam et al., 2018; Zeale et al., 2018) - and with much more available studies on other taxa such as toads (Van Grunsven et al., 2017), beetles (Camacho et al., 2021) or eels (Vowles and Kemp, 2021). This literature indicates that ALAN degrades habitat quality and that illuminated areas are usually avoided for movements. Our study therefore makes an original contribution to increasing knowledge on ALAN as a landscape barrier.

### 4.3. *ALAN may create a (perceived) predation risk*

Several mechanisms may explain the seasonal detrimental effects of ALAN on the crossing probability of European badger and red fox observed in our study. Factually, light contributes to sensory perception, and as a result, artificial light actually enhances animal vision by increasing the photopic level in the environment, leading to a better understanding of its surroundings. However, this mechanism fails to explain our results because it would have made the crossing probability increase while an avoidance effect was observed. We also recorded that European badger reduced its crossing speed in lit underpasses during all seasons. This suggests that lighting might rather create a disturbance in visualising space to move safely (glare), depending on species vision capacities. This result is consistent with moonlight effect previously reported; for instance, Cresswell and Harris (1988) showed that the average and maximum speeds of European badger movements were strongly negatively correlated with moonlight duration. Badger vision might be more easily disturbed by strong light than that of red foxes (Malkemper and Peichl, 2018).

Another explanation of ALAN effects often suggests an increase in food resources near lit sites - mainly insects that demonstrate a flight-to-light behaviour (Deichmann et al., 2021; Justice and Justice, 2016) - which leads to an “attraction” of some predators such as bats, spiders or owls (Mammola et al., 2018; Rodríguez et al., 2021; Schoeman, 2016). However, none of the mammal species studied here are insectivorous (Savouré-Soubelet et al., 2024). Instead, they mainly feed on small mammals which tend to avoid light at night (Hemami et al., 2011; Hernández et al., 2021).

A last and more convincing explanation may be that the increase in light level environment increases risk of predation, or at least the perception of this risk, which prevents animals from using the lit

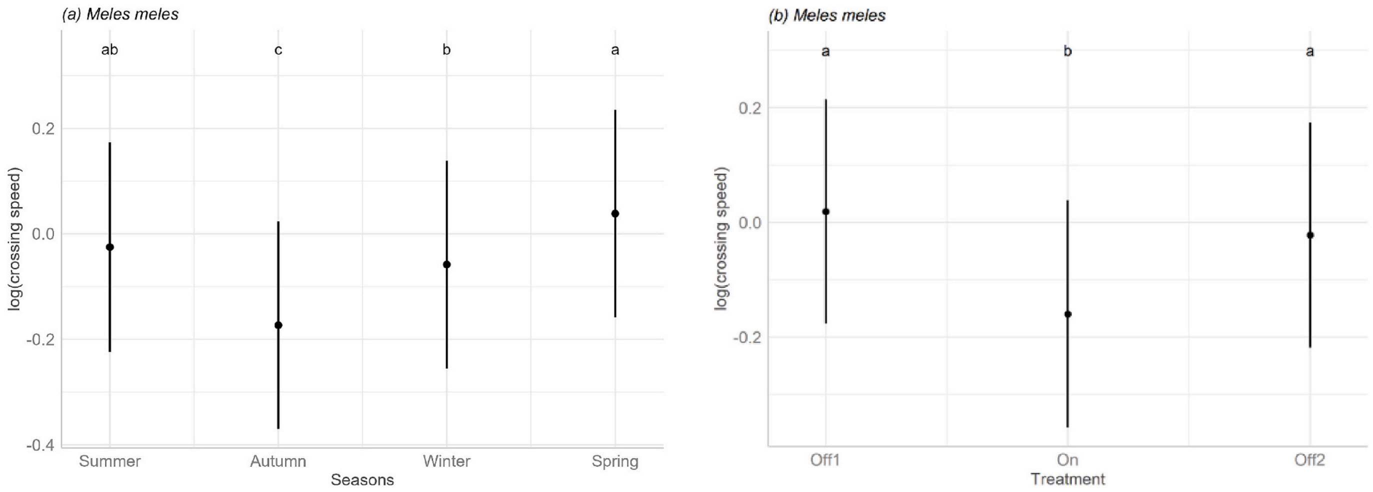


**Fig. 6.** European badger mean crossing speed (log-transformed) at the five underpasses studied in the ‘Causses du Quercy’ regional natural park, France, according to seasons (a) and light treatment (b), as predicted by the model, with 95 % confidence intervals. Letters indicate statistically significant differences between pairs of means (see Additional File 1 - Appendix D for full results of pairwise comparison tests).

underpasses. An antipredator response is often put forward to explain light avoidance observed on some taxa (Clarke, 1983; Hoffmann et al., 2022). Moonlight is known to reduce mammals activity, as shown in bats, rodents and also carnivores (Prugh and Golden, 2014), including European badger (Cresswell and Harris, 1988; Dixon et al., 2006). Red fox seems to be less inhibited by moonlight (Watabe and Saito, 2022); however, light treatment in our study is far brighter than moonlight which may result in inhibition while moonlight is neutral (Dickerson et al., 2023). Actually, the artificial light source used in our study creates a light 'curtain' inside the underpasses that contrasts sharply with the darkness outside and may generate an optic barrier perceived as a landscape of fear (Laundré et al., 2001). As European badgers and red foxes have few predators in our ecosystems today, this could be an ancestral mechanism. This fear would also explain the decrease in crossing speed observed in European badgers, which might be more wary than red foxes and martens for which light did not significantly impact the crossing speed. Both red foxes and beech martens are known to spend more time close to human settlements, suggesting that these species are less stressed of moving under artificial light.

### 4.4. *ALAN effects are reversible*

Unlike other pollutions (e.g. heavy metals or plastics), artificial light has no persistence in the environment. However, whether removing ALAN will have a reversible effect on biodiversity remains uncertain. This point has a major operational importance, as many local authorities want to know whether switching off or even removing street lighting will lead to a return of impacted species. Indeed, in the context of rising energy prices, it is becoming increasingly common for municipalities to completely remove lighting, for instance on certain roads used only by vehicles. Implementing a before–during–after exposure protocol was a way to assess the possible persistence of ALAN effects after having turned the light off.

Our results support a possible resilience of both European badger and red fox behaviour to a long-term lighting (a whole year). As this resilience was observed as early as the first summer following the light extinction, it can be considered as rapid. Indeed, many interventions to restore biodiversity may take longer, sometimes decades (such as restoration of a functional hedge or forest), to be efficient. As a result, from an operational point of view, a recovery delay of one month appears to be very satisfactory by stakeholders involved in biodiversity restoration.

To our knowledge, there is no literature on in-situ lighting removal on biodiversity and in particular on wild terrestrial mammals. Some studies have analysed the effects of part-night or dimming lighting, showing contrasting effects on bats or insects (Azam et al., 2015; Bolliger et al., 2020) - but these lighting managements are not really equating with a total removal of lighting. Studies comparing populations exposed and populations not exposed (control-exposure protocols) do not enable to strictly answer the question of reversibility of ALAN either, since a high variability of response to light exposure can exist between both individuals and populations (Handler et al., 2020). Then, we think our results provide an interesting contribution for a better understanding of what biodiversity may gain by removing lighting after exposure.

## 5. Conclusion

Our results show that ALAN may generate an avoidance behaviour that prevents European badger and red fox from crossing lit underpasses, during some periods of the year. These results argue in favour of reducing night-time lighting as much as possible. Fortunately, our study also highlights that removing lighting quickly produces encouraging results for wildlife; i.e. a reversion of natural crossing behaviour within one month. Our protocol based on wildlife crossings enables to conclude that ALAN acts as a disturbing factor for habitats and even as a fragmenting feature in the landscape at night. In response to habitat loss and fragmentation caused by ALAN, scientists suggest to preserve dark habitat patches and dark corridors as ecological networks named dark infrastructure (Sordello et al., 2022). Our study confirms the value of implementing such public policies to preserve functional nightscapes for wild terrestrial mammals.

## CRediT authorship contribution statement

**Romain Sordello:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Dakis-Yaoba Ouédraogo:** Writing – review & editing, Writing – original draft, Data curation. **Clotilde Chassoulier:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Stéphane Aulagnier:** Writing – review & editing, Supervision, Data curation. **Aurélie Coulon:** Writing – review & editing, Supervision. **Yorick Reyjol:** Writing – review & editing, Supervision.

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## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Romain Sordello reports was provided by PatriNat (OFB-MNHN-CNRS-IRD). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2024.110960.

## Data availability

Data will be made available on request.

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