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Adapting street lighting to limit light pollution's impacts on bats

Julie Pauwels[a,b], Isabelle Le Viol[a,c], Yves Bas[a,d], Nicolas Valet[b], Christian Kerbiriou[a,c,*]

[a] *Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, 61 rue Buffon, 75005 Paris, France*

[b] *Auddicé Environnement, 59286 Roost-Warendin, France*

[c] *Muséum national d'Histoire naturelle, Station de Biologie Marine, 1 place de la Croix, 29900 Concarneau, France*

[d] *CEFE, CNRS, Univ Montpellier, Univ Paul Valéry, Montpellier 3, EPHE, IRD, Montpellier, France*

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ABSTRACT

Artificial light at night (ALAN) affects biodiversity conservation through its impacts on spatio-temporal distribution patterns of species, in particular bat species. The development of this threat underlines the urgency to adopt lighting practices (characteristics) that have the least impact on species, in particular the most vulnerable species still present in semi-natural areas. It is therefore crucial to better assess the relative effects of the different light parameters for a wide variety of species. Our study investigates the relative effects of streetlights characteristics, i.e. height, lamps type (HPS, LED), illuminance, and the distance to a streetlight on the activity of a variety of species (15) according to their flight traits. We compared bat species activity in lit and dark conditions along streets and in hedges at less than 200 m away from streetlights of various characteristics, in a Mediterranean protected area.

Lighting had contrasting effects on the activity of clutter and aerial bat species, with a strong negative effect on clutter species (90% reduction of bat activity), half of which are strictly protected. Illuminance particularly affected their activity.

Among the possible management options to reduce the effect of light pollution at night (reduction of light intrusion by modifying the height of street lamps, lighting intensity, spectral composition), the removal of light sources, or at least the reduction of illuminance, seems to be the most effective option. Due to its strong impact on highly protected species, we urge the need to manage lighting, in particular in protected areas.

Capsule: Artificial light at night had a negative effect on clutter bats activity (90% reduction of bat activity) and among streetlight characteristics illuminance was the most relevant.

Data accessibility: Data used for statistical analysis are include in Appendix C. Acoustic row data was delivered to the citizen science program "VigieChiro" (https://vigiechiro.herokuapp.com/).

* Corresponding author at: Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, 61 rue Buffon, 75005 Paris, France.

E-mail address: christian.kerbiriou@mnhn.fr (C. Kerbiriou).

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1. Introduction

The spread of artificial light at night (ALAN) throughout the world in the past decades has dramatically changed the nocturnal lightscape (Falchi et al. 2016). Through the modification of natural light levels, ALAN disrupt the natural cycle of day and night, i.e. the circadian rhythm, arguably the most important cue to life organization (Bradshaw and Holzapfel, 2010). It has major impacts on nocturnal species (Desouhant et al., 2019; Hölker et al., 2010; Owens and Lewis 2018, Owens et al. 2019), as it can change their behavior (e.g. Downs et al. 2003) disrupt interactions and contribute to decreasing pollinators and their associated ecosystem services (e.g. Knop et al. 2017). Light pollution has come to be considered as a global environmental change (Lyytimäki 2013) that not only affects urban areas but also natural and protected areas (Gaston et al. 2015). Gaston et al. (2012) identified five management options to reduce ALAN: 1) the spatial arrangement of artificial light sources in the landscape and 2) the duration of artificial light sources. Once areas and time periods that actually need to be lit, have been defined, ALAN management should focus on 3) the reduction of light trespass 4) the reduction in the illuminance emitted by light sources; and 5) the adaptation of the spectral composition. While these recommendations reached a consensus (Voigt et al. 2018) that is not the case for how to prioritize them.

Among the taxa sensitive to ALAN and of conservation concern, European Microchiroptera are good model species to study the effects of artificial light as they exhibit contrasting sensitivity to light depending on the scale considered (Lacoeuilhe et al., 2014; Stone et al., 2015). At the local scale (i.e. streetlight scale) fast-flying species foraging in open spaces such as *Pipistrellus* sp and *Nyctalus* sp (hereafter referred to as “aerial” species) can benefit from localized increase in prey abundance due to the attraction of insects to light (Eisenbeis, 2006; van Langevelde et al., 2011, Bolliger et al., 2020, (Rowse et al., 2018)). ***Rhinolophus*** and *Myotis* species are described as light-sensitive as they avoid lit areas (Stone et al., 2009, 2012, (Spoelstra et al., 2017)) and are not present in highly urbanized cities contrary to some aerial species (Bartonicka and Zukal, 2003; Rainho, 2007). They are characterized by a slow low-altitude flight and forage in cluttered vegetation (referred to as “clutter” species). This group contains species that are uncommon or rare and that are strictly protected at the European level (Table 1). Their low abundance makes it difficult to study them, however it is crucial to better understand how they react to artificial lighting as they are the most sensitive species. At the large scale (national or conurbation scales) all species seem to be negatively impacted by artificial lighting, including even fast-flying species (Azam et al., 2016, Pauwels et al., 2019).

Recent scientific literature focusing on ALAN impacts on bat allow to identify some knowledge gaps (see the systematic research, Appendix A). Despite the important conservation issues, few studies have focused on species of conservation concern (20%), i.e on species that justify the designation of protected areas, even though these areas are increasingly submitted to the development of ALAN (Guetteé et al., 2018). Moreover, relatively few studies have been carried out in protected areas (14%) or within biogeographic regions identified as biodiversity hotspot. For example, the majority of studies were conducted in developed countries (89%), and few in tropical areas (17%), while in Europe few studies took place in the Mediterranean region (5%), where several species, including potentially sensitive ones, occur (Wermer et al., 2007). According to this systematic research (see Appendix A), a high proportion of studies were based on field experiments (43%, i.e. introducing artificial lighting in the environment for a limited time) and few (15%) simultaneously took into account several ALAN parameters (illuminance, spectra, streetlight height or distance to streetlight, lamp characteristic’s, see Appendix A) an approach that is needed to identify the most impactful ALAN and hence prioritize the levers of action. In addition, developed countries are experiencing a renewal of their lighting equipment, from conventional lighting technologies (mainly HPS) to light emitting diodes (LEDs) and such shift is expected to have cascading impacts on nocturnal fauna (e.g. changes in abundance). However, few studies have so far dealt with the impact of the renewal of street lighting mainly due to the difficult to monitor the effect of a real-life switch from HPS to LED streetlights with a robust design (before-after-control-impact, see (Kerbiriou et al., 2020). An alternative

Table 1
Number of bat passes, overall occurrence and protection status of the 15 species studied. Protection status refer to the level of protection given by the Habitat Directive in the EU.

	Total number of bat passes	Occurrence	Protection status
Aerial species	**186608**		
P. pipistrellus	45 19	79%	Annex IV
P. kuhlii	89 773	100%	Annex IV
P. pygmaeus	32 380	98%	Annex IV
P. nathusii	5 122	97%	Annex IV
H. savii	2 818	85%	Annex IV
M. schreibersii	2 754	76%	Annex II
E. serotinus	991	87%	Annex IV
N. leisleri	2 234	93%	Annex IV
T. teniotis	5 342	55%	Annex IV
Clutter species	**1277**		
M. daubentonii	169	57%	Annex IV
M. emarginatus	59	29%	Annex II
M. nattereri	196	39%	Annex IV
Plecotus spp.	547	61%	Annex IV
R. hipposideros	240	44%	Annex II
R. ferrumequinum	66	22%	Annex II

approach could consist in simultaneously studying several spectra, (only 17% of published studies focus on difference in spectra composition, and only 3 studies consider HPS vs LED see Appendix A).

Our study investigates the impact of ALAN on bats and strive to prioritize the importance of streetlights characteristics, on bat activity in order to define the most pertinent levers of action to limit the effects of ALAN on these species and produce recommendations for a more environmentally-friendly lighting. According to the conservation issue, we carried out the fieldwork in partnership with land managers, in a Mediterranean protected area of category V, with the aim to collect data on species rarely studied and of conservation concern. We monitored 15 bat species from the clutter and aerial groups (including four species listed in the Annex II of the Habitats Directive) and hence potentially presenting various behavioral responses to light (Lewanzik and Voigt, 2017; Azam et al., 2018).

Among the artificial lighting sources contributing to ALAN pressure, we focused on streetlight because they are responsible for up to 50% of light pollution (Hiscocks and Guömundsson, 2010) and are considered as the most persistent, aggregated and intense source of lighting (Gaston et al., 2012). We designed our study to be able to simultaneously take into account several streetlight characteristics expected to influence bat activity of different species and guilds: (streetlight height (3.6–9 m), lamp type (HPS or LED), illuminance (0.1–51 lux) and distance to streetlight (7–192 m), and in turn to be able to prioritize the importance of streetlights characteristics impacts on bat activity.

Among the resources impacted by ALAN, we focused on forest edges and hedgerows which are landscape elements of great importance for bats for transit and forage (Verboom and Huitema, 1997; Boughey et al., 2011a; Lacoeuilhe et al., 2016). Their lighting by light diffusing from town may result in a decrease of habitat quality and a degradation of ecological corridors (Stone et al., 2009; Hale et al., 2015, Laforge et al., 2019) leading to a reduction of the conservation potential of protected areas that include urban areas. We evaluated the activity of each bat species around streetlights and at forest edges or hedgerows facing a streetlight in relation to streetlight characteristics. We designed our sampling based on simultaneously recording a lit pair and a control dark pair to take into account concomitantly several parameters of ALAN (illuminance, spectra, streetlight height or distance to illuminance) and in turn be able to rank the relative effect of streetlight characteristics on bat activity. To generalize our results, we also explored the response to those characteristics at the level of bat guilds. We expected to find opposite effects on the activity of aerial and clutter species with the latter group being negatively impacted by light.

2. Methods

2.1. Study area

The experiment was carried out, at the end of summer 2016, in the Parc Naturel Régional du Luberon, a protected natural park of 1850 km^2 located in the South-East of France (Fig. 1a). It is a protected area of category V belonging to IUCN Protected Area Categories System, hence the main aims are the protection of nature, the preservation of landscapes of cultural value and the maintenance of balanced interactions with people through traditional management practices (https://www.iucn.org/theme/protected-areas/about/protected-area-categories. Therefore these areas include a significant part of human activities and are prone to suffer increased levels of light. They include small and discontinuous urban areas thus habitats surrounding these urban areas could be impacted by light spillover and be avoided by light sensitive species. The park includes nine Natura 2000 sites covering one third of its surface. It is also recognized as part of a hot spot of bat species richness, harboring 21 of the 34 French bat species (Biotope, 2016). Urban areas represent only 10% of the park surface (including roads with very low traffic < 3000 vehicles/days) and arable lands 14% while semi-natural areas represent 76% of the land (42% of low vegetation and 33% of high vegetation semi-natural areas). The largest city in the park (Cavaillon, 26,000 inhabitants) has a light level 12 times higher than the natural background sky brightness. Aside from this city, the park has a mean artificial brightness about twice as high as the mean natural background sky brightness which means it is within the 40% of France surface receiving the least light pollution (Falchi et al., 2016). Almost 60% of the municipalities have a public lighting extinction scheme but we did not work in these municipalities to avoid biases.

2.2. Sampling design

We selected 28 study sites located at the limit between towns and their semi-natural surroundings to measure bat activity both under streetlights and at hedgerows or forest edges (thereafter, "hedges") directly facing streetlights (Fig. 1b and c). We sampled bat activity at hedges because they represent potential bat commuting routes (Verboom and Huitema, 1997; Boughey et al., 2011b; Lacoeuilhe et al., 2016). In our study hedges were mostly composed of tall oak trees. On each site we placed two pairs of recording points, an experimental lit pair and a control dark pair separated by 450 m on average (min = 56 m, max = 1982 m). For the lit pair, one recording point was placed under a streetlight and the second was placed along a hedge lit by this streetlight. Half of the lit pairs had High Pressure Sodium lamps (HPS, n = 14) and the other half Light Emitting Diode lamps (LED 2500–3000 K, n = 14, see Appendix B for LED and HPS spectra). For the dark pairs, the recording points were placed along a street and at a hedge in a similar fashion and in similar habitats as experimental points but in a dark environment. For a given site, the distance between the two recording points of a pair (i.e. street point and hedge point) was the same for the lit and the dark pair and varied between sites from 7 m to 192 m (see Appendix C – Table C.1).

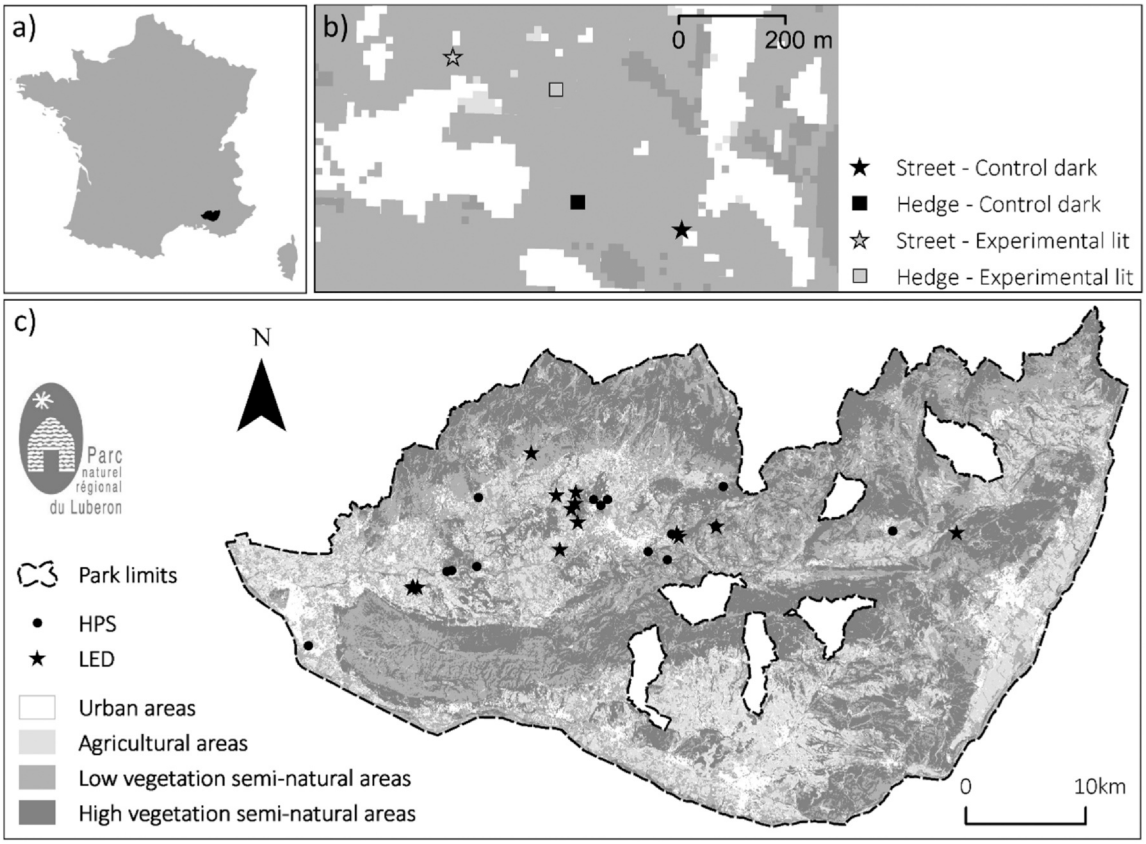

Fig. 1. Presentation of the study area and the sampling design with (a) the location of the Parc Naturel Régional du Luberon (black); (b) an example of site with the experimental lit pair (grey) and the control dark pair (black) both composed of a recording point on a street (stars) and a recording point at a hedge (squares); and (c) the location of the 28 sites with an indication of the lamp type.

2.3. Environmental variables

At each recording point, we measured the vertical illuminance (lux) at 1.20 m above the ground with a lux meter (Digital Light Meter YF-170.) while facing the street point. The luxmeter had a resolution of 0.01 lx, but the accuracy of our measurements under real outdoor conditions was estimated to be ± 0.1 lx The vertical illuminance is the measure of the luminous flux received by a 1 m^2 vertical surface (Azam et al., 2018). We also measured streetlights height. While selecting study sites we paid particular attention to the surroundings land use composition to avoid confounding effects. The site selection was design with the aim that experimental lit points and their associated control dark points had a similar environmental context. We evaluate the independence of light modalities (lit points vs darks points) according to environmental context: (i) we computed the proportion of urban area, agricultural area and semi-natural area for low and high vegetation in a 200 m buffer around the recording points using the CES-OSO (Cesbio http://www.cesbio.ups-tlse.fr/multitemp/?p = 6178, land use map of France (10 m resolution) and (ii) performed Wilcoxon signed rank tests (Appendix C – Table C.2). We did not find any difference in the environmental variables values distribution between experimental and control points either at the street point or at the hedge point. In addition, we also evaluated potential multicollinearity issues between environmental variables and light variables using Spearman's rank correlation coefficient, (as $|rho| \leq 0.6$ no important correlation was detected, Dormann et al., 2013) (Appendix C – Table C.3). Despite no obvious multicolinearity issues were detected, environmental variations between sites were taken into account within models during the final analysis stage.

2.4. Bat monitoring

The fieldwork was carried out between the 28th of August and the 7th of September 2016 when the weather conditions were favorable according to the recommendation of the French national bat-monitoring program Vigie-Chiro (no rain, wind speed below 7 m/s, temperature > 12 °C; Kerbiriou et al. 2018). This period was also between the third and the first quarter of moon to limit the interaction between natural and artificial light (Saldaña-Vázquez and Munguía-Rosas, 2013).

Bat activity was sampled at each point with a Song Meter SM2BAT (http://wildlifeacoustics.com/) which automatically recorded all ultrasounds with an SMX-US omnidirectional microphone. The four recording points of each site were sampled on the same night from

30 min before sunset until 30 min after sunrise, allowing for direct comparison of bat activity between the experimental lit points and their paired dark control point. Bat activity may vary greatly between night this mainly because weather conditions are the main drivers bat activity (Bolliger et al. 2020), this design (i.e. 2 pairs, 4 points sampled the same night, Fig. 1b) allow to control for weather conditions and to evaluate with accuracy the effect of different variables (presence of streetlight, distance to the streetlight).

As it is impossible to identify individual bats from their echolocation calls, we calculated bat activity as the number of bat passes per species. A bat pass is defined as the occurrence of a single or several echolocation calls of the same bat species during a 5-second interval (Millon et al., 2015). Using the software TADARIDA (Bas et al., 2017) in its latest version (online repository (https://github.com/YvesBas), echolocation calls were detected and classified to the most accurate taxonomic level. In addition, for each echolocation TADARIDA provided a confidence score for each automated identification. We follow the approach developed by Barre et al. (2019) for accounting for automated identification errors in acoustic surveys. We used an independent dataset comprising 8405 bat passes recorded throughout France as part of the Vigie-Chiro bat-monitoring program and both checked manually and ran through TADARIDA to perform a logistic regression between the success/failure of automatic species assignation and the confidence index provided by the software. We could hence associate each confidence index with an identification success probability and calculate for each species the minimum confidence index required to tolerate a given maximum error risk, i.e. confidence threshold (methodology detailed in Appendix D). We used the confidence thresholds calculated on the national dataset to create two subsets of this study's dataset: one with a 0.5 Maximum Error Risk Tolerance (MERT) and another subset with a 0.1 maximum error risk tolerance. We performed the analysis on both subsets and found similar results. Hereafter we show results for a 0.5 MERT while results for a 0.1 MERT are presented in Appendix E.

An overlap of the detection volumes of the two recording points of a pair could occur depending on the distance between the points and the species maximum distance of detectability. For example, *Rhinolophus hipposideros* can be detected at a maximum of 5 m, hence for this species the volumes of detection overlapped for only 11% of pairs. For *Tadarida teniotis* which can be detected at 150 m, volumes of detection overlapped for all pairs. When simultaneously detected at the two recording points of a pair, bat passes were associated to the point which recorded the longest sequence of bat calls since it was most probably the closest to the bat flight path. Then we applied a correction on the number of bat passes to account for the subsequent unevenness in the sampling volume of the recording points (Appendix F).

We studied each species activity and also the activity of two groups of species based on their flying and foraging preferences. The "aerial" group was composed of 9 species which are medium to high-altitude fast-flying species: *Pipistrellus kuhlii*, *P. pipistrellus*, *P. pygmaeus*, *P. nathusii*, *Hypsugo savii*, *Miniopterus schreibersii, Eptesicus serotinus*, *Nyctalus leisleri*, *Tadarida teniotis* (Blake et al. 1994; Lacoeuilhe et al. 2014; Azam et al. 2015; Roemer et al. 2017). The "clutter" group was composed of 5 species and 1 genus of low-altitude slow-flying bats that generally forage in cluttered vegetation: *Myotis daubentonii*, *M. emarginatus*, *M. nattereri*, *Plecotus* spp., *Rhinolophus ferrumequinum* and *R. hipposideros* (Blake et al., 1994; Stone et al., 2012; Lacoeuilhe et al., 2014; Azam et al., 2015).

2.5. Statistical analysis

2.5.1. Effect of the presence of streetlight

We tested the effect of the treatment (experimental lit vs control dark) to measure the effect of the presence of a streetlight on bat activity. For each species and group of species, we performed a generalized linear mixed model (GLMM) (R package glmmTMB v.0.2.0; Brooks et al., 2017) using the number of bat passes as the response variable and the recording point type (four levels: street-lit, hedge-lit, street-dark and hedge-dark) as a fixed effect. To account for the paired design in the species models, we used the site as a random effect because we expect some variations of bat activity between night, and each night we sample a site including four points. Models for the aerial and clutter groups contained a random effect on the recording point nested within the site and a second random effect -species identity- to account for the species effect (an approach regularly used to account for differences in abundances between species, see Kerbiriou et al., 2018b, (Pavón-Jordán et al., 2017); (Pellissier et al., 2013). According to the nature of the response variable (i.e. count data) we used a Poisson error distribution or a negative binomial error distribution if overdispersion was detected in the data (Zuur et al., 2009). We performed all models with and without a zero-inflation parameter and to identify the best model, we used AIC scores and examined the dispersion parameter. We did not run models when species was contacted in less than 10% of sampled point or the number of contacts was below 20.

With the aim to (i) take into account the small environmental variations between sites (note that our sampling design reduce drastically environmental variables effect) and weather conditions effects (note that we recorded bats the same night at the four sites, which contribute to reduce drastically weather conditions effects), and (ii) to avoid over-parametrisation, we performed a principal component analysis (PCA) (R package FactoMineR v.1.39; Lê, Josse and Husson, 2008) and include principal components of the PCA as fixed effects in all models. This approach allow to summarize the information included in the 4 environmental variables (proportion of urban, agricultural, high and low vegetation semi-natural areas) and 3 meteorological variables (wind speed, temperature and proportion of visible moon). According that (i) the cumulative proportion of variance explained by the two first principal components of the PCA reached 50% and (ii) the willingness to reduce the number of fixed effect (for ovoid over-parametrization) we only included the first two principal components of the PCA (PC1, PC2) as fixed effects in all models. This technique (see Hoehn et al., 2008, Penone et al., 2018) allowed us to limit the number of co-variables (from seven to two, allowing in turn avoid over parametrization and avoid multi-collinearity problems by using uncorrelated linear combinations of the original co-variables (principal components). The models to test the effect of the presence of the streetlight were written as follow:

Species activity ~ recording point type + PC1 + PC2 + (1|site)

Group activity ~ recording point type + PC1 + PC2 + (1|species) + (1|site/recording point)

They were applied on data for all recording points (n = 112). We performed a post-hoc Tukey HSD test to obtain comparison between experimental lit and control dark points at the street and at the hedge (package lsmeans v.2.27–67; Lenth, 2016).

2.5.2. Effect of the illuminance on bat activity

We evaluated the effect of the illuminance level on bat activity at street and hedge points using both experimental and control recording points. For each species and group of species we performed two GLMMs using bat activity as the response variable and illuminance as a fixed effect, one model focusing on street points and a second model focusing on hedge points. We used the same random effect structures as previously and also included the two first components of the PCA on environmental and meteorological variables. The models to test the effect of the illuminance were written as follow:

Species activity ~ illuminance + PC1 + PC2 + (1|site)

Group activity ~ illuminance + PC1 + PC2 + (1|species) + (1|site/recording point)

Both models were applied separately on data for street points (n = 56) and on data for hedge points (n = 56).

2.5.3. Effect of the streetlights characteristics on bat activity

We measured the effect of three other streetlight characteristics on bat activity: the lamp type (HPS or LED), the streetlight height and the distance to the streetlight. As those variables could only be measured for experimental lit points, we did not consider control points in the following models. For each species and light variable (lamp type, streetlight height and distance to the streetlight), we built two GLM, one for bat activity at the streetlights and one for bat activity at the lit hedges except for the distance variable which could only be measured at hedges. In each model we included one of the three light variables and the two principal components of the PCA as fixed effects. Aerial and clutter groups' models were built as GLMMs with the same fixed effects and two separate random effects, one on the recording point and one on the species.

The models to test the effect of the streetlight characteristics were written as follow:

Species activity ~ streetlight characteristic + PC1 + PC2

Group activity ~ streetlight characteristic + PC1 + PC2 + (1|species) + (1|recording point)

Both were applied separately on data for lit street points (i.e. at streetlights; n = 28) and on data for lit hedge points (n = 28). As we looked at the effect of each characteristics in separate models, we applied a Bonferroni correction on the p-values. In order to be significant, effects of models on street points needed to have a p-value below 0.025 (2 models: lamp height and lamp type) and effects of models on hedge points needed to have a p-values below 0.017 (3 models: lamp height, lamp type and distance to the streetlight). All the analyses were performed in R 3.3.3 (R Core Team, 2017).

3. Results

3.1. Bat monitoring

In the dataset allowing for a maximum error risk of 0.5, there was a total of 187 885 bat passes belonging to 20 species. Five species were not included in the analysis as the number of bat passes recorded was too low (n < 50). The most abundant species were *P. kuhlii* (n = 89 773), *P. pipistrellus* (n = 45 194) and *P. pygmaeus* (n = 32 380) (Table 1). Almost all bat passes were attributed to aerial species with only 1% of bat passes being of clutter species (n = 1277) (see Appendix E and G for more details).

3.2. Effect of the presence of the streetlight

The presence of a streetlight had a significant positive effect on all aerial species activity except for *P. pipistrellus*, *T. teniotis* and *E. serotinus* and on the aerial group activity at the street points compared to a similar environment with no light (Fig. 2a). At the hedge, this positive effect was significant but weaker for the aerial group and for *P. nathusii*, *H. savii*, *M. schreibersii* and *N. leisleri* (Fig. 2b). All these effects were also significant for the 0.1 maximum error risk tolerance (MERT) dataset except for *P. nathusii*. This species number of bat passes dropped drastically from 5122 at the 0.5 MERT to 74 at the 0.1 MERT due to difficulties in its acoustic identification. A significant negative effect was detected on the activity of *M. nattereri*, *R. ferrumequinum*, *R. hipposideros* and *Plecotus* spp. and at the clutter group level at the streetlight. It was only significant for *M. nattereri* activity at the hedge. Results on the dataset with a 0.1 MERT are detailed in Appendix E.

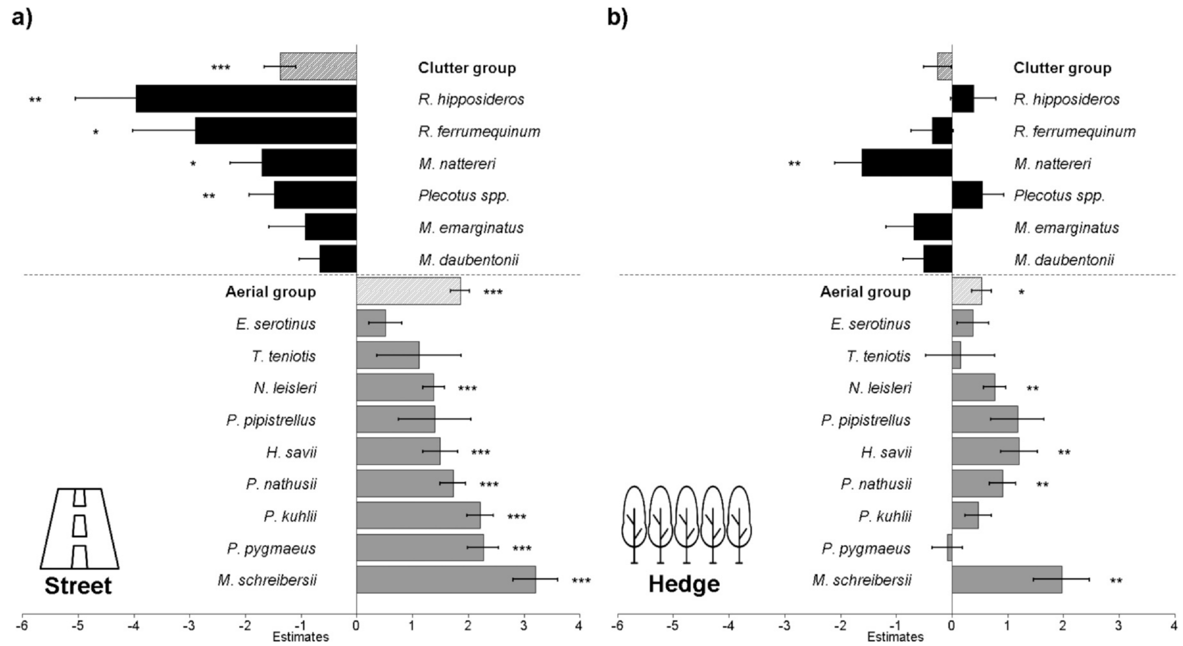

Fig. 2. Effect of the presence of a streetlight on bat activity at the street points (a) and at the hedge points (b) for clutter species (black), aerial species (grey) and groups (hatched). Bars represent estimates of the difference of activity between experimental lit points and control dark points and error bars represent standard errors ('*' refers to p-value < 0.05; '**' refers to p-value < 0.01; '***' refers to p-value < 0.001).

3.3. Effect of the light illuminance on bat activity

Light illuminance had a significant positive effect on the aerial group activity both at the street and hedge points (Fig. 3). At the species level, illuminance had a significant positive effect on *P. kuhlii, P. pygmaeus, P. nathusii, M. schreibersii* and *N. leisleri* but

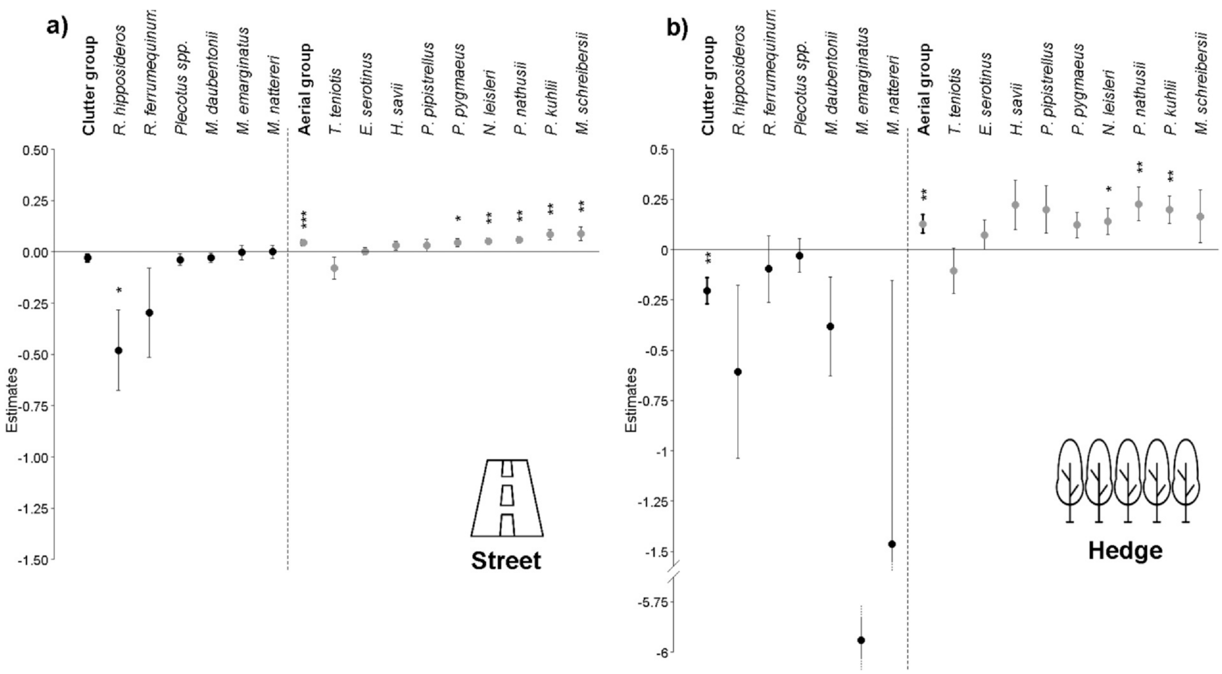

Fig. 3. Effect of the illuminance level on bat activity at the street points (a) and hedge points (b) for clutter species (black) and aerial species (grey). Dots represent the estimates of the effect of illuminance and error bars represent standard errors ('*' refers to p-value < 0.05; '**' refers to p-value < 0.01; '***' refers to p-value < 0.001). For graphical reasons, we broke the y axis on graph (b) to represent *M. emarginatus* estimates but we did not represent the full extent of this species and *M. nattereri* standard error bars.

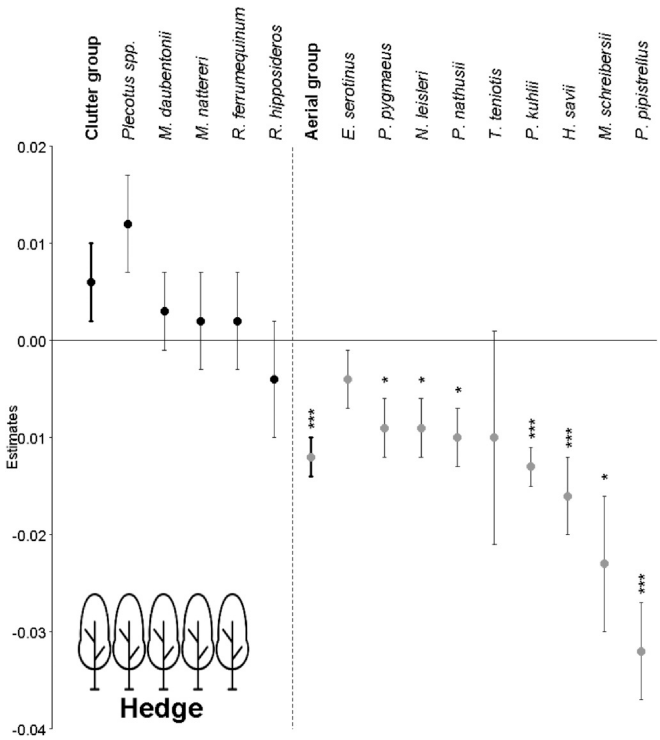

Fig. 4. Effect of the distance of the streetlight on bat activity at the hedge for clutter species (black) and aerial species (grey). Dots represent the estimates of the effect of the distance and error bars represent standard errors. As we tested 3 variables in separate models, we used a Bonferroni correction hence effects are significant for p-values < 0.017 ('*' refers to p-value < 0.017; '***' refers to p-value < 0.0001). We did not run a model for *M. emarginatus* as we had less than 20 contacts in the dataset considered for this model.

these effect disappeared for the 0.1 MERT dataset for *P. pygmaeus* and *P. nathusii*. This positive effect was also present and stronger at the hedge for *P. kuhlii*, *P. nathusii* and *N. leisleri*. Again, it was not significant for *P. nathusii* when using the 0.1 MERT dataset. The illuminance had a negative impact on the clutter group activity at the hedge. At the species level, the illuminance only had a significant negative effect on *R. hipposideros* at street points but it was at least twice as strong as the higher positive effect for aerial species.

3.4. Effect of the streetlight characteristics on bat activity

The lamp height had a negative effect on *P. nathusii* activity at the streetlight but this effect was not significant with the 0.1 MERT dataset (Appendix C, Table C.3). HPS lamps had a significant negative impact on *H. savii* activity at the streetlight compared to LED lamps. There was no other effect of the lamp height or type for any other species or for the two groups either at the streetlight or at the hedge. The distance to the streetlight had a significant negative effect on all aerial species activity except for *T. teniotis* and *E. serotinus* and it was also significant for the aerial group (Fig. 4). The distance to the streetlight had no significant effect on clutter species and group.

4. Discussion

We evaluated the impact of ALAN on 15 bat species activity in a semi-natural context and found opposite effects on aerial (9 species) and clutter (6 species) species. Clutter species activity was negatively impacted by the presence of light which could be explained by a possible intrinsic perception of increased predation risk of these slow-flying species when in lit environments (Rydell et al., 1996). On the opposite, aerial species activity was higher in lit environment both along streets and hedges which reflects the foraging behavior adaptation of most aerial species to take advantage of the accumulation of insects close to lights (Stone et al., 2012; Lewanzik and Voigt, 2017). The illuminance level affected all bat species and notably it negatively impacted clutter bats activity at hedges. Light diffusing outside urban areas and onto potential habitats for bats can decrease their quality and this might alter protected areas capacity to preserve species with conservation issues. We performed all the models (n = 125) on two datasets including a different maximum error risk tolerance (0.5 and 0.1). This allowed us to confirm the robustness of our findings except for five models. Four of these were for *P. nathusii* which acoustic identification is difficult notably due to confusions with *P. kuhlii* (Obrist and Fluckiger, 2004), moreover *P. kuhlii* is more common than *P. nathusii* in the study area , hence results for this species should be considered with caution.

4.1. Influence of light on bat communities

We found a negative effect of lighting at street points on four out of six clutter species activity and a positive effect on six out of nine aerial species activity which is coherent with other studies (Stone et al., 2009; Azam et al., 2015). At the hedge (7–192 m away from streetlights), we only found a negative impact of the streetlight presence on one clutter species. In Azam et al. (2018), the activity of *Myotis* spp. at hedges seemed to be lower in lit conditions as far as 50 m away from the streetlight (positioned along the hedge) but no significant effect was detected further than 10 m away. The difference of sensitivity to light pollution between bat species causes a competition disadvantage for species that cannot forage for insects gathered at light sources. This is most probably accentuated by the “vacuum cleaner” effect, i.e. the long-distance attraction of light-susceptible species to lamps (Voigt and Kingston, 2016), leading surroundings of lit areas to have less food resource available for light-avoider species. This further loss of foraging habitats for light-sensitive species could lead to a distortion in the community composition in favor of aerial species (Arlettaz et al., 2000; Polak et al., 2011). Therefore, light pollution might not only impact activity levels but also bat communities and lead to less rich and more generalist communities thus contributing to a biotic homogenization process. However, the impact of light pollution is not as permanent as land use conversion. If we were to turn off lights illuminating a habitat previously used by light-sensitive bats, we could expect sensitive bats to come back (Stone et al., 2009, 2012) although no research has been done to study bat activity after the extinction of sites lit for a long period of time.

4.2. Effect of the illuminance on bats

We found a significant negative effect of the illuminance on the clutter group at hedge points where illuminance values were low (range 0.1–13.2 lx, 3rd quartile = 0.3 lx). This is coherent with another study that showed a negative impact of illuminance on *Myotis* spp. and *Plecotus* spp. while most sampling sites (77%) had an illuminance level below 5 lx (Lacoeuilhe et al., 2014). Moreover, full moon light which correspond to 0.1–0.3 lx (Gaston et al., 2013) can influence bat activity levels (Saldaña-Vázquez and Munguía-Rosas, 2013) thus small changes in natural light level such as light trespass may have important impacts on bats. As in Stone et al., 2012, we found a significant negative effect of illuminance at street points for *R. hipposideros* but we did not find significant effect for any other clutter species or at the group level. However, our results showed a strong negative effect of the presence of streetlights on clutter species activity at street points when compared to control dark points. The mean number of clutter bat passes was 5 times higher at lit hedges than at streetlights thus it is possible that we find no effect of illuminance at the streetlight because gleaner bats avoid coming close to light sources irrespective of the illuminance level. Moreover, as there was no significant difference in clutter bats activity level between the dark control points along streets and at hedges (p-value = 0.375), our sample design allow us to conclude that the low activity at streetlights is not due to the higher proximity to urban areas of street points.

Studies on artificial light often measure bat activity at streetlights in urban areas and hence mostly record the activity of species exploiting insects attracted by light (Stone et al., 2015; Rowse et al., 2016; Lewanzik and Voigt, 2017). Studying the impact of ALAN in a protected area and at varying distances from streetlights allowed us to evaluate the impact of low levels of light (under 5 lx) on sensitive species. Our results showed that light trespass onto semi-natural areas such as hedges that represent important potential foraging habitats or transiting routes (Verboom and Huitema, 1997; Boughey et al., 2011a; Lacoeuilhe et al., 2016) can reduce habitat quality to a point where light-adverse species will completely avoid the area.

4.3. Streetlight characteristics

We found a negative impact of the distance to streetlights on seven out of nine aerial species activity. Similarly, a study undertaken in a protected area in the North of France, showed that the positive effect of light on *P. nathusii*, *P. kuhlii*, *P. pipistrellus* and *N. leisleri* activity disappeared rapidly with increasing distance steps (no effects at more than 10 m from the streetlight; Azam et al., 2018). However here, while considering distances between 7 and 192 m, we detect a linear negative effect for most aerial species. This is consistent with the positive effect of illuminance on aerial activity as the illuminance decreases proportionally to the inverse of the distance squared (R^2 = 0.9 in our dataset). We did not find any effect of the distance on clutter species either at the species or group level and Azam et al. (2018) showed that the negative effect of light on *Myotis* spp. lost its significance when further than ten meters away from the streetlight. This could suggest that clutter bats are not sensitive to the brilliance of a light source perceived from a distance but only to the illuminance level at the point where they are located.

5. Recommendations and conclusions

New lighting technologies have a higher energy efficiency which decreases the cost of lighting and might trigger a multiplication of light points and an increase in power input (Tsao et al., 2010). Hence it is urgent to consider the impact of light pollution on biodiversity. The constant renovation of public lighting (estimated replacement rate of 3%/year in France in 2011, ADEME, 2011) and the current shift toward more adaptable technologies is also an opportunity to develop lighting planning schemes less harmful to ecosystems. Gaston et al. (2012) proposed five management options to reduce light pollution. According to our result, it appears that three of them are of major importance: reducing the quantity of light, increasing light flux directionality and avoiding lighting at all.

The quantity of light, often measured through illuminance (lux) in ecological studies (when detailed 58% of published studies that measure impact of light intensity used lux, while the other, often used indirect measures such as density of streetlight, see Appendix A). Illuminance is used as a measure of the intensity, as perceived by the human eye, in this measure the power at each wavelength is weighted according to a standardized model of human visual brightness perception. So, this measure adapted to human perception of light potentially did not reflect what bat perceived or their preys (flying insects) perceived. However, this measure is widely used by stakeholder of public lighting and our study show that using this measure we emphasize that illuminance affects the majority of bat species. Clutter species are negatively impacted (90% reduction of bat activity), and sensitive to low levels of light hence they might be disturbed by light trespass. Thus it is important, in public lighting planning and management, to use the lowest amount of light possible considering pedestrians and vehicles use of the area to limit excessive lighting and light spillover into semi-natural habitats. With new technologies light flux can be changed even after being installed. Thus an evaluation of local ecosystems sensitivity to light could technically be followed by a modification in installed streetlights parametrization. In addition, new streetlights are very often installed in full cut-off luminaires that allow for a more directional flux and hence results in less light spillover (Kinzey et al., 2017). It is also possible to add shielding on the streetlight or to plant a hedge to help reduce trespass and preserve dark refuges. However, the most important parameter to control is the placement of the streetlight. The presence of a streetlight irrespective of its characteristics had an impact on the activity of 10 out of the 15 bat species studied. The decision to keep an installed streetlight or add a new one remains the first and principal lever of action to limit light pollution and even more so in protected areas where protected sensitive species exist.

Author Contributions

J.P., C.K., N.V. and I.L.V. designed the study. J.P. collected the data and digitalized environmental data. J.P. analyzed the data with the assistance of C.K., Y.B. and I.L.V and led manuscript writing. All authors critically contributed to manuscript drafts and gave final approval for publication.

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Declaration of Competing Interest

The authors 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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01648.

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