



HAL
open science

Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning

J. Pauwels, I. Le Viol, C. Azam, N. Valet, J.-F. Julien, Y. Bas, C. Lemarchand, A. Sanchez de Miguel, Christian Kerbiriou

► To cite this version:

J. Pauwels, I. Le Viol, C. Azam, N. Valet, J.-F. Julien, et al.. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning*, 2019, 183, pp.12-25. 10.1016/j.landurbplan.2018.08.030 . hal-03952631

HAL Id: hal-03952631

<https://hal.science/hal-03952631>

Submitted on 14 Feb 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning

J. Pauwels^{a,b,*}, I. Le Viol^a, C. Azama, N. Valet^b, J.-F. Julien^a, Y. Bas^{a,h}, C. Lemarchand^c, A. Sanchez de Miguel^{d,e,f,g}, C. Kerbirou^{a,*}

a Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne université, CP 135, 57 rue Cuvier, 75005 Paris, France

b Auddicé Environnement, 59286 Roost-Warendin, France

c Association Les Ecologistes de l'Euzière, Prades-le-Lez, France

d Instituto de Astrofísica de Andalucía, Glorieta de la Astronomía s/n, C.P. 18008 Granada, Spain

e Dept. Física de la Tierra y Astrofísica, Universidad Complutense de Madrid, 28040 Madrid, Spain

f Physics Dept., CEGEP de Sherbrooke, Sherbrooke J1E 4K1, Canada

g Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK

h Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, 1919 route de Mende, 34293 Montpellier, France

* Corresponding author at: MNHN CESCO UMR 7204, CP 135, 43, rue Buffon, 75005 Paris, France (J. Pauwels). CESCO – UMR7204, Museum National d'Histoire Naturelle, Station de biologie marine, 1 place de la croix, 29900 Concarneau, France (C. Kerbirou).

Abstract

Light pollution constitutes a major threat to biodiversity by decreasing habitat quality and landscape connectivity for nocturnal species. While there is an increasing consideration of biodiversity in urban management policies, the impact of artificial light is poorly accounted for. This is in a large part due to the lack of quantitative information and relevant guidelines to limit artificial light's negative effects. This study investigated the impact of light pollution on bat activity in three large cities while comparing two sources of information on artificial light: the location of streetlights and nocturnal pictures taken from the International Space Station (ISS). We tested the relevance of both sources of information by testing 20 different light variables based on either source of information. We used citizen science data to model the activity of *Pipistrellus pipistrellus*, a species considered “light tolerant”, in response to these variables. Our results show that at the city scale, *P. pipistrellus* activity is negatively impacted by light pollution whatever

light variable was used. This detrimental effect was better described by the variables based on ISS pictures than those based on the location of streetlights. We built this methodology with low data requirement so it can be easily reproduced and used in urban planning. We believe it could help take the impact of light pollution into consideration and promote a biodiversity-friendly management of artificial light

2 **1. Introduction**

3 Urbanization is characterized by an increase of impervious surfaces (McKinney, 2002) but also
4 by the emission of environmental stressors such as chemical, noise, and light pollution (Isaksson,
5 2015). Amongst these pollutants the least understood, in terms of impacts on species and
6 ecosystems, is light pollution (Gaston, Visser, & Holker, 2015; Hölker, Moss, Griefahn, &
7 Kloas, 2010), i.e. the emission of artificial light that alter the natural patterns of light and dark in
8 ecosystems (Longcore & Rich, 2004). The modification of the natural day/night rhythm can have
9 considerable impacts on ecosystems (Navara & Nelson, 2007) especially as nocturnal species
10 represent 30% of vertebrates and more than 60% of invertebrates (Hölker, Wolter, Perkin, &
11 Tockner, 2010). In recent decades, light emissions increased globally at an average rate of 6%
12 per year (Hölker, Moss, et al., 2010) and currently, 88% of Europe experience light-polluted
13 nights (Falchi et al., 2016). Moreover, there is a shift in lighting technologies from yellow light
14 sources (e.g., high- and low-pressure sodium vapor lamps) to broader-spectrum white light
15 sources with a higher proportion of blue wavelength (e.g., metal halide and light emitting diodes)
16 that have a higher energy efficiency (Gaston, Visser, & Holker, 2015). This change will most
17 likely result in a global increase in short wavelength (i.e. blue light) emission (Falchi, Cinzano,
18 Elvidge, Keith, & Haim, 2011) and might have major impacts on nocturnal biodiversity.

19

20 A green infrastructure policy was adopted by the European Union to preserve and promote
21 ecological corridors and landscape connectivity. However the green infrastructure policy does
22 not account for the impact of artificial light. Thus the corridors designed following this policy
23 might be ineffective for nocturnal species. Taking into account light pollution's effects on
24 nocturnal species is crucial to design biodiversity-friendly urban lighting plans.

25 Recommendations to mitigate the negative impacts of artificial lighting on biodiversity are
26 scarce with only few studies proposing possible local measures (e.g., Azam et al., 2018; Rydell,
27 Eklöf, & Sánchez-Navarro, 2017). More quantitative information on the impact of artificial light
28 is needed to be able to design a city's lighting plan preserving some dark areas that can be used
29 as habitats and corridors for nocturnal biodiversity.

30

31 Due to their nocturnal lifestyle, bats are good model species to study the impact of artificial light.
32 European bats are long-lived insectivorous species that have great potential as bio-indicators
33 partly because their population trends tend to reflect those of lower trophic levels species such as
34 arthropods (Jones, Jacobs, Kunz, Willig, & Racey, 2009; Stahlschmidt & Brühl, 2012). Some bat
35 species can live in urban areas and are hence directly confronted to light pollution. For instance,
36 species such as *Pipistrellus spp.*, *Plecotus spp.*, *Rhinolophus ferrumequinum*, *R. hipposideros*,
37 *Myotis daubentonii*, and *Myotis myotis* often use man-made structures as breeding roosts and can
38 live in built areas (Marnell & Presetnik, 2010; Simon, Hüttenbügel, & Smit-Viergutz, 2004). In
39 addition, since all bat species are protected at the EU level (Council Directive 92/43/EEC, 1992),
40 they represent one of the few cases of protected species living within urban environments.

41

42 Light-sensitive species such as *Rhinolophus* and *Myotis* species are negatively impacted by
43 artificial lighting through a decrease of their fitness (Boldogh, Dobrosi, & Samu, 2007) and a
44 loss and fragmentation of their habitat (Stone, Jones, & Harris, 2009, 2012). Yet species such as
45 *P. pipistrellus*, *P. kuhlii*, and *Nyctalus leisleri* forage in urbanized and illuminated areas
46 (Bartonicka & Zúkal, 2003; Gaisler, Zúkal, Rehak, & Homolka, 1998; Rainho, 2007). These
47 three species are qualified as light tolerant because they prey on insects that are attracted and

48 trapped within the halo of streetlights (Eisenbeis, 2006; van Langevelde, Ettema, Donners,
49 WallisDeVries, & Groenendijk, 2011). But although the short-term installation of streetlights on
50 a previously dark flying route did not change *Pipistrellus* species activity level (Stone et al.,
51 2012), a study showed that the activity of *P. pipistrellus* was similar or lower in lit areas
52 compared to dark areas in environments with scattered vegetation (Mathews et al., 2015) and
53 another that, *P. pipistrellus* will not cross brightly lit gaps while flying along a hedgerow (Hale,
54 Fairbrass, Matthews, Davies, & Sadler, 2015). While considering a large scale dataset, collected
55 at a national scale across 8 years and mostly looking at permanent street lighting, Azam et al.
56 (2016) showed that bat activity was negatively affected by artificial light even for species
57 described as light tolerant. Hence, overall it would seem that the global effect of light pollution
58 might actually be deleterious even to light tolerant species.

59
60 Assessing the impact of light pollution on biodiversity first requires the ability to measure it.
61 This is not straightforward as artificial light is composed of several measurable characteristics
62 such as intensity, spectral composition, or flux directionality. As street lighting is the most
63 persistent, aggregated, and intense source of lighting in urban areas (Gaston, Davies, Bennie, &
64 Hopkins, 2012), the location of streetlights can be a relevant source of information. Streetlight
65 location data exist for most large cities and are easy to understand, however they do not contain
66 information on the light characteristics or on private lighting which could have a substantial role
67 in light pollution (Gaston et al., 2012). Remote sensing data, such as aerial or satellite pictures
68 are another information source and include all types of lighting (public and private) and also the
69 skyglow (Kyba & Hölker, 2013). Aerial pictures can have a spatial resolution up to 1 m (Hale et
70 al., 2013; Kuechly et al., 2012), but are seldom available as they are very expensive to produce.

71 DMSP OLS and VIIRS Day-Night Band are grey-scale satellite images of the surface of the
72 Earth at night (<https://www.ngdc.noaa.gov/eog/>) but due to their coarse resolution they cannot be
73 used for city-scale land management studies (Fig. 1). Another remote sensing information source
74 are the pictures taken from the International Space Station (ISS ; <https://eol.jsc.nasa.gov>) that
75 have started to be geo-referenced by the citizen science program Cities at Night
76 (<http://citiesatnight.org> – Sánchez De Miguel et al., 2014). ISS pictures can reach a spatial
77 resolution of 10 m, contain four spectral bands in the visible range (one red, two green, one
78 blue), and each pixel's intensity is proportional to the emitted light (Fig. 1). There are a variety
79 of sources of information on artificial light with different spatial resolution, extent, and
80 information on light characteristics. Ground-based and remote sensing data sources both have
81 advantages and drawbacks (presented in Table 1) and represent an opportunity to better
82 understand the impact of artificial light on biodiversity as well as a challenge for their
83 application to an ecological and land management context (Kyba et al., 2014).

84

85 This study investigated the impact of light pollution on bat activity at the city scale comparing
86 two sources of information on artificial light: the location of streetlights and ISS nocturnal
87 pictures. We chose these two sources of information because their resolution was coherent with
88 the scale of our study, they were easily accessible, and their comparison may bring insights on
89 which source of information is the most adapted to measure the impact of light pollution on bats.
90 Our aims were (i) to evaluate how light pollution affected *P.pipistrellus* activity at the city scale,
91 (ii) to determine which source of information on artificial light was the most relevant to measure
92 the effect of light pollution and (iii) to define a reproducible methodology that could be used in
93 land management to make recommendations for a biodiversity-friendly lighting planning and

94 hence keeping low data requirements. To achieve these goals, we examined how *P. pipistrellus*
95 activity was affected by artificial light within three large cities of using a panel of light variables
96 based on either source of information. Although *P. pipistrellus* is considered a light tolerant
97 species, we expected a negative impact of light pollution on its activity as at the national scale
98 the average radiance had a negative effect (Azam et al., 2016).

99 **2. Methods**

100 *2.1 Study sites*

101 To address our main research questions we based the analysis on bat activity and environmental
102 data from three large and highly urbanized cities of France: Paris, Lille, and Montpellier (Fig. 2).
103 These three cities are amongst the most light-polluted areas of France with nights 20 to 40 times
104 brighter than natural illumination in Lille and Montpellier and over 40 times brighter in Paris
105 (Falchi et al., 2016). Paris is the largest of the three cities with 105 km² (Fig. 2.A). There are few
106 green areas in Paris' center but there are two large parks on the outskirts (Vincennes on the East
107 side and Boulogne on the West side) which represent 17 km² in total. Tree cover represented
108 21% of Paris' surface however, when not including the two large parks, it only represented 12%.
109 Montpellier and Lille have a smaller surface than Paris (respectively, 57 and 40 km² – Fig 2.B
110 and 2.C). Only 14% of the surface of Lille corresponded to vegetation whereas Montpellier was
111 the greenest of the tree cities with 21% of vegetation distributed in small patches across the city.
112 The three cities had a similar overall density of streetlights per square kilometer (549 SL/km²).

113

114 *2.2 Bat monitoring*

115 Bat activity recordings were taken following the recommendations of the French national bat-
116 monitoring scheme 'Vigie-Chiro' (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science
117 program running since 2006 and coordinated by the National Museum of Natural History of
118 Paris (France). All recordings occurred between June and October, the seasonal peak in bat
119 activity. Recordings were only carried out when weather conditions were favorable (i.e. no rain,
120 wind speed below 7 m/s, temperature at sunset above 12°C).

121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141

The data for Paris and Montpellier were provided by the French bat-monitoring scheme (<http://vigienature.mnhn.fr/page/vigie-chiro/page/protocoles>) following two different protocols. The first was the *pedestrian protocol* for which volunteer surveyors recorded bat activity for 6 minutes at 10 selected locations within a 4 km² area. The volunteers began their sampling 30 minutes after sunset. In Paris, volunteers used a time expansion detector (Tranquility Transect Bat detector, Courtpan Design Ltd, UK) and in Montpellier, they used a SM2BAT detector (Wildlife Acoustics Inc). The second protocol was the *full-night protocol* for which volunteers placed a SM2BAT detector at a given location 30 minutes before sunset and let it until the morning (30 minutes after sunrise) to record bat activity all night. Data for Lille were recorded by authors following the *full-night protocol* and using SM2BAT detectors. In Paris, 923 recordings lasting 6 minutes were taken at 282 different points following the *pedestrian protocol* between 2008 and 2013. In Lille, each of the 73 points was sampled once in 2015 using the *full-night protocol*. In Montpellier, 82 points were sampled with the *full-night protocol* and 71 points sampled with the *pedestrian protocol* (2011 and 2012). To have a similar data sampling unit among cities, we only took into account recordings of the *full-night protocol* occurring during the first two hours of the night (beginning 30 minutes after sunset) and split the recordings into 6 minutes time slots. Then, to avoid pseudo-replication, we calculated the mean activity per point. When considering entire nights of recordings, bat activity was fairly stable throughout the night, slightly decreasing toward the end of the night (see Appendix A – Fig. A.1).

142 *2.3 Bat acoustic data analysis*

143 All bat calls recorded in Paris and Montpellier were identified by volunteers and then validated
144 by experts using Syrinx software version 2.6 (Burt, 2006). For data recorded in Lille, we used the
145 software SonoChiro (Bas et al. 2013) to automatically classify the echolocation calls to the most
146 accurate taxonomic level possible. All ambiguous calls were then checked manually using
147 Syrinx software. As it is impossible to identify individual bats from their echolocation calls, we
148 calculated bat activity as the number of bat passes per species. A bat pass is defined as the
149 occurrence of a single or several echolocation calls of the same bat species during a 5-second
150 interval (Millon, Julien, Julliard, & Kerbirou, 2015). Although bat activity did not allow us to
151 assess bat abundance, it reflected the suitability of the habitat in terms of food resource. *P.*
152 *pipistrellus* and *P. nathusii* were the only bat species detected in the three cities (Appendix A -
153 Table A.1). However the number of bat passes of *P. nathusii* was very low in Paris and Lille
154 (respectively 6 and 37 bat passes) hence we only performed the analysis on *P. pipistrellus*.

155

156 *2.4 Light pollution variables*

157 We used two sources of information for light pollution. Firstly, we used the location of
158 streetlights. Data for Montpellier were accessible for free at <http://data.montpellier3m.fr/> and
159 data for Paris and Lille were provided by the private companies managing the cities' public
160 lights (Engie Ineo for Lille and Evesa for Paris). Secondly, we used nighttime ISS pictures from
161 the Cities At Night program. The images were corrected for linearity of the sensor, vignetting,
162 and calibrated absolutely using reference stars on other lenses and relatively to the VIIRS image
163 of May 2014 using synthetic photometry (Sánchez De Miguel, 2016). There was no atmospheric

164 correction. The value of each pixel corresponded to the radiance which is the radiant flux
165 reflected or emitted by a given surface (units $\text{nW/cm}^2/\text{sr/A}$).

166

167 A study investigating the impact of light pollution on bat at different scales showed that the best
168 spatial scale to study the impact of artificial light on *P. pipistrellus* was 200 m (the smaller
169 spatial scale tested; Azam et al., 2016). Thus we defined our light variables within a 200 m
170 buffer but also within a 100 m buffer to explore if a smaller spatial scale could bring further
171 insights. We calculated several light variables based on either source using QGIS 2.8.3 (QGIS
172 Development Team, 2017). Using the streetlight location, we calculated the distance to the
173 closest streetlight from each recording point, the number of streetlights within a 100 m and a 200
174 m buffer around each recording point, and the weighted density of streetlights within the same
175 buffers (the sum of the multiplicative inverse of the distance to streetlights within the 100 m and
176 200 m buffers). For several species, the impact of a streetlight seems to be detectable within a 25
177 m distance (Azam et al., 2018) so we built two more variables based on this information: the
178 presence of a streetlight within 25 m of the recording point (binary variable) and the proportion
179 of surface impacted by artificial light within a 100 m and a 200 m buffer. As Azam et al. (2018)
180 found that light had an effect up to 25 m away from a streetlight, we considered that all surface
181 within 25 m of a streetlight was impacted by light pollution. We used the four color bands (one
182 red, one blue, and two green bands) that compose the ISS pictures separately and calculated two
183 variables for each color band: the pixel value at each recording point and the mean pixel value
184 within a 100 m and a 200 m buffer around the recording point. Hence in total there were 8
185 variables based on the location of streetlights and 12 based on the ISS pictures (Table 2). All
186 variables were calculated using the same 60 m x 60 m grid in order to have the same resolution.

187 For the analysis, we removed recordings taken at four points considered as outliers because of
188 their very high radiance value due to a singular urban context (e.g., Eiffel Tower illuminations ;
189 n=12; 1% of the dataset). Note that similar results were obtained when including these
190 recordings in the analysis (see Appendix B).

191

192 *2.5 Environmental and meteorological variables*

193 Bat activity is influenced by environmental conditions both at a fine (i.e. flight path) and
194 intermediate (i.e home range) scale hence we included several variables to account for their
195 effect using BD TOPO data (IGN; Table 2). Several studies identified aquatic habitat as a
196 favorable habitat for bats (Kaňuch et al., 2008; Rainho & Palmeirim, 2011; Russo & Jones,
197 2003) thus we calculated the distance to the closest water source(in meters). In addition, as the
198 distance and the extent of wooded areas are positively correlated with bat presence (Boughey,
199 Lake, Haysom, & Dolman, 2011), we calculated the distance to the nearest tree cover (in
200 meters), and the proportion (%) of tree cover within a 200 m buffer. A set of complementary
201 variables were used as fixed effects to control for specific recording conditions: the method
202 (*pedestrian or full-night protocol*), the year (Kerbiriou et al., 2018), the Julian day and its
203 associated quadratic term as bat activity is expected not to be linear across the study period and
204 include a peak when young start to fly (Kerbiriou et al., 2018; Newson, Evans, & Gillings,
205 2015), and meteorological conditions at sunset (temperature C°, wind speed m/s, and humidity
206 %; Ciechanowski, Zając, Biłas, & Dunajski, 2008; O'Donnell, 2000).

207

208 2.6 Bat activity modeling

209 We built statistical models to test the effect of light pollution on *P. pipistrellus* activity (response
210 variable) while accounting for environmental and meteorological parameters. To outline a
211 general pattern and build robust models, data from the three cities were analyzed as a single
212 dataset. Several light variables were correlated with one another (Spearman's $|r| > 0.7$; Dormann
213 et al., 2013; see Appendix C) thus we built a separate full model for each light variable (i.e. 20
214 models). We ensured that all the variables used within the same model had a Spearman's rho
215 between -0.7 and 0.7. As all variables showed a VIF value < 3 (Heiberger & Holland, 2004) and
216 as the mean of VIF values < 2 (Chatterjee & Bose, 2000) there was no obvious sign of
217 multicollinearity.

218 We performed Generalized Linear Mixed Models (GLMM ; glmmTMB 0.2.0 ; Brooks et al.,
219 2017) using bat activity as the response variable and a light variable, environmental variables
220 and, meteorological variables as fixed effects. According to the nature of the response variable
221 (i.e. count data with over-dispersion) we used a negative binomial error distribution with a log
222 link (Zuur, Ieno, Walker, Saveliev, & Smith, 2009; See Appendix A – Fig A.2). Recording
223 points were distributed within the three cities and sometimes replicated hence we included the
224 city as a fixed effect and a random effect on the recording point. Explanatory variables were
225 standardized to facilitate comparisons between estimates. We added an interaction between the
226 light variable and the proportion of vegetation as a study found a difference in the responses of
227 *P. pipistrellus* activity to the presence of streetlights depending on the local tree cover (Mathews
228 et al., 2015). The full models were written as follow:

229

230 *Bat activity* ~ *light variable* * *proportion of vegetation* + *distance to vegetation*
231 + *distance to water* + *Julian day* + (*Julian day*)² + *Year* + *temperature*
232 + *humidity* + *wind speed* + *recording protocol* + *city*
233 + (1|*recording point*)

234

235 Where *light variable* was one of the 20 light variables listed in Table 2. Hence we had 20 full
236 models. For each full model, we ran all possible combinations (subsets) of fixed effects (MuMIn
237 1.15.6 ; Barton, 2013). Among each ensemble of candidate models (one full model and its subset
238 models), we selected the best model using Akaike’s Information criterion (AIC; Burnham &
239 Anderson, 2002). However, the AIC tends to overestimate the number of parameters in a model
240 by adding uninformative variables that do not improve fit (Guthery, Brennan, Peterson, & Lusk,
241 2005) hence, amongst the best models (i.e. within a Δ AIC of two of the minimum AIC), we
242 selected the simplest model that had significant parameters. Thus, at the end of the selection
243 process, we had 20 best models, one per light variable. We compared these 20 models using the
244 AIC. To explore the possible nonlinear effect of the light variable, we tested a GAMM (mgcv
245 1.8-16 ; Wood, 2011) model with the same structure as the overall best model (lowest AIC) with
246 a smoothing effect on the light variable. The degree of smoothness is left to be estimated as part
247 of the fitting. All analyses were conducted using R 3.3.3 (R Core Team, 2017).

248

249 **3. Results**

250 *3.1 Bat acoustic data analysis*

251 A total of 20,599 bat passes of *P. pipistrellus* were recorded at the 508 recording points (1,205 in
252 Paris, 7,035 in Montpellier, and 12,359 in Lille; see Appendix A – Table A.1 for details on all
253 the species recorded). *P. pipistrellus* represented 47% of the overall bat passes recorded (86% in
254 Paris, 24% in Montpellier, and 98% in Lille) and was detected in 48% of the recordings (27% in
255 Paris, 40% in Montpellier, and 98% in Lille).

256

257 *3.2 Bat activity modeling*

258 We selected one best model for each light variable (Table 3). After model selection on the full
259 models, for five models, the light variable was not retained and the best model was the one
260 without light variable. Three of the light variables not retained were based on streetlight location
261 (streetlight distance, streetlight presence and streetlight density in a 100 m radius) and two on
262 ISS pictures (pixel value for the Red 1 and Green 3 color band). In all models with a light
263 variable, *P. pipistrellus* activity was negatively affected by light. Seven out of the eight models
264 containing a light variable based on streetlight location did not perform better than the model
265 containing no light variable. The three models that performed the best ($\Delta AIC < 2$) were based on
266 mean values of the ISS picture in a 100 m or 200 m radius. Globally, among the 15 models
267 where a light variable was retained, all the models containing a light variable based on the ISS
268 pictures performed better than models containing a light variable based on the streetlight
269 location. For six models, the interaction between the light variable and the proportion of tree
270 cover was retained. Within these six models, five had a light variable based on one of the green
271 color band of the ISS picture and one on the red color band. The interaction showed that for low

272 proportions of tree cover, the radiance level had a negative effect on bat activity whereas for high
273 proportions of tree cover, the radiance level had a positive effect on bat activity (Fig. 3).
274 However no recording were taken at points combining high levels of vegetation and high level of
275 radiance. The GAMM model built with the same structure as the best overall model with a
276 smooth function on the light variable (mean pixel value of the blue color band in a 100 m radius)
277 showed that there was no nonlinear effect of the light variable.

278

279 After model selection, all the best models contained the same environmental and meteorological
280 variables except for the distance to tree cover that was not retained in six models. The distance to
281 water and to tree cover negatively impacted the activity of *P. pipistrellus* and the proportion of
282 tree cover had a positive effect on *P. pipistrellus* activity (Appendix D – Table D.1) as expected.
283 The Julian day and its quadratic term were retained, reflecting the fluctuations of bat activity
284 along the seasons (see Appendix D – Fig. D.1). The wind speed had a positive effect on *P.*
285 *pipistrellus* activity. Wind speed usually has a negative effect on bat activity when considering
286 high wind speed. Here wind speed were always low with 91% of data taken for wind speed
287 below 5.5 m/s.

288 4. Discussion

289 We found that, whatever the light variables tested, *P. pipistrellus* activity was negatively affected
290 by artificial light at the city scale. This result is coherent with large scale studies (Azam et al.,
291 2016; Mathews et al., 2015) although numerous small scale studies showed a local positive effect
292 of artificial light on light tolerant bat species (e.g., Azam et al., 2018; Rydell, 1992). The models
293 containing ISS picture based variables were better in terms of AIC than the models with
294 streetlight location based variables showing that ISS pictures explain the effect of light than
295 streetlight location for bats. The methodology we used to measure the impact of artificial light on
296 bats had low data requirements and could be reproduced elsewhere as these data are available for
297 most cities. Prediction derived from our models could be used to produce maps to identify
298 favorable areas for bats that should be preserved and to work on landscape connectivity.

299

300 The negative effect of light pollution on *P.pipistrellus* at the city scale suggests that the local
301 foraging advantage streetlights can represent (Rydell, 1992) is outweighed by the global negative
302 impact of artificial light. Moths preyed on by bats are attracted to short wavelengths (blue)
303 (Koh, 2008; van Langevelde et al., 2011) thus we could have expected areas with high values of
304 radiance of the blue color band to be areas of high concentration of prey and consequently areas
305 of high bat activity. But on the contrary, our results showed that high radiance values affected
306 negatively the activity of *P. pipistrellus* irrespective of the color band used. The underlying
307 mechanisms that drive the negative response of bats to artificial light are not clear. Rydell (1992)
308 suggested that bats might avoid lit areas due to an intrinsic perception of increased predation
309 risk. However the interaction between the proportion of tree cover and the radiance level showed
310 that the effect of light on bat activity could be positive in areas with important tree cover

311 although this combination was not present in our study areas. Similarly, Mathews et al (2015)
312 found that *P. pipistrellus* activity was higher in lit than dark environments when there was an
313 important tree cover although in open areas, light had a negative effect on this species' activity.
314 Hence it is possible that the tree cover reduces the risk of predation linked to lit areas but also
315 that streetlights close to wooded areas attract more insects and therefore are particularly
316 advantageous foraging grounds. Despite the negative effect of artificial light, *P. pipistrellus* is
317 still present in urbanized and strongly illuminated areas. This species is more resilient to
318 anthropogenic pressures than other species that are seldom found in urban landscapes. Hence
319 species that are more sensitive to light pollution might experience an even more detrimental
320 impact highlighting the importance of including biodiversity in artificial lighting planning
321 schemes.

322

323 Surprisingly, the two sources of data on artificial light were weakly correlated (Spearman's $|r| =$
324 0.13 ± 0.06 , Appendix C). This absence of clear relationship between the two types of data is most
325 likely due to the absence of information on private lighting such as monuments, university or
326 shop lights in the streetlight location data although they can be a major source of illumination
327 within cities. Moreover, location data do not inform on light characteristics (e.g., height, type,
328 intensity) which determine the repartition and brightness of the light. Conversely, ISS pictures
329 include both public and private lighting and are a measure the radiance due direct and reflected
330 light emissions, including skyglow. The ISS pictures encompass the global level of radiance and
331 hence might be a closer representation of what bats experience than streetlight location.
332 Nevertheless, the streetlight density in a 200 m radius was informative and had a similar effect as
333 ISS picture based variables. Hence ideally, using the mean pixel value of an ISS picture within a

334 100 radius would be best but if there is no picture available, streetlight location data can be
335 useful. Moreover, if information on streetlight characteristics are available, this could further
336 increase the explicative power of the ground-based data.

337

338 We deliberately kept a low data requirement to allow our model to be reproducible although
339 complex models using streetlights characteristics and light dispersion models have been
340 developed to map cities nighttime light emissions (Bennie, Davies, Inger, & Gaston, 2014). Our
341 goal was to construct a methodology using fairly simple variables and analysis to be applied to
342 other cities as a management tool. Our model can be used to produce predictive maps of bat
343 activity and to visualize areas where light pollution should be reduced. Furthermore, in addition
344 to preserving dark areas, it is crucial to also consider the landscape scale through which this
345 species move. Favorable habitat patches need to be connected to one another by corridors to
346 sustain populations and allow for daily movement (e.g., foraging), seasonal movement (e.g.,
347 migration), and dispersion (i.e. gene flow). As artificial light can have a barrier effect on bats
348 (Hale et al., 2015), it is important to evaluate its impact on landscape connectivity and our
349 methodology could help map potential ecological corridors for bats at the city scale. Then, to
350 adapt lighting at a fine scale, the information brought by studies on light types (Lewanzik &
351 Voigt, 2017; Rowse, Harris, & Jones, 2016; Stone, Wakefield, Harris, & Jones, 2015) and
352 spectrum (Spoelstra et al., 2017) could help target light sources that might have important
353 impacts on bats. We found a linear negative effect of artificial light on bat activity, whereby
354 increasing radiance was associated with a proportional decrease in bat activity. This relationship
355 suggests that reducing lighting pollution will have a positive effect on bats. Moreover it was
356 shown that even a slight decrease in artificial light intensity could greatly enhance the number of

357 dark patches necessary to nocturnal species (Marcantonio et al., 2015). With the development of
358 adaptable lighting technologies in terms of flux directionality and light intensity, it seems
359 feasible to decrease light intensity and limit trespass while still complying with socio-economic
360 and security constraints (Gaston et al., 2012).

361

362 Remote sensing data offer promising opportunities to account for artificial light impact in urban
363 planning and their availability increases greatly with citizen-science initiatives such as Cities At
364 Night (<http://citiesatnight.org> – Sánchez De Miguel et al., 2014). Although some technical
365 difficulties remain (need for location, calibration, and correction of the images) the technological
366 advances in nocturnal remote sensing represent an opportunity to have a direct representation of
367 the global artificial light emissions at fine resolutions. Thus citizen science programs of
368 biodiversity monitoring and remote sensing imaging and interdisciplinary collaboration between
369 ecologists and astrophysicists will undoubtedly help increase our understanding of light pollution
370 and its impact on the environment.

References

- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., & Kerbiriou, C. (2018). Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning*, *175*(February), 123–135. <http://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., & Kerbiriou, C. (2016). Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecology*, *31*(10), 2471–2483. <http://doi.org/10.1007/s10980-016-0417-3>
- Barton, K. (2013). MuMIn: Multi-Model Inference.
- Bartonicka, T., & Zukal, J. (2003). Flight activity and habitat use of four bat species in a small town revealed by bat detectors. *Folia Zoologica*, *52*(2), 155–166.
- Bennie, J., Davies, T. W., Inger, R., & Gaston, K. J. (2014). Mapping artificial lightscapes for ecological studies. *Methods in Ecology and Evolution*, *5*(6), 534–540. <http://doi.org/10.1111/2041-210X.12182>
- Boldogh, S., Dobrosi, D., & Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, *9*(2), 527–534. [http://doi.org/https://doi.org/10.3161/1733-5329\(2007\)9](http://doi.org/https://doi.org/10.3161/1733-5329(2007)9)
- Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*, *144*(9), 2300–2310.

<http://doi.org/10.1016/j.biocon.2011.06.008>

Brooks, M. E., Kristensen, K., Benthem, K. J. van, Magnusson, A., Berg, C. W., Nielsen, A., ...

Bolker, B. M. (2017). Modeling Zero-Inflated Count Data With glmmTMB. *BioRxiv*, 132753.

<http://doi.org/10.1101/132753>

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition* (Springer-V). New York.

Chatterjee, S., & Bose, A. (2000). VARIANCE ESTIMATION IN HIGH DIMENSIONAL REGRESSION MODELS. *Statistica Sinica*, 10(2), 497–515.

Ciechanowski, M., Zając, T., Biłas, A., & Dunajski, R. (2007). Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology*, 85(12), 1249–1263.
<http://doi.org/10.1139/Z07-090>

Council Directive 92/43/EEC. The conservation of natural habitats and of wild fauna and flora, Official Journal of the European Communities (1992).

de Miguel, A. S., Castano, J. G., Zamorano, J., Pascual, S., Angeles, M., Cayuela, L., ... Kyba, C. C. M. (2014). Atlas of astronaut photos of Earth at night. *Astronomy & Geophysics*, 55(4), 4.36-4.36. <http://doi.org/10.1093/astrogeo/atu165>

Eisenbeis, G. (2006). Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In C. Rich & T. Longcore (Eds.), *Ecological consequences of artificial night lighting* (pp. 281–304). Island Press, Washington, D.C., USA.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., ... Furgoni, R.

- (2016). The new world atlas of artificial night sky brightness. *Science Advances*, 2(6), e1600377–e1600377. <http://doi.org/10.1126/sciadv.1600377>
- Falchi, F., Cinzano, P., Elvidge, C. D., Keith, D. M., & Haim, A. (2011). Limiting the impact of light pollution on human health, environment and stellar visibility. *Journal of Environmental Management*, 92(10), 2714–2722. <http://doi.org/10.1016/j.jenvman.2011.06.029>
- Gaisler, J., Zukal, J., Rehak, Z., & Homolka, M. (1998). Habitat preference and flight activity of bats in a city. *Journal of Zoology*, 244(3), S0952836998003148. <http://doi.org/10.1017/S0952836998003148>
- Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, 49(6), 1256–1266. <http://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Gaston, K. J., Visser, M. E., & Holker, F. (2015). The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140133–20140133. <http://doi.org/10.1098/rstb.2014.0133>
- Guthery, F. S., Brennan, L. A., Peterson, M. J., & Lusk, J. J. (2005). Invited Paper: Information Theory in Wildlife Science: Critique and Viewpoint. *Journal of Wildlife Management*, 69(2), 457–465. [http://doi.org/10.2193/0022-541X\(2005\)069\[0457:ITIWSC\]2.0.CO;2](http://doi.org/10.2193/0022-541X(2005)069[0457:ITIWSC]2.0.CO;2)
- Hale, J. D., Davies, G., Fairbrass, A. J., Matthews, T. J., Rogers, C. D. F., & Sadler, J. P. (2013). Mapping Lightscapes: Spatial Patterning of Artificial Lighting in an Urban Landscape. *PLoS ONE*, 8(5), e61460. <http://doi.org/10.1371/journal.pone.0061460>
- Hale, J. D., Fairbrass, A. J., Matthews, T. J., Davies, G., & Sadler, J. P. (2015). The ecological

- impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology*, 21(7), 2467–2478. <http://doi.org/10.1111/gcb.12884>
- Heiberger, R. M., & Holland, B. (2004). *Statistical Analysis and Data Display*. New York, NY: Springer New York. <http://doi.org/10.1007/978-1-4757-4284-8>
- Hölker, F., Moss, T., Griefahn, B., & Kloas, W. (2010). The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy. *Ecology and Society*, 15(4), art13.
- Hölker, F., Wolter, C., Perkin, E. K., & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*, 25(12), 681–682. <http://doi.org/10.1016/j.tree.2010.09.007>
- Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: A question of evolving, acclimatizing or coping with urban environmental stress. *Functional Ecology*, 29(7), 913–923. <http://doi.org/10.1111/1365-2435.12477>
- Jones, G., Jacobs, D., Kunz, T., Willig, M., & Racey, P. (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, 8, 93–115. <http://doi.org/10.3354/esr00182>
- Kaňuch, P., Danko, Š., Celuch, M., Krištín, A., Pjenčák, P., Matis, Š., & Šmídt, J. (2008). Relating bat species presence to habitat features in natural forests of Slovakia (Central Europe). *Mammalian Biology - Zeitschrift Für Säugetierkunde*, 73(2), 147–155. <http://doi.org/10.1016/j.mambio.2006.12.001>
- Kerbiriou, C., Azam, C., Touroult, J., Marmet, J., Julien, J. F., & Pellissier, V. (2018). Common bats are more abundant within Natura 2000 areas. *Biological Conservation*, 217(September

- 2017), 66–74. <http://doi.org/10.1016/j.biocon.2017.10.029>
- Koh, L. P. (2008). BIRDS DEFEND OIL PALMS FROM HERBIVOROUS INSECTS. *Ecological Applications*, 18(4), 821–825. <http://doi.org/10.1890/07-1650.1>
- Kuechly, H. U., Kyba, C. C. M., Ruhtz, T., Lindemann, C., Wolter, C., Fischer, J., & Hölker, F. (2012). Aerial survey and spatial analysis of sources of light pollution in Berlin, Germany. *Remote Sensing of Environment*, 126, 39–50. <http://doi.org/10.1016/j.rse.2012.08.008>
- Kyba, C. C. M., Garz, S., Kuechly, H., Sanchez de Miguel, A., Zamorano, J., Fischer, J., & Hölker, F. (2014). High-Resolution Imagery of Earth at Night: New Sources, Opportunities and Challenges. *Remote Sensing*, 7(1), 1–23. <http://doi.org/10.3390/rs70100001>
- Kyba, C. C. M., & Hölker, F. (2013). Do artificially illuminated skies affect biodiversity in nocturnal landscapes? *Landscape Ecology*, 28(9), 1637–1640. <http://doi.org/10.1007/s10980-013-9936-3>
- Lewanzik, D., & Voigt, C. C. (2017). Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology*, 54(1), 264–271. <http://doi.org/10.1111/1365-2664.12758>
- Longcore, T., & Rich, C. (2004). Ecological Light Pollution. *Frontiers in Ecology and the Environment*, 2(4), 191. <http://doi.org/10.2307/3868314>
- Marcantonio, M., Pareeth, S., Rocchini, D., Metz, M., Garzon-Lopez, C. X., & Neteler, M. (2015). The integration of Artificial Night-Time Lights in landscape ecology: A remote sensing approach. *Ecological Complexity*, 22(June), 109–120. <http://doi.org/10.1016/j.ecocom.2015.02.008>

- Marnell, F., & Presetnik, P. (2010). Protection of overground roosts for bats. *Eurobats*, 4.
- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., & Langton, S. (2015). Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140124–20140124. <http://doi.org/10.1098/rstb.2014.0124>
- McKinney, M. L. (2002). Urbanization, biodiversity and conservation. *BioScience*, 52(10), 883–890. [http://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](http://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- Millon, L., Julien, J. F., Julliard, R., & Kerbiriou, C. (2015). Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecological Engineering*, 75, 250–257. <http://doi.org/10.1016/j.ecoleng.2014.11.050>
- Navara, K. J., & Nelson, R. J. (2007). The dark side of light at night: physiological, epidemiological, and ecological consequences. *Journal of Pineal Research*, 43(3), 215–224. <http://doi.org/10.1111/j.1600-079X.2007.00473.x>
- Newson, S. E., Evans, H. E., & Gillings, S. (2015). A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation*, 191, 38–49. <http://doi.org/10.1016/j.biocon.2015.06.009>
- O'Donnell, C. (2000). Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *New Zealand Journal of Zoology*, 27(3), 207–221. <http://doi.org/10.1080/03014223.2000.9518228>
- QGIS Development Team. (2017). QGIS Geographic Information System. Open Source

Geospatial Foundation Project.

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria:

R Foundation for Statistical Computing.

Rainho, A. (2007). Summer foraging habitats of bats in a Mediterranean region of the Iberian

Peninsula. *Acta Chiropterologica*, 9(1), 171–181. [http://doi.org/10.3161/1733-5329\(2007\)9\[171:SFHOBI\]2.0.CO;2](http://doi.org/10.3161/1733-5329(2007)9[171:SFHOBI]2.0.CO;2)

Rainho, A., & Palmeirim, J. M. (2011). The Importance of Distance to Resources in the Spatial

Modelling of Bat Foraging Habitat. *PLoS ONE*, 6(4), e19227. <http://doi.org/10.1371/journal.pone.0019227>

Rowse, E. G., Harris, S., & Jones, G. (2016). The switch from low-pressure sodium to light

emitting diodes does not affect bat activity at street lights. *PLoS ONE*, 11(3). <http://doi.org/10.1371/journal.pone.0150884>

Russo, D., & Jones, G. (2003). Use of foraging habitats by bats in a Mediterranean area determined

by acoustic surveys: conservation implications. *Ecography*, 26(2), 197–209. <http://doi.org/10.1034/j.1600-0587.2003.03422.x>

Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional*

Ecology, 6(6), 744–750.

Rydell, J., Eklöf, J., & Sánchez-Navarro, S. (2017). Age of enlightenment: long-term effects of

outdoor aesthetic lights on bats in churches. *Royal Society Open Science*, 4(8), 161077. <http://doi.org/10.1098/rsos.161077>

Sánchez De Miguel, A. (2016). *Variación espacial , temporal y espectral de la contaminación*

lumínica y sus fuentes : Metodología y resultados. Universidad Complutense de Madrid - Facultad de Ciencias Físicas.

Simon, M., Hüttenbügel, S., & Smit-Viergutz, J. (2004). *Ecology and conservation of bats in villages and towns*. Bundesamt für Naturschutz.

Spoelstra, K., van Grunsven, R. H. A., Ramakers, J. J. C., Ferguson, K. B., Raap, T., Donners, M., ... Visser, M. E. (2017). Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society of London B: Biological Sciences*, 284(1855), 11–15.

Stahlschmidt, P., & Brühl, C. A. (2012). Bats as bioindicators - the need of a standardized method for acoustic bat activity surveys. *Methods in Ecology and Evolution*, 3(3), 503–508. <http://doi.org/10.1111/j.2041-210X.2012.00188.x>

Stone, E. L., Jones, G., & Harris, S. (2009). Street Lighting Disturbs Commuting Bats. *Current Biology*, 19(13), 1123–1127. <http://doi.org/10.1016/j.cub.2009.05.058>

Stone, E. L., Jones, G., & Harris, S. (2012). Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, 18(8), 2458–2465. <http://doi.org/10.1111/j.1365-2486.2012.02705.x>

Stone, E. L., Wakefield, A., Harris, S., & Jones, G. (2015). The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140127–20140127. <http://doi.org/10.1098/rstb.2014.0127>

van Langevelde, F., Ettema, J. A., Donners, M., WallisDeVries, M. F., & Groenendijk, D. (2011).

Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144(9), 2274–2281. <http://doi.org/10.1016/j.biocon.2011.06.004>

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73(1), 3–36. <http://doi.org/10.1111/j.1467-9868.2010.00749.x>

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer New York. <http://doi.org/10.1007/978-0-387-87458-6>

List of tables

Table 1

Comparison of the advantages and drawbacks of two sources of information on artificial light: ground-based (GB) data and remote sensing (RS) data.

Table 2

List of all the variables used as explanatory variables to model bat activity. Each light variables were used in a separate full model and all environmental variables, meteorological variables and covariables were included in all full models. Variables based on the ISS pictures are defined for each color band, the red (Red 1), the two green (Green 2 and Green 3), and the blue (Blue 4).

Variables with a (*) are defined for a 100 m and 200 m buffer.

Table 3

Selection of best models to explain bat activity using a light variable. Estimates of the light variable and the interaction between the light variable and the proportion of tree cover (when retained in the model selection) and best model without light variable. After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Individual tables

Table 1

Comparison of the advantages and drawbacks of two sources of information on artificial light: ground-based data (GB; e.g.. streetlights location) and remote sensing data (RS, e.g., ISS pictures).

	Ground-based data (GB)	Remote sensing data (RS)	Comparison
Precision	+	-	GB data give the precise location of light sources whereas RS data give a global radiance value for a pixel
Height perspective relative to bat flight height	+	-	Streetlight heights (GB data) are closer to bats flight height whereas RS data give a radiance value as perceived from space
Exhaustiveness	-	+	RS data include all types of lighting whereas GB data only include public lighting
Light characteristics	-	+	RS data give information on the quantity and the spectrum of the light whereas GB data do not always include information on the light sources characteristics

Table 2

List of all the variables used as explanatory variables to model bat activity. Each light variables were used in a separate full model and all environmental variables, meteorological variables and covariables were included in all full models. Variables based on the ISS pictures are defined for each color band, the red (Red 1), the two green (Green 2 and Green 3), and the blue (Blue 4). Variables with a (*) are defined for a 100 m and 200 m buffer.

	Variable	Description	Units	Reference
LIGHT VARIABLES				
	SL distance	Distance to the closest streetlight	m	
	SL density*	Number of streetlights within a given radius		
	SL weighted density*	Sum of the multiplicative inverse of the distance to streetlights within a given radius	m ⁻¹	
	SL presence	Presence/absence of a streetlight within 25 m		
Streetlight location	Impacted surf.*	Proportion of surface within 25 m of streetlight in a given radius	%	
	Color band - pixel	Pixel value of the ISS picture	nW/cm ² /sr/ A	
ISS pictures	Color band - mean*	Mean pixel value in a given radius	nW/cm ² /sr/ A	
ENVIRONMENTAL VARIABLES				
	Dist. to water	Distance to the closest water surface	m	Kañuch et al., 2008; Rainho & Palmeirim, 2011; Russo & Jones, 2003
	Dist. to tree cover	Distance to the closest tree cover	m	Boughey et al., 2011
	Prop. of tree cover	Proportion of tree cover within 200 m	%	Boughey et al., 2011
METEOROLOGICAL VARIABLES				
	Temperature	Temperature at sunset	°C	
	Humidity	Humidity at sunset	%	?
	Wind speed	Wind speed at sunset	m/s	?
COVARIABLES				

Year	Year of recording	?
Julian Day	Julian day of recording	?
City	City where the recording took place	
Recording point	Identification of the recording point	
Method	Recording method: fullnight or pedestrian protocol	?

Table 3

Selection of best models to explain bat activity using a light variable and best model without light variable. Estimates of the light variable and the interaction between the light variable and the proportion of tree cover (when retained in the model selection). After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates		AIC	Δ AIC	Weights	Marginal R2	Conditional R2
	Light variable	Light variable * Tree cover					
Blue 4 - 100	-0.34 **		3331.3	0.0	0.26	0.33	0.62
Green 2 - 100	-0.21	0.25 .	3332.0	0.7	0.18	0.34	0.63
Red 1 - 200	-0.16	0.27 *	3333.1	1.8	0.11	0.33	0.63
Green 2 - pixel	-0.13	0.31 *	3333.6	2.3	0.08	0.33	0.63
Green 2 - 200	-0.15	0.24 *	3333.9	2.6	0.07	0.33	0.63
Blue 4 - pixel	-0.26 *		3334.4	3.1	0.06	0.32	0.62
Red 1 - 100	-0.31 *		3334.5	3.2	0.05	0.33	0.62
Blue 4 - 200	-0.26 *		3334.8	3.5	0.05	0.32	0.62
Green 3 - 200	-0.10	0.27 *	3335.2	3.9	0.04	0.32	0.63
Green 3 - 100	-0.06	0.28 *	3336.3	5.0	0.02	0.32	0.62
SL density - 200	-0.19 *		3336.6	5.3	0.02	0.31	0.62
Impacted surf. - 200	-0.20 *		3336.8	5.5	0.02	0.31	0.62
Impacted surf. - 100	-0.19 .		3337.0	5.7	0.02	0.31	0.62
SL density - 100	-0.17 .		3337.2	5.9	0.01	0.31	0.63
SL weighted density - 200	-0.15		3337.7	6.4	0.01	0.31	0.62
None			3338.7	7.4	0.01	0.30	0.62

List of figures

Fig. 1. Different possible sources of information on light pollution. DMSP – OLS (A) and VIIRS –DNB (B) satellite images of France with a zoom on Paris and its surrounding. The resolution of the images is too low (930 m for DMSP – OLS and 460 m for VIIRS – DNB) to see the difference of radiance emitted in Paris. The better resolution (60m) of this ISS picture of Paris (C) allows to distinguish areas with low and high radiance at a fine scale. Also, this picture is composed by 4 color bands (2 green, 1 blue, and 1 red) which represent the radiance emitted in each spectral band. Another source of information on light pollution is the location of streetlights (D). Each orange dot represent a streetlight (over 51 000 in Paris).

Fig. 2. Study sites: Lille (A), Paris (B), and Montpellier (C). Triangles represent points of *full-night* recordings and dots represent points of *pedestrian* recordings.

Fig. 3 Interaction between the light variable (mean value of radiance within a 100 m radius for the Green 2 color band of the ISS picture) and the proportion of tree cover. The color scale represent the predicted mean number of bat passes per six minutes. Black dots represent combination of light variable values and tree cover proportion sampled in the data.

Individual figures

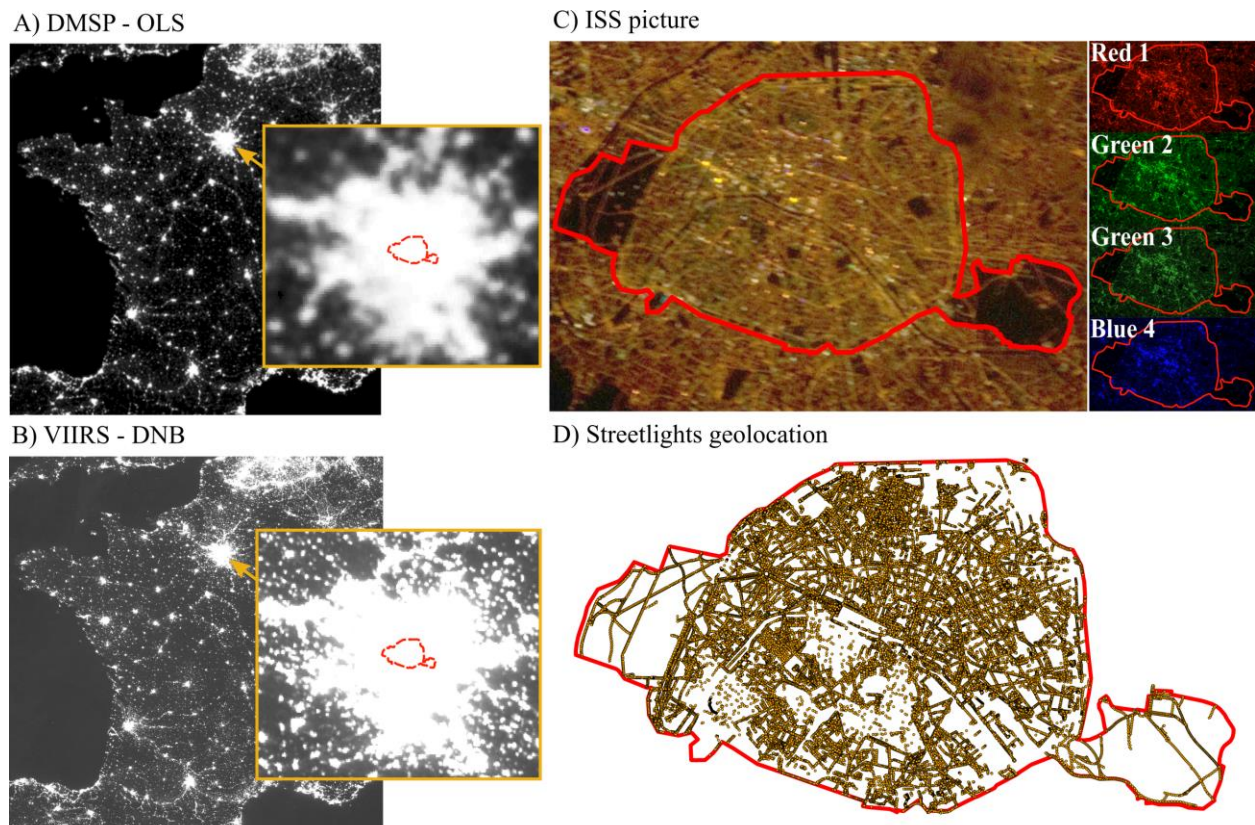


Fig. 1. Different possible sources of information on light pollution. DMSP – OLS (A) and VIIRS –DNB (B) satellite images of France with a zoom on Paris and its surrounding. The resolution of the images is too low (930 m for DMSP – OLS and 460 m for VIIRS – DNB) to see the difference of radiance emitted in Paris. The better resolution (60m) of this ISS picture of Paris (C) allows to distinguish areas with low and high radiance at a fine scale. Also, this picture is composed by 4 color bands (2 green, 1 blue, and 1 red) which represent the radiance emitted in each spectral band. Another source of information on light pollution is the location of streetlights (D). Each orange dot represent a streetlight (over 51 000 in Paris).

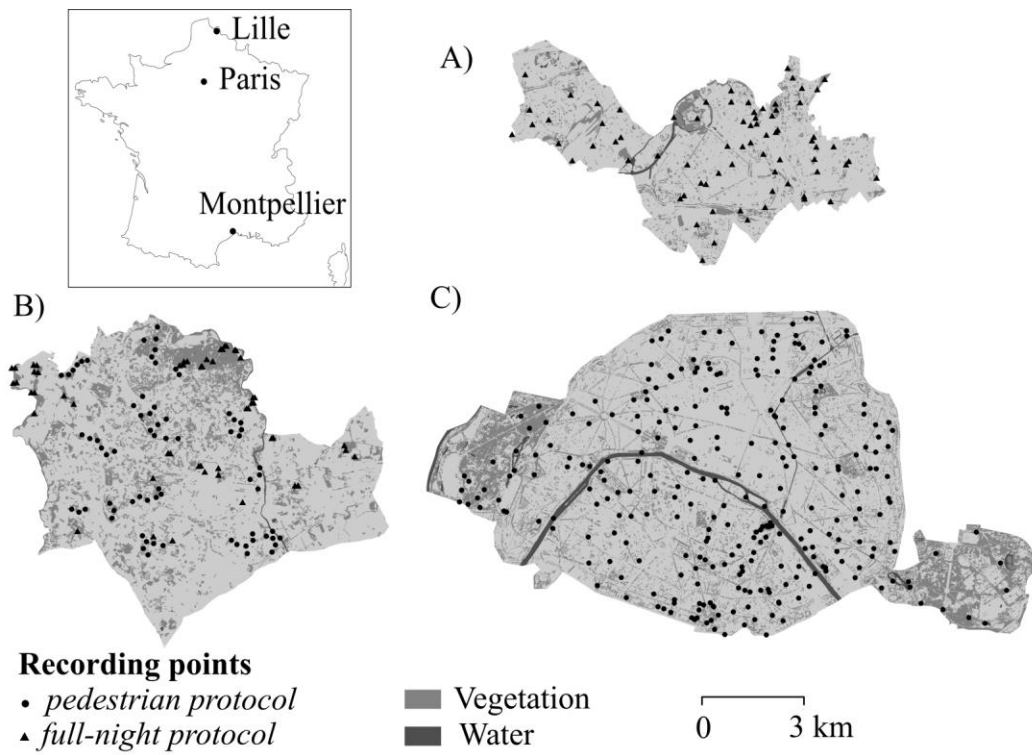


Fig. 2 Study sites: Lille (A), Paris (B), and Montpellier (C). Triangles represent points of *full-night* recordings and dots represent points of *pedestrian* recordings.

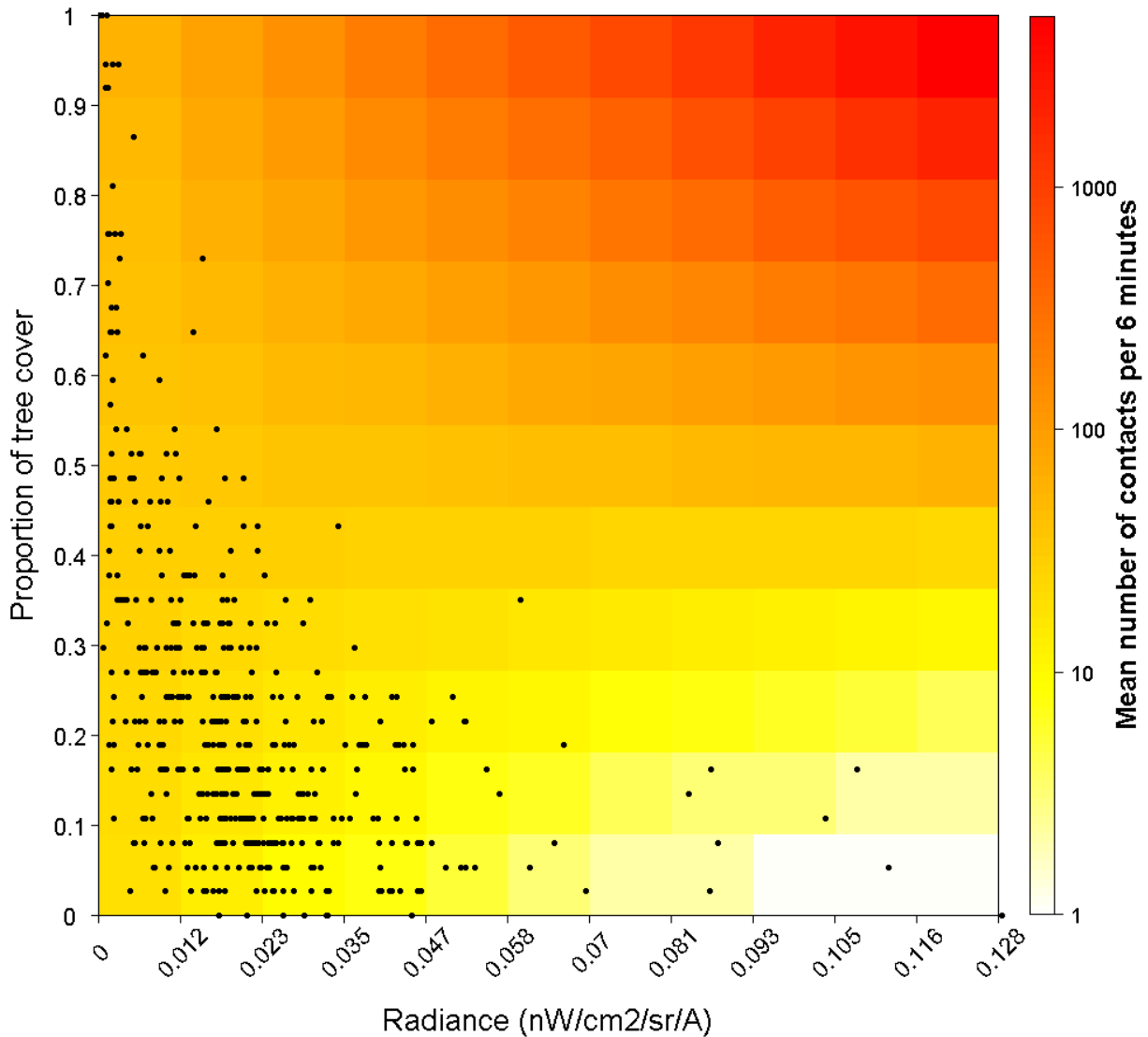


Fig. 3 Interaction between the light variable (mean value of radiance within a 100 m radius for the Green 2 color band of the ISS picture) and the proportion of tree cover. The color scale represent the predicted mean number of bat passes per six minutes (log scale). Black dots represent combination of light variable values and tree cover proportion sampled in the data.

List of appendices

Appendix A. Bat activity data

Appendix B. Definition of the outliers and results when including them in the dataset

Appendix C. Seasonal fluctuation of bat activity

Appendix D. Model results

Appendix A. Bat activity data

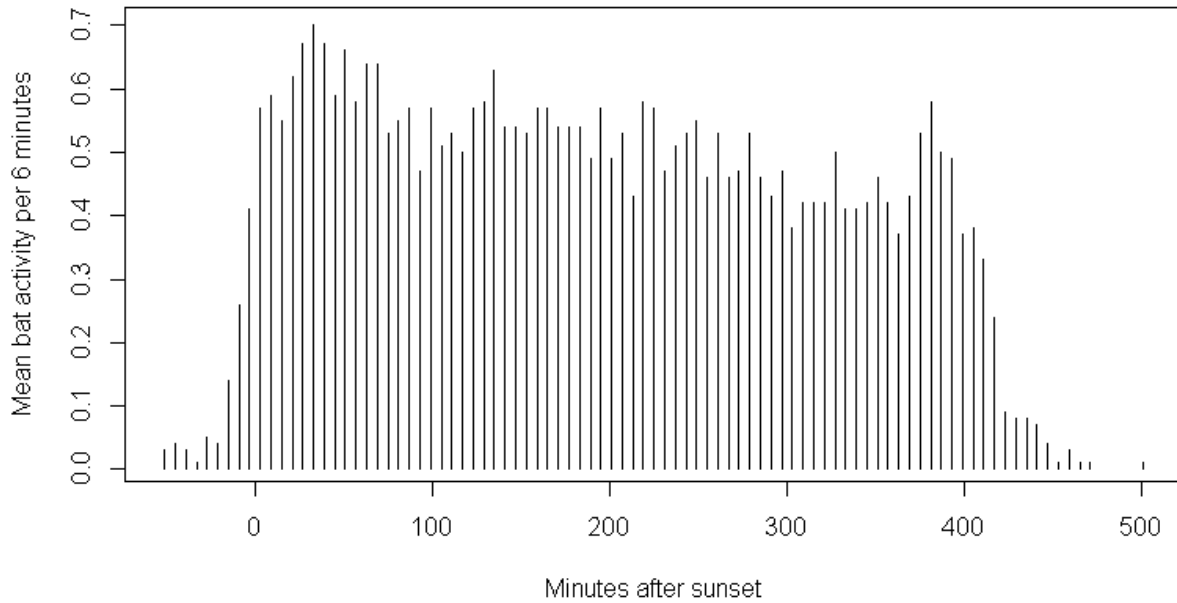


Fig. A.1. Mean activity of *P. pipistrellus* per 6 minutes throughout the night for the full night recordings in Lille.

Table A.1. Number of bat passes during the two first hours of the night per species for each city and occurrence within the recording points of each city.

Species	Paris		Lille		Montpellier	
	Bat passes	Occ.	Bat passes	Occ.	Bat passes	Occ.
<i>Pipistrellus pipistrellus</i>	1,205	27%	12,359	99%	7,035	61%
<i>Pipistrellus pygmaeus</i>	1	0%			13,367	73%
<i>Pipistrellus kuhlii</i>	122	3%			6,581	66%
<i>Pipistrellus nathusii</i>	6	0%	37	1%	723	9%
<i>Nyctalus noctula</i>	45	1%				
<i>Nyctalus leisleri</i>			8	0%	1,032	14%
<i>Eptesicus serotinus</i>			246	5%	150	2%
<i>Myotis daubentonii</i>	22	1%			753	6%

<i>Myotis emarginatus</i>				3	0%	
<i>Myotis nattereri</i>				9	0%	
<i>Miniopterus schreibersii</i>				2	0%	
<i>Plecotus austriacus</i>				45	1%	
<i>Tadarida teniotis</i>				3	0%	
<i>Hypsugo savii</i>				14	0%	
Single-genus group						
<i>P. nathusii</i> / <i>P. kuhlii</i>				5	0%	
<i>Myotis spp.</i>	1	0%			1	0%
<i>Plecotus spp.</i>					2	0%
Multi-genus group						
<i>Nyctalus</i> / <i>Eptesicus</i>				4	0%	

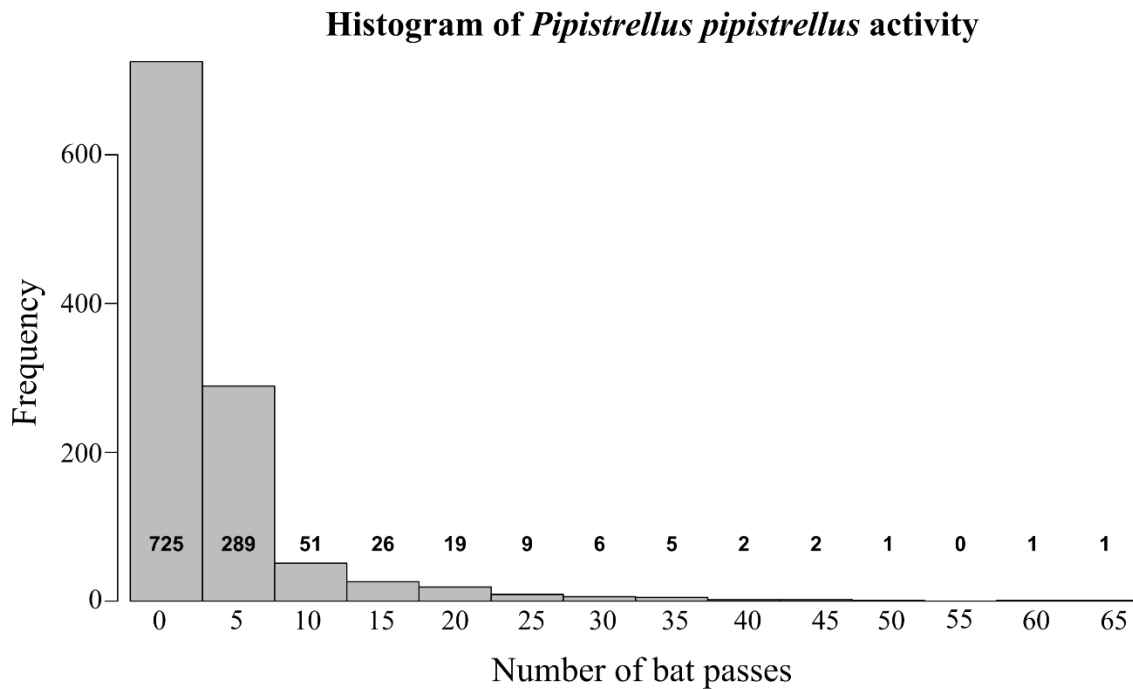


Fig. A.2. Number of *P. pipistrellus* passes in 6 minutes of recording. For *full-night* recordings, we only considered the two first hours of the night and the activity of the night was the average number

of bat passes per 6 minutes time slots. The number of occurrence of each number of bat passes is given in bold above the x-axis.

Appendix B. Definition of the outliers and results when including them in the dataset

We considered four recording points to be outliers because of their particularly high radiance value on the ISS picture (Fig. B.1.). Three recording points with the highest values of radiance are located next to the Eiffel Tower and the fourth one is on the Esplanade Charles de Gaulle, in Montpellier city center.

We carried the same analysis as in the core paper and found similar results when including the 4 outlier points (Table B.1.).

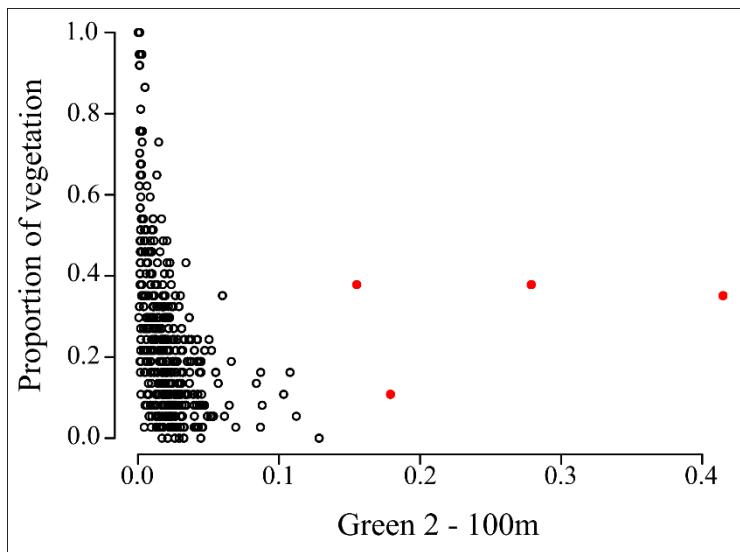


Fig. B.1. The four sites considered as outliers for their particularly high radiance value are represented in red.

Table B.1.

Selection of best models to explain bat activity using a light variable and best model without light variable. After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. The reference level for the factor variable “city” is the city of Lille. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates													Light variable *	AIC	ΔAIC	Weights	Marginal R2	Conc
	Intercept	City - Paris	City - Montpellier	Julian Day	(Julian day)2	Wind speed	Dist. to water	Dist. to tree cover	Prop. of tree cover	Light variable	Tree cover								
Green 2 - 100	2.94 ***	-3.13 ***	-2.60 ***	0.33 ***	-0.28 **	0.16 *	-0.27 **		0.61 ***	-0.35 **	0.50 ***	3363.2	0.0	0.32	0.34	0			
Blue 4 - 100	2.92 ***	-3.12 ***	-2.62 ***	0.32 ***	-0.28 **	0.16 *	-0.27 **		0.55 ***	-0.30 **	0.38 **	3365.0	1.8	0.13	0.34	0			
Red 1 - 200	2.95 ***	-3.14 ***	-2.61 ***	0.34 ***	-0.29 **	0.15 *	-0.26 **		0.65 ***	-0.45 **	0.60 ***	3365.4	2.2	0.11	0.33	0			
Green 2 - pixel	3.00 ***	-3.20 ***	-2.63 ***	0.33 ***	-0.28 **	0.16 *	-0.28 **		0.58 ***	-0.19 *	0.36 **	3365.4	2.2	0.11	0.33	0			
Green 2 - 200	2.94 ***	-3.13 ***	-2.60 ***	0.34 ***	-0.30 **	0.16 *	-0.26 **		0.63 ***	-0.38 **	0.52 ***	3366.0	2.8	0.08	0.33	0			
Blue 4 - pixel	3.02 ***	-3.22 ***	-2.67 ***	0.34 ***	-0.30 **	0.14	-0.26 **	-0.19 *	0.43 ***	-0.22 *	0.25 *	3366.1	2.9	0.08	0.33	0			
Red 1 - 100	2.89 ***	-3.10 ***	-2.56 ***	0.32 ***	-0.28 **	0.17 *	-0.27 **		0.56 ***	-0.27 **	0.37 **	3367.7	4.5	0.03	0.33	0			
Green 3 - 200	3.01 ***	-3.23 ***	-2.68 ***	0.34 ***	-0.29 **	0.16 *	-0.27 **		0.61 ***	-0.42 **	0.55 **	3367.8	4.6	0.03	0.32	0			
Green 3 - 100	2.92 ***	-3.15 ***	-2.60 ***	0.32 ***	-0.28 **	0.16 *	-0.27 **		0.56 ***	-0.40 **	0.50 **	3368.3	5.1	0.03	0.32	0			
Blue 4 - 200	3.04 ***	-3.26 ***	-2.72 ***	0.34 ***	-0.29 **	0.16 *	-0.26 **		0.56 ***	-0.25 *	0.34 **	3368.8	5.6	0.02	0.32	0			
SL density - 200	3.04 ***	-3.33 ***	-2.67 ***	0.34 ***	-0.29 **	0.14	-0.20 *	-0.26 *	0.27 *	-0.20 *		3369.1	5.9	0.02	0.31	0			
SL density - 100	3.00 ***	-3.28 ***	-2.66 ***	0.33 ***	-0.29 **	0.15 *	-0.20 *	-0.27 *	0.29 **	-0.18 *		3369.8	6.6	0.01	0.31	0			
Impacted surf. - 200	2.99 ***	-3.27 ***	-2.63 ***	0.33 ***	-0.29 **	0.16 *	-0.19 *	-0.25 *	0.27 *	-0.20 *		3369.9	6.7	0.01	0.31	0			
Impacted surf. - 100	2.93 ***	-3.21 ***	-2.61 ***	0.33 ***	-0.29 **	0.16 *	-0.19 *	-0.26 *	0.28 **	-0.18 *		3370.1	6.9	0.01	0.31	0			
SL weighted density - 200	3.05 ***	-3.34 ***	-2.70 ***	0.34 ***	-0.29 **	0.15	-0.21	-0.26 *	0.29 **	-0.16		3370.3	7.1	0.01	0.31	0			
None	2.89 ***	-3.18 ***	-2.58 ***	0.33 ***	-0.28 **	0.16 *	-0.23 *	-0.24 *	0.35 ***			3371.7	8.5	0.01	0.30	0			

Appendix C. Correlation between light variables

Table C.1. Correlation (Spearman’s r) between the light variables tested. Values above 0.5 and below -0.5 are in bold. Correlations between variables based on streetlight location are in the dashed rectangle and correlations between variables based on the ISS satellite picture are in the dash-dotted rectangle.

		Streetlights location						ISS satellite picture											
		Distance to streetlight	Streetlights density		Streetlights weighted density		Surface impacted		Pixel value				Valeur moyenne						
			100	200	100	200	100	200	Red 1	Green 2	Green 3	Blue 4	Red 1	Green 2	Green 3	Blue 4			
								100	100	100	100	200	200	200	200				
Streetlight location	Distance to streetlight																		
	Streetlights density	100	-0.52																
		200	-0.50	0.87															
	streetlights weighted density	100	-0.49	0.90	0.79														
		200	-0.50	0.91	0.93	0.94													
	Surface impacted	100	-0.69	0.82	0.74	0.71	0.73												
200		-0.65	0.73	0.86	0.65	0.76	0.84												
ISS satellite picture	Pixel value	Red 1	-0.01	-0.01	-0.03	0.00	-0.02	-0.06	-0.06										
		Green 2	-0.12	0.14	0.13	0.13	0.13	0.09	0.10	0.77									
		Green 3	-0.07	0.08	0.06	0.08	0.07	0.03	0.02	0.93	0.84								
		Blue 4	-0.13	0.15	0.16	0.14	0.15	0.11	0.14	0.55	0.85	0.69							
	Mean value within buffer	Red 1 100	-0.10	0.11	0.11	0.08	0.09	0.05	0.07	0.80	0.79	0.82	0.60						
		Green 2 100	-0.17	0.20	0.18	0.16	0.17	0.14	0.13	0.73	0.81	0.80	0.68	0.93					
		Green 3 100	-0.15	0.19	0.20	0.16	0.18	0.13	0.15	0.74	0.80	0.82	0.67	0.94	0.96				
		Blue 4 100	-0.14	0.18	0.18	0.15	0.16	0.11	0.11	0.63	0.74	0.72	0.73	0.80	0.90	0.87			
		Red 1 200	-0.22	0.28	0.32	0.23	0.28	0.21	0.28	0.48	0.63	0.56	0.54	0.78	0.79	0.80	0.74		
		Green 2 200	-0.24	0.33	0.37	0.26	0.33	0.24	0.30	0.44	0.61	0.54	0.56	0.71	0.79	0.78	0.76	0.95	
		Green 3 200	-0.22	0.30	0.34	0.24	0.30	0.23	0.27	0.42	0.59	0.52	0.54	0.68	0.74	0.75	0.73	0.95	0.97
		Blue 4 200	-0.18	0.28	0.30	0.22	0.28	0.19	0.23	0.35	0.53	0.45	0.53	0.60	0.68	0.67	0.75	0.85	0.92

Appendix D. Model results

Table D.1. Selection of best models to explain bat activity using a light variable and best model without light variable. After model selection on the 20 full models, for five models, the light variable was not retained and the best model was the one without light variable. The reference level for the factor variable “city” is the city of Lille. (**) indicates a p-value between 0.001 and 0.01; (*) indicates a p-value between 0.01 and 0.05 and (.) indicates a p-value between 0.05 and 0.1.

Light variable in the model	Estimates											AIC	ΔAIC	Weights	Marginal R ²	Conditional R ²
	Intercept	City - Paris	City - Montpellier	Julian Day	(Julian day) ²	Wind speed	Dist. to water	Dist. to tree cover	Prop. of tree cover	Light variable	Tree cover					
Blue 4 - 100	2.7 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 *	- *	3331.					
	7 *	3.05 *	-2.59	2 *	0.28 *	8	0.24 *	0.21	5	0.34 *	3	0.0	0.26	0.33	0.62	
Green 2 - 100	2.9 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.5 **	-	3332.					
	2 *	3.11 *	-2.58	2 *	0.27 *	7	0.27 *	-	5 *	0.21	0	0.7	0.18	0.34	0.63	
Red 1 - 200	2.9 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.6 **	-	3333.					
	8 *	3.15 *	-2.59	3 *	0.28 *	6	0.27 *	-	3 *	0.16	1	1.8	0.11	0.33	0.63	
Green 2 - pixel	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.5 **	-	3333.					
	0 *	3.19 *	-2.61	2 *	0.27 *	6	0.28 *	-	7 *	0.13	6	2.3	0.08	0.33	0.63	
Green 2 - 200	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.6 **	-	3333.					
	5 *	3.23 *	-2.67	4 *	0.28 *	6	0.27 *	-	0 *	0.15	9	2.6	0.07	0.33	0.63	
Blue 4 - pixel	2.8 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 **	- *	3334.					
	6 *	3.14 *	-2.61	2 *	0.28 *	7	0.24 *	0.24	8	0.26	4	3.1	0.06	0.32	0.62	
Red 1 - 100	2.7 **	- **	***	0.3 **	- *	0.1 *	- *	-	0.2 *	- *	3334.					
	4 *	3.02 *	-2.55	1 *	0.27 *	7	0.24 *	0.21	6	0.31	5	3.2	0.05	0.33	0.62	
Blue 4 - 200	2.8 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 *	- *	3334.					
	8 *	3.16 *	-2.67	3 *	0.28 *	6	0.24 *	0.23	6	0.26	8	3.5	0.05	0.32	0.62	
Green 3 - 200	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.6 **	-	3335.					
	7 *	3.25 *	-2.65	4 *	0.28 *	6	0.27 *	-	4 *	0.10	2	3.9	0.04	0.32	0.63	
Green 3 - 100	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.6 **	-	3336.					
	0 *	3.19 *	-2.57	2 *	0.27 *	6	0.27 *	-	1 *	0.06	3	5.0	0.02	0.32	0.62	
SL density - 200	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 *	- *	3336.					
	0 *	3.31 *	-2.64	3 *	0.28 *	5	0.20	0.27	7	0.19	6	5.3	0.02	0.31	0.62	
Impacted surf. - 200	2.9 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 *	- *	3336.					
	6 *	3.26 *	-2.61	3 *	0.28 *	6	0.18	0.26	6	0.20	8	5.5	0.02	0.31	0.62	
Impacted surf. - 100	2.8 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 *	-	3337.					
	9 *	3.20 *	-2.58	3 *	0.27 *	7	0.19	0.26	7	0.19	0	5.7	0.02	0.31	0.62	
SL density - 100	2.9 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 **	-	3337.					
	6 *	3.27 *	-2.63	3 *	0.28 *	6	0.20	0.27	8	0.17	2	5.9	0.01	0.31	0.63	

SL weighted density - 200	3.0 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.2 **	- .	3337.				
	1 *	3.32 *	-2.67	3 *	0.28 *	5	0.21	0.27	8	0.15	7	6.4	0.01	0.31	0.62
	2.8 **	- **	***	0.3 **	- *	0.1 .	- *	- *	0.3 **		3338.				
None	5 *	3.17 *	-2.56	2 *	0.27 *	7	0.23	0.25	4 *		7	7.4	0.01	0.30	0.62

The Julian day and its quadratic term were retained in all models as they reflect the fluctuations of bat activity along the seasons. A GAMM model with a smoothed term on the Julian day variable showed a significant nonlinear effect (edf = 4.4, p-value = 0.0006) (Fig. C.1.)

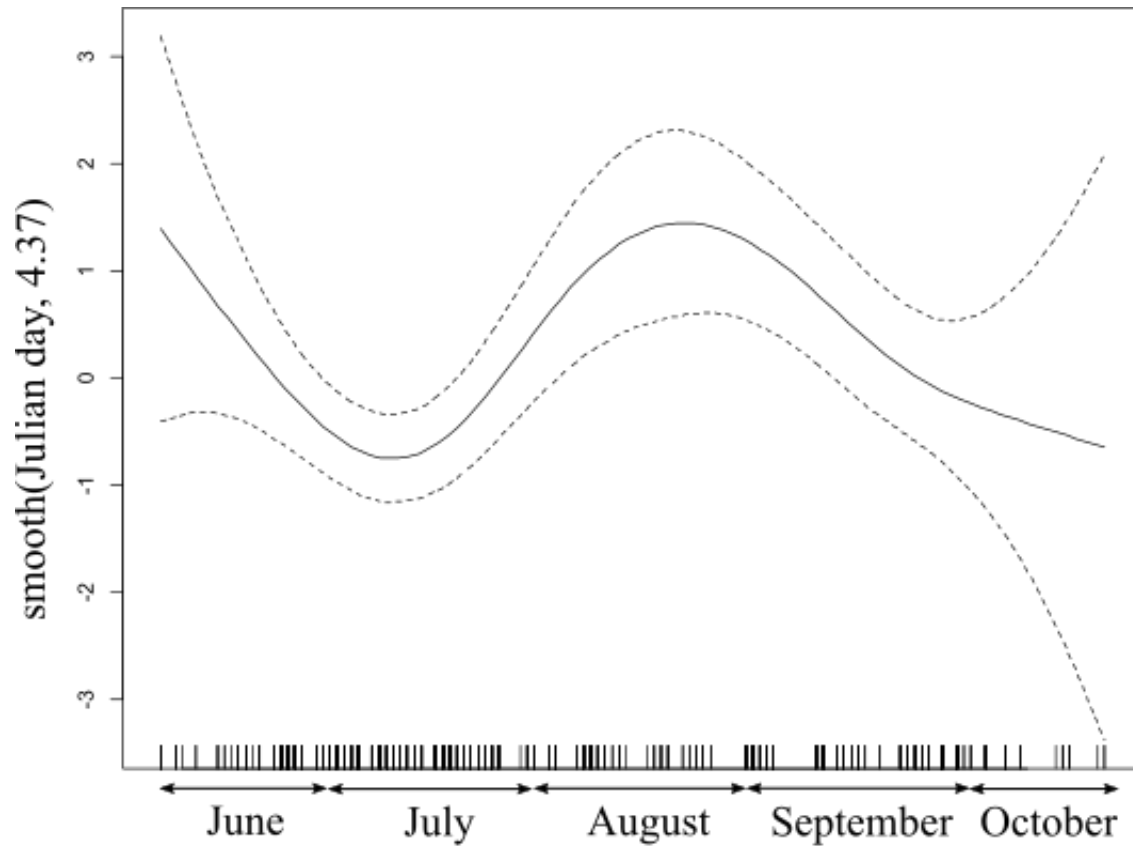


Fig D.1. Representation of the non-linear effect of the date on *P. pipistrellus* activity.

