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## Even low light pollution levels affect the spatial distribution and timing of activity of a “light tolerant” bat species

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### ► To cite this version:

Léa Mariton, Christian Kerbiriou, Yves Bas, Brigitte Zanda, Isabelle Le Viol. Even low light pollution levels affect the spatial distribution and timing of activity of a “light tolerant” bat species. *Environmental Pollution*, 2022, 305, pp.119267. 10.1016/j.envpol.2022.119267 . hal-03638724

**HAL Id: hal-03638724**

**<https://hal.science/hal-03638724v1>**

Submitted on 12 Apr 2022

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6

7 **Even low light pollution levels affect the spatial distribution and timing of activity of a**  
8 **“light tolerant” bat species**

9

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25

26 **Highlights**

27

28 Light pollution decreases bat abundance and delays their timing of activity.

29

30 Even low light levels affect bat abundance and timing of activity.

31

32 Skyglow enhanced by cloud cover increases light impact on the timing of activity.

33

34 Light pollution can even affect “light tolerant” open-space-foraging bat species.

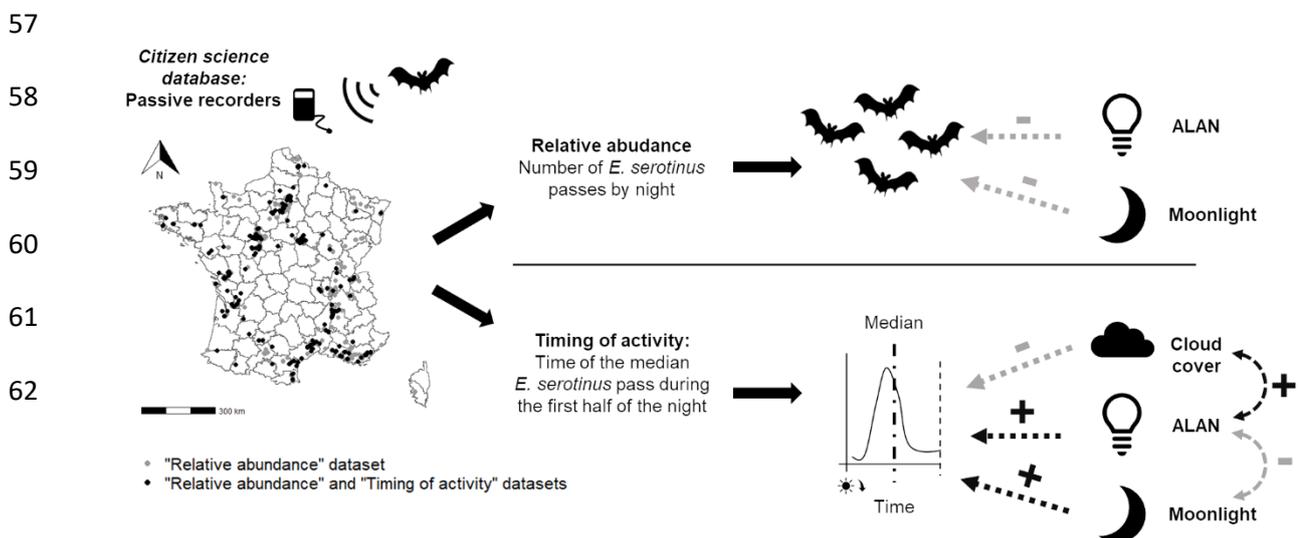
35

36 Reducing direct and indirect light pollution at landscape scale is an urgent need.

37

38 **Abstract:**

39 By disrupting nocturnal landscapes worldwide, light pollution caused by Artificial Light At  
40 Night (ALAN) is recognised as a major threat to biodiversity. As even low light intensities  
41 might affect some taxa, concerns are arising about biological responses to widespread low  
42 light levels. We used data from a French citizen science bat monitoring program (1,894 full-  
43 nights monitored on 1,055 sites) to explore the landscape-scale effects of light on an open-  
44 space-foraging bat species, the Serotine bat (*Eptesicus serotinus*). We assessed this species'  
45 abundance and timing of night-time activity (median time of activity) at foraging sites.  
46 ALAN, and to a lesser extent moonlight, reduced *E. serotinus* abundance. ALAN delayed  
47 activity, and this delay was amplified during overcast nights. On the contrary, where there  
48 was no ALAN, the higher the cloud cover, the earlier the activity occurred. Cloud cover likely  
49 darkened the night sky in rural locations, whereas it amplified skyglow in light-polluted  
50 places, increasing ALAN effects on bats. Interestingly, moonlight also delayed activity but  
51 this effect was weakened where there was ALAN. Our study shows that even fine variations  
52 of light levels could affect the spatiotemporal distribution of a common species usually  
53 considered to be “light tolerant”, with potential cascading effects on individual fitness and  
54 population dynamics. It stresses how urgent it is to preserve and restore dark areas to protect  
55 biodiversity from light pollution while working on light intensity and directivity where ALAN  
56 is needed.



63 **Keywords:** Artificial Light At Night, Bat, Citizen science, Moonlight, Timing of activity,

64 Skyglow

65

## 66        **1. Introduction**

67

68    Given forecasts predicting that, by 2030, global urban land cover will increase by 1.2 million  
69    km<sup>2</sup> (Seto et al., 2012), there are urgent needs to understand mechanisms underlying  
70    urbanisation effects on biodiversity (McKinney, 2002). In addition to leading to an increase in  
71    impervious surfaces, threatening biodiversity hotspots (Seto et al., 2012), it also results in the  
72    emissions of stressors such as noise, chemicals, and artificial light (Isaksson, 2015).

73        Artificial Light At Night (ALAN) and the resulting light pollution spreading even far from  
74    urban areas affect 23% of the globe's surface (Falchi et al., 2016), with a rate of 2.2% of areas  
75    being newly artificially lit per year (Kyba et al., 2017). As it accounts for 16.5% of global  
76    electricity demands (Zissis et al., 2021), it is an energetic use issue, but ALAN impacts on  
77    biodiversity are also a growing concern (Hölker et al., 2010; Koen et al., 2018; Longcore &  
78    Rich, 2004).

79        Light pollution has been shown to impact both nocturnal and diurnal species with  
80    potential dramatic effects on individual fitness, reproduction success and ecosystem  
81    functioning (Gaston et al., 2013; Owens et al., 2019; Svechkina et al., 2020). Many studies  
82    have focused on ALAN alteration of the species' movements and spatial distributions through  
83    attraction/repulsion behaviours (Longcore & Rich, 2004; Stone et al., 2015). However, ALAN  
84    also impacts the species' temporal distribution by changing natural light regimes, inducing  
85    shifts in the timing of activity of many taxa. For instance, it might disrupt the timing of  
86    activity of nocturnal taxa (e.g., arthropods: Lynn et al., 2021; amphibians: Secondi et al.,  
87    2021; mammals: Rotics et al., 2011), expand the timing of activity of diurnal taxa through the  
88    night and disrupt their sleep (e.g., birds: Alaasam et al., 2021; Amichai & Kronfeld-Schor,  
89    2019; Raap et al., 2015), change timings of activity by inducing photoperiod-dependent  
90    behaviours outside of usual periods (e.g., birds: Kempnaers et al., 2010; mammals: Le Tallec

91 et al., 2015). Overall, the cumulative effects of ALAN on the species' behaviour and  
92 community ecology have been recognized as a threat to ecosystem functions (Gaston et al.,  
93 2013; Longcore & Rich, 2004).

94 Developing lighting strategies to mitigate ALAN impacts on biodiversity is therefore  
95 essential (Hölker et al., 2010; Pauwels et al., 2021). Changing lighting intensity has been  
96 suggested as a possible measure (Gaston et al., 2012). However, a few studies suggest that  
97 dim light pollution levels, similar or lower to the full moonlight illuminance under clear skies  
98 (i.e., *c.* 0.1 – 0.3 lx), might impact biodiversity (Azam et al., 2018; Dominoni et al., 2013;  
99 Evans et al., 2007; Secondi et al., 2021).

100 Biological effects of widespread low light levels, induced for instance by skyglow (i.e.,  
101 the artificial light scattered by atmospheric constituents and reflected back towards the Earth  
102 (Gaston et al., 2015; Kyba et al., 2017)), are an emerging concern (Gaston et al., 2013). Cloud  
103 cover has been shown to enhance this indirect light pollution by amplifying and expanding it  
104 to remote areas which are not affected by light pollution on clear nights (Jechow et al., 2017,  
105 2020; Kyba et al., 2015). However, skyglow, and more generally, diffuse light pollution  
106 effects on biodiversity have been scarcely studied (Kupprat et al., 2020; Torres et al., 2020;  
107 Wilson et al., 2021).

108 As they are nocturnal, and directly exposed to light pollution, bats provide a useful system  
109 to study the impacts of ALAN on biodiversity. Natural pattern of light and dark is an  
110 important environmental cue synchronizing bat circadian rhythm (Erkert, 1982). The evening  
111 emergence of bats has been shown to be influenced by the sunset time (Erkert, 1982) while  
112 moonlight appears to influence the activity of some bat species (Saldaña-Vázquez &  
113 Munguía-Rosas, 2013). A perception of higher predation risks has been suggested as a driver  
114 of bat responses to light (Jones & Rydell, 1994; Rydell et al., 1996). Hence light pollution, by

115 disrupting natural light regimes, hiding environmental cues and potentially increasing  
116 predation risks, might have dramatic effects on both bat abundance and timing of activity.

117 It has been shown that bat responses to ALAN depend on their foraging strategies and  
118 flight techniques (Jones & Rydell, 1994). Narrow-space-foraging bat species (mainly short-  
119 range-echolocators that slowly fly in confined spaces (Denzinger & Schnitzler, 2013; Voigt et  
120 al., 2021)) are considered to be light-intolerant at all spatial scales (Lacoeuilhe et al., 2014;  
121 Rydell, 1992; Salinas-Ramos et al., 2021; Spoelstra et al., 2017; Voigt et al., 2021; Zeale et  
122 al., 2018), whereas the responses of edge- and open-space-foraging species (mainly mid- and  
123 long-range-echolocators that fly faster than narrow-space-foraging species (Denzinger &  
124 Schnitzler, 2013; Voigt et al., 2021)) to light pollution are more complex and depend on the  
125 spatial scale considered (Pauwels et al., 2021; Voigt et al., 2021).

126 At local scale, edge- and open-space-foraging species, such as *Pipistrellus spp.* and  
127 *Eptesicus spp.*, tend to be attracted by light sources (Azam et al., 2018; Rydell, 1992; Salinas-  
128 Ramos et al., 2021; Stone et al., 2015; Zeale et al., 2018) probably because of the predictable  
129 foraging opportunities they offer by attracting high insect densities (Owens et al., 2019; Russo  
130 et al., 2019). However, at a slightly higher scale, Azam et al. (2018) showed that Serotine bats  
131 (*Eptesicus serotinus*, Schreber, 1774) experienced an avoidance behaviour from 25 to 50 m  
132 from streetlights probably because of a perception of higher predation risks. Few studies focus  
133 on ALAN effects on bats at landscape scale and they are not consensual regarding the  
134 responses of open-space-foraging species. Laforge et al. (2019) found that, at landscape scale,  
135 *E. serotinus* responded positively to ALAN, and Mathews et al. (2015) found that the Lesser  
136 noctule (*Nyctalus leisleri*, Kuhl, 1817) was more frequent in light-polluted environments.  
137 Conversely, Azam et al. (2016) showed that, at landscape scale, *E. serotine* abundance  
138 decreased because of light pollution and Voigt et al. (2020) showed that the spatial use of the  
139 Common noctule (*Nyctalus noctula*, Schreber, 1774) was largely constrained by ALAN.

140 Hence, bat responses to ALAN may be driven by different mechanisms according to the  
141 considered spatial scales.

142 Several mechanisms might explain ALAN-mediated declines in bat abundance at  
143 landscape scale: (1) ALAN could disrupt bat commuting behaviours by decreasing landscape  
144 connectivity (Hale et al., 2015; Laforge et al., 2019; Stone et al., 2009; Voigt et al., 2020), (2)  
145 ALAN may interfere with insect development, reproductive success, movement behaviours  
146 and foraging behaviours (Boyes et al., 2020; Owens et al., 2019), it could therefore contribute  
147 the decline of insect populations (at local scale: Boyes et al., 2021; van Grunsven et al., 2020,  
148 possibly at global scale: Owens et al., 2019) and deplete landscapes of feeding resources for  
149 bats, (3) ALAN may disrupt the timing of bat nocturnal activity with potential cascading  
150 effects on their fitness and reproductive success, leading to potential population declines  
151 (Stone et al., 2015).

152 Roost illumination has been shown to delay the emergence of narrow-space-foraging bat  
153 species (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021). Some localised studies  
154 also suggest that the timing of bat activity might be disrupted at foraging sites due to ALAN.  
155 Haddock et al. (2019) highlighted that the first recording of Little forest bats (*Vespadelus*  
156 *vulturnus*, Thomas 1914, edge-space foraging) was delayed because of light pollution at forest  
157 edges and Stone et al., (2009) showed that the onset of commuting behaviour of the Lesser  
158 horseshoe bat (*Rhinolophus hipposideros*, Borkhausen, 1797, narrow-space-foraging species)  
159 was delayed by ALAN. Such shifts in the timing of activity – observed at foraging sites –  
160 might result in a desynchronization of bats with the peak of activity of their prey, a reduced  
161 time-budget to forage (Luo et al., 2021; Stone et al., 2015), and eventually it might impact  
162 their fitness and reproduction success. However, such studies are scarce, they focus on local  
163 scale and direct light pollution. Furthermore, there is a lack of studies on potential impacts of  
164 light pollution on the timing of activity of open-foraging-space species.

165 Intensity is an important factor to consider when studying bat responses to light pollution  
166 (Hale et al., 2015; Kerbiriou et al., 2020; Stone et al., 2015). Some studies even suggest that  
167 bat spatiotemporal distribution might be disrupted by slight modifications of light levels such  
168 as those due to moonlight (Appel et al., 2017; Gomes et al., 2020; Kolkert et al., 2020).  
169 However, this moonlight effect has not been much studied in temperate regions and is still  
170 discussed (Saldaña-Vázquez & Munguía-Rosas, 2013). Because the skyglow maintains low  
171 light pollution levels in previously dark areas far from urban centres, it is crucial to determine  
172 if low intensities might disrupt bat spatiotemporal distribution.

173 In this study, we used the data from a national citizen science program to assess if light  
174 pollution, including at low intensities, affects the abundance and timing of activity of open-  
175 space-foraging bat species at their foraging sites, at landscape scale. We chose to focus on *E.*  
176 *serotinus*, an open-space-foraging bat species which is common in France but declining (Bas  
177 et al., 2020). Because their responses to light pollution are known to be complex and scale  
178 dependent (Azam et al., 2016, 2018; Stone et al., 2015), it is a particularly interesting species  
179 to explore the mechanisms explaining the responses of open-space-foraging bat species to  
180 ALAN. We predicted (1) that *E. serotinus* abundance would decrease with light intensities at  
181 foraging sites, (2) that their timing of activity at their foraging sites would be delayed later in  
182 the night because of light pollution, (3) that moonlight and cloud cover, by modifying light  
183 intensity, would also affect *E. serotinus* abundance and timing of activity.

184

## 185        2. Materials and methods

186

### 187            2.1. Bat surveys

188

#### 189                    2.1.1. Vigie-Chiro program

190 We used data from the “stationary points protocol” of the French citizen science bat  
191 monitoring program Vigie-Chiro (<https://www.vigienature.fr/fr/chauves-souris>), which has  
192 been coordinated by the French National Museum of Natural History since 2014. This  
193 standardised passive acoustic monitoring-based protocol encouraged volunteers to set  
194 ultrasonic recorders on hypothetical bat foraging sites for at least one full-night. To limit  
195 heterogeneity between devices, all recorders were configured with recommended settings.

196

#### 197                    2.1.2. Species identification

198 Species identification was made with the Tadarida software which automatically detects and  
199 extracts sound parameters of recorded sound events and classifies them into classes according  
200 to a confidence index value using a random forest algorithm  
201 (<https://github.com/YvesBas/Tadarida-C/> ; Bas et al., 2017). Tadarida-D was used with  
202 default settings. Tadarida-C was used through consecutively Ta\_Tc.R and  
203 ContextualClassif.R with default settings and R 3.2.3 (R Core Team, 2015).

204 We considered bat passes, defined as the occurrence of a single or several bat calls  
205 during a 5-s interval (Kerbiriou et al., 2019a; Millon et al., 2015). This metric had already  
206 been used in many studies (Azam et al., 2015; Barré et al., 2019; Millon et al., 2015; Pauwels  
207 et al., 2019), and, as 5 s is the mean call duration recorded for *E. serotinus* in France  
208 (Kerbiriou et al., 2019b), it was the best compromise between the risk of counting several  
209 times the same individual and the risk of missing another individual.

210 As automated identification can generate significant error rates, we chose to follow  
211 Barré et al., (2019) approach to ensure result robustness against automated identification  
212 errors. We considered *E. serotinus* passes with a maximum error rate tolerance of 0.5 to  
213 minimize false positives while keeping a high number of *E. serotinus* passes. Then, in order to  
214 ensure result robustness, we confirmed our results using a maximum error rate tolerance of  
215 0.1 in Supplementary material A. Such a rate permitted us to limit false positives but  
216 discarded more true positives.

217

### 218 2.1.3. Spatiotemporal restrictions

219 We excluded surveys that might have been carried out near bat roosts, as we expected relative  
220 abundance to be higher there and driven by other factors than at foraging sites. There, we also  
221 expected an earlier timing of activity driven by specific events such as emergence. We also  
222 excluded surveys carried out in mountain environments (defined as sites above 500 m above  
223 sea level) to restrict our dataset to *E. serotinus* distribution range (Arthur & Lemaire, 2015)  
224 and to avoid any bias due to mountain environments (e.g., shades, specific climate) or to bat  
225 specific behaviours in these kind of environments (Cryan et al., 2000; McCain, 2007).

226 It had been shown by Catto et al. (1995) that while the timing of *E. serotinus* activity  
227 was unimodal to bimodal during gestation, it became more complex and multimodal during  
228 lactation. Therefore, we restricted our study to the gestation period of *E. serotinus* (from May  
229 1<sup>st</sup> to 21<sup>st</sup> June (Catto et al., 1995; Harbusch & Racey, 2006)) because we expected that the  
230 timing of *E. serotinus* activity would be consistent during this period. Moreover, during  
231 gestation, female bats experience a greater wing loading that might affect their flight  
232 performance and make them more likely to be vulnerable to predation (Duvergé et al., 2000).  
233 Therefore, bats are likely to be prone to suffer from light pollution during this period. Finally,

234 during this period, controlling for the potential confounding effect of night length is easier, as  
235 it is only decreasing.

236

## 237 *2.2. Biological and environmental metrics*

238

### 239 *2.2.1. Abundance*

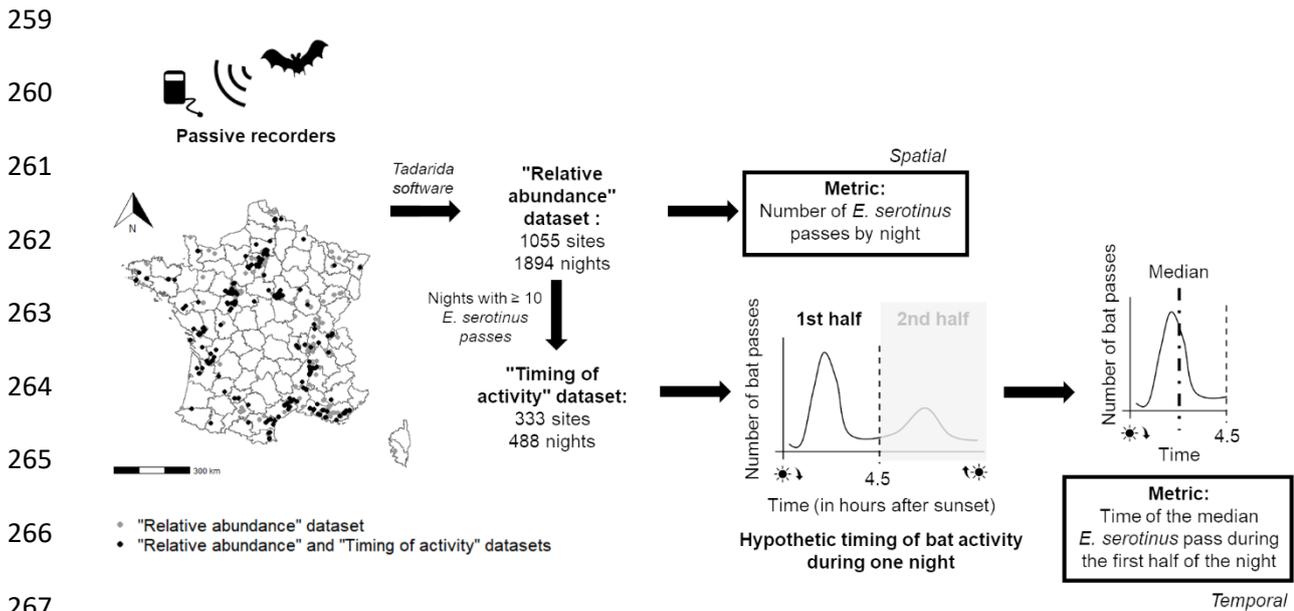
240 We used the number of *E. serotinus* passes (named hereinafter “relative abundance”) during  
241 the night (from 30 min before sunset to 30 min after sunrise) as a proxy for abundance. As a  
242 matter of fact, because the number of feeding buzzes (i.e., call sequences produced by bats  
243 prior to a successful, or attempted, prey capture (Griffin & Lindsay, 1959)) has been shown to  
244 be strongly related to the overall number of bat passes, relative abundance can be used as  
245 reliable estimator of foraging activity (Put et al., 2019; Russo & Jones, 2003; Salvarina et al.,  
246 2018). Furthermore, commuting and foraging are not fully distinct activities for *E. serotinus*  
247 (Catto et al., 1996).

248 Our “relative abundance” dataset was made up of 21,452 *E. serotinus* passes, across  
249 1894 full nights, on 1055 sites, from 2014 to 2020 (Fig. 1). As *E. serotinus* can be found  
250 across the whole French territory (except in mountain areas that we discarded from our  
251 datasets) and, as this species is highly flexible when choosing their foraging habitats (Arthur  
252 & Lemaire, 2015), we hypothesised that all our survey sites were inside the range/habitat  
253 requirements of *E. serotinus*. We hence kept for our analyses the nights with no *E. serotinus*  
254 pass.

255

### 256 *2.2.2. Timing of activity*

257 As we postulated that no metric would be robust enough with less than 10 *E. serotinus* passes  
258 by night, we only kept nights with at least 10 passes during the whole night. We confirmed



268 *Fig. 1: Data processing and construction of the biological metrics.*

269

270 the pertinence of such a threshold according to the metric chosen to study the timing of

271 activity by resampling the *E. serotinus* passes of the 100 nights with the most passes of our

272 dataset (Supplementary material B). Among the 1894 full nights of the “relative abundance”

273 dataset, 488 had at least 10 *E. serotinus* passes and they covered 333 sites. These nights

274 constituted our “timing of activity” dataset (Fig. 1).

275 Catto et al. (1995) showed that the timing of *E. serotinus* activity was unimodal to

276 bimodal during pregnancy with a high peak after sunset and, possibly, a lower one before

277 sunrise. We thus chose to focus only on the first part of the night (from 30 min before sunset

278 to 4 h and 30 min after sunset) as it covered the first and higher peak of activity observed

279 during gestation. The 488 first parts of night had 19,489 *E. serotinus* passes. The time of the

280 first bat call recorded has been used in studies focusing on timings of bat activity at foraging

281 sites (Haddock et al., 2019; Stone et al., 2009). However, in studies on bat emergence from

282 roost, the median is preferred, even if it requires to monitor bats over a longer period (Bullock

283 et al., 1987). It is less vulnerable to extreme values, as it does not rely on a single event and

284 does not only reflect the onset of bat activity, but also its spreading across time. Therefore, to  
285 characterise the timing of activity, we chose to calculate the time of the median *E. serotinus*  
286 pass during the first 4 h and 30 min of the night, in seconds after sunset.

287

### 288 2.2.3. ALAN

289 To characterise light pollution around sites, we used radiance data (in  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ , excluding  
290 lunar contamination and cloud cover degradation) from the average radiance composite raster  
291 produced by the Earth Observation Group (EOG) using night-time data from the Visible  
292 Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (EOG, Annual VNL V1 2016,  
293 <https://eogdata.mines.edu/products/vnl/>, Elvidge et al., 2017).

294 We hypothesised that *E. serotinus* spatiotemporal distribution at foraging sites would  
295 be influenced by the presence of light pollution across their whole vital domain at landscape  
296 scale (e.g., ALAN might delay their emergence from roosts and delay their arrival at foraging  
297 sites because of the barrier effect, or even result in lower feeding resources at the landscape  
298 scale). Therefore, we considered buffer zones with a 3000 m radius around the studied sites,  
299 as it covered the mean distance between foraging sites and roosts (Catto et al., 1996; Kervyn,  
300 2001; Robinson & Stebbings, 1997). We ensured that the radiance gradient of our datasets  
301 was representative of the French radiance gradient (Supplementary material C).

302 To ensure the robustness of our approach, we re-analysed our datasets with the  
303 radiance value at the recorder sites rather than the mean value in 3000 buffer zones around  
304 sites (Supplementary material D).

305

### 306 2.2.4. Other factors affecting light levels

307 We considered other meteorological and astronomical factors that might influence light  
308 levels: (1) cloud cover (extracted from the NCEP/NCAR Reanalysis dataset, Kalnay et al.,

309 1996) and (2) moonlight (we computed a variable that synthesised moon illumination values  
310 and moonrise hours (Supplementary material E)). We confirmed that the gradients of cloud  
311 cover and moonlight were wide enough to ensure robust analyses (respectively  
312 Supplementary materials F and G).

313

#### 314 2.2.5. Weather

315 Temperature, precipitations and windspeed are known to influence bat spatiotemporal  
316 distributions, including *E. serotinus* one (Catto et al., 1996; Vaughan et al., 1997; Verboom &  
317 Huitema, 1997). As the timing of *E. serotinus* activity might be influenced not only by the  
318 weather conditions of the night but also by those of previous ones (Catto, Racey, et  
319 Stephenson 1995), we considered the daily weather and the difference with previous days.

320 Absolute measures of temperature may be misleading if *E. serotinus* populations adapt  
321 to local climatic conditions: a given temperature may represent a mild day for one population  
322 but a cold day for another. We therefore analysed temperature as anomalies relative to long-  
323 term (1980-2010) averages for each site.

324 Eventually, because of correlation issues, we did not include the precipitations of the  
325 day and the difference between the windspeed of the day and the windspeed of the previous  
326 days (further details on the calculation and selection of the weather variables are given in  
327 Supplementary material E).

328

#### 329 2.2.6. Land-use

330 The higher the landscape quality for bats, the greater the relative abundance will be, and the  
331 less bats may have to commute to arrive at their foraging sites. We chose to calculate seven  
332 environmental variables known to influence the spatiotemporal distribution of bats, especially  
333 *E. serotinus*, in 3000 m buffer zones around sites: proportions of deciduous forest, conifer

334 forest, grasslands and artificialized surfaces (dense and diffuse impervious surfaces, industrial  
335 and commercial estates), habitat diversity (Shannon's diversity index), density of small  
336 woody features, minimum distance from freshwater. The buffer zones around the sites of our  
337 datasets covered the same land-use type gradient as buffer zones around sites randomly  
338 selected in France. Correlation issues led us not to include road density and proportion of  
339 crops despite their potential effects on the spatiotemporal distribution of bats (Supplementary  
340 material E).

341 ALAN and artificialized surfaces were highly correlated (Pearson correlation  
342 coefficient equal to 0.88 for the "relative abundance" dataset and 0.83 for the "timing of  
343 activity" dataset). However, as this study aimed at assessing if ALAN by itself might impact  
344 *E. serotinus* spatiotemporal distribution, we had to consider these two variables. Thus, we  
345 chose to adapt our statistical modelling methods (see below) to consider both artificialized  
346 surfaces and ALAN despite their correlation.

347

### 348 *2.3. Statistical analyses*

349

#### 350 2.3.1. Full models

351 We used Generalized linear mixed models (GLMM) to test the influence of light level on the  
352 biological metrics (R 4.0.4 (R Core Team, 2021), R package *glmmTMB*). We used a negative  
353 binomial distribution with a quadratic parameterization for "relative abundance" analyses and  
354 a gaussian distribution for "timing of activity" analyses.

355 We included all variables previously described in our models as fixed effects along  
356 with Julian day and its quadratic effect to control any potential effect of the night length or of  
357 the gestation progress. For "relative abundance" analyses, we added the recorder type used as  
358 a fixed effect, to control the different performances of recorders in detecting bats. All

359 quantitative fixed effects were scaled, so that the regression coefficients calculated would be  
360 comparable in their effects and magnitudes (Schielzeth, 2010).

361 We tested several interactions that could affect light levels: interaction (1) between  
362 cloud cover and ALAN as cloud cover might amplify light pollution (Jechow et al., 2017;  
363 Kyba et al., 2015), (2) between moonlight and ALAN as, for instance, light pollution could be  
364 so strong that moonlight does not have an effect on bats anymore, (3) between moonlight and  
365 cloud cover as the latter could conceal the moon. Note that we also added an interaction  
366 between temperature anomaly of the day and difference with temperature anomalies of the  
367 previous days because bat responses to temperature extremes may depend upon whether  
368 previous days have also been too hot or cold to forage effectively.

369 Our dataset had a spatiotemporal structure: (1) a site might have been monitored  
370 several nights, (2) if these nights were consecutive, they formed a single “participation” (i.e.,  
371 a single monitoring session during which the same recorder stayed at the same place during at  
372 least one full night to several in a row); if they were not consecutive, they formed several  
373 “participations”. Thus, we included a random effect on participations nested on sites for  
374 “relative abundance” analyses. For “timing of activity” analyses, the smaller dataset did not  
375 allow the use of such a random structure. As we already considered Julian day, we did not  
376 include the random effect on participation but we kept the random effect on sites.

377 We hypothesised that, the more *E. serotinus* passes there would be during the night,  
378 the more accurate the calculation of the metric used to characterise the timing of activity  
379 would be. We therefore put a weight on the logarithm of the number of *E. serotinus* passes  
380 during the first 4 h and 30 min after sunset for the analyses on the timing of activity.

381 The 3000 m buffer zones around some sites of our datasets overlapped, however,  
382 according to Zuckerberg et al. (2020), overlapping landscapes are not a violation of  
383 independence and they do not induce nor protect from spatial autocorrelation. There was

384 some spatial autocorrelation for both the “relative abundance” and the “timing of activity”  
385 analyses. We added latitude as a fixed effect to correct it. As some spatial autocorrelation  
386 remained for the “timing of activity” analyses, we corrected it by adding an autocovariate  
387 computed with the `autocov_dist` function (R package *spdep*).

388 The full models were the following ones (all variables are summarized in Table H;  
389 model assumptions were checked according the procedure described in Supplementary  
390 material I):

391

$$\begin{aligned} 392 \text{Metric} \sim & \text{ALAN} + \text{Conifer\_forest} + \text{Deciduous\_forest} + \text{Grasslands} + \text{Artificialized\_surfaces} \\ 393 & + \text{Habitat\_diversity} + \text{Small\_woody\_features} + \text{Min\_distance\_freshwater} + \text{Temperature} + \\ 394 & \text{Difference\_temperature} + \text{Windspeed} + \text{Difference\_precipitations} + \text{Cloud\_cover} + \\ 395 & \text{Moonlight} + \text{Julian\_day} + \text{Julian\_day}^2 + \text{Recorder\_type}^* + \\ 396 & \text{Temperature:Difference\_temperature} + \text{Moonlight:Cloud\_cover} + \text{Moonlight:ALAN} + \\ 397 & \text{Cloud\_cover} : \text{ALAN} + \text{Latitude} + \text{autocov}^{**} + (1|\text{site/participation})^* + (1|\text{site})^{**} \end{aligned} \quad \text{Eq. (1)}$$

398

399 With:

400 *Metric*: “relative abundance” or “timing of activity” metric

401 \*: only for “relative abundance” analyses

402 \*\*: only for “timing of activity” analyses

403

#### 404 2.3.2. Model averaging

405 We chose the model averaging approach so that we could assess both the effects of  
406 artificialized surfaces and ALAN despite their correlation. The aim was to compare their  
407 relative importance on the relative abundance and timing of activity.

408           We processed all the models resulting from all the combinations of the fixed effects  
409 with this condition: never include artificialized surfaces and ALAN in the same combinations  
410 (i.e., never include these two variables in the same models) (R package *MuMIn* and *snow*).  
411 For “relative abundance” analyses, we always included latitude (to correct spatial  
412 autocorrelation) and recorder type (to control possible bias). For “timing of activity” analyses,  
413 we always included latitude and the autocovariate (to correct spatial autocorrelation). Then, a  
414 model averaging was computed within a  $\Delta AICc$  (second order bias correction for Akaike  
415 Information Criterion) of six points (Burnham et al., 2011; Grueber et al., 2011; Richards,  
416 2007). Since the inclusion of models with interaction terms involving ALAN might favour  
417 selection of ALAN over artificialized surfaces, we repeated all analyses excluding those terms  
418 and found similar results as those obtained with interaction terms (Supplementary material J).

419           To assess if the variables had an effect on the relative abundance or the timing of  
420 activity, we compared the relative importance of the variables (i.e., the sum of weights (SW)).  
421 However, as it has been shown that only considering this criterion is hazardous, we crossed it  
422 with the 95% confidence intervals of regression coefficients obtained with the model  
423 averaging (Galipaud et al., 2014). Hence, we considered that a variable had an effect when the  
424 confidence interval of its regression coefficient did not overlap zero and its SW was above  
425 0.6.

426           We checked the robustness of our results by comparing them to those we would have  
427 obtained by only considering the best model and the significance of the estimates included in  
428 it, and we found concordant results. We also confirmed that not discarding complex versions  
429 of any other model with a lower  $AICc$  value (as suggested by Richards et al., (2011)), was not  
430 an issue in our analyses. Furthermore, to ensure that our results were sound against the  
431 multicollinearity issues raised by Cade, (2015), we also computed model averaging on  
432 standardised estimates based on partial standard deviations for their variables and found

433 similar results as with a “classical” standardisation of estimates (see Supplementary material  
434 K for these additional analyses).

435

### 436 **3. Results**

437

#### 438 *3.1. Relative abundance*

439

440 ALAN had a strong negative effect on relative abundance. It was the variable with the  
441 greatest effect size of all those tested (Table 1) (see Table L for details on the model  
442 averaging results) and its SW was much greater than the artificialized surfaces one. For an  
443 average mid-sized town (mean radiance  $7.8 \text{ nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ , Table M), there was 18% less *E.*  
444 *serotinus* passes than in a dark place (radiance =  $0 \text{ nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ ; assuming all other variables  
445 held at mean levels).

446 When considering the ALAN value at the recorder sites rather than the mean ALAN  
447 value in the 3000 m buffer zones, the AICc of the best model was higher and artificialized  
448 surfaces had a greater SW than ALAN (Supplementary material D). The estimate (-0.014) and  
449 confidence interval (-0.020 ; -0.007) of ALAN when considering ALAN at the recorder sites  
450 were nonetheless similar to those obtained when considering the mean ALAN value in the  
451 3000 m buffers zones (Table 1).

452 Moonlight also had a negative impact on relative abundance while there was no clear  
453 effect of cloud cover and interactions.

454 Besides variables reflecting light levels around sites, relative abundance increased with  
455 favourable meteorological conditions (high temperature, higher temperature than the previous  
456 days, less rain than the previous days), with Julian day and with habitats known to

457

458 *Table 1: Model averaging results for a  $\Delta AICc$  of six points for the “relative abundance” and*  
459 *“timing of activity” analyses: estimate, sum of weights (SW) and 95% confidence interval*  
460 *(CI) for each variable (apart from latitude and recorder type that were fixed for “relative*  
461 *abundance” analyses and latitude and the autocovariate that were fixed for “timing of*  
462 *activity” analyses) (estimates in bold when the 95% confidence interval did not overlap zero*  
463 *and the SW was above 0.60). All quantitative fixed effects were scaled and estimates were*  
464 *standardized by dividing them by the standard deviation of the response variable.*

Variables	Relative abundance			Timing of activity		
	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	<b>0.010</b>	1.00	0.005 ; 0.015	0.031	0.31	-0.047 ; 0.110
Difference_temperature	<b>0.012</b>	1.00	0.007 ; 0.016	<b>0.114</b>	1.00	0.064 ; 0.165
Windspeed	-0.002	0.47	-0.006 ; 0.001	<b>-0.093</b>	1.00	-0.136 ; -0.050
Difference_precipitations	<b>-0.006</b>	1.00	-0.010 ; -0.002	<b>-0.053</b>	0.91	-0.099 ; -0.006
Julian_Day	<b>0.012</b>	1.00	0.008 ; 0.017	-0.031	1.00	-0.119 ; 0.057
(Julian_Day) <sup>2</sup>	-0.002	0.32	-0.007 ; 0.003	<b>0.142</b>	1.00	0.061 ; 0.223
Cloud_cover	0.003	0.67	-0.001 ; 0.006	<b>-0.155</b>	1.00	-0.199 ; -0.110
Artificialized_surfaces	-0.016	0.11	-0.023 ; -0.009	NA	NA	NA
Grassland	-0.005	0.50	-0.011 ; 0.002	0.012	0.18	-0.111 ; 0.135
Deciduous_forest	<b>0.010</b>	1.00	0.004 ; 0.015	-0.059	0.26	-0.189 ; 0.072
Conifer_forest	<b>0.012</b>	1.00	0.006 ; 0.019	-0.017	0.18	-0.138 ; 0.104
Habitat_diversity	<b>0.007</b>	0.82	0.000 ; 0.013	0.017	0.18	-0.090 ; 0.123
Min_distance_freshwater	-0.004	0.37	-0.012 ; 0.004	0.041	0.20	-0.107 ; 0.190
Small_woody_features	<b>0.008</b>	1.00	0.003 ; 0.014	-0.067	0.36	-0.181 ; 0.047
ALAN	<b>-0.019</b>	0.89	-0.027 ; -0.010	<b>0.235</b>	1.00	0.117 ; 0.354
Moonlight	<b>-0.006</b>	1.00	-0.010 ; -0.002	<b>0.092</b>	1.00	0.032 ; 0.152
Difference_temperature :Temperature	0.001	0.24	-0.003 ; 0.004	-0.024	0.09	-0.066 ; 0.019
Cloud_cover:Moonlight	0.002	0.21	-0.002 ; 0.005	-0.013	0.21	-0.055 ; 0.030
ALAN:Cloud_cover	-0.001	0.14	-0.006 ; 0.003	<b>0.059</b>	0.95	0.011 ; 0.106
Moonlight:ALAN	-0.001	0.19	-0.005 ; 0.004	<b>-0.073</b>	1.00	-0.120 ; -0.027

466 increase bat abundance (deciduous and conifer forests, habitat diversity and small woody  
467 features).

468

### 469 *3.2. Timing of activity*

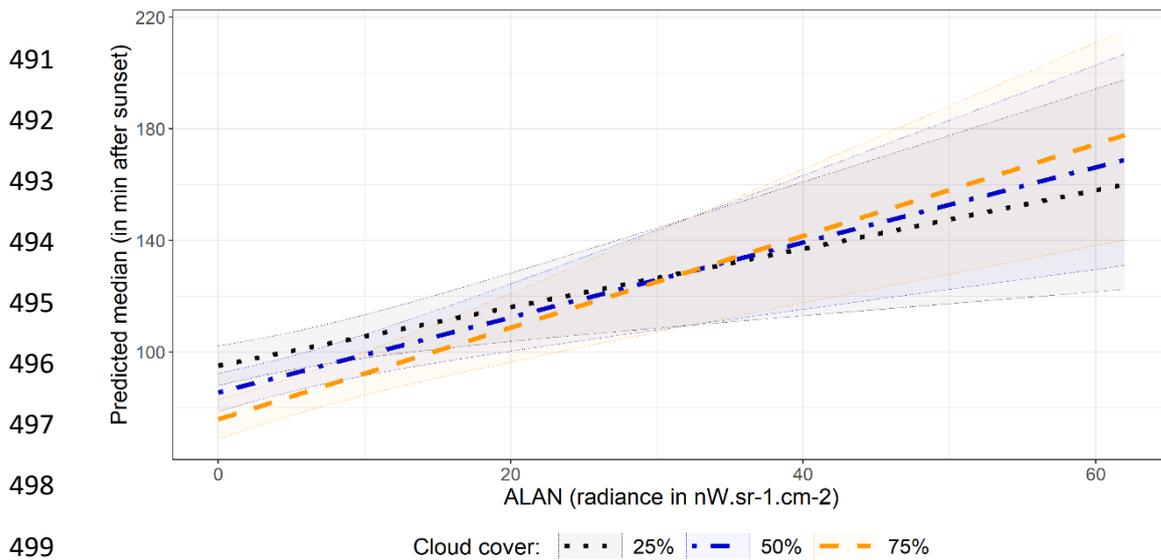
470

471 Increased ALAN delayed the timing of activity, and this delay was increased by a higher  
472 cloud cover (Table 1, Figure 2, Figure N). For an average mid-sized town (mean radiance 7.8  
473  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ , Table M), activity was delayed by 6 minutes on a clear night and by 10 minutes  
474 on a night with a 50% cloud cover, compared to a site with no ALAN (radiance = 0  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ ;  
475 assuming all other variables held at mean levels). Where there was no ALAN,  
476 increased cloud cover provoked an earlier activity, whereas above an ALAN value of 31.04  
477  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ , the cloud cover seemed to delay the timing of activity.

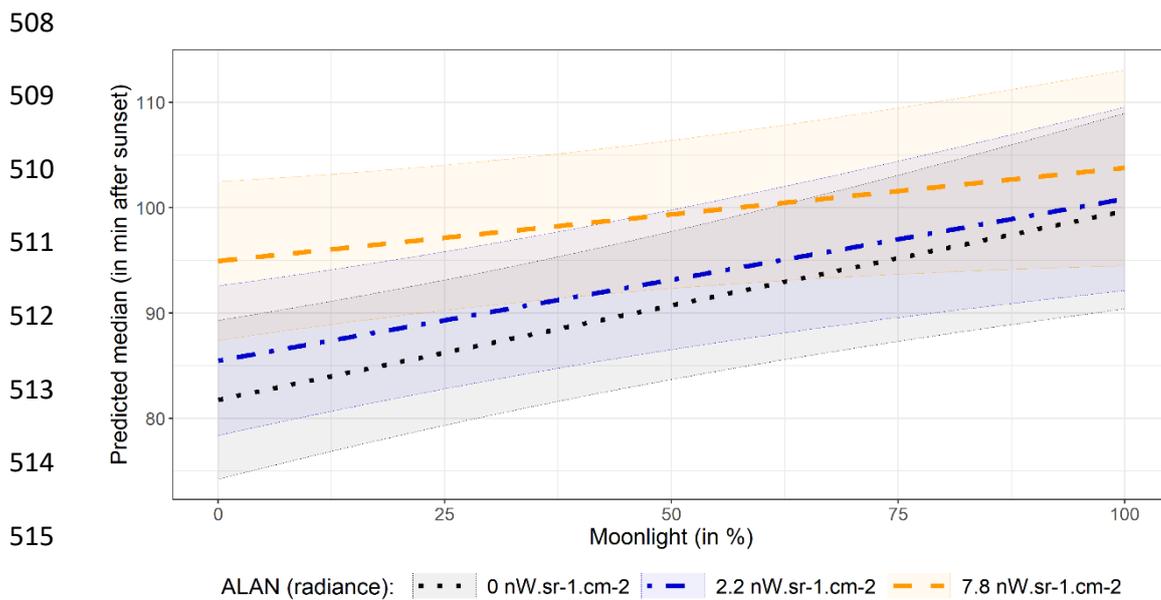
478 Moonlight also delayed the timing of activity. However, this effect was weakened by  
479 increasing ALAN (Table 1, Figure 3, Figure O). Compared to a night with no moonlight  
480 (0%), a moonlight of 50% delayed activity by 4 minutes at the average mid-sized town, and  
481 by 9 minutes at a site with no ALAN (assuming all other variables held at mean levels).  
482 Above an ALAN value of 15.40  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ , the moonlight effect even seemed to shift the  
483 timing of activity earlier.

484 When considering the ALAN value at the recorder sites rather than the mean ALAN value  
485 in 3000 m buffer zones, the AICc of the best model was higher and these two interactions no  
486 longer had any significant effect (Supplementary material D).

487 The timing of activity was not affected by any of the land-use variables, in particular,  
488 artificialized surfaces were not included in any models of the model set. The timing of activity  
489 was delayed by favourable meteorological conditions (higher temperature than the previous  
490 days, less rain than the previous days, less wind) and varied according to Julian day (Julian



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501 *Fig. 2: Interaction between ALAN and cloud cover: Predicted values and 95% confidence*  
502 *intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first*  
503 *half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as*  
504 *they were previously scaled) apart from ALAN and cloud cover. This graph represents the*  
505 *median time of activity according to ALAN (radiance back transformed in  $nW.sr^{-1}.cm^{-2}$ ) for*  
506 *three values of cloud cover (see to visualise the median time of activity according to cloud*  
507 *cover for three values of ALAN).*



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517 *Fig. 3: Interaction between moonlight and ALAN: Predicted values and 95% confidence*  
518 *intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first*

519 *half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as*  
520 *they were previously scaled) apart from moonlight and ALAN. This graph represents the*  
521 *median time of activity according to moonlight (back transformed in %) for three values of*  
522 *ALAN (2.2 nW.sr<sup>-1</sup>.cm<sup>-2</sup> being the mean radiance of French municipalities of 1,000 to 5,000*  
523 *inhabitants and 7.8 nW.sr<sup>-1</sup>.cm<sup>-2</sup> being the mean radiance for municipalities of 5,000 to*  
524 *10,000 inhabitants, see Table M) (see Fig. O to visualise the median time of activity*  
525 *according to ALAN for three values of moonlight).*

526

527 day led to an earlier activity until approximately the two-third of the period considered, then  
528 it delayed activity) (Table 1).

529

#### 530 **4. Discussion**

531

532 This study is one of the first to test natural and artificial light effects on both the spatial and  
533 temporal distributions of an open-space-foraging bat species at their foraging sites, at  
534 landscape scale. Light pollution reduced *E. serotinus* relative abundance and delayed their  
535 timing of activity. The use of a seven-year citizen science database allowed us to consider a  
536 whole national territory and gave us the unique opportunity to show the impact of fine light  
537 intensity variations (moonlight, skyglow amplified by cloud cover) on *E. serotinus*  
538 spatiotemporal distribution.

539

##### 540 *4.1. Relative abundance*

541

542 At landscape scale, ALAN was responsible for a decrease in *E. serotinus* relative abundance  
543 at their foraging sites. The obtained results when considering ALAN at local scale confirmed

544 that this decrease in abundance was not the reflection of a localised avoidance behaviour.  
545 Such results are consistent with Azam et al. (2016) study results on open-space-foraging bat  
546 species. Using a different dataset from the Vigie-Chiro program (data from one-hour car  
547 surveys), they found that *E. serotinus* abundance was lower when exposed to light pollution at  
548 landscape scale. On the contrary, Laforge et al. (2019) found that *E. serotinus* had a positive  
549 response to light pollution at a city scale. The authors hypothesized that in their highly  
550 urbanized study sites, with few optimal foraging areas, streetlights might have become sub-  
551 optimal foraging areas; this could explain the difference between their own results and those  
552 obtained by Azam et al. (2016).

553         Furthermore, we found that even the low light levels created by moonlight reduced *E.*  
554 *serotinus* abundance. In South America, some authors found that moonlight affected bat  
555 abundance making it higher or lower depending on the species (Appel et al., 2017; Gomes et  
556 al., 2020; Vásquez et al., 2020). However, to our knowledge, this study is one of the first to  
557 show such an effect, called “lunar phobia”, on the abundance of a European open-space-  
558 foraging bat species. Ciechanowski et al., (2007) detected a decreasing abundance of  
559 Daubenton's bat (*Myotis daubentonii*, Kuhl 1817), an edge-space-foraging species, when  
560 exposed to moonlight but they did not detect any effect on *E. serotinus*. This result difference  
561 can be explained by the fact that they did not consider the hours of moonrise in their analyses.  
562 Furthermore, they began to record bats 30 min after sunset. If moonlight impacted the early  
563 activity, it might therefore not have been detected. Overall, the effect we found of moonlight  
564 on abundance indicates that even low, occasional or periodic increases of light levels could  
565 result in lower *E. serotinus* abundance.

566         The decrease of an open-space-foraging species abundance when exposed to light,  
567 despite potential positive impacts locally, could be explained by several mechanisms. In the  
568 short-term, light might impact bat abundance by modifying prey availability. For instance,

569 insect abundance has been shown to vary according to moonlight (Bowden & Church, 1973;  
570 Williams & Singh, 1951) and Lang et al. (2006) linked White-throated round-eared bat  
571 (*Lophostoma silvicolum*, D'Orbigny, 1836) higher abundance during new moon compared to  
572 full moon periods to a higher activity of the katydids they prey on. Furthermore, a perception  
573 of increased predation risks when exposed to light has also been suggested as a potential  
574 driver of bat responses to light (Jones & Rydell, 1994; Rydell et al., 1996). This may result in  
575 changes of the timing and duration of bat activity during bright nights to limit predation risks.  
576 In this context, the tolerance of open-space-foraging bat species to light pollution when  
577 foraging could only be the result of a local trade-off between their energetic needs and the risk  
578 of predation, the higher prey concentrations around light sources offsetting greater risks of  
579 being seen by predators.

580         When bright conditions are created by moonlight, bats may be able to compensate  
581 their lower activity during those bright nights by being more active during darker ones. But,  
582 when these bright conditions are due to ALAN, they are constant, and bats could then either  
583 not be able to reach their energetic needs in the long-term or be compelled to be active despite  
584 higher predation risks. It could result in lower individual fitness and dramatic disruptions of  
585 population dynamics.

586         Furthermore, in the medium- and long-terms, light pollution might not only impact bat  
587 fitness, but also the fitness of the insect they eat. Some authors suggested that ALAN may be  
588 a driver of insect population declines in light-polluted areas (Boyes et al., 2021; Grubisic et  
589 al., 2018; van Grunsven et al., 2020) or even globally (Owens et al., 2019). Therefore, light  
590 pollution may affect bat abundance by decreasing the overall available feeding resources at  
591 landscape scale.

592         Eventually, light pollution might not only disrupt bat foraging behaviours, but also  
593 their commuting ones. For instance, Hale et al. (2015) showed that *P. pipistrellus* movements

594 were restricted in brightly lit gaps, ALAN creating a barrier effect impairing landscape  
595 connectivity. Bats may hence have to find longer routes to reach their foraging sites with  
596 potential greater energetic costs that can affect their individual fitness and, *in fine*, their  
597 abundance (Stone et al., 2009). If the energetic costs of alternative routes are too high, ALAN  
598 might even result in a reduction of the accessible lands to forage for bats at landscape scale.

599 Further research would be needed to determine if this decrease in abundance at  
600 landscape scale when exposed to ALAN results from a redistribution of *E. serotinus*  
601 populations in darker places at a wider scale and/or from lower individual fitness which might  
602 lead to population declines. In particular, it is worth noting that Bas et al. (2020) showed that  
603 *E. serotinus* population declined by -30% between 2006 and 2019 in France. It raises the  
604 question of the causes of such a strong decline and, what role light pollution could be playing.

605

#### 606 *4.2. Timing of activity*

607 Increased ALAN delayed the timing of activity, and this delay was increased by higher cloud  
608 cover when considering ALAN at landscape scale. Firstly, the overall ALAN delaying effect  
609 we found is consistent with the few and localised studies focusing on edge- and narrow-space-  
610 foraging bat species at foraging sites (Haddock et al., 2019; Stone et al., 2009) which also  
611 showed that ALAN delayed the timing of activity, our study expanding it to open-space-  
612 foraging species at wide scale. Secondly, cloud cover amplifying the ALAN effect at  
613 landscape scale is consistent with studies showing that skyglow (i.e., diffuse light pollution  
614 glow at landscape scale, even affecting areas that are not directly lit (Kyba et al., 2017)) is  
615 amplified during overcast nights (Jechow et al., 2017; Kyba et al., 2015). By amplifying  
616 skyglow, cloud cover can thus increase the effects of ALAN on wildlife (van Hasselt et al.,  
617 2021). On the contrary, where there was no ALAN, cloud cover shifted the timing of activity

618 earlier likely by darkening the night sky in rural locations (Jechow et al., 2016). Hence,  
619 dynamic and fine variations of light levels affect the timing of *E. serotinus* activity.

620 Interestingly, moonlight also delayed the timing of activity. However, this effect was  
621 weakened by increasing ALAN. Such results suggest that light pollution masks other  
622 luminous environmental cues. It also shows that even periodic or occasional increases of light  
623 levels could impact *E. serotinus* timing of activity.

624 The delayed timing of activity around light-polluted foraging sites could be explain by  
625 several hypotheses. First, bat emergence from roosts might be delayed because of ALAN, as  
626 shown by a few studies on narrow-space-foraging species (Boldogh et al., 2007; Duvergé et  
627 al., 2000; Luo et al., 2021; McAney & Fairley, 1988). Also, as light pollution is known to  
628 decrease landscape connectivity for bats (Hale et al., 2015; Laforge et al., 2019; Stone et al.,  
629 2009), a delayed timing of activity at foraging sites could be the result of longer flights to  
630 reach them. Then, if bats arrive later, they might potentially suffer from a desynchronization  
631 with the peak of activity of their prey (Luo et al., 2021). It could result in a reduced efficient  
632 time-budget (i.e., a reduced period during which bats may feed on the prey their diets are  
633 mainly composed of) and/or in longer foraging durations to reach their energetic needs.

634 Delayed timing of activity could potentially lead to a reduced efficient time-budget to  
635 forage for bats and/or higher energetic costs to forage. If these delays are occasional, for  
636 instance because of brighter nights caused by moonlight, bats may be able to compensate  
637 potential harmful effects by taking advantage of darker nights to reach their energetic needs.  
638 However, as light pollution is a constant stressor, delays caused by ALAN may eventually  
639 prevent bats from reaching their energetic needs in the medium- and long-terms, which could  
640 have cascading effects on individual fitness and population dynamics, and thus result in lower  
641 bat abundance at landscape scale when exposed to ALAN. For instance, Boldogh et al. (2007)  
642 showed that juveniles of narrow-space-foraging bat species were smaller in illuminated

643 buildings, where bat emergence was delayed because of ALAN. However, our study only  
644 focuses on the gestation period and further investigations should be carried out for the  
645 lactation one – when energetic needs are even higher – to assess whether ALAN still has an  
646 effect on the timing of *E. serotinus* activity.

647

#### 648 *4.3. Management consequences*

649 Abundant and widespread bats such as *E. serotinus* provide important ecosystem functions  
650 (Mathews et al., 2015). Tiede et al. (2020) showed that, among the most frequent taxa *E.*  
651 *serotinus* fed on, there were many potential pests of forestry and agriculture, this bat species  
652 therefore contributing to biological control. More generally, they suggested that *E. serotinus*  
653 contributes to the stabilization of food webs and ecosystems, by exploiting seasonally  
654 abundant insect prey. Hence, ALAN impacts on *E. serotinus* spatiotemporal distribution may  
655 have dramatic consequences on the ecosystem services they provide and might, more  
656 generally, have harmful effects on ecosystem functioning.

657 These effects of light levels on the spatiotemporal distribution of an open-space-foraging  
658 bat species show that even species considered to be “light tolerant”, that mainly roost in  
659 buildings (Marnell & Presetnik, 2010), can suffer from light pollution. Because bat species of  
660 the same foraging guild tend to respond to ALAN in a similar way (Voigt et al., 2021), other  
661 open-space-foraging bat species are likely to suffer from similar impacts of light pollution on  
662 their abundance and timing of activity. Narrow-space-foraging species that are known to be  
663 particularly sensitive toward ALAN (Rydell, 1992; Voigt et al., 2021) and/or species that  
664 usually roost in trees may experience even more drastic effects. It stresses the urge to reduce  
665 light pollution to protect bats, and more generally biodiversity.

666 Gaston et al., (2012) suggested five levers to reduce light pollution: prevent dark areas  
667 from being lit, limit the duration of artificial lighting, reduce light trespass, reduce light

668 intensity and change ALAN spectral composition. Bats are known to present different  
669 responses to light with different spectra (Barré et al., 2021; Lewanzik & Voigt, 2017;  
670 Spoelstra et al., 2017; Straka et al., 2020). However, in this study, we could not assess how  
671 different spectral compositions would have affected our results, as the light pollution data  
672 available at landscape scale were not made of multiple spectral bands. Hence, further studies  
673 would particularly be necessary to explore how ALAN spectral composition may modify how  
674 light pollution affects the timing of bat activity at landscape scale.

675       Limiting the lighting duration might only be efficient if part-night lighting schemes  
676 overlap with the range of bat activity (for instance streetlights should be switched off during  
677 emergence and during the first and higher foraging peak), which is not the case today (Azam  
678 et al., 2015; Day et al., 2015). As even low light intensities (similar to moonlight) could  
679 disrupt bat spatiotemporal distribution, the intensity under which light stops affecting bats  
680 might be very low. Therefore, even if reducing light intensity might reduce light impacts on  
681 bats, it might not be a very efficient measure. Our study, by highlighting that, at landscape  
682 scale, bats suffer from light pollution and its intensity variation due to cloud cover, shows the  
683 need of lighting installations that reduce horizontally- and upward-directed lighting, and more  
684 generally light trespass.

685

## 686       **5. Conclusion**

687

688       This study highlights that the abundance and timing of activity of an open-space-  
689 foraging bat species, at foraging sites, are both affected by light pollution at landscape scale.  
690 It stresses that even species often considered to be “light tolerant” could suffer from ALAN.  
691 The intensity under which light stops impacting bat activity could be very low as moonlight,  
692 cloud cover and the amplifying of skyglow during overcast nights seem to impact the

693 spatiotemporal distribution of bats. By showing that the bat abundance was reduced and the  
694 timing of bat activity was delayed when exposed to light, our study raises the urge to  
695 investigate further how delayed timings of activity might affect individual fitness,  
696 reproduction success and eventually result in population dynamic disruptions.

697

## 698 **Acknowledgements**

699

700 This work was funded by the Institut de la Transition Environnementale de l'Alliance  
701 Sorbonne Université (SU-ITE). We thank Kévin Barré for helping us checking the robustness  
702 of our results according to different identification success thresholds and for his numerous  
703 advices. We are also grateful for Nolwenn Le Touz's help with proofreading. We thank CC-  
704 IN2P3 and PCIA-MNHN for providing computing and storage facilities, and Didier Bas for  
705 his help in this process. The success of such a large-scale study relies on the continuous  
706 participation of the volunteers of the Vigie-Chiro program, who we warmly thank. We also  
707 thank the two anonymous reviewers for all their insightful comments on the manuscript.

708

## 709 **Conflict of interest**

710

711 The authors declare no conflict of interest.

712

## 713 **Data availability statement**

714

715 The data supporting this study are available at <https://doi.org/10.5281/zenodo.6418651> .

716 **References**

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1091 **Supplementary material**

1092

1093 Supplementary material A: Consistency of the results obtained for datasets built with a  
1094 maximum error rate tolerance of 0.5 with datasets built with a maximum error rate tolerance  
1095 of 0.1

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1097 Supplementary material B: Threshold on the number of *E. serotinus* passes for the “timing of  
1098 activity” analyses

1099

1100 Supplementary material C: Comparison of the French radiance gradient with the radiance  
1101 gradient in our datasets

1102

1103 Supplementary material D: Influence of the spatial scale at which the ALAN metric is  
1104 calculated

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1106 Supplementary material E: Details the calculation and selection of environmental variables

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1108 Supplementary material F: Gradient of cloud cover for the studied nights

1109

1110 Supplementary material G: Gradient of moonlight for the studied nights

1111

1112  
1113 Table H: Variables extracted to control exogenous factors that could impact *E. serotinus*  
1114 relative abundance and timing of activity at their foraging site. The variables that have been  
1115 discarded due to multi-collinearity issues are in brackets. Ab = “relative abundance” dataset,  
1116 Ta = “timing of activity” dataset.

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1118 Supplementary material I: Checks of model assumptions

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1121 Supplementary material J: Analyses when considering full models without interactions  
1122 including ALAN

1123  
1124 Supplementary material K: Checking of the robustness of the model averaging results

1125 Table L: Results of the model averaging for the “relative abundance” and the “timing of  
1126 activity” analyses. Even if a lot of models were selected in these analyses, the differences  
1127 between the AICc of the null model and the AICc of the best model were always high.

1128  
1129 Table M: Mean of the mean radiances (in  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ ) of the French municipalities  
1130 according to their population size (only municipalities that are below 500 m above sea levels  
1131 are considered).

1132  
1133 Fig. N: Interaction between cloud cover and ALAN: Predicted values and 95% confidence  
1134 intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first  
1135 half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they  
1136 were previously scaled) apart from cloud cover and ALAN. This graph represents the median  
1137 time of activity according to cloud cover (back transformed in %) for three values of ALAN  
1138 ( $2.2 \text{ nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$  being the mean radiance of French municipalities of 1000 to 5000  
1139 inhabitants and  $7.8 \text{ nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$  being the mean radiance for municipalities of 5000 to 10,000  
1140 inhabitants, see Table M).

1141  
1142 Figure O: Interaction between ALAN and moonlight: Predicted values and 95% confidence  
1143 intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first  
1144 half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they  
1145 were previously scaled) apart from ALAN and moonlight. This graph represents the median  
1146 time of activity according to ALAN (radiance back transformed in  $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$ ) for three  
1147 values of moonlight.