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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.

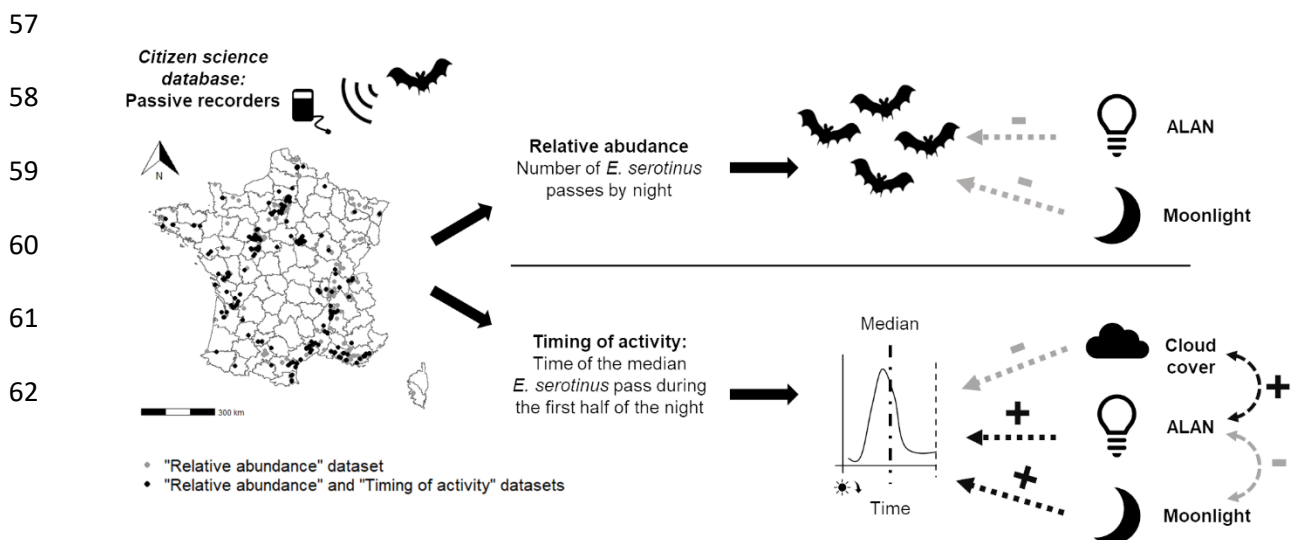
35

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 km² (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 1st to 21st 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*

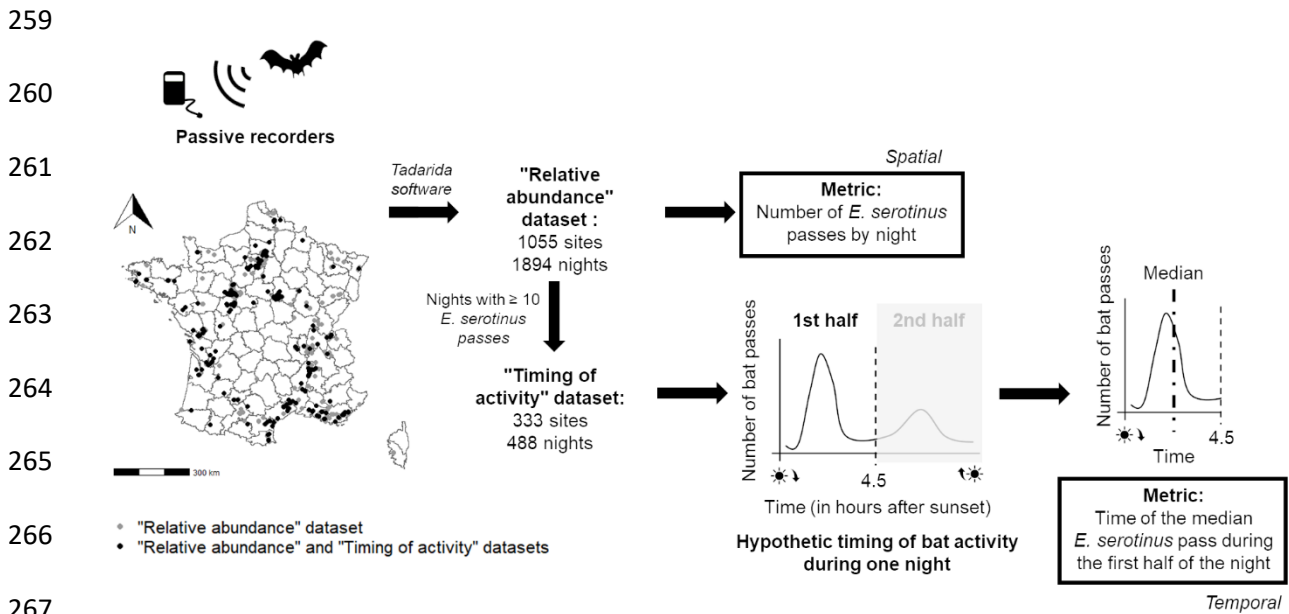
240 We used the number of *E. serotinus* passes (named hereinafter “relative abundance”) during
241 the night (from 30 min before sunset to 30 min after sunrise) as a proxy for abundance. As a
242 matter of fact, because the number of feeding buzzes (i.e., call sequences produced by bats
243 prior to 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	0.010	1.00	0.005 ; 0.015	0.031	0.31	-0.047 ; 0.110
Difference_temperature	0.012	1.00	0.007 ; 0.016	0.114	1.00	0.064 ; 0.165
Windspeed	-0.002	0.47	-0.006 ; 0.001	-0.093	1.00	-0.136 ; -0.050
Difference_precipitations	-0.006	1.00	-0.010 ; -0.002	-0.053	0.91	-0.099 ; -0.006
Julian_Day	0.012	1.00	0.008 ; 0.017	-0.031	1.00	-0.119 ; 0.057
(Julian_Day) ²	-0.002	0.32	-0.007 ; 0.003	0.142	1.00	0.061 ; 0.223
Cloud_cover	0.003	0.67	-0.001 ; 0.006	-0.155	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	0.010	1.00	0.004 ; 0.015	-0.059	0.26	-0.189 ; 0.072
Conifer_forest	0.012	1.00	0.006 ; 0.019	-0.017	0.18	-0.138 ; 0.104
Habitat_diversity	0.007	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	0.008	1.00	0.003 ; 0.014	-0.067	0.36	-0.181 ; 0.047
ALAN	-0.019	0.89	-0.027 ; -0.010	0.235	1.00	0.117 ; 0.354
Moonlight	-0.006	1.00	-0.010 ; -0.002	0.092	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	0.059	0.95	0.011 ; 0.106
Moonlight: ALAN	-0.001	0.19	-0.005 ; 0.004	-0.073	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*

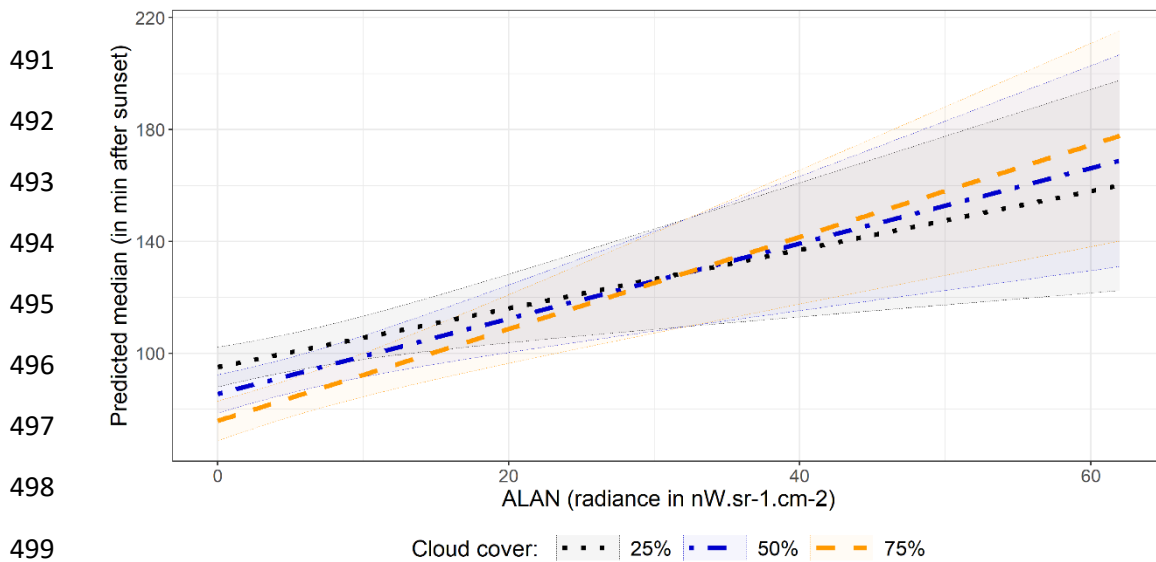
470

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.

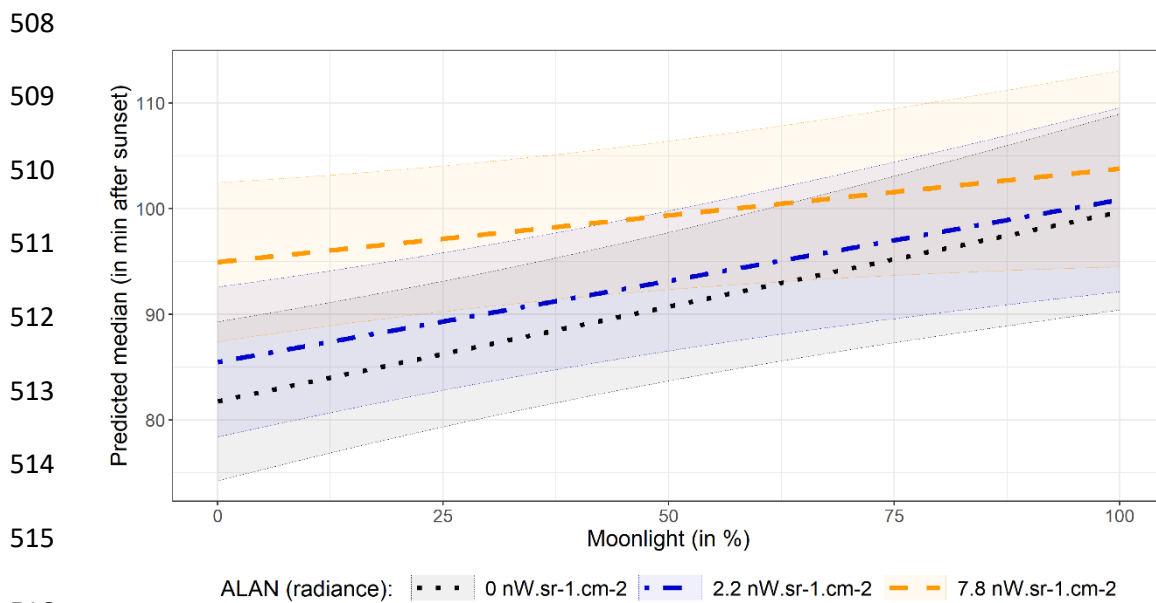
478 Moonlight also delayed the timing of activity. However, this effect was weakened by
479 increasing ALAN (Table 1, Figure 3, Figure O). Compared to a night with no moonlight
480 (0%), a moonlight of 50% delayed activity by 4 minutes at the average mid-sized town, and
481 by 9 minutes at a site with 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



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).*



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⁻¹.cm⁻² being the mean radiance of French municipalities of 1,000 to 5,000*
523 *inhabitants and 7.8 nW.sr⁻¹.cm⁻² 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

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699

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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**

- 717
718 Alaasam, V. J., Liu, X., Niu, Y., Habibian, J. S., Pieraut, S., Ferguson, B. S., Zhang, Y., &
719 Ouyang, J. Q. (2021). Effects of dim artificial light at night on locomotor activity,
720 cardiovascular physiology, and circadian clock genes in a diurnal songbird.
721 *Environmental Pollution*, 282, 117036. <https://doi.org/10.1016/j.envpol.2021.117036>
- 722 Amichai, E., & Kronfeld-Schor, N. (2019). Artificial Light at Night Promotes Activity
723 Throughout the Night in Nesting Common Swifts (*Apus apus*). *Scientific Reports*,
724 9(1), 11052. <https://doi.org/10.1038/s41598-019-47544-3>
- 725 Appel, G., López-Baucells, A., Magnusson, W. E., & Bobrowiec, P. E. D. (2017). Aerial
726 insectivorous bat activity in relation to moonlight intensity. *Mammalian Biology*, 85,
727 37–46. <https://doi.org/10.1016/j.mambio.2016.11.005>
- 728 Arthur, L., & Lemaire, M. (2015). *Les chauves-souris de France, Belgique, Luxembourg et*
729 *Suisse*. Biotope ; Museum national d'Histoire Naturelle.
- 730 Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J., & Le
731 Viol, I. (2015). Is part-night lighting an effective measure to limit the impacts of
732 artificial lighting on bats? *Global Change Biology*, 21(12), 4333–4341.
733 <https://doi.org/10.1111/gcb.13036>
- 734 Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., & Kerbiriou, C. (2018).
735 Evidence for distance and illuminance thresholds in the effects of artificial lighting on
736 bat activity. *Landscape and Urban Planning*, 175, 123–135.
737 <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- 738 Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., & Kerbiriou, C. (2016). Disentangling the relative
739 effect of light pollution, impervious surfaces and intensive agriculture on bat activity
740 with a national-scale monitoring program. *Landscape Ecology*, 31(10), 2471–2483.
741 <https://doi.org/10.1007/s10980-016-0417-3>
- 742 Barré, K., Kerbiriou, C., Ing, R.-K., Bas, Y., Azam, C., Le Viol, I., & Spoelstra, K. (2021).
743 Bats seek refuge in cluttered environment when exposed to white and red lights at
744 night. *Movement Ecology*, 9(1), 3. <https://doi.org/10.1186/s40462-020-00238-2>
- 745 Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S. E., Julien, J.-F., Claireau, F.,
746 Kerbiriou, C., & Bas, Y. (2019). Accounting for automated identification errors in
747 acoustic surveys. *Methods in Ecology and Evolution*, 10(8), 1171–1188.
748 <https://doi.org/10.1111/2041-210X.13198>

749 Bas, Y., Bas, D., & Julien, J.-F. (2017). Tadarida: A Toolbox for Animal Detection on
750 Acoustic Recordings. *Journal of Open Research Software*, 5(1), 6.
751 <https://doi.org/10.5334/jors.154>

752 Bas, Y., Roemer, C., & Julien, J.-F. (2020). *Bat population trends*. Team-Chiro.
753 <https://croemer3.wixsite.com/teamchiro/population-trends?lang=fr>

754 Boldogh, S., Dobrosi, D., & Samu, P. (2007). The effects of the illumination of buildings on
755 house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, 9(2),
756 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)

757 Bowden, J., & Church, B. M. (1973). The influence of moonlight on catches of insects in
758 light-traps in Africa. Part II. The effect of moon phase on light-trap catches. *Bulletin of*
759 *Entomological Research*, 63(1), 129–142.
760 <https://doi.org/10.1017/S0007485300050938>

761 Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2020). Is light
762 pollution driving moth population declines? A review of causal mechanisms across the
763 life cycle: Light pollution and moth life cycles. *Insect Conservation and Diversity*,
764 14(2), 167–187. <https://doi.org/10.1111/icad.12447>

765 Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2021). Street
766 lighting has detrimental impacts on local insect populations. *Science Advances*, 7,
767 eabi8322. <https://doi.org/10.1126/sciadv.abi8322>

768 Bullock, D. J., Combes, B. A., Eales, L. A., & Pritchard, J. S. (1987). Analysis of the timing
769 and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrettus*). *Journal of*
770 *Zoology*, 211(2), 267–274. <https://doi.org/10.1111/j.1469-7998.1987.tb01533.x>

771 Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and
772 multimodel inference in behavioral ecology: Some background, observations, and
773 comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.
774 <https://doi.org/10.1007/s00265-010-1029-6>

775 Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96(9),
776 2370–2382. <https://doi.org/10.1890/14-1639.1>

777 Catto, C. M. C., Hutson, A. M., Racey, P. A., & Stephenson, P. J. (1996). Foraging behaviour
778 and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal*
779 *of Zoology*, 238(4), 623–633. <https://doi.org/10.1111/j.1469-7998.1996.tb05419.x>

780 Catto, C. M. C., Racey, P. A., & Stephenson, P. J. (1995). Activity patterns of the serotine bat
781 (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, 235(4), 635–
782 644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>

- 783 Ciechanowski, M., Zając, T., Biłas, A., & Dunajski, R. (2007). Spatiotemporal variation in
784 activity of bat species differing in hunting tactics: Effects of weather, moonlight, food
785 abundance, and structural clutter. *Canadian Journal of Zoology*, 85(12), 1249–1263.
786 <https://doi.org/10.1139/Z07-090>
- 787 Cryan, P. M., Bogan, M. A., & Altenbach, J. S. (2000). Effect of elevation on distribution of
788 female bats in the Black Hills, South Dakota. *Journal of Mammalogy*, 81(3), 719–725.
789 [https://doi.org/10.1644/1545-1542\(2000\)081<0719:EOEODO>2.3.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0719:EOEODO>2.3.CO;2)
- 790 Day, J., Baker, J., Schofield, H., Mathews, F., & Gaston, K. J. (2015). Part-night lighting:
791 Implications for bat conservation: Part-night lighting and bats. *Animal Conservation*,
792 18(6), 512–516. <https://doi.org/10.1111/acv.12200>
- 793 Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse
794 foraging and echolocation behaviors of microchiropteran bats. *Frontiers in*
795 *Physiology*, 4, 164. <https://doi.org/10.3389/fphys.2013.00164>
- 796 Dominoni, D. M., Quetting, M., & Partecke, J. (2013). Long-Term Effects of Chronic Light
797 Pollution on Seasonal Functions of European Blackbirds (*Turdus merula*). *PLoS ONE*,
798 8(12), e85069. <https://doi.org/10.1371/journal.pone.0085069>
- 799 Duvergé, P. L., Jones, G., Rydell, J., & Ransome, R. D. (2000). Functional significance of
800 emergence timing in bats. *Ecography*, 23(1), 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- 802 Elvidge, C. D., Baugh, K., Zhizhin, M., Hsu, F.-C., & Ghosh, T. (2017). VIIRS night-time
803 lights. *International Journal of Remote Sensing*, 38(21), 5860–5879.
804 <https://doi.org/10.1080/01431161.2017.1342050>
- 805 Erkert, H. G. (1982). Ecological Aspects of Bat Activity Rhythms. In T. H. Kunz (Ed.),
806 *Ecology of Bats* (pp. 201–242). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_5
- 808 Evans, J. A., Elliott, J. A., & Gorman, M. R. (2007). Circadian Effects of Light No Brighter
809 Than Moonlight. *Journal of Biological Rhythms*, 22(4), 356–367.
810 <https://doi.org/10.1177/0748730407301988>
- 811 Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B.
812 A., Rybnikova, N. A., & Furgoni, R. (2016). The new world atlas of artificial night
813 sky brightness. *Science Advances*, 2(6), e1600377.
814 <https://doi.org/10.1126/sciadv.1600377>
- 815 Galipaud, M., Gillingham, M. A. F., David, M., & Dechaume-Moncharmont, F.-X. (2014).
816 Ecologists overestimate the importance of predictor variables in model averaging: A

817 plea for cautious interpretations. *Methods in Ecology and Evolution*, 5(10), 983–991.
818 <https://doi.org/10.1111/2041-210X.12251>

819 Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of
820 nighttime light pollution: A mechanistic appraisal. *Biological Reviews*, 88(4), 912–
821 927. <https://doi.org/10.1111/brv.12036>

822 Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). REVIEW: Reducing the
823 ecological consequences of night-time light pollution: options and developments.
824 *Journal of Applied Ecology*, 49(6), 1256–1266. [https://doi.org/10.1111/j.1365-
825 2664.2012.02212.x](https://doi.org/10.1111/j.1365-2664.2012.02212.x)

826 Gaston, K. J., Visser, M. E., & Hölker, F. (2015). The biological impacts of artificial light at
827 night: The research challenge. *Philosophical Transactions of the Royal Society B:
828 Biological Sciences*, 370(1667), 20140133. <https://doi.org/10.1098/rstb.2014.0133>

829 Gomes, D. G. E., Appel, G., & Barber, J. R. (2020). Time of night and moonlight structure
830 vertical space use by insectivorous bats in a Neotropical rainforest: An acoustic
831 monitoring study. *PeerJ*, 8, e10591. <https://doi.org/10.7717/peerj.10591>

832 Griffin, D. R., & Lindsay, R. B. (1959). *Listening in the Dark*. *Physics Today*, 12(1), 42–42.
833 <https://doi.org/10.1063/1.3060644>

834 Grubisic, M., van Grunsven, R. H. A., Kyba, C. C. M., Manfrin, A., & Hölker, F. (2018).
835 Insect declines and agroecosystems: Does light pollution matter?: Insect declines and
836 agroecosystems. *Annals of Applied Biology*, 173(2), 180–189.
837 <https://doi.org/10.1111/aab.12440>

838 Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in
839 ecology and evolution: Challenges and solutions: Multimodel inference. *Journal of
840 Evolutionary Biology*, 24(4), 699–711. [https://doi.org/10.1111/j.1420-
841 9101.2010.02210.x](https://doi.org/10.1111/j.1420-9101.2010.02210.x)

842 Haddock, J. K., Threlfall, C. G., Law, B., & Hochuli, D. F. (2019). Light pollution at the
843 urban forest edge negatively impacts insectivorous bats. *Biological Conservation*, 236,
844 17–28. <https://doi.org/10.1016/j.biocon.2019.05.016>

845 Hale, J. D., Fairbrass, A. J., Matthews, T. J., Davies, G., & Sadler, J. P. (2015). The
846 ecological impact of city lighting scenarios: Exploring gap crossing thresholds for
847 urban bats. *Global Change Biology*, 21(7), 2467–2478.
848 <https://doi.org/10.1111/gcb.12884>

849 Harbusch, C., & Racey, P. A. (2006). The sessile serotine: The influence of roost temperature
850 on philopatry and reproductive phenology of *Eptesicus serotinus* (Schreber, 1774)
851 (Mammalia: Chiroptera). *Acta Chiropterologica*, 8(1), 213–229.

852 Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., Hänel, A., Kappeler,
853 P. M., Völker, S., Schwöpe, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R.,
854 Wolter, C., & Tockner, K. (2010). The Dark Side of Light: A Transdisciplinary
855 Research Agenda for Light Pollution Policy. *Ecology and Society*, 15(4), 13.
856 <https://doi.org/10.5751/ES-03685-150413>

857 Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: A question of evolving,
858 acclimatizing or coping with urban environmental stress. *Functional Ecology*, 29(7),
859 913–923. <https://doi.org/10.1111/1365-2435.12477>

860 Jechow, A., Hölker, F., Kolláth, Z., Gessner, M. O., & Kyba, C. C. M. (2016). Evaluating the
861 summer night sky brightness at a research field site on Lake Stechlin in northeastern
862 Germany. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 181, 24–32.
863 <https://doi.org/10.1016/j.jqsrt.2016.02.005>

864 Jechow, A., Kolláth, Z., Ribas, S. J., Spoelstra, H., Hölker, F., & Kyba, C. C. M. (2017).
865 Imaging and mapping the impact of clouds on skyglow with all-sky photometry.
866 *Scientific Reports*, 7(1), 6741. <https://doi.org/10.1038/s41598-017-06998-z>

867 Jechow, A., Kyba, C. C. M., & Hölker, F. (2020). Mapping the brightness and color of urban
868 to rural skyglow with all-sky photometry. *Journal of Quantitative Spectroscopy and*
869 *Radiative Transfer*, 250, 106988. <https://doi.org/10.1016/j.jqsrt.2020.106988>

870 Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing
871 emergence time in echolocating bats. *Philosophical Transactions of the Royal Society*
872 *of London. Series B: Biological Sciences*, 346(1318), 445–455.
873 <https://doi.org/10.1098/rstb.1994.0161>

874 Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha,
875 S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, E., Higgins, W.,
876 Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., ... Joseph, D. (1996).
877 The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological*
878 *Society*, 77(3), 437–472.

879 Kempnaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial Night
880 Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds.
881 *Current Biology*, 20(19), 1735–1739. <https://doi.org/10.1016/j.cub.2010.08.028>

882 Kerbiriou, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A., & Le Viol, I. (2020).
883 Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of
884 Bats. *Diversity*, 12(4), 165. <https://doi.org/10.3390/d12040165>

885 Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J., & Julien, J.-F. (2019a).
886 Potential of bat pass duration measures for studies of bat activity. *Bioacoustics*, 28(2),
887 177–192. <https://doi.org/10.1080/09524622.2017.1423517>

888 Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J., & Julien, J.-F. (2019b). Bat
889 Pass Duration Measurement: An Indirect Measure of Distance of Detection. *Diversity*,
890 11(3), 47. <https://doi.org/10.3390/d11030047>

891 Kervyn, T. (2001). *Ecology and ethology of the serotine bat, Eptesicus serotinus (Chiroptera,*
892 *Vespertilionidae): Perspectives for the conservation of bats*. University of Liège.

893 Koen, E. L., Minnaar, C., Roeber, C. L., & Boyles, J. G. (2018). Emerging threat of the 21st
894 century lightscape to global biodiversity. *Global Change Biology*, 24(6), 2315–2324.
895 <https://doi.org/10.1111/gcb.14146>

896 Kolkert, H., Smith, R., Rader, R., & Reid, N. (2020). Insectivorous bats foraging in cotton
897 crop interiors is driven by moon illumination and insect abundance, but diversity
898 benefits from woody vegetation cover. *Agriculture, Ecosystems & Environment*, 302,
899 107068. <https://doi.org/10.1016/j.agee.2020.107068>

900 Kupprat, F., Hölker, F., & Kloas, W. (2020). Can skyglow reduce nocturnal melatonin
901 concentrations in Eurasian perch? *Environmental Pollution*, 262, 114324.
902 <https://doi.org/10.1016/j.envpol.2020.114324>

903 Kyba, C. C. M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F.,
904 Bennie, J., Elvidge, C. D., Gaston, K. J., & Guanter, L. (2017). Artificially lit surface
905 of Earth at night increasing in radiance and extent. *Science Advances*, 3(11),
906 e1701528. <https://doi.org/10.1126/sciadv.1701528>

907 Kyba, C. C. M., Tong, K. P., Bennie, J., Birriel, I., Birriel, J. J., Cool, A., Danielsen, A.,
908 Davies, T. W., Outer, P. N. den, Edwards, W., Ehlert, R., Falchi, F., Fischer, J.,
909 Giacomelli, A., Giubbilini, F., Haaima, M., Hesse, C., Heygster, G., Hölker, F., ...
910 Gaston, K. J. (2015). Worldwide variations in artificial skyglow. *Scientific Reports*, 5,
911 8409. <https://doi.org/10.1038/srep08409>

912 Lacoueilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., & Kerbiriou, C. (2014). The Influence
913 of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context.
914 *PLoS ONE*, 9(10), e103042. <https://doi.org/10.1371/journal.pone.0103042>

915 Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbiriou, C., Fonderflick, J., & Besnard, A.
916 (2019). Reducing light pollution improves connectivity for bats in urban landscapes.
917 *Landscape Ecology*, 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>

918 Lang, A. B., Kalko, E. K. V., Römer, H., Bockholdt, C., & Dechmann, D. K. N. (2006).
919 Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia*, 146, 659–
920 666. <https://doi.org/10.1007/s00442-005-0131-3>

921 Le Tallec, T., Théry, M., & Perret, M. (2015). Effects of light pollution on seasonal estrus and
922 daily rhythms in a nocturnal primate. *Journal of Mammalogy*, 96(2), 438–445.
923 <https://doi.org/10.1093/jmammal/gyv047>

924 Lewanzik, D., & Voigt, C. C. (2017). Transition from conventional to light-emitting diode
925 street lighting changes activity of urban bats. *Journal of Applied Ecology*, 54(1), 264–
926 271. <https://doi.org/10.1111/1365-2664.12758>

927 Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the*
928 *Environment*, 2(4), 191–198. [https://doi.org/10.1890/1540-9295\(2004\)002\[0191:ELP\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2)

930 Luo, B., Xu, R., Li, Y., Zhou, W., Wang, W., Gao, H., Wang, Z., Deng, Y., Liu, Y., & Feng,
931 J. (2021). Artificial light reduces foraging opportunities in wild least horseshoe bats.
932 *Environmental Pollution*, 288, 117765. <https://doi.org/10.1016/j.envpol.2021.117765>

933 Lynn, K. D., Quintanilla-Ahumada, D., Anguita, C., Widdicombe, S., Pulgar, J. M.,
934 Manríquez, P. H., Quijón, P. A., & Duarte, C. (2021). Artificial light at night alters the
935 activity and feeding behaviour of sandy beach amphipods and pose a threat to their
936 ecological role in Atlantic Canada. *Science of The Total Environment*, 780, 146568.
937 <https://doi.org/10.1016/j.scitotenv.2021.146568>

938 Marnell, F., & Presetnik, P. (2010). *Protection of overground roosts for bats.*
939 UNEP/EUROBATS.

940 Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., & Langton, S. (2015).
941 Barriers and benefits: Implications of artificial night-lighting for the distribution of
942 common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society*
943 *B: Biological Sciences*, 370(1667), 20140124. <https://doi.org/10.1098/rstb.2014.0124>

944 McAney, C. M., & Fairley, J. S. (1988). Activity patterns of the lesser horseshoe bat
945 *Rhinolophus hipposideros* at summer roosts. *Journal of Zoology*, 216(2), 325–338.
946 <https://doi.org/10.1111/j.1469-7998.1988.tb02433.x>

947 McCain, C. M. (2007). Could temperature and water availability drive elevational species
948 richness patterns? A global case study for bats. *Global Ecology and Biogeography*,
949 16(1), 1–13. <https://doi.org/10.1111/j.1466-822X.2006.00263.x>

950 McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation. *BioScience*, 52(10),
951 883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)

952 Millon, L., Julien, J.-F., Julliard, R., & Kerbiriou, C. (2015). Bat activity in intensively
953 farmed landscapes with wind turbines and offset measures. *Ecological Engineering*,
954 75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>

955 Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K., & Seymoure, B. M.
956 (2019). Light pollution is a driver of insect declines. *Biological Conservation*, 241,
957 108259. <https://doi.org/10.1016/j.biocon.2019.108259>

958 Pauwels, J., Le Viol, I., Azam, C., Valet, N., Julien, J.-F., Bas, Y., Lemarchand, C., Sánchez
959 de Miguel, A., & Kerbiriou, C. (2019). Accounting for artificial light impact on bat
960 activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning*,
961 183, 12–25. <https://doi.org/10.1016/j.landurbplan.2018.08.030>

962 Pauwels, J., Le Viol, I., Bas, Y., Valet, N., & Kerbiriou, C. (2021). Adapting street lighting to
963 limit light pollution’s impacts on bats. *Global Ecology and Conservation*, 28, e01648.
964 <https://doi.org/10.1016/j.gecco.2021.e01648>

965 Put, J. E., Fahrig, L., & Mitchell, G. W. (2019). Bats respond negatively to increases in the
966 amount and homogenization of agricultural land cover. *Landscape Ecology*, 34(8),
967 1889–1903. <https://doi.org/10.1007/s10980-019-00855-2>

968 R Core Team. (2015). *R: A language and environment for statistical computing* (3.2.3)
969 [Computer software]. R Foundation for Statistical Computing. URL [https://www.R-](https://www.R-project.org/)
970 [project.org/](https://www.R-project.org/)

971 R Core Team. (2021). *R: A language and environment for statistical computing* (4.0.4.)
972 [Computer software]. R Foundation for Statistical Computing. URL [https://www.R-](https://www.R-project.org/)
973 [project.org/](https://www.R-project.org/)

974 Raap, T., Pinxten, R., & Eens, M. (2015). Light pollution disrupts sleep in free-living animals.
975 *Scientific Reports*, 5, 13557. <https://doi.org/10.1038/srep13557>

976 Richards, S. A. (2007). Dealing with overdispersed count data in applied ecology:
977 Overdispersed count data. *Journal of Applied Ecology*, 45(1), 218–227.
978 <https://doi.org/10.1111/j.1365-2664.2007.01377.x>

- 979 Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model
980 averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral*
981 *Ecology and Sociobiology*, 65(1), 77–89. <https://doi.org/10.1007/s00265-010-1035-8>
- 982 Robinson, M. F., & Stebbings, R. E. (1997). Home range and habitat use by the serotine bat,
983 *Eptesicus serotinus*, in England. *Journal of Zoology*, 243(1), 117–136.
984 <https://doi.org/10.1111/j.1469-7998.1997.tb05759.x>
- 985 Rotics, S., Dayan, T., & Kronfeld-Schor, N. (2011). Effect of artificial night lighting on
986 temporally partitioned spiny mice. *Journal of Mammalogy*, 92(1), 159–168.
987 <https://doi.org/10.1644/10-MAMM-A-112.1>
- 988 Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., & Ancillotto, L.
989 (2019). Artificial illumination near rivers may alter bat-insect trophic interactions.
990 *Environmental Pollution*, 252(Part B), 1671–1677.
991 <https://doi.org/10.1016/j.envpol.2019.06.105>
- 992 Russo, D., & Jones, G. (2003). Use of foraging habitats by bats in a Mediterranean area
993 determined by acoustic surveys: Conservation implications. *Ecography*, 26(2), 197–
994 209. <https://doi.org/10.1034/j.1600-0587.2003.03422.x>
- 995 Rydell, J. (1992). Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional*
996 *Ecology*, 6(6), 744–750. <https://doi.org/10.2307/2389972>
- 997 Rydell, J., Entwistle, A. C., & Racey, P. A. (1996). Timing of Foraging Flights of Three
998 Species of Bats in Relation to Insect Activity and Predation Risk. *Oikos*, 76(2), 243–
999 252. <https://doi.org/10.2307/3546196>
- 1000 Saldaña-Vázquez, R. A., & Munguía-Rosas, M. A. (2013). Lunar phobia in bats and its
1001 ecological correlates: A meta-analysis. *Mammalian Biology*, 78(3), 216–219.
1002 <https://doi.org/10.1016/j.mambio.2012.08.004>
- 1003 Salinas-Ramos, V. B., Ancillotto, L., Cistrone, L., Natasi, C., Bosso, L., Smeraldo, S.,
1004 Sánchez-Cordero, V., & Russo, D. (2021). Artificial illumination influences niche
1005 segregation in bats. *Environmental Pollution*, 284, 117187.
1006 <https://doi.org/10.1016/j.envpol.2021.117187>
- 1007 Salvarina, I., Gravier, D., & Rothhaupt, K.-O. (2018). Seasonal bat activity related to insect
1008 emergence at three temperate lakes. *Ecology and Evolution*, 8(7), 3738–3750.
1009 <https://doi.org/10.1002/ece3.3943>
- 1010 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
1011 *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041->
1012 [210X.2010.00012.x](https://doi.org/10.1111/j.2041-210X.2010.00012.x)

- 1013 Secondi, J., Mondy, N., Gippet, J. M. W., Touzot, M., Gardette, V., Guillard, L., & Lengagne,
1014 T. (2021). Artificial light at night alters activity, body mass, and corticosterone level in
1015 a tropical anuran. *Behavioral Ecology*, arab044.
1016 <https://doi.org/10.1093/beheco/arab044>
- 1017 Seto, K. C., Guneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to
1018 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National*
1019 *Academy of Sciences*, 109(40), 16083–16088.
1020 <https://doi.org/10.1073/pnas.1211658109>
- 1021 Spoelstra, K., van Grunsven, R. H. A., Ramakers, J. J. C., Ferguson, K. B., Raap, T., Donners,
1022 M., Veenendaal, E. M., & Visser, M. E. (2017). Response of bats to light with
1023 different spectra: Light-shy and agile bat presence is affected by white and green, but
1024 not red light. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855),
1025 20170075. <https://doi.org/10.1098/rspb.2017.0075>
- 1026 Stone, E. L., Harris, S., & Jones, G. (2015). Impacts of artificial lighting on bats: A review of
1027 challenges and solutions. *Mammalian Biology*, 80(3), 213–219.
1028 <https://doi.org/10.1016/j.mambio.2015.02.004>
- 1029 Stone, E. L., Jones, G., & Harris, S. (2009). Street Lighting Disturbs Commuting Bats.
1030 *Current Biology*, 19(13), 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>
- 1031 Straka, T. M., Greif, S., Schultz, S., Goerlitz, H. R., & Voigt, C. C. (2020). The effect of cave
1032 illumination on bats. *Global Ecology and Conservation*, 21, e00808.
1033 <https://doi.org/10.1016/j.gecco.2019.e00808>
- 1034 Svechkina, A., Portnov, B. A., & Trop, T. (2020). The impact of artificial light at night on
1035 human and ecosystem health: A systematic literature review. *Landscape Ecology*, 35,
1036 1725–1742. <https://doi.org/10.1007/s10980-020-01053-1>
- 1037 Tiede, J., Diepenbruck, M., Gadau, J., Wemheuer, B., Daniel, R., & Scherber, C. (2020).
1038 Seasonal variation in the diet of the serotine bat (*Eptesicus serotinus*): A high-
1039 resolution analysis using DNA metabarcoding. *Basic and Applied Ecology*,
1040 S1439179120300992. <https://doi.org/10.1016/j.baae.2020.09.004>
- 1041 Torres, D., Tidau, S., Jenkins, S., & Davies, T. W. (2020). Artificial skyglow disrupts celestial
1042 migration at night. *Current Biology*, 30(12), R696–R697.
1043 <https://doi.org/10.1016/j.cub.2020.05.002>
- 1044 van Grunsven, R. H. A., van Deijk, J. R., Donners, M., Berendse, F., Visser, M. E.,
1045 Veenendaal, E. M., & Spoelstra, K. (2020). Experimental light at night has a negative

1046 long-term impact on macro-moth populations. *Current Biology*, 30(12), R694–R695.
1047 <https://doi.org/10.1016/j.cub.2020.04.083>

1048 van Hasselt, S. J., Hut, R. A., Allocca, G., Vyssotski, A. L., Piersma, T., Rattenborg, N. C., &
1049 Meerlo, P. (2021). Cloud cover amplifies the sleep-suppressing effect of artificial light
1050 at night in geese. *Environmental Pollution*, 273, 116444.
1051 <https://doi.org/10.1016/j.envpol.2021.116444>

1052 Vásquez, D. A., Grez, A. A., & Rodríguez-San Pedro, A. (2020). Species-specific effects of
1053 moonlight on insectivorous bat activity in central Chile. *Journal of Mammalogy*,
1054 101(5), gyaa095. <https://doi.org/10.1093/jmammal/gyaa095>

1055 Vaughan, N., Jones, G., & Harris, S. (1997). Habitat Use by Bats (Chiroptera) Assessed by
1056 Means of a Broad-Band Acoustic Method. *Journal of Applied Ecology*, 34(3), 716–
1057 730. <https://doi.org/10.2307/2404918>

1058 Verboom, B., & Huitema, H. (1997). The importance of linear landscape elements for the
1059 pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape*
1060 *Ecology*, 12, 117–125. <https://doi.org/10.1007/BF02698211>

1061 Voigt, C. C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D.,
1062 Limpens, H. J. G. A., Mathews, F., Rydell, J., Spoelstra, K., & Zagamajster, M. (2021).
1063 The Impact Of Light Pollution On Bats Varies According To Foraging Guild And
1064 Habitat Context. *BioScience*, 71(10), 1103–1109.
1065 <https://doi.org/10.1093/biosci/biab087>

1066 Voigt, C. C., Scholl, J. M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., & Gras, P.
1067 (2020). Movement responses of common noctule bats to the illuminated urban
1068 landscape. *Landscape Ecology*, 35, 189–201. [https://doi.org/10.1007/s10980-019-](https://doi.org/10.1007/s10980-019-00942-4)
1069 [00942-4](https://doi.org/10.1007/s10980-019-00942-4)

1070 Williams, C. B., & Singh, B. P. (1951). Effect of Moonlight on Insect Activity. *Nature*,
1071 167(4256), 853. <https://doi.org/10.1038/167853a0>

1072 Wilson, A. A., Seymoure, B. M., Jaeger, S., Milstead, B., Payne, H., Peria, L., Vosbigian, R.,
1073 & Francis, C. D. (2021). Direct and ambient light pollution alters recruitment for a
1074 diurnal plant-pollinator system. *Integrative and Comparative Biology*, 31(3), 1122–
1075 1133. <https://doi.org/10.1093/icb/icab010>

1076 Zeale, M. R. K., Stone, E. L., Zeale, E., Browne, W. J., Harris, S., & Jones, G. (2018).
1077 Experimentally manipulating light spectra reveals the importance of dark corridors for
1078 commuting bats. *Global Change Biology*, 24(12), 5909–5918.
1079 <https://doi.org/10.1111/gcb.14462>

1080 Zissis, G., Bertoldi, P., & Serrenho, T. (2021). *Update on the status of LED-lighting world*
1081 *market since 2018* (JRC Technical Report EUR 30500 EN). Publications Office of the
1082 European Union. <https://data.europa.eu/doi/10.2760/759859>

1083 Zuckeberg, B., Cohen, J. M., Nunes, L. A., Bernath-Plaisted, J., Clare, J. D. J., Gilbert, N. A.,
1084 Kozidis, S. S., Maresh Nelson, S. B., Shipley, A. A., Thompson, K. L., & Desrochers,
1085 A. (2020). A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring
1086 in Landscape Ecology? *Current Landscape Ecology Reports*, 5(4), 140–148.
1087 <https://doi.org/10.1007/s40823-020-00059-4>

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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

1096

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

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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

1107

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

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

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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.