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► To cite this version:

Kévin Barré, Kamiel Spoelstra, Yves Bas, Samuel Challéat, Ros Kiri Ing, et al.. Artificial light may change flight patterns of bats near bridges along urban waterways. *Animal Conservation*, 2021, 24 (2), pp.259-267. 10.1111/acv.12635 . hal-02914600

HAL Id: hal-02914600

<https://hal.science/hal-02914600>

Submitted on 12 Aug 2020

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1 **Artificial light may change flight patterns of bats near bridges**
2 **along urban waterways**

3

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31 Running head: Waterway lighting changes bat flight patterns

32

33 **Abstract**

34 Artificial light at night (ALAN) is considered as a major threat to biodiversity, especially to
35 nocturnal species, as it reduces availability, quality and functionality of habitats. However, its
36 effects on the way species use landscape elements such as rivers are still largely understudied,
37 especially the effect of crossing infrastructure lighting on bridges. These elements are
38 nevertheless key commuting and foraging habitats in heavily urbanised landscapes for several
39 taxa such as bats that are particularly affected by ALAN. We studied the effects of the
40 illumination of facades and undersides of bridges on the relative abundance of pipistrelle bats,
41 on their 3D distribution and their behavioural response (i.e. flight speed) close to bridges. We
42 set-up an innovative approach based on a microphone-array to reconstruct positions and flight
43 trajectories in 3D. We studied the effect of lighting on bats in the close proximity of six
44 similar bridges, mostly differentiated by the presence or absence of lighting (3 lit and 3 unlit).
45 All bridges cross the same waterway, within a uniformly and highly urbanized agglomeration
46 (Toulouse, France). We found that bat activity was 1.7 times lower in lit sites. Bats tended to
47 keep a larger distance, and to fly faster close to illuminated bridges. These results suggest that
48 bridge lighting strongly reduces habitat availability and likely connectivity for bats. In that
49 case, results call for switching off the illumination of such bridges crossing riverine
50 ecosystems to preserve their functionality as habitats and corridors for bats.

51

52 Key words: acoustic localisation, artificial light, Chiroptera, ecological corridor, flight
53 behaviour, light pollution, microphone array, river

54

55 **1. Introduction**

56 Among the most prevalent sources of change in biodiversity state, Artificial Light At Night
57 (ALAN) is increasingly recognized as a new threat (Koen et al., 2018). ALAN impacts a wide
58 range of taxa, from individual physiological response to ecosystem functioning, interactions
59 between species and regulatory processes (Bennie et al., 2018; Hölker et al., 2010; Knop et
60 al., 2017; Salinas-Ramos et al., 2020) at many spatiotemporal scales (Altermatt and Ebert,
61 2016; Gaston et al., 2017).

62 ALAN particularly affects nocturnal species such as bats. ALAN affects the availability,
63 quality and functionality of habitats for bats, by changing environmental conditions in which
64 bats interact with other taxa at different spatial scales: their prey, their predators, and likely
65 their competitors (Cravens et al., 2017; Jones and Rydell, 1994; Minnaar et al., 2015; Russo et
66 al., 2019). First of all, it affects the abundance and the distribution of their prey, i) by
67 massively attracting insects around light sources at the streetlight scale ii) and by inducing a
68 suspected vacuum cleaner effect in the surrounding dark areas (Eisenbeis, 2006; Perkin et al.,
69 2014). ALAN also induces mortality and changes in community composition of insects
70 (Davies et al., 2012) in such a way that ALAN is suggested to be a major driver of large scale
71 decline in insects' populations (Fox, 2013; Frank, 1988) and consequently in bat prey
72 availability. By illuminating the scene, ALAN is also suggested to increase predation risk of
73 bats by owls and other raptors (Jones and Rydell, 1994), and in turn bats increase their flight
74 speed (Polak et al., 2011). Bat species respond differently to these changes in interactions
75 with other taxa according to their flight type. Slow-flying species adapted to forage on insects
76 in cluttered vegetation, such as *Myotis* spp., *Plecotus* spp. and *Rhinolophus* spp. avoid lit areas
77 (Clémentine Azam et al., 2015; Zeale et al., 2018), while fast-flying species adapted to hunt
78 insects in open space, such as *Pipistrellus* spp., may appear to benefit locally from the
79 aggregated prey resources around streetlight (Clémentine Azam et al., 2015; Rydell, 1992),

80 although at a wider scale, ALAN negatively impacts their relative abundance (Azam et al.,
81 2016; Pauwels et al., 2019).

82 By reducing habitat availability and quality, ALAN was also suggested to decrease the
83 functional connectivity of landscapes for bats (Laforge et al., 2019) and can have dramatic
84 impacts on their relative abundance at a larger scale (Azam et al., 2016; Pauwels et al., 2019).

85 Linear landscape elements such as hedgerows and rivers play an essential role for bats
86 commuting between roosts and foraging patches (Akasaka et al., 2012; Lacoeylthe et al.,
87 2016; Pinaud et al., 2018; Smith and Racey, 2008). Such landscape elements also provide
88 dark corridors in dimly lighted situations (full moon or distant lighting) (Ancillotto et al.,
89 2019; Zeale et al., 2018) and are specifically important in illuminated urban landscape.

90 ALAN is nevertheless worldwide increasing, in particular close to protected areas and
91 biodiversity hotspots (Guetté et al., 2018), for security, use or aesthetic reasons. This lighting
92 hinders bats when crossing gaps in wooded linear corridors (Hale et al., 2015) and reduces the
93 number of bat commuting along hedgerows (Zeale et al., 2018). Among linear landscape
94 elements, riverine ecosystems are key habitats for bats. Their riparian vegetation and water
95 surface are important foraging areas for many bat species and are recognized as determinants
96 to explain bat abundance across the landscape (Carrasco-Rueda and Loiselle, 2019; Downs
97 and Racey, 2006; Grindal et al., 1999; Lloyd et al., 2006; Lookingbill et al., 2010; Sirami et
98 al., 2013). In highly urbanized areas rivers or waterways and their associated riparian
99 vegetation are often the only corridors still relatively dark, and are thus of high importance for
100 bat moving through such illuminated landscapes (Laforge et al., 2019; Lintott et al., 2015;
101 Todd and Williamson, 2019). However, ecological consequences of the illumination of rivers
102 remain largely understudied (Jechow and Hölker, 2019). Only one study to our knowledge
103 investigated the effect of ALAN on commuting bats by recording Daubenton's bats (*Myotis*
104 *daubentonii*) passing through culverts. In this study the bat activity was found to be

105 unaffected by the presence of light (Spoelstra et al., 2018). However, another study showed
106 that most bat species, including *Myotis* species, significantly reduced their number of drinking
107 and activity above water in presence of artificial light (Russo et al., 2019, 2018, 2017).
108 However, studying bats using such activity metrics from acoustic recordings does not inform
109 on all behavioural changes (e.g. flight speed, spatial position). The development of
110 microphone arrays allows high-resolution localization of bats using their echolocation calls,
111 and hence tracking the animal's movement (Koblitz, 2018). Precise tracking of bats appears
112 as an innovative and a promising method for assessing poorly studied impacts of light on
113 flight behaviour, such as flight speed and changes in flight path.
114 Here, we aim to assess how the illumination of bridges over waterways affects bat activity
115 and their flight behaviour along riverine ecosystems. We studied six bridges above a
116 waterway in a highly urbanized area to assess the impact of facade and underbridge lighting
117 on bats. In addition to activity measurements, we used a microphone-array to record bat
118 positions to construct 3D bat flight trajectories in order to calculate flight speeds. When
119 approaching a lighted structure across a riverine ecosystem, we hypothesize that bats have to
120 deal with a trade-off that includes the benefits of foraging and commuting along this corridor,
121 and the drawback of increased predation risk by exposure to light. In the case of bats limit the
122 risk of exposure to light (Jones and Rydell, 1994; Russo et al., 2018), we predict a decrease in
123 passing bats through light cone and in approaches of individuals to lit bridges. Light sources
124 at riverine ecosystems could therefore form a barrier for moving along it (Hale et al., 2015).
125 In case bats do fly through light cone, they possibly try to minimize the risk of predation by
126 increasing their flight speed (Polak et al., 2011).

127

128 **2. Material and methods**

129 *Study sites*

130 We carried out the study on three lit and three unlit bridges. These six bridges were across
131 two branches of a waterway with a comparable width (around 30 m) and stagnant water (i.e.
132 low current), at the centre of a highly urbanized area (in the city of Toulouse, France, N 43.60
133 E 1.43; Fig. S1). Among bridges studied, four were road bridges (two lit and two unlit) and
134 two were footbridges (one lit and one unlit). Bridges were chosen such that these were
135 comparable in shape (height and width; Table 1 & Fig. S1) and surrounding vegetation (Fig.
136 S1). The lit bridges have been illuminated for many years, with all-year lighting of the facade
137 and underside from the sunset until 1:00 a.m., while unlit bridges had no illumination at all
138 (Fig. S1). Since all the sites were located in very dense urban areas, we assumed that
139 background light from the surrounding city was comparable for all sites. Lit sites were on
140 average exposed to twice as much light than unlit sites: respectively 7.4 ± 1.4 lux for lit sites
141 and 3.6 ± 1.6 lux for unlit sites (Table 1; see Supporting information S1 for details about light
142 measurements).

143

144 *Sampling design and 3D acoustic tracking*

145 We studied the effect of bridge-illumination on bat activity, bat-bridge distance and associated
146 flight speed, through comparisons between lit and unlit sites. We therefore recorded and
147 localized bats in three dimensions on the three first hours starting from sunset during 6
148 consecutive nights between the 19th and 25th of June 2018 (Koblitz, 2018). Weather
149 conditions were highly stable and optimal throughout this sampling period (average
150 temperature: 24.5 ± 1.5 °C, average wind: 3.3 ± 1.1 m/s, no rain and no cloud; Table S1).
151 Between consecutive nights, we alternated each night sampling near lit and unlit bridges.

152 To sample bats, we used an acoustic localisation system (hereafter named microphone array)
153 designed at the Institut Langevin by Ros Kiri Ing (see Supporting Information S2 for more
154 details about the system) (Ing et al., 2016), with a detection radius of about 20 m. Arrays
155 were placed as close as possible to the bridge where the nature of the ground allowed to install
156 the microphone array (i.e. 16.2, 11.7 and 10.5 m from lit bridges, and 10.5, 8.5 and 6 m from
157 unlit bridges). Consequently, the microphone array was placed at the same distance from
158 bridges for only one pair of lit/unlit bridges (i.e. 10.5 m), We accounted for these differences
159 in array-bridge distances in statistical analysis (see statistical analysis section).
160 Each position of bats was reconstructed in 3D using time differences of arrival (TDOA)
161 (Koblitz, 2018) of one echolocation call following the Ing et al. (2016) approach. While
162 relatively seldom used for bat studies, this innovative approach of acoustic localisation has
163 already proven its worth (Götze et al., 2020; Ing et al., 2016; Koblitz, 2018; Polak et al.,
164 2011). We chose to discard positions with a cumulated imprecision greater than one meter on
165 the three dimensions (i.e. the sum of the imprecision on each dimension). Spatial location of
166 bats around the microphone array then allowed the computation of the distance of each
167 emitted bat call to the bridge (see Supporting information S3 for more details on calculation).
168 We then computed flight speed (Equation 1) as follows:

$$169 \quad V_i = \frac{\sqrt{(x_i - x_j)^2 + (y_i - y_j)^2 + (z_i - z_j)^2}}{t_i - t_j} \quad (\text{Eq. 1})$$

170 where x , y and z represent distances to the microphone array for each of the three-dimension
171 axis, and t is the time of call arrival to the microphone array of a given position i and its
172 previous position j (see Supporting information S3 for more details).

173 Although the number of sampled sites was low due to technical constraints, the method using
174 microphone arrays allowed to measure a high number of positions with high precisions.

175

176 *Assigning species to 3D positions and quantification of the number of passing bats*

177 The microphone arrays continuously recorded the echolocation calls of passing bats which
178 were stored in sound files (Ing et al., 2016). These files were divided in five-second files, a
179 sufficient interval for the average duration of a bat pass (Kerbiriou et al., 2019). Hereafter, a
180 bat pass was thus defined as a single or several echolocation calls within a five-second
181 interval. Only 0.6% of 5-second recordings contained more than one individual. Each five-
182 second file was classified to the closest taxonomic level using Tadarida software (Bas et al.,
183 2017). We also visually inspected sound files for feeding buzzes during each bat pass, i.e.
184 rapid sequences of short linear calls before the prey capture.

185 Because the identification at the species level can be problematic, we limited identification
186 level to the species group. We limited further analysis to the *Pipistrellus* group, which
187 includes *Pipistrellus kuhlii*, *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, and *Pipistrellus*
188 *nathusii*. The other bat species groups were absent or showed only a couple of passes
189 preventing any analyses. We subsequently linked the 3D bat position calculated for each call
190 to the species group assigned to it by Tadarida. See Supporting information S4 and R script
191 for more details about automated identification and assigning species to 3D positions.

192

193 *Statistical analysis*

194 We first compared bat activity between lit and unlit sites, using the number of bat passes
195 instead of the number of bat positions, because increasing flight speed reduces the number
196 and the precision of positions (Table 1).

197 To test for potential difference of bat-bridge distances between unlit and lit bridge sites, we
198 built a Linear Mixed Model (LMM, R package *TMB*) using the bat-bridge distance as the
199 response variable following a Gaussian error distribution (Fig. 1), and the lighting treatment
200 (i.e. lit or unlit bridge), the array-bridge distance, the square of the array-bridge distance, and

201 the interaction between both array-bridge distance variables and the lighting treatment as
202 fixed explanatory variables. We used the array-bridge distance as a covariate because lit sites
203 were sampled on average slightly closer to bridges than unlit sites due to field constraints
204 (Table 1; Fig. S2). We included the site as a random effect in models to account for the
205 spatial-temporal structure of the sampling design of recordings (i.e. several recordings per
206 site, one site sampled per night)

207 We then tested whether flight speed changed according to the distance to light. We performed
208 LMM using the flight speed as the response variable associated with a Gaussian error
209 distribution (Fig. S3), the lighting treatment (i.e. lit or unlit bridge), the array-bridge distance,
210 the bat-bridge distance (i.e. for every position for which a flight speed was computed), the
211 square of the bat-bridge distance as fixed explanatory variables. The square of the bat-bridge
212 distance was included as explanatory variable after visual inspection of their non-linear nature
213 in a Generalized Additive Mixed Model using the *gamm* function (R package *mgcv*). As flight
214 speed is expected to vary with lighting (Polak et al., 2011), we also included two interaction
215 terms between the bat-bridge distance, respectively the square of the bat-bridge distance, and
216 the lighting treatment (i.e. lit or unlit bridge). Since flight speed was computed for positions
217 which were part of bat individual trajectories composed of several positions (see Supporting
218 Information S2 for trajectory reconstruction), we accounted for this individual nesting by
219 adding a random effect on the trajectory identity. We also included the site as a second
220 random effect. Given that imprecisions of positions were positively correlated with their
221 distance to the microphone array and the flight speed (Pearson correlation tests: $t=18.5$,
222 $df=2185$, $p\text{-value} < 0.001$ and $t=17.2$, $df=1349$, $p\text{-value} < 0.001$, respectively), we gave to the
223 response variable different weights according to their associated precision by adding a weight
224 term in LMMs (i.e. one per imprecision squared; Penone et al., 2013). We then selected for
225 models with the lowest AIC values, and with VIF values lower than 2 to avoid collinearity

226 issues (Zuur et al., 2010). We re-ran this model for road and footbridges separately to assess
227 the potential dependence of results to the type of bridge. Finally, because the microphone
228 array was placed at the same distance from bridges for only one pair of lit/unlit bridges (i.e.
229 10.5 m), we focused a last model only on positions that were located between 10.4 to 13.5 m
230 from bridges, i.e. that corresponded to the overlap of the 95% confidence interval of bat
231 distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges
232 (see right panel of the Fig. 1). This model was identical to the previous ones but without the
233 bat and array-bridge distance variables as it only focuses on a restricted range of distances,
234 where there is maximum confidence in the results by limiting the array-bridge distance bias.
235 Finally, it was not technically possible to measure light intensity with sufficient precision for
236 each bat position due to the presence of the waterway. We therefore used the bat-bridge
237 distance variable assuming it could be a good proxy due to the relationship between the light
238 intensity and the distance to light. All analyses were performed using a significance threshold
239 of 5% in the R statistical software (R Core Team, 2018).

240

241 **3. Results**

242 We recorded 644 bat passes of *Pipistrellus* spp. at unlit sites (respectively 179, 212, 253 bat
 243 passes per site) while only 386 at lit sites (respectively 106, 136, 144 bat passes per site; Table
 244 1), i.e. 1.7 times less bat passes at lit compared to unlit sites. We also recorded four passes of
 245 *Myotis* spp. and 12 passes of *Nyctalus* spp. The *Pipistrellus* group was composed of 73.1%
 246 *Pipistrellus kuhlii/nathusii*, 26.4% *Pipistrellus pipistrellus* and 0.5% *Pipistrellus pygmaeus*.
 247 *Pipistrellus* spp. emitted in total 21 feeding buzzes (i.e. during 2% of all passes), all at unlit
 248 sites (Table 1). We also recorded more 3D bat position at unlit sites (i.e. 2036) than at lit sites
 249 (i.e. 151) (Table 1).

250 Bat positions were located significantly closer to unlit bridges than lit bridges (Table 2). At
 251 the 10.5 m array-bridge distance at which unlit and lit sites were both sampled, bats were in
 252 average 1.6 m closer to unlit bridges than to lit bridges (Fig. 1). This difference tends to
 253 become higher when sites are sampled closer to bridges (Fig. 1). Bats never approached lit
 254 bridges closer than 7.9 m while for unlit bridges they regularly flew along, over or under
 255 bridges (Fig.2).

256 Table 1. Summary per site of study sites characteristics, sampling design and bat survey results.

Sites	Date	Lighting treatment	Bridge type (height – width in meters)	Array-bridge distance (m)	Light intensity \pm SD (Lux)	Number of 3D positions	Number of 5 seconds bat passes (buzzes)	Average bat-bridge distance \pm SD (m)	Average flight speed \pm SD (m/s)	Average imprecision on positions \pm SD (cm)
1	19/06/2018	Lit	Road bridge (7.2 – 29.7)	16.2	9.1 \pm 8.8	107	144 (0)	15.7 \pm 1.8	8.2 \pm 1.3	54.1 \pm 27.0
2	21/06/2018	Lit	Road bridge (5.5 – 17.8)	11.7	7.9 \pm 8.2	26	106 (0)	10.7 \pm 1.8	6.8 \pm 2.0	48.2 \pm 22.9
3	24/06/2018	Lit	Footbridge (6.0 -2.5)	10.5	5.3 \pm 3.6	18	136 (0)	12.6 \pm 1.5	8.5 \pm 1.3	54.5 \pm 22.0
4	20/06/2018	Unlit	Road bridge (5.7 – 22.8)	8.5	4.7 \pm 8.8	779	179 (3)	7.1 \pm 2.9	6.5 \pm 2.3	16.0 \pm 13.8
5	22/06/2018	Unlit	Road bridge (6.5 – 29.3)	10.5	4.9 \pm 4.1	263	253 (10)	10.0 \pm 2.1	5.7 \pm 2.0	59.2 \pm 27.7
6	25/06/2018	Unlit	Footbridge (6.2 – 2.6)	6.0	1.2 \pm 0.3	994	212 (8)	5.7 \pm 3.6	6.3 \pm 2.4	12.3 \pm 14.3
1+2+3	/	Lit	/	14.7	7.4 \pm 1.4	151	386	14.5 \pm 2.7	8.1 \pm 1.5	53.1 \pm 25.8
4+5+6	/	Unlit	/	7.5	3.6 \pm 1.6	2036	644	6.8 \pm 3.5	6.3 \pm 2.3	19.8 \pm 22.5

257

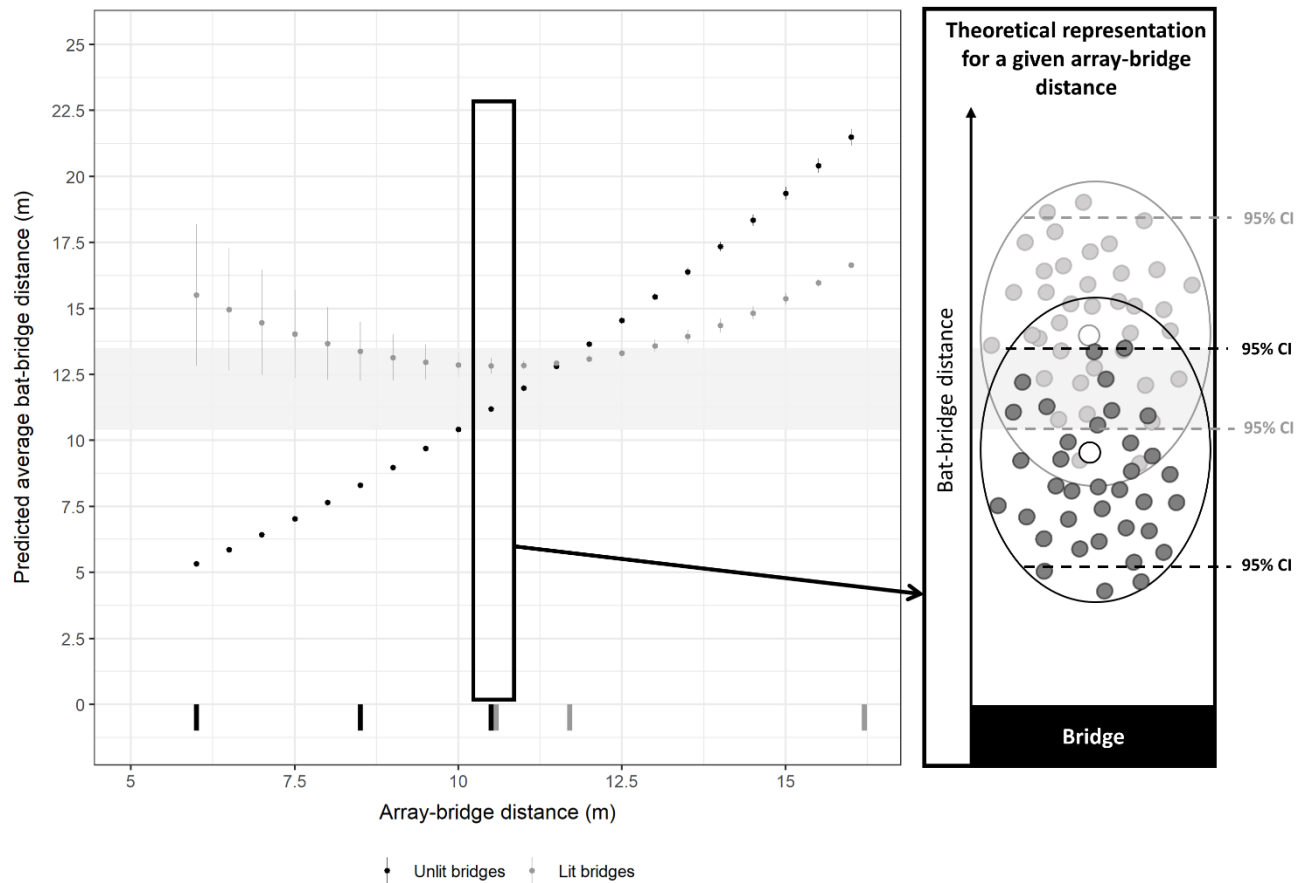
258

259 Table 2. Bridge lighting effects on bat-bridge distance and flight speed from linear mixed models, respectively
 260 including the bat-bridge distance and the flight speed as response variables. Delta AIC are shown as a difference
 261 with respective null models.

Response variable	Explanatory variables	Estimate \pm SE	z value	p-value	Δ AIC
Bat-bridge distance	Intercept	27.230 \pm 4.527	6.015	< 0.001	- 60
	Unlit vs.lit bridge	-26.145 \pm 4.529	-5.773	< 0.001	
	Array-bridge distance	-2.727 \pm 0.673	-4.055	< 0.001	
	Array-bridge distance ²	0.129 \pm 0.024	5.315	< 0.001	
	Unlit vs.lit bridge : Array-bridge distance	3.093 \pm 0.673	4.593	< 0.001	
	Unlit vs.lit bridge : Array-bridge distance ²	-0.072 \pm 0.024	-2.964	0.003	
Flight speed	Intercept	-0.961 \pm 2.537	-0.379	0.705	- 2565
	Unlit vs.lit bridge	8.832 \pm 2.221	3.977	< 0.001	
	Bat-bridge distance	2.043 \pm 0.294	6.954	< 0.001	
	Bat-bridge distance ²	-0.082 \pm 0.011	-7.573	< 0.001	
	Array-bridge distance	-0.185 \pm 0.096	-1.929	0.054	
	Unlit vs.lit bridge : Distance to the bridge	-2.083 \pm 0.294	-7.088	< 0.001	
	Unlit vs.lit bridge : Distance to the bridge ²	0.089 \pm 0.011	8.250	< 0.001	
Flight speed in the overlap between 95% confidence intervals of positions of lit and unlit sites	Intercept	8.708 \pm 0.625	13.930	< 0.001	-5.5
	Unlit vs.lit bridge	-2.175 \pm 0.677	-3.214	0.001	

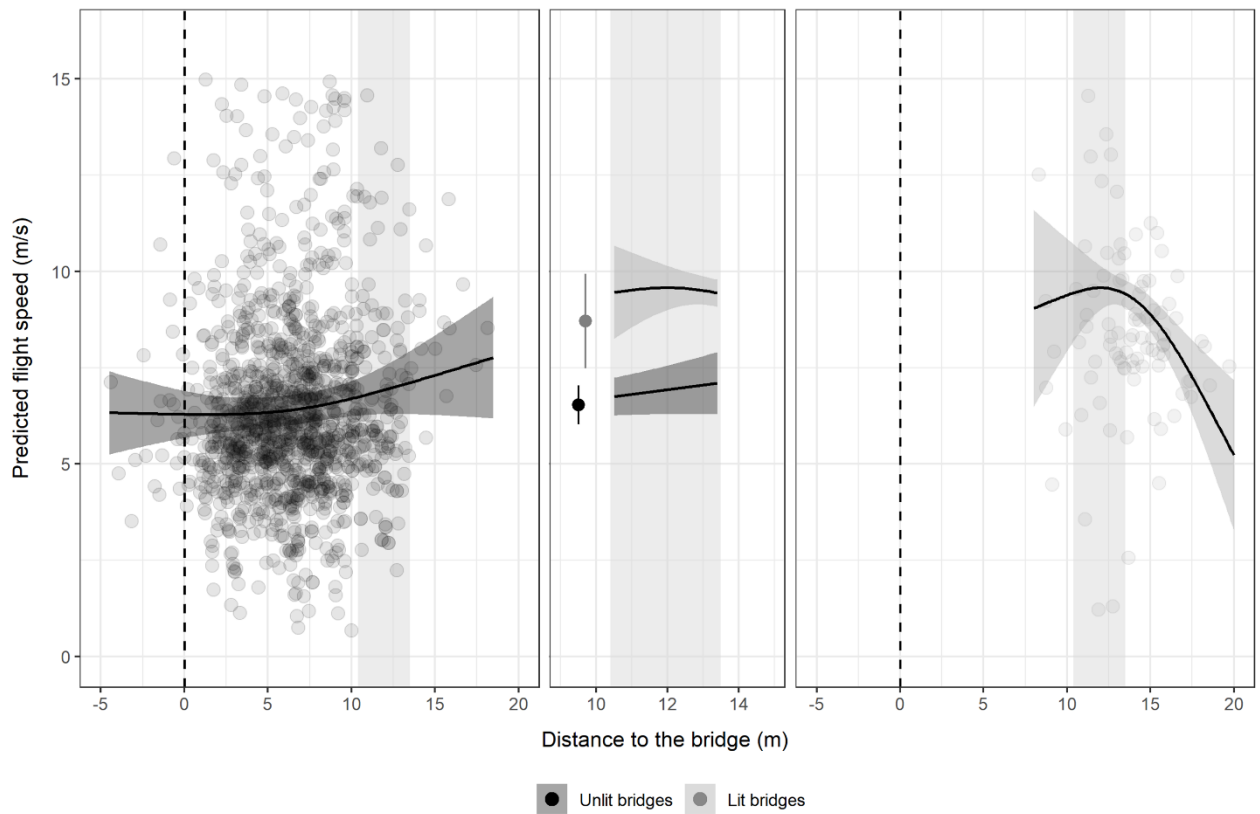
262
 263 Bats were overall flying significantly faster in nearby lit bridges compared to unlit bridges.
 264 Flight speeds were for example 8.7 m/s for lit sites and 6.5 m/s for unlit sites on average
 265 within the range of distances between 10.4 and 13.5 m from bridges (i.e. the range including
 266 an overlap of 95% between bat positions from lit and bat positions from unlit bridges; Table
 267 2; Fig. 2). The relationship between the flight speed and the bat-bridge distance was thus
 268 found to strongly differ between unlit and lit bridges (Table 2; Fig.2): Flight speed was found
 269 to significantly decrease when bats approached unlit bridges, while we found significant
 270 increasing of speeds when bats approached lit bridges (Table 2; Fig. 2). The array-bridge
 271 distance was not found to significantly influence results about flight speeds (Table 2). Finally,
 272 bats responded the same to footbridges and road bridges (Figs. S4 & S5), the results were thus
 273 independent of differences in usage, structure and lighting way.

274



275

276 Figure 1. Predicted average bat-bridge distances in unlit and lit sites according to the array-bridge distance of
 277 sampling. This interaction comes from the linear mixed model presented in Table 2. Vertical bars at the bottom
 278 show the three array-bridge distances sampled in unlit sites (black), and the three sampled in lit sites (grey). The
 279 representation on the right panel shows a theoretical top-view of bat localisations (filled circles) and average bat
 280 localisation (blank circles) according to the lighting type of bridges, and shown for the array-bridge distance of
 281 10.5 m shared by two sampling sites. The light grey rectangles show the overlap of the 95% confidence interval
 282 of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges.



283

284 Figure 2. Predicted relationships between the flight speed and the bat-bridge distance for unlit (dark grey, left
 285 panel) and lit sites (light grey, right panel) and associated 95% confidence intervals from the linear mixed model
 286 presented in Table 2. The light grey rectangles and the focus on it in the middle panel show the overlap of the
 287 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from
 288 unlit bridges, for which direct comparison is the most reliable. Solid dots in the middle panel show predicted
 289 average flight speeds in the overlap zone. Vertical dashed lines show the bridge location, and empty circles show
 290 raw data used in models.

291

292 **4. Discussion**

293 Results show that compared to unlit bridges, bats approaching illuminated bridges kept a
294 greater distance, were less abundant, and increased flight speed instead of slowing down.

295 Although these results have to be taken with cautious given the number of sampled sites (i.e.
296 6 bridges) due to technical constraints, we think we can be confident in their accuracy thanks
297 to the innovative approach of 3D acoustic localisation which allowed to measure a high
298 number of positions (i.e. 2 187) with high precisions (i.e. 22.1 ± 24.2 cm). In addition, we
299 cannot exclude an effect of particular conditions in samples correlated to lit-unlit
300 characteristics of sites. However, the sampling was designed to control for environmental
301 conditions by selecting sites as similar as possible, and we found a bat activity always lower
302 at unlit sites (i.e. 179, 212, 253 bat passes per site) than at lit sites (i.e. 106, 136, 144). Further
303 studies with a higher sample size to limit potential effects of inherent site characteristics
304 would therefore be necessary to confirm our results.

305 These results are also consistent with previous studies showing that for this group (i.e.
306 *Pipistrellus* species), light at night can result in a decrease of bat activity (Azam et al., 2016),
307 can limit the presence of feeding buzzes (Kerbiriou et al., 2020), reduces the crossing
308 probability of gaps in wooded corridors within a city (Hale et al., 2015), and that flight speeds
309 are much higher in presence of light (Polak et al., 2011).

310 Given the high importance of riverine corridors for bats in urbanized areas with little green
311 spaces (Lintott et al., 2015), our results suggest that bridge lighting reduces bat activity in an
312 important habitat and could potentially constitute a barrier for moving along waterways by
313 preventing individuals from approaching and crossing bridges, and hence affect the functional
314 connectivity for bats in urban landscapes (Laforge et al., 2019; Pauwels et al., 2019).

315 The considerably lower number of bat passes found near illuminated bridges, and the increase
316 in flight speed in response to light is particularly interesting as *Pipistrellus* species are

317 commonly considered as light-tolerant when studied at a similar spatial scale (Clémentine
318 Azam et al., 2015; Azam et al., 2018; Spoelstra et al., 2017; Zeale et al., 2018). Indeed, as
319 light sources used for street lighting massively attract insects (Wakefield et al., 2016),
320 *Pipistrellus* species often increase foraging activity around these and reduce their flight speed
321 (Grodzinski et al., 2009). We hypothesise that bats may increase flight speed when their fear
322 for predators outweighs the benefits of foraging at a specific location. The absence of feeding
323 buzzes (i.e. foraging) at lit sites is consistent with this hypothesis: individuals fly faster in
324 highly lit environments reduce foraging behaviour (Grodzinski et al., 2009). This response has
325 been observed in other mammal taxa as well (Farnworth et al., 2019; Hof et al., 2012). We
326 finally show that bats decrease their flight speed while approaching unlit bridges. This is
327 presumably linked to the bridge that forces individuals to slow down to avoid it.

328 Although we accounted for differences in sampling bat-bridge distances between unlit and lit
329 sites by adding the array-bridge distance as a covariate in models, the range of array-bridge
330 distances shared by unlit and lit sites was narrow, which calls for caution in interpreting
331 results about bat-bridge distances for the whole lighting influence area. However, even though
332 we lack data between zero and seven meters from lit bridges (Fig. 2), flight speed response to
333 the distance to bridges and number of bat passes are different enough between lit and unlit
334 sites to be confident about these results.

335 In our study, we were able to only explore the response of fast-flying species such as
336 *Pipistrellus* species often described as light-tolerant at the street light scale (Lacoeuilhe et al.,
337 2014), but the response of other bat groups – such as slow-flying light-shy bats – that also rely
338 on aquatic corridors as we tested here will be highly interesting as well. Such negative effects
339 on *Pipistrellus* species thus raise numerous questions about less tolerant species, especially in
340 more rural landscapes where light-shy bats are regularly more abundant than in urban
341 landscape (Gili et al., 2020). In addition, *P. pipistrellus* and *P. pygmaeus* may respond

342 differently to light as these species are smaller than *P. kuhlii/nathusii* (Dietz et al., 2009), and
343 hence have different flight characteristics (e.g. Azam et al., 2018; C. Azam et al., 2015; Russo
344 et al., 2018). Further studies are needed to assess species-specific changes in flight patterns
345 due to artificial light.

346 Our results highlight that even for the most common bat species in urban habitat, which is
347 considered as light-tolerant in direct response to light, we found a strong impact of light on
348 the relative abundance near bridges, and on the spatial distribution and flight behaviour. The
349 effects we report here call for keeping bridges dark to preserve the functionality of river
350 corridors and to limit habitat loss for bats.

351

352 **Acknowledgments**

353 This work was supported by the Infrastructures de Transports Terrestres, Ecosystèmes et
354 Paysages (ITTECOP-MTES) program, including funding sources from the Agence de
355 l'Environnement et de la Maîtrise de l'Énergie (ADEME), the Fondation pour la Recherche
356 sur la Biodiversité (FRB) and the Club Infrastructures Linéaires et Biodiversité (CIL&B). We
357 are grateful towards Julie Pauwels and Charlotte Roemer which recently help to improve R
358 script allowing to reconstruct 3D bat trajectories. We also thank Danilo Russo and one
359 anonymous reviewer for their comments which improved our manuscript.

360

361 **Author's contribution**

362 K.B., I.L., C.K, R.K.I. and K.S. conceived the ideas and designed the methodology; K.B. and
363 S.C. collected the data, K.B. and Y.B. prepared the data and wrote R scripts; K.B, C.K. and
364 I.L. analysed the data; K.B., I.L., K.S, C.K, and Y.B. led the writing of the manuscript. All
365 authors gave their final approval for publication.

366

367 **Data availability**

368 Data and R scripts used to prepare data are available at the following link
369 <https://doi.org/10.5281/zenodo.3929723>.

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