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

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Abstract

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

Introduction

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

ALAN particularly affects nocturnal species such as bats. ALAN affects the availability, quality and functionality of habitats for bats, by changing environmental conditions in which bats interact with other taxa at different spatial scales: their prey, their predators and likely their competitors (Jones & Rydell, 1994; Minnaar et al., 2015; Cravens et al., 2017; Russo et al., 2019). First of all, it affects the abundance and

the distribution of their prey, (i) by massively attracting insects around light sources at the streetlight scale (ii) and by inducing a suspected vacuum cleaner effect in the surrounding dark areas (Eisenbeis, 2006; Perkin *et al.*, 2014). ALAN also induces mortality and changes in community composition of insects (Davies *et al.*, 2012) in such a way that ALAN is suggested to be a major driver of large scale decline in insects' populations (Frank, 1988; Fox, 2013) and consequently in bat prey availability. By illuminating the scene, ALAN is also suggested to increase predation risk of bats by owls and other raptors (Jones & Rydell, 1994), and in turn bats increase their flight speed (Polak *et al.*, 2011). Bat species respond differently to these changes in interactions with other taxa according to their flight type. Slow-flying species adapted to forage on insects in cluttered vegetation, such as *Myotis* spp., *Plecotus* spp. and *Rhinolophus* spp. avoid lit areas (Azam *et al.*, 2015; Zeale *et al.*, 2018), while fast-flying species adapted to hunt insects in open space, such as *Pipistrellus* spp., may appear to benefit locally from the aggregated prey resources around streetlight (Rydell, 1992; Azam *et al.*, 2015), although at a wider scale, ALAN negatively impacts their relative abundance (Azam *et al.*, 2016; Pauwels *et al.*, 2019).

By reducing habitat availability and quality, ALAN was also suggested to decrease the functional connectivity of landscapes for bats (Laforge *et al.*, 2019) and can have dramatic impacts on their relative abundance at a larger scale (Azam *et al.*, 2016; Pauwels *et al.*, 2019). Linear landscape elements such as hedgerows and rivers play an essential role for bats commuting between roosts and foraging patches (Smith & Racey, 2008; Akasaka *et al.*, 2012; Lacoeuilhe *et al.*, 2016; Pinaud *et al.*, 2018). Such landscape elements also provide dark corridors in dimly lighted situations (full moon or distant lighting) (Zeale *et al.*, 2018; Ancillotto *et al.*, 2019) and are specifically important in illuminated urban landscape. ALAN is nevertheless worldwide increasing, in particular close to protected areas and biodiversity hotspots (Guetté *et al.*, 2018), for security, use or aesthetic reasons. This lighting hinders bats when crossing gaps in wooded linear corridors (Hale *et al.*, 2015) and reduces the number of bat commuting along hedgerows (Zeale *et al.*, 2018). Among linear landscape elements, riverine ecosystems are key habitats for bats. Their riparian vegetation and water surface are important foraging areas for many bat species and are recognized as determinants to explain bat abundance across the landscape (Grindal *et al.*, 1999; Downs & Racey, 2006; Lloyd *et al.*, 2006; Lookingbill *et al.*, 2010; Sirami *et al.*, 2013; Carrasco-Rueda & Loiselle, 2019). In highly urbanized areas rivers or waterways and their associated riparian vegetation are often the only corridors still relatively dark, and are thus of high importance for bat moving through such illuminated landscapes (Lintott *et al.*, 2015; Laforge *et al.*, 2019; Todd & Williamson, 2019). However, ecological consequences of the illumination of rivers remain largely understudied (Jechow & Hölker, 2019). Only one study to our knowledge investigated the effect of ALAN on commuting bats by recording Daubenton's bats (*Myotis daubentonii*) passing through culverts. In this study, the bat

activity was found to be unaffected by the presence of light (Spoelstra *et al.*, 2018). However, another study showed that most bat species, including *Myotis* species, significantly reduced their number of drinking and activity above water in presence of artificial light (Russo *et al.*, 2017, 2018, 2019). However, studying bats using such activity metrics from acoustic recordings does not inform on all behavioural changes (e.g. flight speed, spatial position). The development of microphone arrays allows high-resolution localization of bats using their echolocation calls, and hence tracking the animal's movement (Koblitz, 2018). Precise tracking of bats appears as an innovative and a promising method for assessing poorly studied impacts of light on flight behaviour, such as flight speed and changes in flight path.

Here, we aim to assess how the illumination of bridges over waterways affects bat activity and their flight behaviour along riverine ecosystems. We studied six bridges above a waterway in a highly urbanized area to assess the impact of facade and underbridge lighting on bats. In addition to activity measurements, we used a microphone-array to record bat positions to construct 3D bat flight trajectories in order to calculate flight speeds. When approaching a lighted structure across a riverine ecosystem, we hypothesize that bats have to deal with a trade-off that includes the benefits of foraging and commuting along this corridor, and the drawback of increased predation risk by exposure to light. In the case of bats limit the risk of exposure to light (Jones & Rydell, 1994; Russo *et al.*, 2018), we predict a decrease in passing bats through light cone and in approaches of individuals to lit bridges. Light sources at riverine ecosystems could therefore form a barrier for moving along it (Hale *et al.*, 2015). In case bats do fly through light cone, they possibly try to minimize the risk of predation by increasing their flight speed (Polak *et al.*, 2011).

Material and methods

Study sites

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

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

Sampling design and 3D acoustic tracking

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

To sample bats, we used an acoustic localization system (hereafter named microphone array) designed at the Institut Langevin by Ros Kiri Ing (see Supporting Information S2 for more details about the system) (Ing *et al*., 2016), with a detection radius of about 20 m. Arrays were placed as close as possible to the bridge where the nature of the ground allowed to install 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 unlit bridges). Consequently, the microphone array was placed at the same distance from bridges for only one pair of lit/unlit bridges (i.e. 10.5 m). We accounted for these differences in array-bridge distances in statistical analysis (see statistical analysis section).

Each position of bats was reconstructed in 3D using time differences of arrival (TDOA) (Koblitz, 2018) of one echolocation call following the Ing *et al*. (2016) approach. While relatively seldom used for bat studies, this innovative approach of acoustic localisation has already proven its worth (Polak *et al*., 2011; Ing *et al*., 2016; Koblitz, 2018; Götze *et al*., 2020). We chose to discard positions with a cumulated imprecision greater than one meter on the three dimensions (i.e. the sum of the imprecision on each dimension). Spatial location of bats around the microphone array

then allowed the computation of the distance of each emitted bat call to the bridge (see Supporting information S3 for more details on calculation). We then computed flight speed (Equation 1) as follows:

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

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

Although the number of sampled sites was low due to technical constraints, the method using the microphone array allowed to measure a high number of positions with high precision.

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

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

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

Statistical analysis

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

To test for potential difference of bat-bridge distances between unlit and lit bridge sites, we built a Linear Mixed Model (LMM, R package *TMB*) using the bat-bridge distance as the response variable following a Gaussian error distribution (Fig. 1), and the lighting treatment (i.e. lit or unlit bridge), the array-bridge distance, the square of the array-bridge distance, and the interaction between both array-bridge distance variables and the lighting treatment as fixed explanatory variables. We used the array-bridge distance as a covariate because lit sites were sampled on average slightly closer to bridges than unlit sites due to field constraints (Table 1; Fig. S2). We included the site as a random effect in models to account for the spatial-temporal structure of the sampling design of recordings (i.e. several recordings per site, one site sampled per night).

We then tested whether flight speed changed according to the distance to light. We performed LMM using the flight speed as the response variable associated with a Gaussian error distribution (Fig. S3), the lighting treatment (i.e. lit or unlit bridge), the array-bridge distance, the bat-bridge distance (i.e. for every position for which a flight speed was computed), the square of the bat-bridge distance as fixed explanatory variables. The square of the bat-bridge distance was included as explanatory variable after visual inspection of their non-linear nature in a Generalized Additive Mixed Model using the *gamm* function (R package *mgcv*). As flight speed is expected to vary with lighting (Polak *et al.*, 2011), we also included two interaction terms between the bat-bridge distance, respectively the square of the bat-bridge distance, and the lighting treatment (i.e. lit or unlit bridge). Since flight speed was computed for positions which were part of bat individual trajectories composed of several positions (see Supporting Information S2 for trajectory reconstruction), we accounted for this individual nesting by adding a random effect on the trajectory identity. We also included the site as a second random effect. Given that imprecisions of positions were positively correlated with their distance to the microphone array and the flight speed (Pearson correlation tests: t = 18.5, df = 2185, p-value < 0.001 and

t = 17.2, df = 1349, p-value < 0.001, respectively), we gave to the response variable different weights according to their associated precision by adding a weight term in LMMs (i.e. one per imprecision squared; Penone *et al.*, 2013). We then selected for models with the lowest AIC values, and with VIF values lower than 2 to avoid collinearity issues (Zuur *et al.*, 2010). We re-ran this model for road and footbridges separately to assess the potential dependence of results to the type of bridge. Finally, because the microphone array was placed at the same distance from bridges for only one pair of lit/unlit bridges (i.e. 10.5 m), we focused a last model only on positions that were located between 10.4 and 13.5 m from bridges, that is, that corresponded to the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges (see right panel of the Fig. 1). This model was identical to the previous ones but without the bat and array-bridge distance variables as it only focuses on a restricted range of distances, where there is maximum confidence in the results by limiting the array-bridge distance bias.

Finally, it was not technically possible to measure light intensity with sufficient precision for each bat position due to the presence of the waterway. We therefore used the bat-bridge distance variable assuming it could be a good proxy due to the relationship between the light intensity and the distance to light. All analyses were performed using a significance threshold of 5% in the R statistical software (R Core Team, 2018).

Results

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

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

Bats were overall flying significantly faster in nearby lit bridges compared to unlit bridges. Flight speeds were for example 8.7 m/s for lit sites and 6.5 m/s for unlit sites on average within the range of distances between 10.4 and 13.5 m from bridges (i.e. the range including an overlap of 95% between bat positions from lit and bat positions from
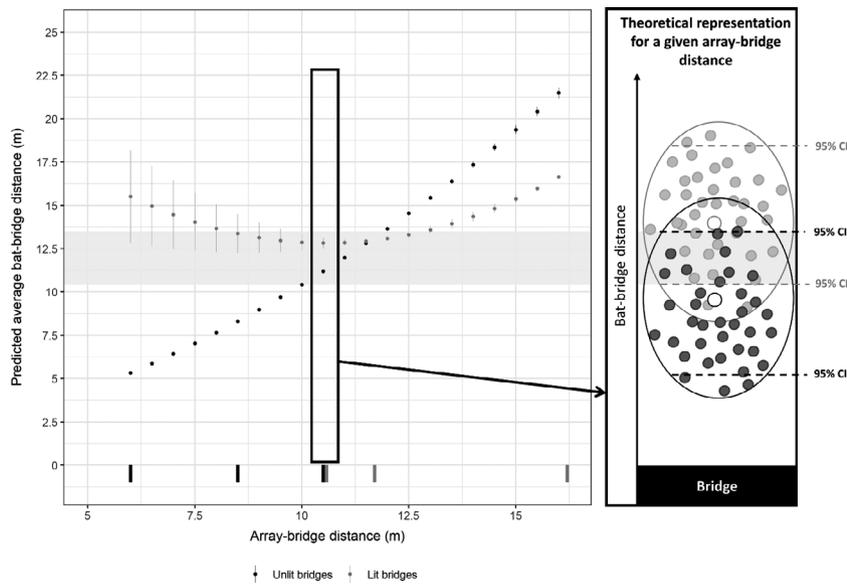
Figure 1 Predicted average bat-bridge distances in unlit and lit sites according to the array-bridge distance of sampling. This interaction comes from the linear mixed model presented in Table 2. Vertical bars at the bottom show the three array-bridge distances sampled in unlit sites (black), and the three sampled in lit sites (grey). The representation on the right panel shows a theoretical top-view of bat localisations (filled circles) and average bat localisation (blank circles) according to the lighting type of bridges, and shown for the array-bridge distance of 10.5 m shared by two sampling sites. The light grey rectangles show the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges.

unlit bridges; Table 2; Fig. 2). The relationship between the flight speed and the bat-bridge distance was thus found to strongly differ between unlit and lit bridges (Table 2; Fig. 2). Flight speed was found to significantly decrease when bats approached unlit bridges, while we found significant increasing of speeds when bats approached lit bridges (Table 2; Fig. 2). The array-bridge distance was not found to significantly influence results about flight speeds (Table 2). Finally, bats responded the same to footbridges and road bridges (Figs. S4 & S5), the results were thus independent of differences in usage, structure and lighting way.

Discussion

Results show that compared to unlit bridges, bats approaching illuminated bridges kept a greater distance, were less abundant, and increased flight speed instead of slowing down. Although these results have to be taken with cautious given the number of sampled sites (i.e. 6 bridges) due to technical constraints, we think we can be confident in their accuracy thanks to the innovative approach of 3D acoustic localisation which allowed to measure a high number of positions (i.e. 2 187) with high precisions (i.e. 22.1 ± 24.2 cm). In addition, we cannot exclude an effect of particular conditions in samples correlated to lit-unlit characteristics of sites. However, the sampling was designed to control for environmental conditions by selecting sites as similar as possible, and we found a bat activity always higher at unlit sites (i.e. 179, 212, 253 bat passes per site) than at lit sites (i.e. 106, 136, 144). Further studies with a

higher sample size to limit potential effects of inherent site characteristics would therefore be necessary to confirm our results.

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

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

The considerably lower number of bat passes found near illuminated bridges, and the increase in flight speed in response to light is particularly interesting as *Pipistrellus* species are commonly considered as light-tolerant when studied at a similar spatial scale (Azam *et al.*, 2015; Spoelstra *et al.*, 2017; Azam *et al.*, 2018; Zeale *et al.*, 2018). Indeed, as light sources used for street lighting massively attract insects (Wakefield *et al.*, 2016), *Pipistrellus* species often increase foraging activity around these and reduce their flight speed (Grodzinski *et al.*, 2009). We hypothesise that bats may increase flight speed when their fear for predators

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

Response variable	Explanatory variables	Estimate ± SE	z value	P-value	Δ AIC
Bat-bridge distance	Intercept	27.230 ± 4.527	6.015	<0.001	−60
	Unlit *vs.* lit bridge	-26.145 ± 4.529	-5.773	<0.001	
	Array-bridge distance	-2.727 ± 0.673	-4.055	<0.001	
	Array-bridge distance^2	0.129 ± 0.024	5.315	<0.001	
	Unlit *vs.* lit bridge: Array-bridge distance	3.093 ± 0.673	4.593	<0.001	
	Unlit *vs.* lit bridge: Array-bridge distance^2	-0.072 ± 0.024	-2.964	0.003	
Flight speed	Intercept	-0.961 ± 2.537	-0.379	0.705	−2565
	Unlit *vs.* lit bridge	8.832 ± 2.221	3.977	<0.001	
	Bat-bridge distance	2.043 ± 0.294	6.954	<0.001	
	Bat-bridge distance^2	-0.082 ± 0.011	-7.573	<0.001	
	Array-bridge distance	-0.185 ± 0.096	-1.929	0.054	
	Unlit *vs.* lit bridge: Distance to the bridge	-2.083 ± 0.294	-7.088	<0.001	
	Unlit *vs.* lit bridge: Distance to the bridge^2	0.089 ± 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 ± 0.625	13.930	<0.001	−5.5
	Unlit *vs.* lit bridge	-2.175 ± 0.677	-3.214	0.001	
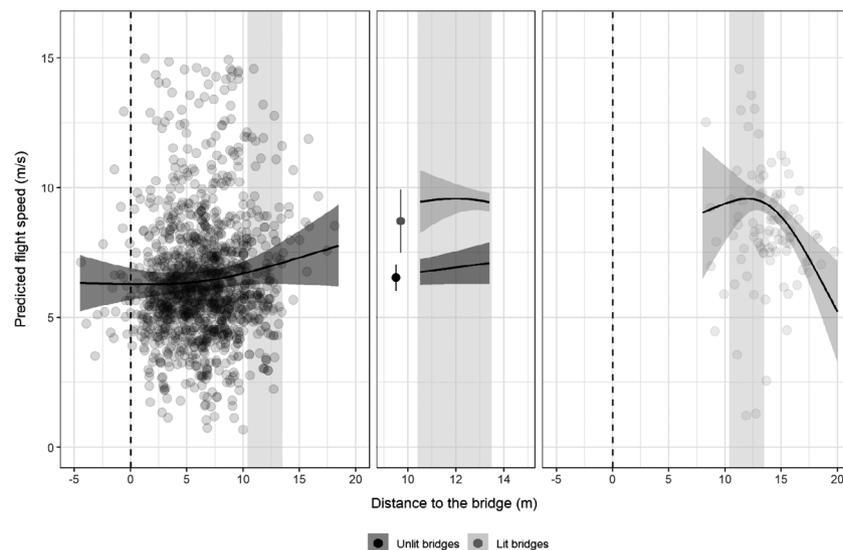
Figure 2 Predicted relationships between the flight speed and the bat-bridge distance for unlit (dark grey, left panel) and lit sites (light grey, right panel) and associated 95% confidence intervals from the linear mixed model presented in Table 2. The light grey rectangles and the focus on it in the middle panel show the overlap of the 95% confidence interval of bat distances from lit bridges and the 95% confidence interval of bat distances from unlit bridges, for which direct comparison is the most reliable. Solid dots in the middle panel show predicted average flight speeds in the overlap zone. Vertical dashed lines show the bridge location, and empty circles show raw data used in models.

outweighs the benefits of foraging at a specific location. The absence of feeding buzzes (i.e. foraging) at lit sites is consistent with this hypothesis: individuals fly faster in highly lit environments and in turn reduce foraging behaviour (Grodzinski *et al.*, 2009). This response has been observed in other mammal taxa as well (Hof *et al.*, 2012; Farnworth *et al.*, 2019). We finally show that bats decrease their flight speed while approaching unlit bridges. This is presumably linked to the bridge that forces individuals to slow down to avoid it.

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

In our study, we were able to only explore the response of fast-flying species such as *Pipistrellus* species often described as light-tolerant at the street light scale (Lacoeuilhe *et al.*, 2014), but the response of other bat groups – such as slow-flying light-shy bats – that also rely on aquatic corridors as we tested here will be highly interesting as well. Such negative effects on *Pipistrellus* species thus raise numerous questions about less tolerant species, especially in more rural landscapes where light-shy bats are regularly more abundant than in urban landscape (Gili *et al.*, 2020). In addition, *P. pipistrellus* and *P. pygmaeus* may respond differently to light as these species are smaller than *P. kuhlii/nathusii* (Dietz *et al.*, 2009), and hence have different flight characteristics (e.g. Azam *et al.*, 2015; Azam *et al.*, 2018; Russo *et al.*, 2018). Further studies are needed to assess species-specific changes in flight patterns due to artificial light.

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

Acknowledgements

Author's contribution

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

Data Availability Statement

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

References

Akasaka, T., Akasaka, M. & Nakamura, F. (2012). Scale-independent significance of river and riparian zones on three sympatric Myotis species in an agricultural landscape. *Biol.*

Conserv. **145**, 15–23. https://doi.org/10.1016/j.biocon.2011.08.017.

Altermatt, F. & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biol. Lett.* **12**, 3–6. https://doi.org/10.1098/rsbl.2016.0111.

Ancillotto, L., Bosso, L., Salinas-Ramos, V.B. & Russo, D. (2019). The importance of ponds for the conservation of bats in urban landscapes. *Landsc. Urban Plan.* **190**, 103607. https://doi.org/10.1016/j.landurbplan.2019.103607.

Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J. & Le Viol, I. (2015). Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? *Glob. Chang. Biol.* **21**, https://doi.org/10.1111/gcb.13036.

Azam, C., Le Viol, I., Julien, J.F., Bas, Y. & Kerbiriou, C. (2016). Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landsc. Ecol.* **31**, 2471–2483. https://doi.org/10.1007/s10980-016-0417-3.

Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F. & Kerbiriou, C. (2018). Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landsc. Urban Plan.* **175**, 123–135. https://doi.org/10.1016/j.landurbplan.2018.02.011.

Bas, Y., Bas, D. & Julien, J. (2017). Tadarida : A Toolbox for animal detection on acoustic recordings. *J. open Res. Softw.* **5**, 1–8. https://doi.org/10.5334/jors.154.

Bennie, J., Davies, T.W., Cruse, D., Inger, R. & Gaston, K.J. (2018). Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *J. Appl. Ecol.* **55**, 2698–2706. https://doi.org/10.1111/1365-2664.13240.

Carrasco-Rueda, F. & Loiselle, B.A. (2019). Do riparian forest strips in modified forest landscapes aid in conserving bat diversity? *Ecol. Evol.* 4192–4209, https://doi.org/10.1002/ece3.5048.

Cravens, Z.M., Brown, V.A., Divoll, T.J., Boyles, J.G., Abdullah, E., Idris, A. & Saparon, A. (2017). Illuminating prey selection in an insectivorous bat community, exposed to artificial light at night. *J. Appl. Ecol.* **12**, 3218–3221. https://doi.org/10.1111/ijlh.12426.

Davies, T.W., Bennie, J. & Gaston, K.J. (2012). Street lighting changes the composition of invertebrate communities. *Biol. Lett.* **8**, 764–767. https://doi.org/10.1098/rsbl.2012.0216.

Dietz, C., VonHelversen, O. & Nill, D. (2009). *Bats of Britain, Europe and Nortwest Africa*. London: A&C Black Publishers.

Downs, N.C. & Racey, P.A. (2006). The use by bats of habitat features in mixed farmland in Scotland NICK. *Acta chiropterologica* **8**, 169–185. https://doi.org/10.3161/1733-5329(2006)8.

Eisenbeis, G.2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In *Ecological Consequences of Artificial Night*

Lighting: pp. 281–304. Rich, C. & Longcore, T. (Eds), Washington, DC: Island Press. https://doi.org/10.1017/CBO9780511609763.016.

Farnworth, B., Meitern, R., Innes, J. & Waas, J.R. (2019). Increasing predation risk with light reduces speed, exploration and visit duration of invasive ship rats (Rattus rattus). *Sci. Rep.* **9**, 3739. https://doi.org/10.1038/s41598-019-39711-3.

Fox, R. (2013). The decline of moths in Great Britain: A review of possible causes. *Insect Conserv. Divers.* **6**, 5–19. https://doi.org/10.1111/j.1752-4598.2012.00186.x.

Frank, K.D. (1988). Impact of outdoor lighting on moths. *J. Lepid. Soc.* **2**, 63–93. https://doi.org/10.1017/s0252921100003687.

Gaston, K.J., Davies, T.W., Nedelec, S.L. & Holt, L.A. (2017). Impacts of artificial light at night on biological timings. *Annu. Rev. Ecol. Evol. Syst.* **48**, 49–68. https://doi.org/10.1146/annurev-ecolsys-110316-022745.

Gili, F., Newson, S.E., Gillings, S., Chamberlain, D.E. & Border, J.A. (2020). Bats in urbanising landscapes: habitat selection and recommendations for a sustainable future. *Biol. Conserv.* **241**, 108343. https://doi.org/10.1016/j.biocon.2019.108343.

Götze, S., Denzinger, A. & Schnitzler, H. (2020). High frequency social calls indicate food source defense in foraging Common pipistrelle bats. *Sci. Rep.* **10**, 5764. https://doi.org/10.1038/s41598-020-62743-z.

Grindal, S.D., Morissette, J.L. & Brigham, R.M. (1999). Concentration of bat activity in riparian habitats over an elevational gradient. *Can. J. Zool.* **77**, 972–977. https://doi.org/10.1139/z99-062.

Grodzinski, U., Spiegel, O., Korine, C. & Holderied, M.W. (2009). Context-dependent flight speed: evidence for energetically optimal flight speed in the bat Pipistrellus kuhlii? *J. Anim. Ecol.* **78**, 540–548. https://doi.org/10.1111/j.1365-2656.2009.01526.x.

Guetté, A., Godet, L., Juigner, M. & Robin, M. (2018). Worldwide increase in Artificial Light At Night around protected areas and within biodiversity hotspots. *Biol. Conserv.* **223**, 97–103. doi.org/S0006320717319043.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G. & Sadler, J.P. (2015). The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Glob. Chang. Biol.* **21**, 2467–2478. https://doi.org/10.1111/gcb.12884.

Hof, A.R., Snellenberg, J. & Bright, P.W. (2012). Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Anim. Behav.* **83**, 1099–1106. https://doi.org/10.1016/j.anbehav.2012.01.042.

Hölker, F., Wolter, C., Perkin, E.K. & Tockner, K. (2010). Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681–682. https://doi.org/10.1016/j.tree.2010.09.007.

Ing, R.K., Colombo, R., Gembu, G.-C., Bas, Y., Julien, J.-F., Gager, Y. & Hassanin, A. (2016). Echolocation calls and flight behaviour of the elusive pied butterfly bat (*Glauconycteris superba*), and new data on its morphology and ecology. *Acta Chiropterologica* **18**, 477–488. https://doi.org/10.3161/15081109ACC2016.18.2.014.

Jechow, A. & Hölker, F. (2019). How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements. *Wiley Interdiscip. Rev. Water* **1–19**, https://doi.org/10.1002/wat2.1388.

Jones, G. & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philos. Trans. R. Soc. B Biol. Sci.* **346**, 445–455. https://doi.org/10.1098/rstb.1994.0161.

Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J. & Julien, J.-F. (2019). Bat pass duration measurement: an indirect measure of distance of detection. *Diversity* **11**, 47. https://doi.org/10.3390/d11030047.

Kerbiriou, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A. & Le Viol, I. (2020). Switching LPS to LED streetlight may dramatically reduce activity and foraging of bats. *Diversity* **12**, https://doi.org/10.3390/d12040165.

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M. & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature* **548**, 206–209. https://doi.org/10.1038/nature23288.

Koblitz, J.C. (2018). Arrayvolution: using microphone arrays to study bats in the field. *Can. J. Zool.* **96**, 933–938. https://doi.org/10.1139/cjz-2017-0187.

Koen, E.L., Minnaar, C., Roever, C.L. & Boyles, J.G. (2018). Emerging threat of the 21st century lightscape to global biodiversity. *Glob. Chang. Biol.* **24**, 2315–2324. https://doi.org/10.1111/gcb.14146.

Lacoeuilhe, A., Machon, N., Julien, J.F., Le Bocq, A. & Kerbiriou, C. (2014). The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLoS One* **9**, https://doi.org/10.1371/journal.pone.0103042.

Lacoeuilhe, A., Machon, N., Julien, J.F. & Kerbiriou, C. (2016). Effects of hedgerows on bats and bush crickets at different spatial scales. *Acta Oecologica* **71**, 61–72. https://doi.org/10.1016/j.actao.2016.01.009.

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

Lintott, P.R., Bunnefeld, N. & Park, K.J. (2015). Opportunities for improving the foraging potential of urban waterways for bats. *Biol. Conserv.* **191**, 224–233. https://doi.org/10.1016/j.biocon.2015.06.036.

Lloyd, A., Law, B. & Goldingay, R. (2006). Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. *Biol. Conserv.* **129**, 207–220. https://doi.org/10.1016/j.biocon.2005.10.035.

Lookingbill, T.R., Elmore, A.J., Engelhardt, K.,Churchill, J.B., Edward Gates, J. & Johnson, J.B, (2010). Influence of

wetland networks on bat activity in mixed-use landscapes. *Biol. Conserv.* **143**, 974–983. https://doi.org/10.1016/j.biocon.2010.01.011.

Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L. & Mckechnie, A.E. (2015). Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *J. Appl. Ecol.* **52**, 522–531. https://doi.org/10.1111/1365-2664.12381.

Pauwels, J., Viol, I.Le, Azam, C., Valet, N., Julien, J. Bas, Y., Lemarchand, C., Sanchez de Miguel, A. & Kerbiriou, C. (2019). Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landsc. Urban Plan.* **183**, 12–25. https://doi.org/S0169204618311939 .

Penone, C., Kerbiriou, C., Julien, J.-F., Julliard, R., Machon, N. & Le Viol, I. (2013). Urbanisation effect on Orthoptera: which scale matters? Insect Conserv. *Divers.* **6**, 319–327. https://doi.org/10.1111/j.1752-4598.2012.00217.x.

Perkin, E.K., Hölker, F. & Tockner, K. (2014). The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshw. Biol.* **59**, 368–377. https://doi.org/10.1111/fwb.12270.

Pinaud, D., Claireau, F., Leuchtmann, M. & Kerbiriou, C. (2018). Modelling landscape connectivity for greater horseshoe bat using an empirical quantification of resistance. *J. Appl. Ecol.* **55**, 2600–2611. https://doi.org/10.1111/1365-2664.13228.

Polak, T., Korine, C., Yair, S. & Holderied, M.W. (2011). Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. *J. Zool.* **285**, 21–27. https://doi.org/10.1111/j.1469-7998.2011.00808.x.

R Core Team, 2018. R: A Language and Environment for Statistical Computing [WWW Document]. Vienna, Austria: R Found. Stat. Comput. https://www.r-project.org/.

Russo, D., Cistrone, L., Libralato, N., Korine, C., Jones, G. & Ancillotto, L. (2017). Adverse effects of artificial illumination on bat drinking activity. *Anim. Conserv.* **20**, 492–501. https://doi.org/10.1111/acv.12340.

Russo, D., Ancillotto, L., Cistrone, L., Libralato, N., Domer, A., Cohen, S. & Korine, C. (2018). Effects of artificial illumination on drinking bats: a field test in forest and desert habitats. *Anim. Conserv.* **1–10**, https://doi.org/10.1111/acv.12443.

Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P. & Ancillotto, L. (2019). Artificial illumination near rivers may alter bat-insect trophic interactions. *Environ. Pollut.* **252**, 1671–1677. https://doi.org/10.1016/j.envpol.2019.06.105.

Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* **6**, 744. https://doi.org/10.2307/2389972.

Salinas-Ramos, V.B., Ancillotto, L., Bosso, L., Sánchez-Cordero, V. & Russo, D. (2020). Interspecific competition in bats: state of knowledge and research challenges. *Mamm. Rev.* **50**, 68–81. https://doi.org/10.1111/mam.12180.

Sirami, C., Jacobs, D.S. & Cumming, G.S. (2013). Artificial wetlands and surrounding habitats provide important foraging habitat for bats in agricultural landscapes in the Western Cape, South Africa. *Biol. Conserv.* **164**, 30–38. https://doi.org/10.1016/j.biocon.2013.04.017.

Smith, P.G. & Racey, P.A. (2008). Natterer's bats prefer foraging in broad-leaved woodlands and river corridors. *J. Zool.* **275**, 314–322. https://doi.org/10.1111/j.1469-7998.2008.00445.x.

Spoelstra, K., van Grunsven, R.H.A., Ramakers, J.J.C., Ferguson, K.B., Raap, T., Donners, M., Veenendaal, E.M. & Visser, M.E. (2017). Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proc. R. Soc. B Biol. Sci.* **284**, 20170075. https://doi.org/10.1098/rspb.2017.0075.

Spoelstra, K., Ramakers, J.J.C., van Dis, N.E. & Visser, M.E. (2018). No effect of artificial light of different colors on commuting Daubenton's bats (Myotis daubentonii) in a choice experiment. J. *Exp. Zool. Part A Ecol. Integr. Physiol.* **329**, 506–510. https://doi.org/10.1002/jez.2178.

Todd, V.L.G. & Williamson, L.D. (2019). Habitat usage of Daubenton's bat (Myotis daubentonii), common pipistrelle (Pipistrellus pipistrellus), and soprano pipistrelle (Pipistrellus pygmaeus) in a North Wales upland river catchment. *Ecol. Evol.* 4853–4863, https://doi.org/10.1002/ece3.5085.

Wakefield, A., Broyles, M., Stone, E.L., Jones, G. & Harris, S. (2016). Experimentally comparing the attractiveness of domestic lights to insects: Do LEDs attract fewer insects than conventional light types? *Ecol. Evol.* **6**, 8028–8036. https://doi.org/10.1002/ece3.2527.

Zeale, M.R.K., Stone, E.L., Zeale, E., Browne, W.J., Harris, S. & Jones, G. (2018). Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. *Glob. Chang. Biol.* **24**, 5909–5918. https://doi.org/10.1111/gcb.14462.

Zuur, A., Ieno, E. & Elphick, C. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

Supporting information

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