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Manipulating spectra of artificial light affects movement patterns of bats along ecological corridors

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Abstract

Animal movement throughout the landscape is a key concept for population viability. Human footprint can reduce animal movement through barrier effects such as habitat change and fragmentation, or through enhanced resources. Artificial light at night (ALAN) can affect the movement of nocturnal animals such as bats that are highly mobile in the landscape. Very few studies have explicitly quantified the choices that moving bats make when they encounter a light source on their flight routes. We assessed whether ALAN of different colours (green, red and white) compared to control conditions affected the use of ecological corridors, considering (i) activity and (ii) movement along the corridor, for open, edge (i.e. light-opportunistic) and narrow-space (i.e. light-averse) foraging bats. We modelled the effects of 28 independent lampposts at four experimental sites on bat activity and movement (i.e. the number of trajectories towards the lamppost and the probability of lamppost crossing). Each lamppost was sampled two to three times over eight complete nights using paired passive acoustic stereo recorders to record bat activity and reconstruct bat trajectories. Narrow-space foragers were much less active in presence of any light source, and fewer flew towards any lit lampposts. Open and edge-space foragers were more active close to white and green lights, and to a lesser extent red light, compared to unlit control sites. Edge-space foragers overall flew more towards white and green lampposts, but had a lower probability of fully crossing a white and red-lighted site. The study shows that ALAN can strongly alter bat movements along landscape structures, for light-averse but also light-opportunistic species. Such changes in flight behaviour may involve bypasses or detours, which may force bats to fly longer distances at night which could ultimately affect fitness. Our findings suggest that avoiding artificial lighting close to flight routes will benefit bats.

Introduction

The ability of animals to move throughout the landscape is essential for individual fitness and hence population viability (e.g. Hanski & Ovaskainen, 2000; Allan, Keesing, & Ostfeld, 2003). For many species, mobility is essential for daily foraging or seasonal reproduction. Mobility influences biotic interactions (e.g. predator–prey relationships or competition for resources) and ecological services species can provide to ecosystems (e.g. pest regulation, seed dispersal, disease dynamics and gene flow) (e.g. Lundberg & Moberg, 2003; Bauer & Hoye, 2014).

The degree to which landscape traits facilitate or impede individuals in their spatial behaviour, the so-called 'functional connectivity', is of crucial importance (Kindlmann & Burel, 2008). The ability for animals to move in a landscape is driven by the amount of their dispersal habitats, and their compositional and configurational heterogeneity (Fahrig *et al.*, 2011). Human footprint (e.g. impervious surfaces, intensive agriculture) can strongly affect animal movements (Tucker *et al.*, 2018). Specifically, animal movement can be reduced through barrier effects such as habitat change and fragmentation due to human infrastructures (e.g. Fahrig, 2007; Kamler *et al.*, 2012), or through enhanced resources (e.g. due to insects aggregation around streetlights) reducing movement requirements (e.g. Prange, Gehrt, & Wiggers, 2004; Jones *et al.*, 2014).

Artificial light at night (ALAN) used for human needs (e.g. street and road lighting for movements) is a global threat (Koen *et al.*, 2018) that can strongly affect the movement of nocturnal animals across landscapes on various scales (e.g. Degen *et al.*, 2016; Roeleke *et al.*, 2018; Van Doren *et al.*, 2017), and in turn community composition due to species-specific sensitivities and an alteration of interspecific competition dynamics (Salinas-Ramos *et al.*, 2021). Indeed, many taxa may be repelled or attracted by lit areas when moving. Effects may be caused by increased predation risk (Jones & Rydell, 1994; Farnworth *et al.*, 2019), direct attraction (e.g. Eisenbeis, 2006; Van Doren et al., 2017) or physiological consequences of light (Cravens & Boyles, 2019; Touzot *et al.*, 2019). Such spatial alteration of landscape use by species due to ALAN can even have genetic implications (Altermatt & Ebert, 2016), which may be an evolutionary driver contributing to population differentiation across urban–rural landscapes (Hopkins et al. 2018).

Bats are a very interesting biological model in this context, as this group has highly various and marked sensitivities to artificial light (Stone, Harris, & Jones, 2015). Bats can be light-opportunistic or light-averse depending on species and their traits, with fast-flying species (i.e. edge- and open-space foragers) being more opportunistic than slow-flying species (i.e. narrow-space foragers). Impact of light can be reduced by using long wavelengths and reduced intensity (Spoelstra *et al.*, 2017; Azam *et al.*, 2018). This aspect is all the more important as old narrow light spectrum sources (such as orange low-pressure sodium and yellow high-pressure sodium lights) are currently being renewed by broad spectrum lighting technologies such as white light emitting diodes. In addition, bats are very mobile compared to other small mammals, with a high dependency on landscape structure, using key features such as hedgerows to forage and move (Pinaud *et al.*, 2018; Froidevaux *et al.*, 2019). Daily movements vary, from just a few to several tens of km per night (Laforge *et al.*, 2021). Most work about the effects of ALAN on bats so far has focused on species abundance and activity, but very few studies to date have explicitly quantified the choices that moving bats make when they encounter a light source on their flight route. Specifically, gaps of open space in between tree cover are important corridors for bats (Verboom & Huitema, 1997; Pinaud *et al.*, 2018). However, even a light-opportunistic species such as *Pipistrellus* has a lower chance of crossing such a gap with increasing lighting level (Hale *et al.*, 2015). Another study showed that when one side of a hedgerow was lit, a light-averse species (*Rhinolophus hipposideros*) preferred to be active at the unlit side (Zeale *et al.*, 2018). Bats can also alter their flight behaviour when approaching a light source, by flying faster, seeking refuge in cluttered habitats or keeping distance with light (Polak *et al.*, 2011; Barré *et al.*, 2020, 2021). However, no study to our knowledge has explicitly quantified the local alteration of bat ability to move along ecological corridors, that is, using their flight paths, and the choice they make when encountering different lighting colour sources, and determining this for different bat groups having contrasting sensitivities to light.

In this study, we assess whether artificial light of different colours affects how bats move in flyways along a forest edge, considering (i) their overall activity (i.e. including foraging and commuting behaviours) and (ii) their movement along the corridor (i.e. commuting behaviour), for open, edge and narrow-space foraging bat species. We used paired passive acoustic stereo recorders to record bat activity and reconstruct bat trajectories along forest edges. When bats flying along a woody corridor are confronted with a light source, we hypothesise a trade-off will occur. The benefits include greater foraging success because of arthropods attracted to light (Rydell, 1992; Owens & Lewis, 2018), and the drawback entails an increased predation risk by exposure to light itself (e.g. nocturnal birds of prey; Jones & Rydell, 1994). In comparison with fully dark corridors, we predict the activity of edge and open-space foraging species (i.e. fast-flying species) to increase close to lights thanks to foraging opportunities, especially for spectral compositions with short wavelengths which attract more arthropods (Russo *et al.*, 2019). Conversely, we predict that the activity of narrow-space foraging species (i.e. slow-flying species) decreases close to any light source due to increased fear of predation. Then, when bats use the corridor to move, we predict any benefits of lighting sources for foraging to disappear and lit areas to be avoided by all bat groups, leading to a decrease in the probability of light crossing by bats along ecological corridors compared to unlit sites.

Materials and methods

Experimental sites

We carried out the study in 2018 at five experimentally illuminated sites in The Netherlands (Figure S1), each with four rows of five 4 m tall lampposts placed perpendicular in a forest edge habitat. Each row was randomly assigned to emit white, green or red light (Fortimo white, ClearField red, and ClearSky green light, Philips, Amsterdam, The Netherlands), with one of the rows kept dark (just poles). All lights were switched on at sunset, and switched off at sunrise since spring 2012. All lights emitted broad spectrum light and had negligible UV emission. However, green lamps had an increased blue and reduced red light emission, and red lamps had an increased red and reduced blue light emission (see Fig. 1 for spectral composition). The light beam of each light was directed downwards by Philips Residium FGS224 (1xPL-L36WHFP) fixtures commonly used for street lighting, which did not emit light in radial symmetry; most light was projected on one side of the light post (see Fig. 2). The light intensity at ground level was on average 8.7 ± 3.0 lux, which was comparable to the illumination levels of countryside roads. Further description of these experimental sites can be found in Spoelstra *et al.* (2015).

Bat recording and sampling design

To assess whether artificial light at forest edges altered the movement of commuting bats and disrupted their activity, we placed a pair of passive acoustic recorders at each location (Song Meter SM2Bat+, Wildlife Acoustic Inc., Maynard, MA, USA), at both sides at 20 m distance from the

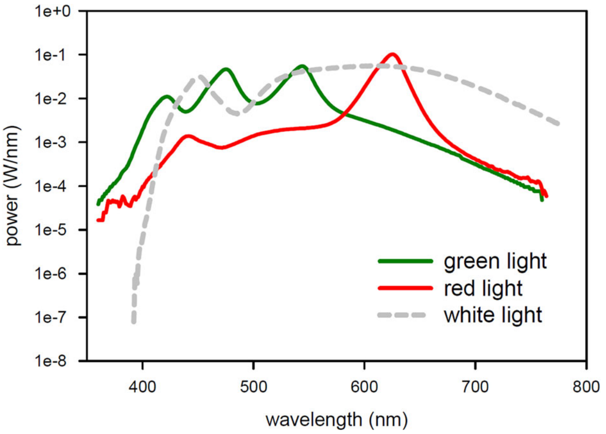
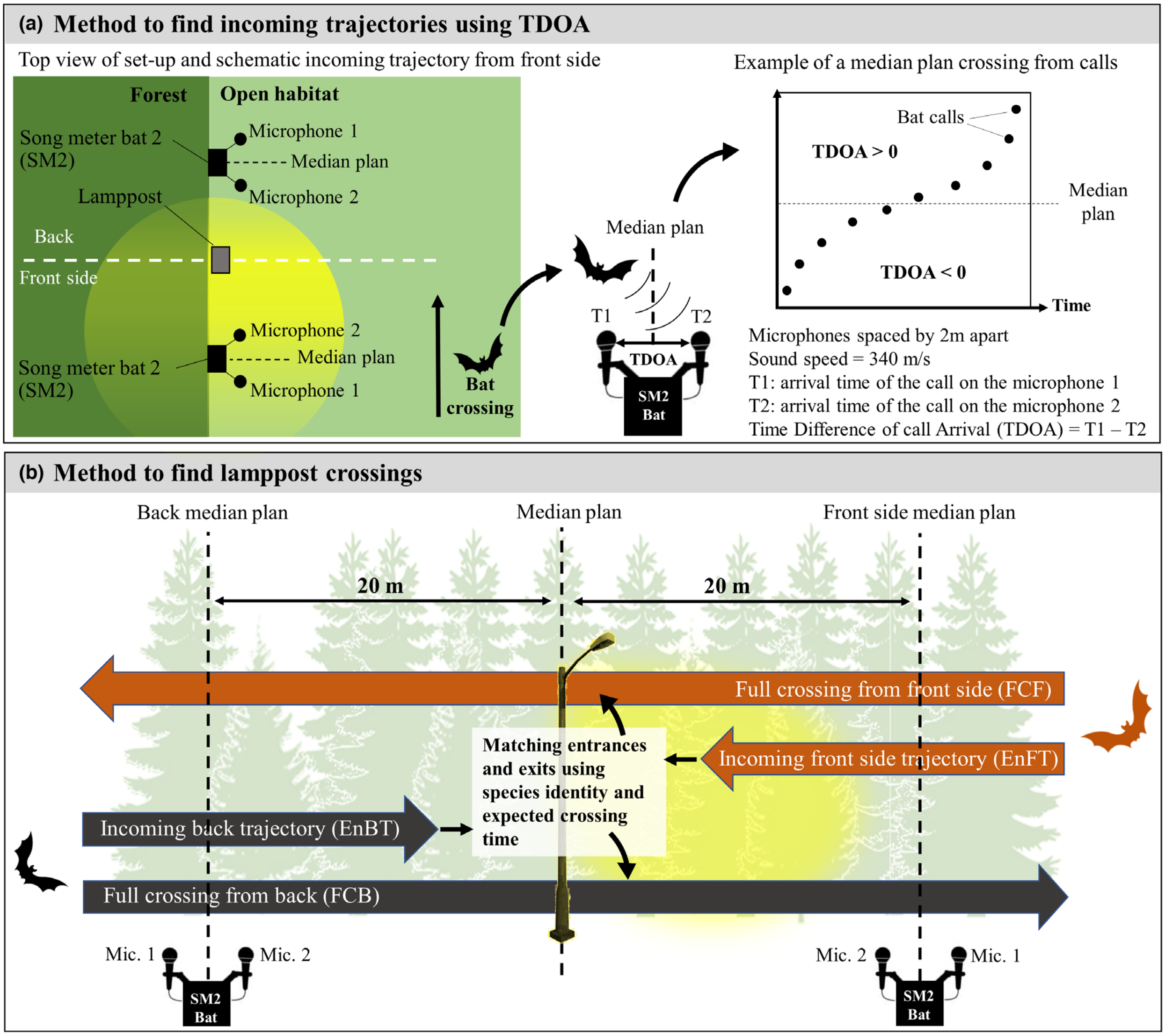


Figure 1 Spectral composition of the light installed on lampposts studied at experimental sites.

lamppost (Fig. 1). For stereo recording, we used two microphones (SMX-US, Wildlife Acoustic Inc.) placed 2 m apart per recorder. The microphone closest to the lamppost was always connected to the left channel, and all microphones were always placed at 1 m above the ground facing the open area. The recorders automatically recorded all ultrasound using predefined settings as recommended by the French bat monitoring program 'Vigie-Chiro' (trigger level set to 6 dB signal-to-noise ratio and set to continue recording until 2.0 s after the last trigger event, 384 kHz sampling rate; https://www.vigienature.fr/fr/chauves-souris). Recordings were started 30 min before sunset and ended 30 min after sunrise.

Except for one night, we recorded simultaneously around eight lampposts each night (two of each colour and two unlit control). In total, we recorded during eight consecutive nights from 9 to 16 July, 2018, around 28 unique lampposts. We recorded bat flight behaviour during two to three nights


(a) Method to find incoming trajectories using TDOA

Top view of set-up and schematic incoming trajectory from front side

Example of a median plan crossing from calls

Microphones spaced by 2m apart
Sound speed = 340 m/s
T1: arrival time of the call on the microphone 1
T2: arrival time of the call on the microphone 2
Time Difference of call Arrival (TDOA) = T1 – T2

(b) Method to find lamppost crossings

Figure 2 Schematic overview of the method to find incoming trajectories (i.e., towards the lamppost) (a) and lamppost crossings (b).

per lamppost, resulting in total of 60 night-lamppost measurements (see Table S1 for more details). Weather conditions were highly favourable for bats during each of these nights (Table S2).

Recorded sound files were segmented into 5 s intervals which is sufficient to cover the average duration of a bat pass (Kerbiriou *et al.*, 2019). Each 5 s file was then automatically classified to the closest taxonomic level using Tadarida software (Bas, Bas, & Julien, 2017). To avoid identification errors and keep enough data for analyses, we limited identification to the following species groups: the *Eptesicus/Nyctalus* group including *Eptesicus* sp. and *Nyctalus* sp., the *Myotis/Plecotus* group including *Myotis* sp. and *Plecotus* sp., and the *Pipistrellus* group including *P. pipistrellus* (largely dominant) and *Pipistrellus nathusii*. At a local scale such as that of our study, these three groups respond differently to light: the *Eptesicus/Nyctalus* group (i.e. open-space and fast-flying foragers) and the *Pipistrellus* group (i.e. edge-space and fast-flying foragers) are considered as light-opportunistic with an ability to exploit insects accumulated around light sources, while species in the *Myotis/Plecotus* group (i.e. narrow-space and slow-flying foragers) are strictly light-averse (Voigt *et al.*, 2021).

Computing bat activity and trajectories

From acoustic recordings, we first derived a bat activity metric for each night and lamppost sampled (white, green, red, and unlit control). We calculated bat activity as the number of 5 s files per night of each species groups, by pooling 5 s files from each of the four microphones (i.e. two microphones in stereo for each of the two recorders per night-lamppost measurement).

Then, following the Claireau *et al.* (2018) approach based on time difference of echolocation call arrivals (TDOA) between two microphones, we computed three types of trajectories: (i) incoming trajectories (i.e. a bat flying in a trajectory towards the lamppost), (ii) leaving trajectories (i.e. when a bat flew in a trajectory away from the lamppost), and (iii) full crossings (i.e. when a bat flew along an incoming trajectory, followed by a leaving trajectory, thus crossing the lamppost). An incoming trajectory was identified when a bat crossed the median plan in between both microphones of a stereo recorder at either side of the lamppost, when flying towards the lamppost. The median plan crossing was detected by a change of TDOA sign, from negative to positive (Fig. 2a, b; see Claireau *et al.* (2018) for more details). We also computed leaving trajectories using the same method, with bats flying away from the lamppost. Then, we computed full crossings, that is, when a bat passed the lamppost by crossing the median plan of the first recorder and then the median plan of the second recorder (Fig. 2b). A full crossing was identified when an incoming flight on one side of the lamppost was directly followed by a leaving flight of the same species group on the other side of the lamppost. The maximum interval between incoming and leaving flights for a full crossing was defined according to the distance between the paired acoustic recorders (40 m) and the expected time of full crossing by bats (Claireau *et al.*, 2018). We assumed that the *Pipistrellus*, *Eptesicus/Nyctalus* and *Myotis/Plecotus* groups take up to 5, 5.4 and 5.6 s to make a full crossing (i.e. 40 m), corresponding at least to their respective average flight speed (i.e. 7.99, 7.43 and 7.08 m s^{-1}, respectively; Barré *et al.*, 2021). Hence, full crossings are more likely to include commuting (i.e. moving between foraging patches) than foraging bats as higher flight speeds are expected to be mainly associated with commuting behaviour (Grodzinski *et al.*, 2009). Finally, we computed the ratio between the number of full crossings and the number of incoming trajectories including those not linked to full crossings. This variable informed on the full crossing probability, which constituted a metric not biased by bat abundance or activity.

Incoming trajectories and full crossings were computed for bats flying in either direction along the forest edge corridor (i.e. from the back or front side of the lamppost; Fig. 2b), and for both directions pooled together.

Statistical analyses

We examined the effects of lampposts and their colour on bat activity and moving along forest edges. We ran Generalised Linear Mixed Models (GLMMs, R package glmmTMB) including as response variable either (i) bat activity, (ii) the number of incoming trajectories, both associated with a negative binomial distribution; and (iii) the proportion of incoming bats that crossed the lamppost associated with a binomial distribution. Then, we used as explanatory variables the spectrum type (i.e. control, green, red and white), and the site identifier as random effect to control for inter-site variations in bat activity (4–8 lampposts sampled each night per site). For trajectory response variables, we performed three models per bat group: for trajectories incoming (i) from the back of the lamppost, (ii) from lamppost front side, and from (iii) both directions pooled together. For each model, we then performed post hoc pairwise comparisons (R package lsmeans) using Tukey's method for *P*-value adjustment in order to test differences between each couple of spectrum type. Finally, we compared corrected Akaike Information Criterion (AICc) of each full model with those of the null ones.

Results

Bat activity and trajectories

We collected a total of 494 018 5 s files with bat activity, including 79.9% of *Pipistrellus* passes, 18.6% of *Eptesicus/Nyctalus* passes, and 1.5% of *Myotis/Plecotus* passes (Table 1). Then, we identified a total of 11 026 incoming bat trajectories, composed of 82.2% *Pipistrellus*, 16.3% *Eptesicus/Nyctalus*, and 1.4% *Myotis/Plecotus* (Table 1). Finally, we found a total of 324 full crossings of bats, composed of 59.6% *Pipistrellus*, 40.1% *Eptesicus/Nyctalus*, and 0.3% *Myotis/Plecotus* (only one at a control site) (Table 1).

Table 1 Summary for each type of site (i.e., lit with green, red or white lampposts, or unlit controls) and for each bat group of the number of bat passes and occurrence (i.e., the proportion of nights with at least one pass), the number of incoming bat trajectories, and the number of light crossings (i.e., full crossings) in total and from back and front side of the lamppost

	Eptesicus/Nyctalus group	*Myotis/Plecotus* group	*Pipistrellus* group
Control			
Number of bat passes (occurrence)	17 568 (0.98)	2783 (0.96)	42 595 (1.00)
Number of incoming trajectories	447	88	1399
Number of light crossings (from back/from frontside)	32 (16/16)	1 (1/0)	48 (28/20)
Green light			
Number of bat passes (occurrence)	27 641 (1.00)	1482 (1.00)	132 716 (1.00)
Number of incoming trajectories	376	20	2549
Number of light crossings (from back/from frontside)	30 (17/13)	0 (0/0)	77 (51/26)
Red light			
Number of bat passes (occurrence)	20 569 (1.00)	1702 (1.00)	65 200 (1.00)
Number of incoming trajectories	647	25	1576
Number of light crossings (from back/from frontside)	43 (19/24)	0 (0/0)	32 (8/24)
White light			
Number of bat passes (occurrence)	26 101 (1.00)	1535 (1.00)	154 126 (1.00)
Number of incoming trajectories	330	26	3543
Number of light crossings (from back/from frontside)	25 (16/9)	0 (0/0)	36 (22/14)

Effects of light spectrum on bat activity

We found the activity of the *Eptesicus/Nyctalus* group to be higher at green and white sites compared to control and red sites which exhibited similar activity levels (Fig. 3; Table S3). Then, we found the activity of the *Myotis/Plecotus* group to be lower at any lit sites compared to control sites (Fig. 3; Table S3). Finally, the activity of the *Pipistrellus* group was higher at green and white sites compared to control sites, while at red sites the activity was lower compared to green and white sites and higher compared to control sites (Fig. 3; Table S3).

Effects of light spectrum on bat movement

Regarding flight pattern towards the lamppost, we found that green, red and white lampposts equally reduced the number of incoming trajectories of the *Myotis/Plecotus* group compared to unlit control lampposts, except for red lamppost when bats came from the back of the lamppost (Table 2; Fig. 4). Conversely, green and white lampposts increased the number of incoming trajectories of the *Pipistrellus* group, except for green lampposts when bats came from lamppost front side, while red lampposts never significantly increased the number of incoming trajectories from either direction (Table 2; Fig. 4).

Concerning the full crossing of the sites, we found that white lampposts always reduced the probability of full crossing for the *Pipistrellus* group compared to unlit control lampposts, as well as red lampposts reducing the probability of full crossing when bats came from the back of the lamppost (Table 2; Fig. 4). No effect of green lampposts on full crossings was found. Since only one full crossing was detected at an unlit control site, it was not possible to

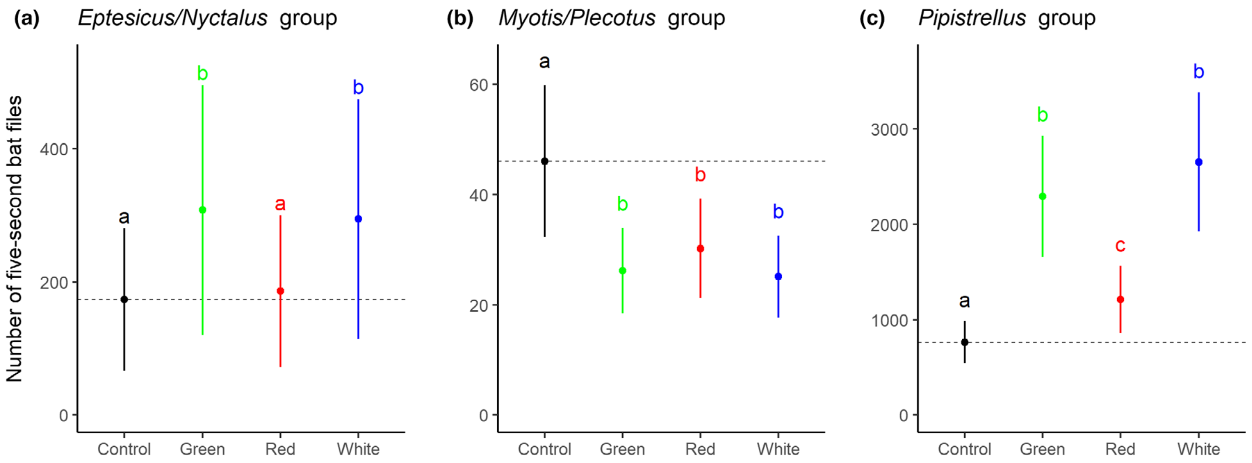


Figure 3 Predicted number of 5 s bat files per night from Generalised Linear Mixed models at each type of site (i.e., lit with green, red or white lampposts, or unlit controls) for each bat group. The differences in letters show the significant differences in bat activity between lighting colours.

Table 2 Estimates, standard errors and *P*-values from Generalised Linear Mixed models of the effect of the lamppost spectrum on the number of incoming trajectories and the probability of full crossing of each bat group when considering all entering trajectories, entering trajectories from the back of the lamppost, or incoming trajectories from lamppost front side, using unlit control lamppost as intercept

		Eptesicus/Nyctalus group				*Myotis/Plecotus* group				*Pipistrellus* group			
Response variables	Spectrum	Delta AICc	Estimate	SE	*P*	Delta AICc	Estimate	SE	*P*	Delta AICc	Estimate	SE	*P*
Number of incoming trajectories													
All data	Green vs. control	−4.59	0.17	0.31		17.86	−1.33	0.32	***	12.93	0.68	0.24	**
	Red vs. control		0.25	0.31			−0.89	0.28	**		0.24	0.23	
	White vs. control		−0.09	0.31			−1.06	0.28	***		0.96	0.23	***
From back	Green vs. control	−5.09	0.23	0.41		−0.45	−0.91	0.44	*	4.70	0.84	0.32	**
	Red vs. control		0.45	0.42			−0.51	0.42			0.50	0.33	
	White vs. control		0.10	0.40			−0.97	0.46	*		1.08	0.33	***
From frontside	Green vs. control	−5.67	0.05	0.48		14.46	−1.65	0.46	***	2.70	0.36	0.35	
	Red vs. control		0.14	0.46			−1.26	0.37	***		−0.14	0.33	
	White vs. control		−0.25	0.49			−1.11	0.35	**		0.76	0.33	*
Probability of full crossing													
All data	Green vs. control	−5.56	0.19	0.27		–	–	–		20.77	0.15	0.19	
	Red vs. control		0.15	0.25			–	–			−0.21	0.23	
	White vs. control		0.13	0.28			–	–			−0.84	0.23	***
From back	Green vs. control	−6.00	0.15	0.37		–	–	–		12.10	−0.11	0.25	
	Red vs. control		0.00	0.38			–	–			−1.22	0.41	**
	White vs. control		0.13	0.38			–	–			−0.82	0.29	**
From frontside	Green vs. control	−6.00	0.08	0.39		–	–	–		15.72	0.36	0.32	
	Red vs. control		0.18	0.34			–	–			0.54	0.31	
	White vs. control		0.04	0.44			–	–			−0.89	0.36	*

Delta AICc shows the difference in AICc with the AICc of the null model, when the value is >2 the interest model outperforms the null one. It was not possible to model the probability of full crossing for *Myotis*/*Plecotus* group due to insufficient number of full crossings.
*** $P < 0.001$.
** $P < 0.01$.
* $P < 0.05$.

perform models testing the probability of full crossing for this group (Table 1).

All models of this movement analysis on the *Eptesicus*/*Nyctalus* group exhibited a higher AICc than null models and no significant effects.

Discussion

We show that narrow-space bat species flew less often towards the lampposts of all colours compared to the unlit control ones, while edge-space species flew more often towards white and green lampposts. However, edge-space species had a lower probability of fully crossing a lamppost, that is, fly from 20 m before to 20 m after the lamppost, when a white and to a lesser extent a red light was present. We also show that open and edge-space species (the *Eptesicus*/*Nyctalus* and *Pipistrellus* groups, respectively) were more active close to white and green lights, as well as red lights for the *Pipistrellus* group to a lesser extent, compared to unlit control sites. However, narrow-space species (the *Myotis*/*Plecotus* group) were much less active in the presence of artificial light regardless of its colour. The response of both groups is fully comparable to the data earlier reported (Spoelstra *et al.*, 2017). These results provide important functional knowledge on how bats deal with light when they move along a woody corridor. The study explicitly shows that artificial light of different colours can alter the patterns of bat movements across landscapes, for at least narrow and edge-space species, which are commonly considered as light-averse and light-opportunistic, respectively. The results also show contrasted responses between activity and movement metrics for edge-space foragers, highlighting that the commonly used activity metric does not inform on bat movement patterns alteration due to artificial light, and that using trajectories with flight direction information is essential to highlight such effects.

Positive effects of green and white light on the activity of edge-space species is consistent with the literature (Spoelstra *et al.*, 2017; Zeale *et al.*, 2018), and can be attributed to the accumulation of arthropods around light sources with more blue light (Rydell, 1992; Owens & Lewis, 2018; Russo *et al.*, 2019). However, the fact that red light increases the activity of edge-space species was previously unreported. This positive response to red light could nevertheless also be linked to the accumulation of arthropods which, even if their number is lower than under white and green light, remains much higher than in dark conditions (Owens & Lewis, 2018).

In contrast, positive effects of green and white light on the activity of open-space species corroborate only a part of the existing literature. Indeed, there is variation in the

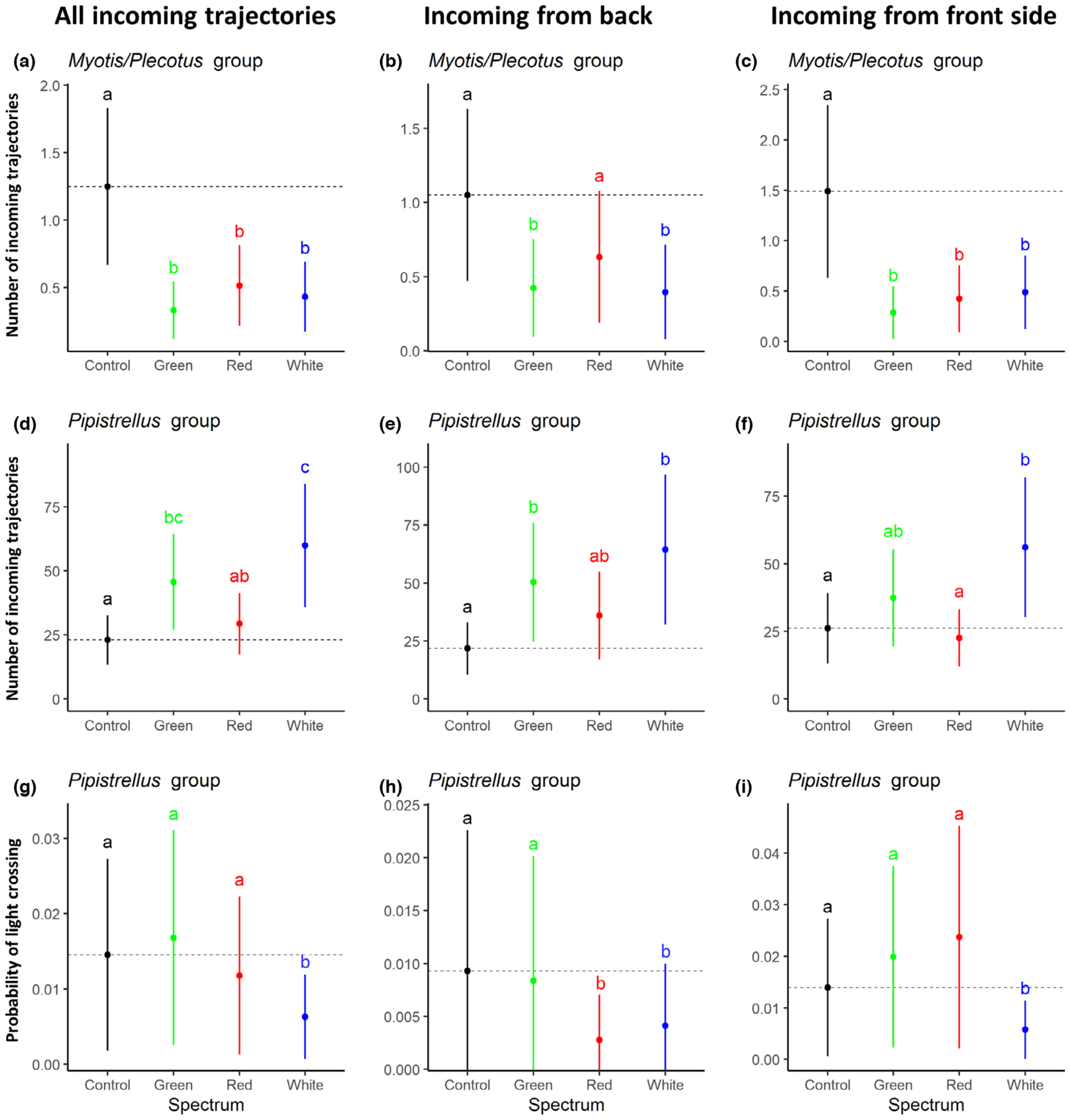


Figure 4 Predicted number of incoming trajectories (i.e., towards the lamppost) (a–f) and probability of full crossing (g–i) per night from Generalised Linear Mixed models at each type of site (i.e., lit with green, red or white lampposts, or unlit control lampposts) for *Myotis/Plecotus* (a–c) and *Pipistrellus* (d–i) groups, when considering all incoming trajectories (a, d and g), incoming trajectories from the back of the lamppost (b, e and h), and incoming trajectories from lamppost front side (c, f and i). The differences in letters show the significant differences in the number of incoming trajectories or the probability of full crossing between lighting colours.

reported responses to light for these species (Spoelstra *et al.*, 2017; Azam *et al.*, 2018; Zeale *et al.*, 2018; Pauwels *et al.*, 2019, 2021), that may depend on context, such as landscape composition (Pauwels *et al.*, 2019; Barré *et al.*, 2022). Finally, negative effects of artificial light on narrow-space species regardless of colour is consistent with the main literature (e.g. Azam *et al.*, 2015, 2018; Pauwels *et al.*, 2021), except for red light, which is previously reported to have limited to absent effects on these species (Spoelstra *et al.*, 2017).

Incoming flights towards lampposts was qualitatively similar to bat activity responses, with a reduced number of flights towards the light for narrow-space species and the opposite for edge-space species. Since the number of incoming trajectories is more likely to be high if bat activity is also high, it is not surprising to find similar results between these two metrics. Hence, a reduced number of flights towards the light simply mean that individuals avoid lit areas more, which nevertheless already constitute a form of barrier effect and habitat loss. An increased number of flights towards the light could mean that individuals come to take advantage of the food resource at the periphery of the light. The study by Azam *et al.* (2018) confirmed these hypotheses, showing that the *Myotis* group species kept greater distances (25 m) to light sources, and that *P. pipistrellus* activity was predominant at intermediate (10 m) from the light compared to the area under the lamppost.

In terms of full crossings of study areas, moving edge-space species had a lower probability of crossing sites lit with white light regardless of whether flying in from the back or front side of lampposts. This result corroborates previous results from Hale *et al.* (2015) and Barré *et al.* (2020) on pipistrelles showing a reduced crossing probability for lighted corridors and bats keeping larger distances to light sources, respectively. Such a result would mean that when they are commuting, bats may be more wary of light. However, results also showed that when a bat comes from the back of the lamppost, red light reduced their crossing probability as well, a finding not previously reported to our knowledge. One explanation could refer to the respective position of the recorders in relation to the light halo: individuals coming from the back are not yet exposed to the halo of the lamppost when they pass the first stereo recorder and can still turn around, while individuals arriving from the front side are directly in the halo of the lamppost when they pass the stereo recorder. Longer distances between the recorders and the lamppost could help confirm this hypothesis. Finally, it was somewhat surprising that green light did not affect the probability of crossing as short wavelengths are relatively well represented. One explanation may be the absence of a peak in wavelengths >580 nm in contrast to white and red lights (see Fig. 1 for spectral compositions), meaning that the mechanisms involved in the decision to cross the light (e.g., the sensitivity of bat eyes to wavelengths, which is poorly studied (Hölker *et al.*, 2021)) could be different from those involved in the attraction for foraging (i.e. arthropods are mainly attracted by short wavelengths). However, although this subject is largely understudied, it would seem that echolocating bats have a lower visual sensitivity at very long wavelengths (Hope & Bhatnagar, 1979; Winter, López, & Von Helversen, 2003).

Our study demonstrates that light prevents bats from crossing freely; however, we do not know specifically how they change their flight paths. Future studies could determine whether incoming individuals which do not fully pass, experience a barrier effect by just bypassing the lit location or turn around, or whether they do not pass though and proceed exploring enhanced resources around or inside the light halo. In this study, a barrier effect is more likely since the lower probability of full crossing by the *Pipistrellus* group for white compared to green light is driven by a reduction in the number of full crossings, and not the number of incomings that can contain individuals exploring enhanced resources without fully crossing the site. Indeed, the number of incoming trajectories and activity level does not differ between white and green lights, unlike the number of full crossings. This is supported by a recent study showing that bats tend to keep a larger distance to artificial light (Barré *et al.*, 2020). In addition, we did not find any movement alteration for open-space species despite effects were previously found on the activity of these species. One explanation could be the greater distance of call detection making measurements of crossings less accurate, a shortcoming that could be improved by using GPS tracking which is possible on species of this size (Roeleke *et al.*, 2016). Finally, the abundance of narrow-space species was too low to reconstruct sufficient full crossings for modelling, making this metric impossible to test in our study, but strong negative effects of all light colours on activity and the number of incoming trajectories already show a barrier effect as individuals simply use much less of any artificially lit area.

In conclusion, this study shows strong alteration of bat movements at a fine scale by all lighting colours for narrow-space species and white and even red for edge-space species. Such local disturbances can affect habitat availability due to avoidance responses, and movements at the landscape scale (Laforge *et al.*, 2019; Voigt *et al.*, 2019) by generating bypasses or detours, consequently probably increasing flight distances, which may have implications for individual fitness. Our results show that manipulating light spectra does not avoid adverse effects of artificial light on bats. In cases where switching off lights would be not possible regarding human needs, mitigation measures should be implemented by avoiding lighting during bat activity peaks (Mariton *et al.*, 2023), and by considerably reducing light intensities to enable bats to commute freely (Hale *et al.*, 2015). However, these measures would have incomplete effectiveness since hourly peaks of bat activity correspond to human time needs and bat behavioural responses begin at very low light intensities (Azam *et al.*, 2018; Barré *et al.*, 2021; Mariton *et al.*, 2023). As a consequence, the most effective solution for restoring or maintaining the functionality of corridors for bat movement is to avoid sources of artificial light at the flight routes and foraging habitats of these species.

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Author contributions

K.B. conceived the ideas, designed the methodology and processed the data; K.B. and K.S. collected the data; K.B. and I.T. analysed the data; K.B. led writing of the manuscript with the support of all authors. All authors critically contributed to the drafts and gave their final approval for publication.

Conflict of Interest

None to declare.

Data availability statement

Data used for analyses are available at https://doi.org/10.5281/zenodo.7560697.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Study sites plotted on a nightly light-emission map of the Netherlands (map image courtesy of Avex's files).

Table S1. Summary of sampled sites and lampposts each night. Capital letters indicate lamppost colour (C: control; G: green; R: red; W: white).

Table S2. Weather conditions at the beginning of each night (for temperature, humidity and wind speed) and over the whole night for the cumulated rain.

Table S3. Estimates, standard errors and *P*-values from Generalised Linear Mixed models of the effect of the lamppost spectrum on the activity of each bat group using unlit control lamppost as intercept (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$). Delta AICc shows the difference in AICc with the AICc of the null model, when the value is >2 the interest model outperforms the null one.