RESEARCH NOTE



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Guild-specific response of bats to motion-triggered LED lighting of bicycle trails

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Abstract

Motion-triggered light-emitting diodes (LED) could reduce light pollution; however, its effect on nocturnal animals is poorly known. Here, we investigated how bats respond to the motion-triggered lighting of a bicycle path, an infrastructure that is increasingly being built to support human mobility. We measured the acoustic activity of bats in relation to the activity of LED lights. The responses of bats varied during the night and between functional guilds: Edge-space foraging bats avoided LED lighting, but the response was less clear during early and late night. Open-space foraging and narrow-space foraging bats avoided the LED lighting, especially late at night. The foraging intensity remained relatively stable across the night for bats of all guilds. We conclude that the motion-sensitive LED lighting of bicycle paths induces a guild-specific avoidance response in bats, which could be mitigated by shorter lighting periods.

KEYWORDS

ALAN, bicycle trails, functional bat guilds, LED, motion-triggered lighting, sustainable mobility

1 | INTRODUCTION

Globally, artificial light at night (ALAN) is increasing by 7%–10% per year (Kyba et al., 2023). If this trend continues, more and more organisms and ecosystems will be affected by ALAN in the future (Bennie et al., 2015; Falchi et al., 2016). Many nocturnal animals avoid ALAN and may thus suffer from habitat degradation and fragmentation when areas are illuminated at night (Hölker et al., 2010), for example, as part of urbanization (Korpach et al., 2022). Among mammals, bats have evolved in a primarily nocturnal niche (Speakman, 2001), which makes them susceptible to ALAN (Rowse

et al., 2016; Stone et al., 2015). All bats are capable of perceiving light at even low intensities (Childs & Buchler, 1981), yet the response of bats to ALAN varies across functional guilds (Voigt, Dekker, et al., 2021). In the temperate zone, bats that hunt insects in vegetation, that is, narrow-space foraging bats, avoid ALAN under almost all circumstances (Voigt, Dekker, et al., 2021). However, relatively fast-flying bats, for example, genera *Pipistrellus* and *Nyctalus*, that are adapted to foraging at the edge of structures and in the open space beyond structures, respectively, may occasionally hunt insects attracted by street lamps at night (Rydell, 1992). Although these species are often described as

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light-tolerant, they may still avoid strong light sources or illuminated areas at the landscape level (Hale et al., 2015; Mariton et al., 2023; Voigt et al., 2020).

In Europe, guidelines have been established for appropriate interventions following the avoidancemitigation-compensation hierarchy (Arlidge et al., 2018; Voigt et al., 2018). A general recommendation of these guidelines is to use ALAN only in those circumstances where it is needed for human safety. A promising approach to mitigate the adverse effects of ALAN on bats is to switch off streetlights during part of the night. Acoustic surveys at roads illuminated by part-night lighting have shown that the response of bats to this lighting scheme varies between species. However, most light-sensitive bat species still avoided illuminated areas (Azam et al., 2015; Day et al., 2015). Recent technological innovations, such as motion-triggered lighting, may be more efficient in avoiding ALAN when it is not needed (Gagliardi et al., 2020). Bats and other wildlife are too small to trigger the sensor, so the environment remains dark in the absence of a large moving object. Recently, it was shown that traffic-regulated dimming of street lighting resulted in a lower number of insects and reduced bat activity compared to permanent lighting, but light-sensitive bats responded negatively toward LED light (Bolliger et al., 2020). Here, we investigated whether motiontriggered LED lighting can help to reduce the negative effects of ALAN on bats at a regional bicycle trail, which are currently established in many parts of Europe to promote ecologically friendly, sustainable mobility.

Specifically, we studied the acoustic activity of bats in response to motion-triggered LED lighting at a regional bicycle trail. We hypothesized that the response of bats toward motion-triggered LED lighting varies over the course of a night and between bats of different guilds. We expected that bats would be most sensitive toward the LED lighting during the first half of the night, because this time is the primary foraging period of bats (Mariton et al., 2023) and because this is the time when the bicycle trail is most often used. Also, we predicted that narrow-space foraging bats avoid LED lighting more than bats from other guilds. We expected edge-space foraging bats to respond positively to the LED lighting because of insects attracted to the light, and open-space foraging bats to respond neutrally toward the LED lighting (Voigt, Dekker, et al., 2021).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is a 1.5 km section of a bicycle trail near the city of Münster, Germany (Supporting Information, SI; Figures S1 and S2). The trail is a 4-m broad tarred road that follows at 10–20 m distance the Dortmund-Ems canal. The area between the trail and the canal is covered by grassland, shrubs, and trees. The following habitat types (from north to south) are located to the east along the 1.5 km of the trail: (1) \sim 240 m of open grassy lands and a patch of farmland (both \sim 5 ha), (2) \sim 380 m of a forest patch ("Große Lodden," \sim 100 ha large), (3) \sim 630 m of a residential area characterized by detached houses with gardens (\sim 36 ha), and (4) \sim 230 m of a 10-ha large park.

2.2 | Motion-triggered LED lighting scheme and light characteristics

LED lamps with a correlated color temperature of 2700K (Figure S3) were positioned every 30 m along the bicycle trail. At ground level (i.e., about 5 m below lamps), illuminance ranged between 15 and 16 lux. The motion-triggering of lamps was activated when natural illuminance was below 34 lux at a sensor in the city center of Münster. When triggered, light intensity increased from 0% to 100% in 2 s, stayed on for 36 s and decreased to 0% in 2 s, resulting in an on-phase of a total of 40 s (Figure S4).

2.3 | Study design

We selected five lampposts spaced between 210 and 300 m apart along the trail for passive acoustic monitoring and simultaneous light measurement. Each lamppost was located next to a different habitat type (open field, forest, forest-residential area, residential area, park) to collect data from sites that are representative of the local land-scape structure (Figures S1 and S2). Passive acoustic monitoring and light measurements were conducted during the reproduction season of bats (June/July) and in late summer (August/September), with three nights of recording per season within a period of 2 weeks around the new moon (Table S1). Hereafter, we also refer to the late summer as the migration season following Heim et al. (2016).

2.4 | Echolocation call recordings, bat species identification, and measures of bat activity

We used Batloggers A+ (Elekon AG, Luzern, Switzerland) that were attached to the lamppost at 3.5 m height above ground, with the microphone about 20 cm above the Batlogger box, facing away from the bicycle

TABLE 1 List of bat species in the library "European bats DE" and classification based on the local abundance and general biology (Voigt, Dekker, et al., 2021; Voigt, Russo, et al., 2021).

Genus	Species	Abbreviations	Abundant	Less abundant	Absent	Guild	Foraging
Barbastella	barbastellus	Bbar		X		ESF	Aerial
Eptesicus	serotinus	Eser	X			OSF	Aerial
	nilssonii				X	OSF	Aerial
Hypsugo	savii				X	ESF	Aerial
Miniopterus	schreibersii				X	OSF	Aerial
Myotis	alcathoe				X	NSF	Gleaning
	bechsteinii	Mbec	X			NSF	Gleaning
	blythii				X	NSF	Gleaning
	brandtii	Mbra	X			NSF	Gleaning
	capaccinii				X	ESF	Trawling
	dasycneme	Mdas	X			ESF	Trawling
	daubentonii	Mdau	X			ESF	Trawling
	emarginatus	Mema		X		NSF	Gleaning
	myotis	Mmyo	X			NSF	Gleaning
	mystacinus	Mmys	X			NSF	Gleaning
	nattereri	Mnat	X			NSF	Gleaning
Nyctalus	lasiopterus				X	OSF	Aerial
	leisleri	Nlei		X		OSF	Aerial
	noctula	Nnoc	X			OSF	Aerial
Pipistrellus	kuhlii				X	ESF	Aerial
	nathusii	Pnat	X			ESF	Aerial
	pipistrellus	Ppip	X			ESF	Aerial
	pygmaeus	Ppyg		X		ESF	Aerial
Plecotus	auritus	Plau	X			NSF	Gleaning
	austriacus				X	NSF	Gleaning
	kolombatovici				X	NSF	Gleaning
	macrobullaris				X	NSF	Gleaning
Rhinolophus	euryale				X	NSF	Flutter detecti
	ferrumequinum				X	NSF	Flutter detecti
	hipposideros				X	NSF	Flutter detecti
Tadarida	teniotis				X	OSF	Aerial
Vespertilio	murinus	Vmur		X		OSF	Aerial

Note: Bat species that are locally present are highlighted in bold (NSF = Narrow-space foraging bat, OSF = Open-space foraging bat, Edge-space foraging bat).

trail. During all recording nights and at each site, ambient temperature was recorded by a logger (see below), while wind speeds were measured about 5 km away at Münster University.

We used the software BatExplorer (version 2.1.10.1, Elekon AG, Luzern, Switzerland) to identify automatically species based on echolocation calls after adjusting the species library "European bats DE" of the BatExplorer to the local bat fauna (Table 1). Then, we analyzed

the accuracy of the automatic identification by manually checking a subset of recordings (SI Accuracy test). Based on the results of this accuracy test, we derived rules about when automatic species identifications may prove acceptable without further manual checks and when recordings have to be double-checked manually (SI Accuracy test).

Due to similar echolocation call features of species of the genera Nyctalus, Eptesicus, and Vespertilio, we classified all recordings from these species into the group of

open-space foraging bats (also called "NEV"). Similarly, we assigned all recordings from species of the genus *Myotis* and those of *Plecotus auritus* to the group of narrow-space foraging bats. All species of the genus *Pipistrellus* were lumped into the functional guild of edge-space foraging bats. Additionally, we counted the number of terminal buzzes in a recording as a proxy for foraging activity. A terminal buzz is a characteristic sequence of echolocation calls with a short duration, a decreasing interval length between subsequent pulses and decreasing peak frequency, indicating the attempted capture of an insect (Griffin, 1958).

2.5 | Light measurements

At each recording site, we tied a light sensor logger (HOBO light sensor; 1 lux precision; Datenlogger-Store, Eichstetten, Germany) to the lamppost a few cm above the Batlogger. From sunset to sunrise of a recording night, we measured the relative illuminance at 1 s intervals, which integrates over all present light.

2.6 | Statistical analyses

2.6.1 | Flight activity

Because bat species differ in the probability of being detected by ultrasonic detectors, we corrected for this factor (SI Correction for detection probability). Since we related the activity of bats to the time stamp of the light sensor, we decided to keep both data sets on the level of seconds. Thus, for the bat activity, we registered for each second of each recording night and site whether a member of the respective bat guild was active or not. We combined this activity data with the light-sensor data and thus, each second of bat activity presence or absence was also associated with an illuminance value. Then, we kept all time points that were associated with the lights being unambiguously at full power or off (n = 786,529) and discarded the other 19.8% of time points that were either associated with twilight or that were associated with LED being in a transition state between full power and off.

For the statistical analysis, we used the platform R (R Core Team, 2022, Version 4.2.2). First, we counted the number of seconds with guild-specific flight activity per hour and illustrated these using ggplot2 (version 3.4.0; Wickham, 2016). Second, we analyzed the effect of the light status, site, and hours of the night on the guild-specific presence/absence activity using linear mixed-effects models fitted with spaMM (version 4.1.0; Rousset & Ferdy, 2014). These analyses were conducted

after aggregating the data into an hourly presence/ absence activity for each given night, site, and light status (on or off) and accounted for the effect of temporal autocorrelation. For details see SI "Statistical analysis of bat activities."

2.6.2 | Foraging intensity

We also investigated the guild-specific foraging intensity in relation to the light status. For this, we summarized the guild-specific activity into sums of active seconds per hour and counted the number of terminal buzzes per hour. Then, we modeled the number of terminal buzzes (feeding) relative to the flight activity without terminal buzzes (non feeding) using linear mixed-effects models with the same predictors as those used for analyzing flight activity (SI "Statistical analysis of bat activities").

3 | RESULTS

3.1 | Light and climate data

During recording nights, mean ambient temperature ranged between 15°C and 19°C and wind speed between 1 and 5 m/s (Table S5). The percentage of lighting per hour varied considerably across the night and among sites as well as among recording nights (Figure S5). On an hourly basis, LED lights were on for a longer period early and late at night with shorter lighting periods around midnight (Figure S5). However, at some locations, LED lights were also on around midnight for cumulative periods of 20–25 min/h. Frequent use of the trail in the early evening and morning resulted in an almost constant lighting.

3.2 | Flight activity of bats

We recorded a total of 60,445 files of bat echolocation calls. The files ranged in length from 224 to 2536 s per night. With an average of 955 s of nightly activity, edge-space foraging bats were most active (interquartile range [IQR]: 772–2226), while narrow-space and open-space foraging bats were moderately active, showing a median of 164 (IQR: 53–342) and 113 (IQR: 68–271) activity seconds, respectively (Figure S6). In general, the activity of open-space foraging bats decreased during the night (Figure 1A), while edge-space foraging bats were most active early at night and shortly before dawn (Figure 1B). The activity of narrow-space foraging bats was relatively



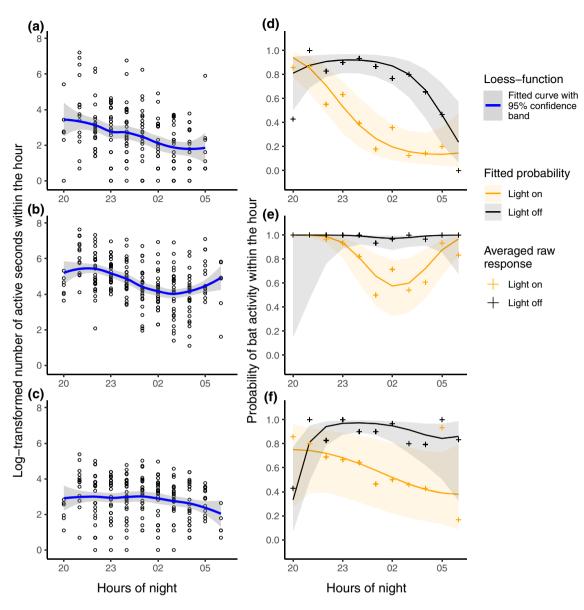


FIGURE 1 (a-c) Echolocation call activity of bats (log-transformed number of active seconds per hour, $n_{\text{open-space}} = 205$, $n_{\text{edge-space}} = 247$, and $n_{\text{narrow-space}} = 229$) across the night and (d-f) probability of activity (each guild: n = 489) in relation to lighting scheme (on/off) for the local functional guilds of open- (a and d), edge- (b and e), and narrow-space foraging bats (c and f) (Table 1). The blue line in (a-c) indicates a loess function (as $y \sim x$) that was fitted to the data, while the gray band represents the 95% confidence intervals. Please note that bat activity in (a-c) appears pulsed due to hourly aggregation, but was continuous. Mixed models fitted without the factor "site" were used to achieve a siteindependent illustration of the interactive effect between light and time of night (d-f).

stable, but declined gradually toward the end of the night (Figure 1C). We observed a significant effect of LED light in interaction with the time of night for open- and narrow-space foraging bats (Table S6). The probability of activity of edge-space bats was significantly affected by the LED lights, however not in significant interaction with the time of night. We could not model the interactive effect between the light and the site ID for the edgespace foraging bats, because species from this guild were so active that the factor combination of "no activity" and "light off" was non-existent at four out of five sites.

Overall, the probability of activity was higher for open- and narrow-space foraging bats when the LED lights were off compared to when they were on (Figure 1D,F). The strength of the effect varied across the night with no evident light avoidance during early night, and also late night in the case of open-space foraging bats. In edge-space foraging bats, we observed a higher acoustic activity in darkness compared to the LED light independent of the time of night (Figure 1E). However, the confidence intervals for the period of darkness were very broad at the beginning and at the end of the night.

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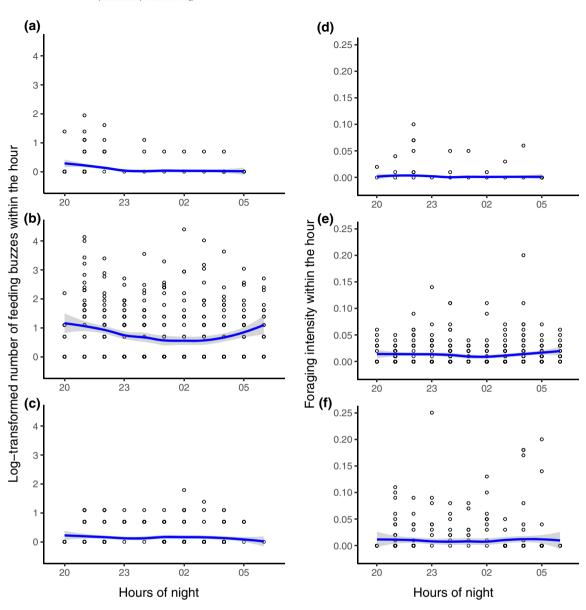


FIGURE 2 (a-c) Log-transformed number of terminal buzzes per hour (1 was added to all zero data points to avoid negative infinite values) and (d-f) the foraging intensity as the proportion of terminal buzzes versus flight activity per hour across the hours of the night for (a and d) open- (n = 288), (b and e) edge- (n = 494), and (c and f) narrow-space foraging bats (n = 366) (Table 1). Note that one data point at foraging intensity of 1 in (f) is not displayed to ensure a better representation of curves and to facilitate comparison among bat guilds. The blue line indicates a loess function (as $y \sim x$) that was fitted to the data, while the gray band represents the 95% confidence intervals. Please note that the number of terminal buzzes and the foraging intensity appear pulsed due to hourly aggregation, but were continuous.

3.3 | Foraging activity and intensity

Foraging activity ranged from 1 to 299 s with terminal buzzes per night (Figure S7). The log-transformed number of terminal buzzes across the night (Figure S7; Figure 2A–C) followed the flight activity patterns of functional guilds (Figure 1A–C). The foraging intensity—as the proportion of terminal buzzes per flight activity within a given hour—remained almost stable across the night for all three functional guilds (Figure 2D–F). For guild-specific models, we did not find a significant effect

of lighting (on/off), time of night (hour of night), and site ID on the degree of foraging relative to the flight activity (Table S6).

4 | DISCUSSION

We evaluated at a regional bicycle path if motiontriggered LED lighting is reducing the negative impact of ALAN on bats. Since cyclists used the trail at night most often after dusk and before dawn, motion-triggered LED lighting turned into an almost constant lighting during these periods. Overall, bats showed a negative response toward ALAN, yet patterns differed between guilds and during the course of a night. Early at night, LED light had no or only a minor adverse effect on open-space and narrow-space foraging bats, most likely because bats were in strong need of finding food, and thus more tolerant toward ALAN. Open-space foraging bats avoided ALAN strongest after around the first 2 h of feeding activity. In contrast, edge-space foraging bats avoided LED light around midnight, which mirrors the feeding activities of this guild early and late at night (Mariton et al., 2023). The observed pattern is also consistent with findings from common pipistrelles (P. pipistrellus) that show a behavior during light-averse commuting et al., 2015), but not during feeding (Hale et al., 2012; Lacoeuilhe et al., 2014; Laforge et al., 2019). In contrast to our prediction, open-space foraging bats avoided LED lighting, which supports recent findings, that bats of this functional guild may not necessarily tolerate ALAN even when commuting and foraging (Mariton et al., 2023; Voigt et al., 2020). The avoidance response of narrowspace foraging bats toward ALAN was less pronounced than expected (Voigt, Dekker, et al., 2021).

We acknowledge the following constraints and limitations of our study. The detection range of ultrasonic detectors for bats depends on the species' ultrasonic frequencies and sound intensities (Voigt, et al., 2021). Accordingly, we were more likely to record low-frequency calling open-space foraging than highfrequency calling edge-space foraging bats. Narrow-space foraging bats emit calls with the highest ultrasonic frequencies and the lowest sound amplitudes. We corrected for this effect in the number of seconds with bat activity. Nonetheless, the guild-specific sensitivity of microphones might have influenced the results on the modeled probability of activity per hour for the observed feeding guilds. Site-specific clutter may have excluded some species from foraging at street lights (Li & Wilkins, 2022), but we consider our approach to be comprehensive in sampling the acoustic activity of bats at street lights in representative habitats. Therefore, we do not consider site-specific clutter to have biased our results. Since the study sites were located close to the Dortmund-Ems-canal, we most probably also recorded Myotis daubentonii and M. dasycneme. Although these two species are edge-space trawling bats (Voigt, Dekker, et al., 2021), we lumped them with the guild of narrow-space foraging bats because we could not differentiate echolocation calls unambiguously between these two guilds. Possibly, patterns observed for bats of the genus *Myotis* are confounded by this pooling. We also acknowledge that we collected data only over a stretch of 1.5 km of a bicycle trail, which may not be representative

for the total 27 km length of the trail. Moreover, each type of site considered only involved one type of LED, so the effect of the site is confounded with the possible effect of slight difference in illumination. However, the two types of LED present similar correlated color temperature and intensity and we placed recording devices at sites that were most representative of the surrounding landscape. Finally, it is important to note that the response behavior of bats is most likely caused by a combination of changes in the lighting and noises produced by cyclists, but our experimental design cannot differentiate between these two variables.

In summary, bats from all guilds responded negatively to the motion-triggered LED lighting, yet this effect was absent or mild early at night and it varied between guilds. We conclude that motion-triggered LED lighting may potentially reduce light pollution at bicycle trails, yet the adverse effect of LED light on bats could be further reduced by using shorter light intervals. However, we highlight that even motion-triggered lighting substantially reduces the activity of bats of all studied feeding guilds during on-times as compared to dark periods. Therefore, we suggest using motion-triggered lighting as an alternative for permanent lighting where ALAN is truly needed, but we discourage the installation of any new lighting-including motion-triggered lighting-in areas that are not yet illuminated.

AUTHOR CONTRIBUTIONS

Olga Heim: Methodology; software; formal analysis; investigation; data curation; writing—original draft; writing—review and editing; visualization; supervision. Fernanda Chávez: Formal analysis; investigation; writing—review and editing. Alexandre Courtiol: Methodology; software; formal analysis; writing—review and editing; visualization. Frederike Paul: Investigation; writing—review and editing. Christian C. Voigt: Conceptualization; investigation; resources; data curation; writing-original draft; writing-review and editing; visualization; supervision; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that have been used in this study are accessible via the DOI 10.5281/zenodo.7797077 on the platform Zenodo.

ETHICS STATEMENT

This study did not involve any animal experiments.

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SUPPORTING INFORMATION

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

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