Environmental Pollution 307 (2022) 119552

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats☆

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ARTICLE INFO

Keywords:
Anthropogenic impacts
Bats
Light pollution
Urbanisation
Biodiversity conservation
Chiroptera
Foraging
ALAN

ABSTRACT

Increasing levels of artificial light at night (ALAN) are a major threat to global biodiversity and can have negative impacts on a wide variety of organisms and their ecosystems. Nocturnal species such as bats are highly vulnerable to the detrimental effects of ALAN. A variety of lighting management strategies have been adopted to minimise the impacts of ALAN on wildlife, however relatively little is known about their effectiveness. Using an experimental approach, we provide the first evidence of negative impacts of part-night lighting (PNL) strategies on bats. Feeding activity of *Myotis* spp. was reduced along rivers exposed to PNL despite no reduction in overall bat activity. We also provide the first evidence of negative effects of PNL on both feeding and activity for *Pipistrellus pipistrellus* which has previously been recorded feeding under artificial light.

Despite having considerable energy-saving benefits, we outline the potential negative impacts of PNL schemes for bats in riparian habitats. PNL are unlikely to provide desired conservation outcomes for bats, and can potentially fragment important foraging habitats leading to a breakdown of functional connectivity across the landscape. We highlight the potential dichotomy for strategies which attempt to simultaneously address climate change and biodiversity loss and recommend alternative management strategies to limit the impacts of ALAN on biodiversity.

1. Introduction

Rapidly increasing urbanisation is regarded as a major threat to global biodiversity and a significant factor in current and future species extinctions (McKinney, 2006; Mcdonald et al., 2008). Urban expansion can create profound ecosystem changes, including shifts in local climate, habitat loss, fragmentation, and the introduction of ecological stressors such as anthropogenic noise, artificial illumination, disturbance and chemical and physical pollutants (e.g. Markovchick-Nicholls et al., 2008; Francis and Barber, 2013; Stone et al., 2009, 2012; 2015; Russo and Ancillotto, 2015; Voigt et al., 2021). Artificial light at night (ALAN) associated with urban expansion ranks amongst the most important global threats to biodiversity conservation (Gaston et al., 2014; Gaston, Visser and Hölker, 2015; Davies and Smyth, 2018). ALAN is a global problem with nearly a quarter of the world's land surface impacted by light pollution (Falchi et al., 2016). Negative impacts of ALAN have been demonstrated in a wide variety of organisms ranging from individual physiological responses to changes in ecosystem functioning which may trigger ecological effects spanning trophic levels (Hölker et al., 2010; Bennie et al., 2016; Knop et al., 2017; Bennie et al., 2018). Artificially lit areas are growing by ~2% per year in both radiance and extent (Kyba et al., 2017), therefore it is imperative to understand the impact of ALAN and test the effectiveness of mitigation strategies to minimise impacts on wildlife.

Nocturnal taxa such as bats are highly vulnerable to the detrimental effects of ALAN due to their evolutionary adaptations for dark environments, likely as a result of protection from diurnal predators, either perceived or real (Rydell and Speakman, 1995; Mikula et al., 2016). Bats exhibit differential sensitivity to light that can be both species and scale dependent (Lacoeuilhe et al., 2014; Stone et al., 2015; Rowse et al., 2018). Some light types, including newer technologies such as white metal halide and LED (e.g. Stone et al., 2015; Russo et al., 2017), can provide increased foraging opportunities for fast-flying bat species due to the accumulation of insects around lights along with a light-induced impairment for insects to evade predation by bats (Minnaar et al., 2015; Wakefield et al., 2015, 2018; Voigt et al., 2021). These opportunistic bats may be able to forage and commute through illuminated areas as they are fast-flying, largely feed by aerial hawking on crepuscular prey

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☆ This paper has been recommended for acceptance by Prof. Pavlos Kassomenos.

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https://doi.org/10.1016/j.envpol.2022.119552
Received 15 February 2022; Received in revised form 7 May 2022; Accepted 26 May 2022

and are able to escape diurnal predation more effectively (Mathews et al., 2015). These factors when taken together thereby lessen the risk at increased light levels. Overall, most bat species avoid sites that are subjected to ALAN due to its negative effect on roosting and foraging behaviour, the composition and abundance of insect prey sources as well as the increased risk of predation (e.g. Stone et al., 2009, 2012; Davies et al., 2012; Lewanzik and Voigt, 2014; Pauwels et al., 2021). Such light-induced habitat fragmentation can reduce the quality and availability of habitat as well as functional connectivity across the landscape (Azam et al., 2015; Pauwels et al., 2021; Laforge et al., 2019).

Linear habitat features such as waterways are important for bats, both as commuting corridors linking roosts and foraging/drinking areas (Smith and Racey, 2008; Lacoeuilhe et al., 2016; Pinaud et al., 2018); as well as being important foraging habitats in their own right, due to the increased insect biomass associated with riparian vegetation and water surfaces (Lintott et al., 2015; Laforge et al., 2019; Todd and Williamson, 2019). Urbanisation has increased the amount of light pollution along waterways due to light trespass from buildings as well as an increasing prevalence of security and aesthetic light installations. Despite the ecological importance of waterways, there is a paucity of research on the impacts of ALAN on riparian biodiversity with recent studies only just starting to quantify the extent of light pollution in aquatic environments and its impact on bat behaviour and distribution as well as ecosystem functioning (Russo et al., 2017, 2019; Jechow and Hölker, 2019; Barré et al., 2020). Waterways are particularly important areas for specialist bat species such as *Myotis daubentonii* which rely on these habitats for foraging and represent a genus that has been found to be negatively impacted by ALAN at the local and landscape level (Spoelstra et al., 2018; Laforge et al., 2019; Voigt et al., 2021).

As new research on the negative impacts of ALAN on nocturnal fauna emerges, local authorities are utilising more flexible lighting technologies to both reduce energy consumption in order to address climate change targets and mitigate potential negative impacts of light pollution on biodiversity (Bennie et al., 2014; Azam et al., 2015). Several policy and management responses have been proposed such as altering the spectrum or intensity of artificial lighting, reducing light trespass and the implementation of part-night lighting regimes (Gaston et al., 2012; Spoelstra et al., 2017; Bolliger et al., 2020). Part-night lighting (PNL) involves switching off street-lights during periods of low human activity and has been implemented widely in urban areas throughout Europe, primarily motivated by the need to reduce public expenditure and carbon emissions (Gaston et al., 2013). However, activity for many nocturnal species (including bats) peaks at dusk which corresponds with high human activity and demand for lighting, therefore the effectiveness of PNL for reducing negative impacts on biodiversity is questionable (Gaston et al., 2012). Simulations of PNL regimes (Day et al., 2015) and studies assessing the effectiveness of existing PNL regimes indicate they fail to mitigate the negative effects of ALAN for most bat species, despite some success for late-emerging species (Azam et al., 2015). However, previous studies have not assessed the impacts of PNL on feeding behaviours, nor have they focused on specific aquatic habitats or bat assemblages. Waterways represent a habitat of particular importance to a number of slow-flying bat species (e.g. *Myotis* spp.) that have echolocation and wing morphology adapted for cluttered, low-light environments, yet these habitats are increasingly subjected to ALAN (Norbery and Rayner, 1987; Stone et al., 2015). Increased light levels around these habitats may compromise crucial foraging areas as well as fragmenting dark corridor networks and limiting functional connectivity. For trawling bats (i.e. those who specialise in foraging over water) such as M. *daubentonii* echolocation plays a crucial role in detecting the water surface and surrounding environment in order to execute safe manoeuvres (Siemers and Swift, 2006; Russo et al., 2012). Under artificial illumination, bats rely more on vision than in the dark which reduces their ability to avoid obstacles (Orbach and Fenton, 2010). This shift in sensory ecology, along with higher potential predation risk could impair their ability to successfully forage which could have severe negative impacts for both individual bats and populations. This is especially important for those species who have low aspect ratios and wing loading (e.g. *Myotis* spp.), traits that correlate with an already heightened extinction risk (Jones et al., 2003).

To our knowledge no study has experimentally tested the effect of PNL on bat communities along waterways in riparian habitats or assessed its impact on specific behaviours such as feeding (despite some studies on the effect of ALAN on bat drinking behaviours, see Russo et al., 2017, 2019). In this study, we used an experimental approach to assess the impact of artificial lighting on bat activity and feeding behaviour in riverine ecosystems. We compared activity levels of four bat species/groups (*Myotis* spp., *Nyctalus/Eptesicus* spp. *P. pipistrellus*, *P. pygmaeus*) under dark (unlit), full-night lighting and different durations of PNL.

We hypothesised that bats would respond to PNL regimes according to species specific adaptations for flight and foraging (Stone et al., 2012; Zeale et al., 2016). We predicted that activity would be reduced during full-night lighting but activity would be higher during PNL for slower-flying species (i.e. *Myotis* spp.) due to the overall reduction in illuminated hours in which bats would perceive an increased predation threat (Rydell and Speakman, 1995). Furthermore, as *Myotis* spp. emerge later from roosts (Jones and Rydell, 1994) there is less potential overlap between bat activity and illuminated hours under PNL compared to full-night lighting. In contrast, we predicted no effects of light treatments on the activity of fast-flying species (i.e. *Pipistrellus* spp., *Nyctalus/Eptesicus* spp.) as operational hours for both PNL and full-night lighting would align with peak emergence and activity for these species (Spoelstra et al., 2017; Russo et al., 2018). In addition, fast-flying species are better adapted to increased light-levels due to their reduced perceived light-dependent predation risk and will often utilise illuminated sites opportunistically (Mathews et al., 2015).

2. Material and methods

Lighting experiments were conducted along eight unconnected waterways in south west England (Bristol, Gloucestershire and Somerset; mean river width 5.5 m, SD = 2.39 m, range = 3–10 m, n = 8) between August and October 2020 (Fig. 1a). Each experiment lasted for four nights per site and comprised of a single dark unlit (control) treatment on night one followed by one of three lit treatments whereby lights were switched on at sunset for either 2 h, 4 h or for the full night until sunrise (Table 1). The order of the lit treatments was randomized between sites to control for order effects and sites were separated by a minimum of 10 km to ensure collection of independent samples.

Sites were located within dark (<0.05 lux) agricultural landscapes consisting predominantly of pasture, semi-natural woodland/scrub and managed grassland. Waterways were illuminated with three portable cool white RL20K LED Floodlights (Right Light, Chesterfield, Derbyshire, UK) that consist of 40 × 3 W high-powered LEDs powered by a 52 Ah Li-ion battery and dimmed to an output of 13,000 lumens (Pulse-width modulation 70 kHz). This LED lamp type was chosen due to its wide commercial usage for outdoor illumination owing to its energy efficiency and perceived benefit to nocturnal biodiversity (Davies and Smyth, 2018; Kyba et al., 2017). The lighting system did not emit any audible nor ultrasonic noise (assessed with Anabat Swift Full Spectrum Bat Recorder for a full-nights illumination) and therefore any potential noise effects as a result of the experimental protocol could be omitted from the study. At each site lights were placed 2 m from the top of the river bank and mounted 3 m above the ground on portable columns and directed downwards. Light columns were placed 5 m apart from each other and we ensured that the entire cross section of the experimental stretch of river was illuminated. Due to the variation of lighting unit distances and orientations when deployed adjacent to waterways, lamp placement was ascertained based on overall illuminance (lux) (Fig. 1c).

Illuminance (in lux) was measured 1 h after sunset using a T-10 illuminance metre (Konica Minolta Sensing Inc, Osaka, Japan) held

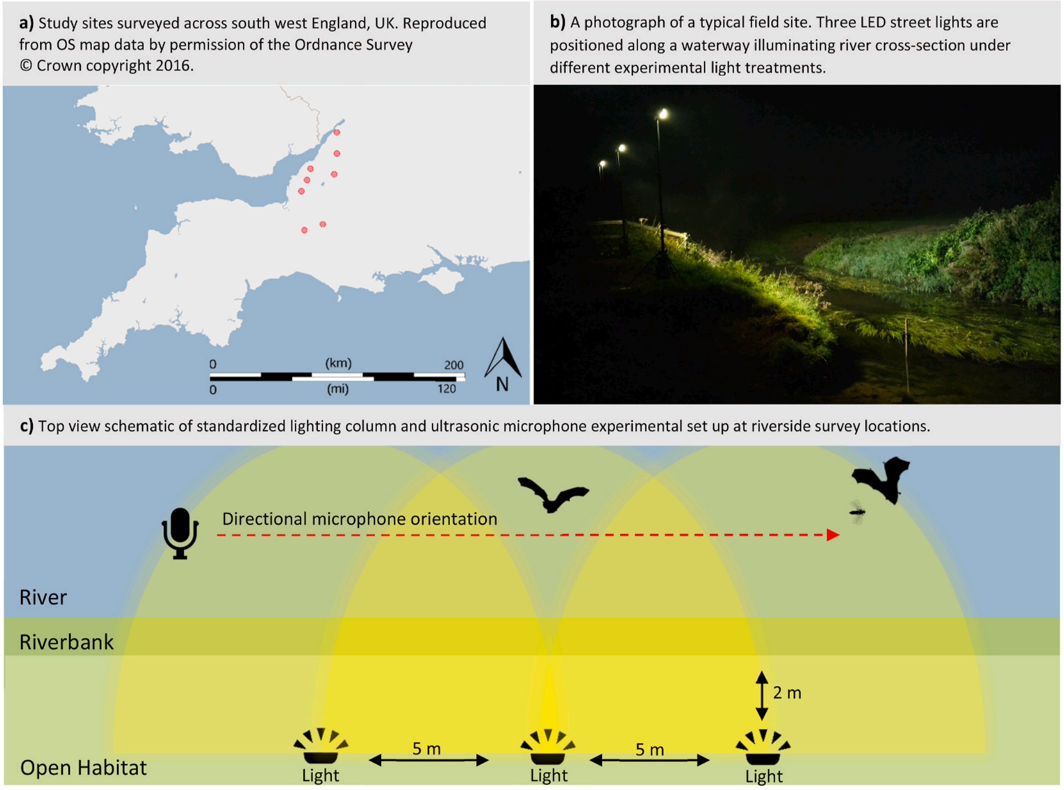


Fig. 1. A) Location of study sites surveyed within the south west of England, UK, B) a photograph of a typical field site and C) a top view schematic of standardized lighting columns and ultrasonic microphone experimental set up. Light columns were positioned at a height of 3 m and orientated downward toward river corridor.

Table 1
Experimental treatment regime conducted at waterways (n = 8). The sequence of light treatments was randomized among nights two to five to control for any potential order effects.

Night	Treatment	Description
1	Control (unlit)	Detectors installed at waterway, no lighting treatment
2	LED	Detectors installed, lighting units installed and illuminated for durations of 2-hr, 4-hr or full night. Sequence of lit treatments randomly selected at each site.
3	LED	As night 2 with second randomized light treatment.
4	LED	As night 2 with remaining light treatment.

horizontally 2 m from the edge of the river bank and 1 m above the water's surface in front of the lighting columns. Waterways were illuminated to a mean light intensity of 44.8 ± 6.8 lux which is in the range used during previous experiments utilising white LED (Stone et al., 2012; Zeale et al., 2018) and is equivalent to that emitted by street-lighting in public areas in the UK (Stone et al., 2009). Field work was only conducted in suitable conditions in accordance with Bat Conservation Trust guidance (i.e. sunset temperature 10 °C or above, no rain or strong wind). Mean nightly temperatures (°C) were recorded using in-built thermometers within the bat detectors and mean nightly wind speed (mph) and total nightly rainfall (mm) was obtained from Met Office weather stations (http://www.metoffice.gov.uk) within 15 km of each site (mean distance 10.24 km, SD 2.6 km).

Bat activity was recorded from 30 min before sunset to 30 min after sunrise using Anabat Swift Full Spectrum Bat Recorders (Titley Scientific, Brendale, QLD, Australia) with directional microphones orientated centrally down the river corridor to limit recordings from bats flying in adjacent habitats. Echolocation calls were analysed in Anabat Insight v.1.9.2 (Titley Scientific, Brendale, QLD, Australia) and identified manually using call parameters as described in Russ (2012). Mean number of bat passes per treatment night was used as an index of relative bat activity with a single bat pass identified as a continuous sequence from a passing bat containing two or more echolocation pulses within 1 s of each other (Fenton, 1970; Walsh and Harris, 1996). Bat passes from multiple bats of the same species were identified using distinguishable differences in pulse interval and/or peak frequency of overlapping echolocation pulse sequences. Calls were grouped into four species/species groups: *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus*, *Myotis* spp. and *Nyctalus/Eptesicus* spp. with rarely recorded species such as *Rhinolophus ferrumequinum, Rhinolophus hipposideros, Barbastella barbastellus* and *Plecotus* spp. (total 185 bat passes; 0.7% of overall bat activity), not included in subsequent analysis.

Relative feeding activity of recorded bat species was examined by identifying diagnostic terminal phase calls (feeding buzzes) within recordings calculated as the ratio of feeding buzzes to total number of passes per species per night (buzz ratio) (Vaughan et al., 1997). A buzz ratio of one indicates that on average every bat pass contains a feeding buzz.

All analyses were performed in R v.4.0.4 (R Core Team, 2012) using the significance level $p < 0.05$. Repeated measures general linear models (RMGLMs) were used to test for differences between environmental variables with treatment conditions fitted as a within-factor effect. As there were no significant differences in mean nightly temperature ($F_{3,21} = 0.97$, $n = 8$, $P = 0.43$), total nightly rainfall ($F_{3,14} = 0.50$, $n = 8$, $P = 0.69$) and mean nightly wind speed ($F_{3,21} = 1.60$, $n = 8$, $P = 0.22$) across treatments these variables were excluded from further analyses to achieve model simplification. We fitted RMGLMs to examine the effect of light treatment on bat activity (number of bat passes per night per species/species group). Counts of bat passes for each species group were log transformed to meet assumptions of homoscedasticity and normality. Light treatment was fitted as a within-factor effect with 4 levels corresponding to the light treatment types (Unlit, 2-h, 4-h and full night). Species/species group were then assessed to examine the effect of lighting treatment of bat feeding activity. RMGLMs with log transformed data were fitted for *Myotis* spp. and *Nyctalus/Eptesicus* spp. whilst *P. pipistrellus* and *P. pygmaeus* were tested using Friedman's non-parametric ANOVA due to their non-normal distribution despite data transformation attempts. RMGLM statistics are presented as *F* and *p* values with effect sizes presented as Cohen's d or Kendall's W in the case of non-parametric ANOVAs.

3. Results

3.1. Bat activity

A total of 25,178 bat passes belonging to seven species/species groups were recorded during the 32 nights of monitoring. The majority of echolocation recordings belonged to *P. pygmaeus* (18,119 passes; 71.9%) followed by *P. pipistrellus* (3837 passes; 15.2%), *Myotis* spp. (1964 passes; 7.8%), *Nyctalus/Eptesicus* spp. (1073 passes; 4.3%) with *Rhinolophus* spp. and *Plecotus* spp. <1% of species recorded. A total of 15,491 feeding buzzes were recorded from six species/species groups comprising *P. pygmaeus* (12,736 buzzes; 82.2% buzz ratio 0.70) followed by *P.pipistrellus* (1206 buzzes; 7.8% buzz ratio 0.31), *Myotis* spp. (1362 buzzes; 8.8% buzz ratio 0.69), *Nyctalus/Eptesicus* spp. (167 buzzes; 1.1% buzz ratio 0.16) with *Rhinolophus* spp. and *Plecotus* spp. making up the remaining <1% of feeding buzzes recorded.

We found statistically significant effects of light on bat activity for *Myotis* spp., *P. pygmaeus* and *P. pipistrellus*. *Myotis* spp. activity declined by an average of 71% along waterways under full-night lighting compared to unlit nights (P = 0.033; Table 2; Fig. 2a), but did not decline significantly under PNL (2 or 4-h PNL treatments) compared to unlit nights (2- hours P = 0.88 4-h P = 0.630; Table 2; Fig. 2a). *Myotis* spp. activity recorded under full-night lighting treatment was significantly lower compared to PNL (2- hours P = 0.044; 4-h P = 0.011; Table 2, Fig. 2a) with no significant differences between the 2-h and 4-h PNL treatments. In addition, we found temporal variation in *Myotis* spp. activity between unlit and lit treatments over the course of the night (Fig. 3). During unlit nights, peak bat activity occurred between 0 and 2 h after sunset (35% of mean bat passes) whereas peak bat activity for both the 2-h and 4-h PNL treatments corresponded with hours following the lights being switched off (3–5 h after sunset; 31% mean bat passes and 4–6 h after sunset; 28% mean bat passes respectively). In contrast, under full-night lighting treatments bat activity was highest 0–2 h after sunset (32% of mean bat passes) with no further peaks of activity throughout the night.

Table 2
Results for bat activity (mean bat passes) and relative feeding activity (mean buzz ratio) of *Myotis* spp., *P. pygmaeus*. and *P. pipistrellus* and *Nyctalus/Eptesicus* spp. species from repeated measures general linear models and within-subject differences during post-hoc comparisons.

	Bat Activity (passes)			Feeding Activity (Buzz Ratio)		
Myotis spp.	*F*	*d*	*P*	*F*	*D*	*P*
Treatment	3.040	0.932	0.052	3.923	1.2729	0.023*
Control (Unlit) vs 2 h		0.032	0.888		0.160	0.692
Control (Unlit) vs 4 h		0.105	0.630		0.989	0.048*
Control (Unlit) vs Full-night		0.544	0.033*		1.410	0.008*
2 h vs 4 h		0.130	0.534		0.819	0.103
2 h vs Full-night		0.474	0.044*		1.249	0.018*
4 h vs Full-night		0.619	0.011*		0.550	0.401
P.pygmaeus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	3.383	0.983	0.037*	3.32	0.415	0.019*
Control (Unlit) vs 2 h		0.250	0.105			0.068
Control (Unlit) vs 4 h		0.187	0.233			0.059
Control (Unlit) vs Full-night		0.179	0.253			0.017*
2 h vs 4 h		0.450	0.008*			0.961
2 h vs Full-night		0.077	0.612			0.281
4 h vs Full-night		0.381	0.026*			0.761
P.pipistrellus	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	2.817	0.969	0.068	3.077	0.440	0.026*
Control (Unlit) vs 2 h		0.600	0.028*			0.011*
Control (Unlit) vs 4 h		0.198	0.972			0.690
Control (Unlit) vs Full-night		0.539	0.158			0.073
2 h vs 4 h		0.874	0.026*			0.196
2 h vs Full-night		0.031	0.369			0.912
4 h vs Full-night		0.755	0.149			0.550
Nyctalus/Eptesicus spp.	***F***	***d***	***P***	***F***	***W***	***P***
Treatment	0.679	0.44	0.575	1.000	0.125	0.392
Control (Unlit) vs 2 h		0.100	0.658			0.281
Control (Unlit) vs 4 h		0.315	0.205			1.000
Control (Unlit) vs Full-night		0.037	0.870			0.787
2 h vs 4 h		0.202	0.399			0.181
2 h vs Full-night		0.066	0.780			0.423
4 h vs Full-		0.285	0.266			0.423

There was no significant effect of any light treatments on *P. pygmaeus* activity compared to unlit nights. However, significantly more *P. pygmaeus* passes were recorded (+164%) under the 4-h PNL treatment compared to 2-h PNL (P = 0.008; Table 2; Fig. 2c) which also represented an average 191% increase compared to full-night lighting treatments (P = 0.026; Table 2; Fig. 2c). *Pipistrellus pipistrellus* activity declined by an average of 79% under 2-h PNL compared to unlit nights (P = 0.028; Table 2; Fig. 2e) but no significant differences in activity were recorded during the 4-h PNL or the full-night lighting treatments compared to unlit nights (Table 2; Fig. 2e). A significant increase in *P. pipistrellus* activity was recorded for the 4-h PNL compared to the 2-h (P = 0.026; Table 2; Fig. 2e).

We found no statistically significant effects of any light treatments on *Nyctalus/Eptesicus* spp. activity compared to unlit nights (P = 0.575; Table 2).

3.2. Bat feeding activity

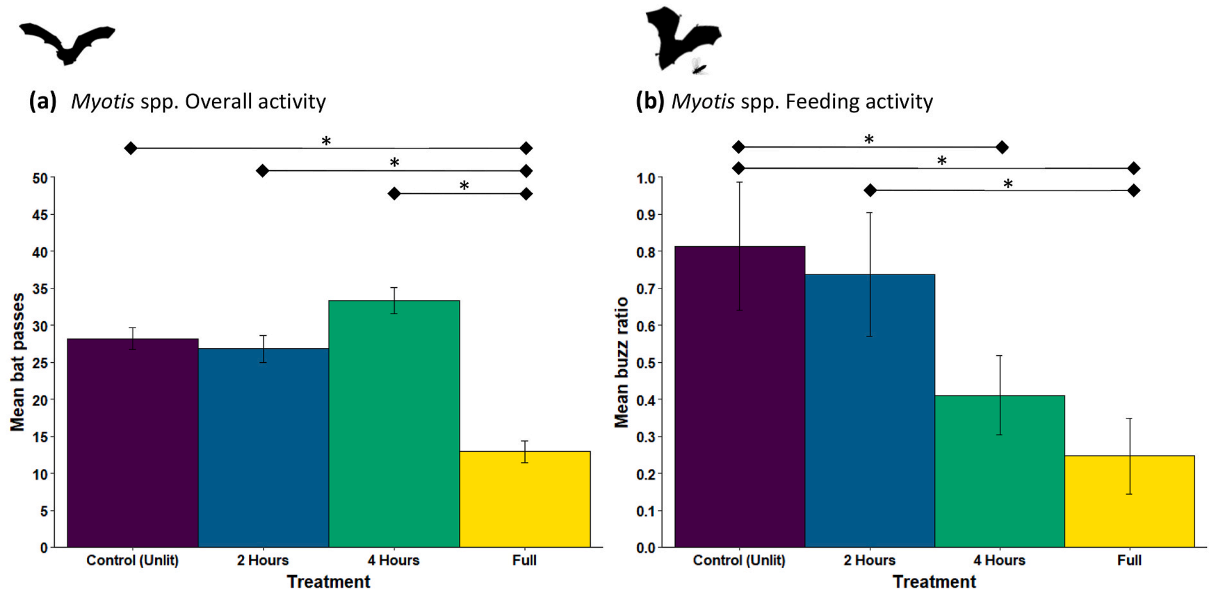
Relative feeding activity (buzz ratio) was lower for *Myotis* spp., *P. pygmaeus* and *P.pipistrellus* species under all lit treatments with significant (or marginally significant) negative effects recorded during both part-night and full-night lighting treatments. Relative feeding activity for *Myotis* spp. declined as the number of hours under lit treatments increased. Buzz ratios declined by an average of 50% during the 4-h PNL (P = 0.048; Table 2; Fig. 2b) and by 70% in full-night lighting treatments (P = 0.008; Table 2; Fig. 2b) compared to unlit nights. *Myotis* spp. feeding activity was significantly higher during 2-h PNL compared with full-night lighting treatments (P = 0.018; Table 2; Fig. 2b).

P. pygmaeus feeding activity declined by an average of 75% during full lit treatments compared to unlit nights (P = 0.017; Table 2; Fig. 2d). Marginally significant reductions in feeding activity were recorded in both 2-h and 4-h PNL treatments compared to unlit nights (P = 0.068 and P = 0.059 respectively; Table 2; Fig. 2d). *P.pipistrellus f*eeding activity declined by an average of 77% during 2-h PNL compared to unlit nights (P = 0.011; Table 2; Fig. 2f) and marginally significant reduction in feeding activity were recorded under full-night lighting compared to unlit nights (P = 0.073; Table 2; Fig. 2f).

We found no statistically significant effects of any light treatments on *Nyctalus/Eptesicus* spp. feeding activity compared to unlit nights (P = 0.392; Table 2).

4. Discussion

To our knowledge this is the first study to experimentally test the effectiveness of part-night LED lighting schemes along waterways on the activity and behaviour of a bat assemblage. Here we show that light treatment had a significant or marginally-significant effect on the overall activity and feeding behaviour of a riparian bat assemblage compared to unlit nights. Furthermore, we show species-specific responses in overall activity and feeding behaviour by bats to different light treatments. This is of particular importance as LEDs are rapidly

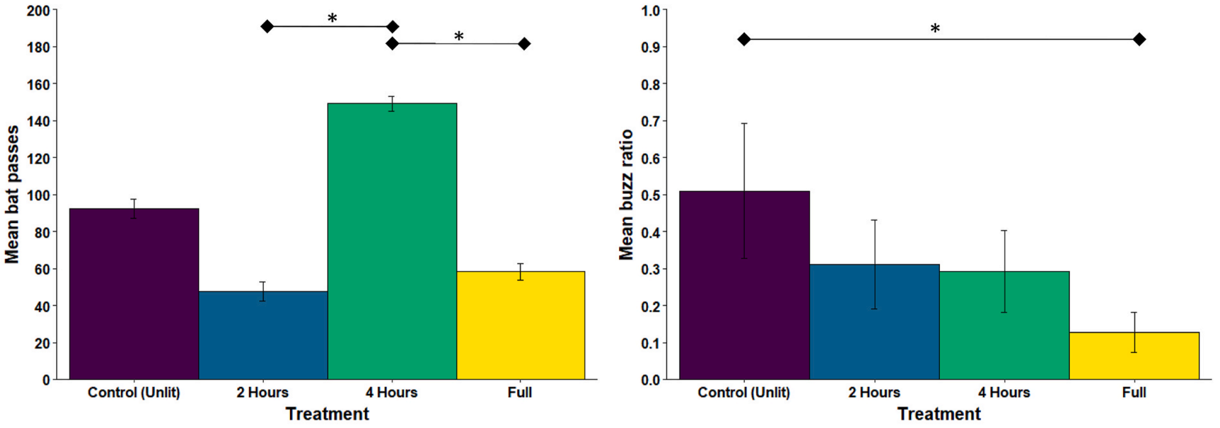


(a) *Myotis* spp. Overall activity

(b) *Myotis* spp. Feeding activity

(c) *P.pygmaeus* Overall activity

(d) *P.pygmaeus* Feeding activity



(e) *P.pipistrellus* Overall activity

(f) *P.pipistrellus* Feeding activity

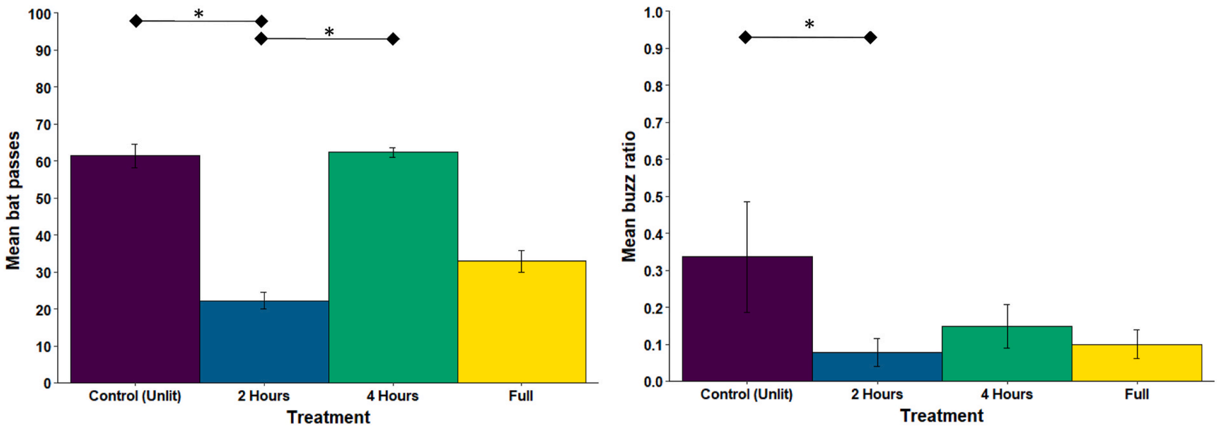


Fig. 2. Bat activity (Mean bat passes) and relative feeding activity (Mean buzz ratio) by (a,b) *Myotis* spp. (c,d) *P.pygmaeus*. and (e,f) *P.pipistrellus* along experimental waterways during dark control and three light treatment nights. Data are presented as mean ± SEM with significant within-subject differences during post hoc tests highlighted.

replacing older lighting technologies and measures such as part-night lighting schemes are already being readily adopted in a bid to limit light pollution and mitigate the harmful impacts of urbanisation. Our results therefore demonstrate that part-night lighting still presents a risk to wildlife and appropriate assessment and mitigation should be deployed prior to their use.

Slow-flying *Myotis* spp. are generally considered to be less tolerant of lighting and therefore the reduction in relative activity under full-night

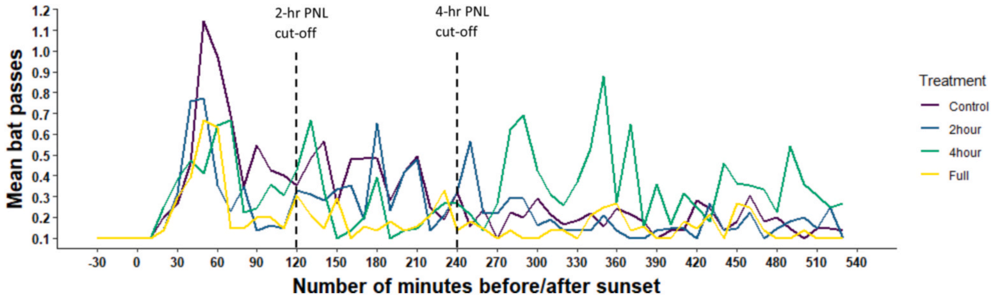


Fig. 3. Average number of *Myotis* spp. registrations recorded per 10-min period before and after sunset under control (unlit), 2-h PNL, 4-h PNL and full-night lighting treatments.

lighting treatments was expected and is consistent with previous studies using both high pressure sodium (HPS) and LED lighting systems (e.g. Azam et al., 2015; Stone et al., 2012; Spoelstra et al., 2017). Overall activity under full-night light treatments was significantly lower in comparison to both unlit nights and PNL treatments. This suggests that, to some extent, PNL does limit the negative impacts of ALAN over the course of the night by allowing *Myotis* bats to have peaks of activity later in the night after lights are switched off (Fig. 3).

Superficially this may seem to highlight the efficacy of PNL as a mitigation method, however our results show that this is not true for all behaviours. Whilst no negative impact in overall *Myotis* spp. activity for PNL treatments was recorded, a 50% reduction in relative feeding activity occurred under the 4-h part-night lighting treatment suggesting that PNL reduces the feeding activity window for these species.

Despite *Myotis* species being grouped together in a genera-wide category due to the similarities in call structure between species within the same genus (Schnitzler and Kalko, 2001), it is likely that the majority of the calls were of *M. daubentonii* given that this species is widespread throughout the study area and strongly associated with riverine habitats (Warren et al., 2000). *M. daubentonii* primarily feed on insects of the orders Diptera (most frequently those of the Chironomidae family), Trichoptera and Lepidoptera (Vaughan et al., 1997; Vesterinen et al., 2013; Todd and Waters, 2017) whose activity peaks in the evening and early part of the night (Holzenthal et al., 2015; Vebrová et al., 2018). Therefore, a delay in bat activity as a result of ALAN can create a mis-match with prey availability leading to an overall reduction in feeding. Previous studies assessing the effect of artificial lighting on *M. daubentonii* show that changes in food availability do not explain the decrease in foraging seen for this species under lit treatments as ALAN does not induce any significant qualitative or quantitative changes in typical prey abundance or availability (Russo et al., 2019).

The response of *Myotis* spp. to ALAN supports findings by Kuijper et al. (2008) who found that feeding activity of *M. dasycneme* reduced by more than 60% under lit conditions despite overall activity levels remaining unaffected and insect prey being in higher abundance. Our results suggest that *Myotis* species are more light-sensitive when foraging compared to commuting, likely due to their longer exposure to illumination and subsequent predation threat (Russo et al., 2019). This is consistent with findings by Spoelstra et al. (2018) who found that commuting *M. daubentonii* did not respond strongly to any of the four different light treatment combinations deployed in a choice experiment. Disturbances to bat foraging sites caused by ALAN can significantly impact the fitness and reproductive success of light-sensitive species especially *Myotis* spp. who are particularly sensitive to habitat fragmentation (Duvergé et al., 2000; Safi and Kerth, 2004; Frey-Ehrenbold et al., 2013) and are typically of greater conservation concern than their light-opportunistic counterparts (Lacoeuilhe et al., 2014). The impacts of ALAN along waterways can be especially detrimental for specialist trawling bats who rarely move out of the river corridor whilst hunting (Nardone et al., 2015) and therefore any illumination constitutes a potential barrier, fragmenting their foraging habitat.

A similar reduction in *Myotis* spp. feeding activity was not found under the 2-h PNL treatment, suggesting that a mitigation scheme of this duration may have little negative impact on overall activity and feeding for *Myotis* bats. This may be due to the limited overlap of operational lighting and peak activity windows as a result of their later emergence times (Mean emergence times for *M. daubentonii* from previous studies were found to be between 40 min and 73 min after sunset (see Warren et al., 2000; Jones and Rydell, 1994). Despite the potential benefits of shorter PNL schemes (i.e. 2-h PNL) to light-sensitive bats, this mitigation option is unlikely to be adopted as the hours in which street lighting would be turned off are also those most important to humans (Gaston et al., 2012).

Whilst our study showed no significant differences in overall activity between PNL treatments and unlit nights for *Myotis* spp., there is likely to be a species-specific response from this genus based on habitat preference and foraging guild. Species such as *M. daubentonii, M. capaccinii* and *M. dasycneme* constitute edge-space foragers that uses stretches of open water for commuting and foraging and therefore are likely to be more tolerant of ALAN than their narrow-space foraging counterparts who consistently avoid areas subjected to ALAN (Voigt et al., 2021). This differential response to ALAN by *Myotis* spp. is supported by findings from Azam et al. (2015) and our own study, showing that *Myotis* spp. in terrestrial ecosystems are more sensitive to PNL than those is aquatic or riparian ecosystems. These forest-dwelling bat assemblages are more likely to comprise narrow-space-foraging species such as *M. emarginatus* or *M. nattereri* who will avoid both commuting and foraging areas that are subjected to ALAN (Voigt et al., 2021).

Unlike *Myotis* spp. both *P.pipistrellus* and *P. pygmaeus* showed different overall activity responses to PNL dependent on the duration for which the lights were operational, with both species being significantly more active under the 4-h than the 2-h PNL treatment (*P. pygmaeus* 164% increase; *P.pipistrellus* 110% increase). For *P. pygmaeus* this also represented a significant 66% increase over full-night lighting treatments and may indicate a temporal delay in exploratory behaviour around these novel light sources after initial avoidance behaviour.

However, as with *Myotis* spp., changes in feeding activity do not always mirror changes in overall activity, as even though an increased amount of activity was recorded for both *P.pipistrellus* and *P.pygmaeus* under 4-h PNL, feeding activity of both species was lower for all light treatments when compared to unlit nights. These findings are particularly important for this species group as while some previous studies highlight the negative impacts of ALAN on *Pipistrellus* spp. feeding behaviour (see Kerbiriou et al., 2020; Barré et al., 2020), it is commonly assumed that Pipistrelle bats represent a species group that benefit from increased feeding opportunities at artificial lighting due to increased insect biomass (e.g. Perkin et al., 2014; Wakefield et al., 2018; Spoelstra et al., 2017; Zeale et al., 2018). Our results add to the body of evidence highlighting the negative impacts of ALAN on *Pipistrellus* species through reducing feeding activity and may suggest that *Pipistrellus* spp. are responding to urbanisation through increasing individual flight speed through illuminated areas and transiting at commuting rather than foraging speed (Grodzinski et al., 2009; Polak et al., 2011; Barré et al., 2020). Our results therefore raise important questions about negative impacts of ALAN on supposedly "light-opportunistic" species and the implications for individual fitness and reproductive success.

Lastly, we found no significant effects of any light treatments on *Nyctalus/Eptesicus* spp. overall bat activity or foraging which is consistent with our hypothesis for fast-flying aerial hawking bat species that are known to emerge at dusk to coincide with crepuscular activity peaks of their prey species (Jones and Rydell, 1994). For this species group, prey availability rather than light levels will be a key driver of their activity patterns, due to their increased ability to escape diurnal predators, and they may even forage opportunistically at illuminated sites in order to exploit swarms of insects attracted by street lights (Mathews et al., 2015; Laforge et al., 2019; Voigt et al., 2020).

5. Conclusions

With increasing attention paid to the financial and environmental impacts of light pollution, the use of flexible management approaches such as PNL are an attractive option to limit the harmful impacts of ALAN on the nocturnal landscape. However, despite being a valuable approach in terms of reducing carbon emissions and public sector costs, we demonstrate that PNL schemes are unlikely to provide desired biodiversity benefits especially for bats due to species-specific impacts on activity and feeding. The use of PNL is particularly limited for light-sensitive bat species due to the standoff between humans' requirement for light and bats requirement for darkness occupying the same space in time. Therefore, if the aim it to limit the negative impacts of ALAN on biodiversity, it would be more beneficial to pursue alternative management strategies such as reducing light trespass, changing the intensity or spectrum of lighting and increasing dark corridor networks (Gaston et al., 2012; Pauwels et al., 2021).

Author declaration

- We the undersigned declare that this manuscript is original, has not been published before and is not currently being considered for publication elsewhere.
- We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.
- We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.
- We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.
- We understand that the Corresponding Author is the sole contact for the Editorial process (including Editorial Manager and direct communications with the office). He is responsible for communicating with the other authors about progress, submissions of revisions and final approval of proofs. We confirm that we have provided a current, correct email address which is accessible by the Corresponding Author and which has been configured to accept email from biomaterials@online.be.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We wish to thank all those farmers and landowners who provided advice and access on the location and suitability of waterways for surveying. We also thank Eleanor Delaney for her assistance during the field work.

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