



Wooded streets, but not streetlight dimming, favour bat activity in a temperate urban setting

Christopher Stanley ^{1*} Joanna Maria Bagniewska,^{1,2}
Ada Grabowska-Zhang^{1,2} and Thomas Hesselberg ^{1,3,*}

¹Department for Continuing Education, University of Oxford, Oxford OX1 2JA, UK, ²Department of Life Sciences, College of Health, Medicine and Life Sciences, Brunel University London, London, Uxbridge UB8 3PH, UK and ³Department of Biology, University of Oxford, Oxford OX1 3SZ, UK

*Corresponding author. E-mail: christopherstanley@outlook.com (C.J.S.); thomas.hesselberg@biology.ox.ac.uk (T.H.)

Submitted: 8 December 2022; Received (in revised form): 25 May 2023. Accepted: 1 June 2023

Abstract

Urbanization damages biodiversity, reducing people's connection to nature and negatively impacting the survivability of local species. However, with small adjustments, the damage could be mitigated. In temperate regions, several bat species inhabit urban areas, and with urbanization set to increase, adapting urban areas to improve their suitability for bats is imperative. Therefore, we investigated if wooded streets and streetlight dimming in an urban setting influenced bat activity. Static bat detectors were used to compare wooded versus non-wooded, and bright versus dim streets in Leicester, UK, on predominantly residential streets. The collected calls were quantified into bat activity (passes per night). Six species were identified, but the common pipistrelle (*Pipistrellus pipistrellus*) was dominant, making up 94.1% of all calls, so it was the sole species included in the statistical model. Wooded streets had significantly higher bat activity than non-wooded streets, but bright and dim streets were not significantly different. The results suggest that wooded streets were being used as green corridors, with common pipistrelles possibly following them to conceal themselves from predators, such as the tawny owl, and the proliferation of wooded streets in urban areas could allow the formation of better-connected populations. Streetlight dimming did not affect bat activity, but no light-averse bats were detected, likely because even the most dimmed streets deterred them despite street lighting increasing food availability by attracting insects. Therefore, an alternate solution, such as part-night lighting, may be required to increase the suitability of urban areas to light-averse species.

Key words: artificial light at night (ALAN), bat activity, bat conservation, streetlight dimming, green corridors, light-emitting diode (LED) streetlights

Introduction

Urban areas can be challenging for wildlife to inhabit, with many factors reducing their suitability (Grimm et al. 2008), including roads and traffic (Fahrig et al. 1995; Benítez-López, Alkemade, and Verweij 2010; Claireau et al. 2019), fragmented and species-poor habitats (Krauss et al. 2010), as well as air quality, noise and light pollution (Kunc and Schmidt 2019; Murray et al. 2019; Owens et al. 2020). The UK is highly urbanized, with 83.9% of its population in urban areas, following an

almost 3% increase over the past decade (O'Neill 2021). Therefore, enhancing urban spaces for wildlife is vital in aiding population viability and species survival, and helps connect people to nature, with associated health benefits (Shwartz et al. 2014; Carrus et al. 2015; Wood et al. 2018). Bats are valuable in many environments, acting as pollinators, as pest control agents, and importantly, as indicator species (Jones et al. 2009; Kunz et al. 2011; Russo et al. 2021). Studies into drivers of bat population change (Burns et al. 2016) and the habitat selection of bats in urban and surrounding areas (Gili et al. 2020) indicate

that urbanization likely has a negative impact on bats, even if there are gaps in the evidence (Browning et al. 2021). Therefore, with the global urban land area set to triple between 2000 and 2030 (Seto, Güneralp, and Hutrya 2012), it is imperative to adapt urban areas to improve their suitability for bats, despite overall bat populations appearing to be stable or increasing in the UK (Barlow et al. 2015) and Europe (van der Meij et al. 2015).

The increasing density of urban landscapes is leading to their green spaces inevitably becoming fragmented (Dallimer et al. 2011), reducing their ability to support wildlife and bats (Hale et al. 2012). Wooded streets can act as green corridors connecting these fragmented green spaces, with Fernández-Juricic (2000) finding wooded streets were used by numerous bird species, with their use increasing when adjacent to urban parks. Bats are known to benefit from urban green spaces, having higher activity in large parks than in residential areas (Avila-Flores and Fenton 2005), and following linear features when commuting between habitats (Verboom and Huitema 1997). Therefore, their use of wooded streets as green corridors is feasible. Oprea et al. (2009) investigated this in Vitória, Brazil, concluding that bats did not use wooded streets as green corridors, but the species present differ from those in the temperate regions. Therefore, an investigation of this within the UK is timely, providing evidence towards bat conservation and wildlife-benefitting planning reforms. For example, in the UK, a 'Tree-lined Streets Bill 2019-21' was recently discussed (parliament.uk 2020).

Bats could be using wooded streets for a number of reasons, including as flight corridors, as foraging habitats, with trees offering habitat for invertebrates, or as roosting habitats, with mature trees possibly offering roosting opportunities. Bioacoustics provides a powerful tool to investigate both overall bat activity and foraging activity. It has seen widespread use in urban bat research (Parkins and Clark 2015; Rowse et al. 2018), demonstrating its validity.

Artificial light at night (ALAN) affects many nocturnal species (Gaston, Visser, and Hölker 2015; Davies and Smyth 2018; Sanders et al. 2021) and continues to increase in prevalence globally (Hölker et al. 2010). Bat responses to ALAN vary, with some species, such as common pipistrelle (*Pipistrellus pipistrellus*), being considered 'light-opportunistic' (Blake et al. 1994), and preying upon the many insects attracted to the light (Stone, Harris, and Jones 2015). This streetlight foraging behaviour is found to reduce overall foraging time, offering further advantages to light-opportunistic species (Salinas-Ramos et al. 2021). Other species, such as *Myotis* spp., are considered 'light-averse' and avoid lit areas (Stone, Jones, and Harris 2012), possibly to reduce their predation risk (Jones and Rydell 1994; Rydell and Speakman 1995; Rydell, Entwistle, and Racey 1996). Streetlight dimming, an approach that allows local governing authorities to reduce their carbon footprint and energy costs, could result in bats responding to ALAN differently (Stone, Harris, and Jones 2015). Rowse et al. (2018) investigated this previously, comparing activity at differently dimmed sites containing three adjacent dimmed streetlights, and found that high light levels increase light-opportunistic bat activity, but decrease light-averse bat activity. However, being able to investigate this on a whole street-by-street basis may yield different and more relevant results.

Our main aim was to investigate if urban wooded streets, and streetlight dimming, influence bat activity in a medium-sized British city. Two hypotheses were tested:

- i. Overall bat activity (defined as the number of passes per night) will increase on wooded streets in comparison to non-wooded streets.
- ii. Overall bat activity (defined as the number of passes per night) will increase on brightly lit streets in comparison to dimly lit streets.

Methods

Experimental design

The study was conducted in Leicester, UK (Fig. 1), located at lat: 52.633688, long: -1.1300468, with an area of 73.3 km². Leicester has a population of 354,224, and a population density of 4832 per km² (Office for National Statistics 2021). The city council operates city-wide streetlight dimming, with eight differing dimming programmes (Leicester City Council 2021), as well as having many wooded streets, making it suitable for this study.

Before selecting the streets, the four street types were defined. Wooded streets contained trees at intervals of at most 50 m, at a minimum height of 3 m to avoid undeveloped trees. Non-wooded streets contained few to no trees, at intervals of at most 100 m. Streets with rural areas directly adjacent were excluded. The brightest and dimmest dimming programmes operated in Leicester were examined. Bright streets had programme A: 100% brightness at 18:00 (hours), then 75% brightness at 22:00, while dim streets had programme K: 60% brightness at 18:00, then 45% at 19:00, and 30% at 22:00. The lights are all light-emitting diode (LED) bulbs, replaced during the white light programme between 2012 and 2015 (Leicester City Council 2021).

Sixteen streets were assessed, across eight paired bat detector deployments of five nights each, with a total of 80 samples collected. The street types were paired, allowing wooded and non-wooded, and bright and dim streets, to always be concurrently recorded. To choose the streets, a dataset containing Leicester's programme A and K streets (Leicester City Council 2021) was randomly selected using QGIS (QGIS.org 2021), with satellite images (Google Maps 2021) used to determine their wooded type. Cul-de-sacs were excluded. Only streets with speed limits up to 30 mph were selected to increase the similarity of each road's structure, traffic load and traffic noise. There was at least 1 km between concurrently recorded streets to attempt to achieve independence, double the minimum used in Threlfall et al.'s (2011) study.

Two AudioMoth static bat detectors were used to collect bat calls (Open Acoustic Devices 2020), which were concurrently recorded on two streets. Data were collected between June and August 2021. The mean nightly temperature varied between 9°C and 19°C, and the mean nightly rainfall between 0.0 and 2.8 mm. They recorded between 21:00 and 05:00, maintaining equal recording times between streets. The sample rate was 192 kHz, the gain set to medium, with a high pass filter at 25 kHz. No amplitude threshold was used. Recording was continuous, but each audio file was 1-minute long. The detectors were attached to streetlight poles, similar to Rowse et al. (2018). The pole closest to the midpoint along the length of the street was preferred. The detectors were attached at a height of 1.5 m, and at least 1.5 m from any trees or obstacles following the methods of Alder et al. (2021), to avoid reflected sounds, decrease chances of vandalism, and attempt to reduce the background noise from passing vehicles. Heavy-duty cases and bike cable locks were used for attachment, to further reduce the risk of vandalism. In February 2023, an LX1010BS lux meter was



Figure 1: Map of Leicester and its boundary, with its position within the UK also shown. The 16 streets where data were collected are labelled: black triangle for wooded/dim streets, white triangle for wooded/bright streets, black cross for non-wooded/dim streets and white cross for non-wooded/bright streets.

used to collect illuminance (lux) readings from three streetlights on each street, allowing an average to be calculated. The lux meter was positioned directly underneath the lantern, at 2 m from the ground. Two sets of data were collected due to the staggered dimming: between 20:00 and 22:00, and after 22:00—specifically between 22:05 and 23:00.

Data processing

The recordings were analysed using Kaleidoscope Pro version 5.4.2 (Wildlife Acoustics 2021). Its auto-identification feature was used to identify any calls present in the recordings, using the Bats of Europe 5.4.0 classifier with the UK species selected, and the more sensitive feature to attempt to highlight all possible bat calls. All automatically identified calls were manually vetted, to avoid incorrect identifications.

Bat activity was defined as the number of passes per night, with each call-containing sound file considered as one pass. If a file contained two species' calls, this was recorded as two passes. Every call had its species identified.

Distance to green space was calculated using QGIS (QGIS.org 2021), measuring from where the detector was deployed to the

closest area which could support bats, defined as areas containing clusters of at least 10 mature trees in close proximity. This avoided green spaces which might not support bats. Nightly temperature and rainfall (mm) data were obtained from a Leicester weather station (WorldWeatherOnline 2021), allowing for the effect of weather to be accounted for in the analyses.

Statistical analyses

R version 3.5.3 (R Core Team 2019) was used for the analyses. Generalized linear-mixed effects models (GLMMs) with negative binomial distributions, as Poisson models were found to be over-dispersed, were fitted using 'glmmTMB' from the glmmTMB package (Brooks et al. 2017) to identify potential influences on bat activity. Only common pipistrelle (*Pipistrellus pipistrellus*) calls were used within the model. The fixed effects analysed included wooded type, dim type, distance to green space, mean nightly rainfall and mean nightly temperature, with the random effects of location (street) and date to control for variation between sites and over the 3 months of survey. The mean street illuminance data collected after 22:00 (Fig. 2C), these data used as it included most of the recording period, had

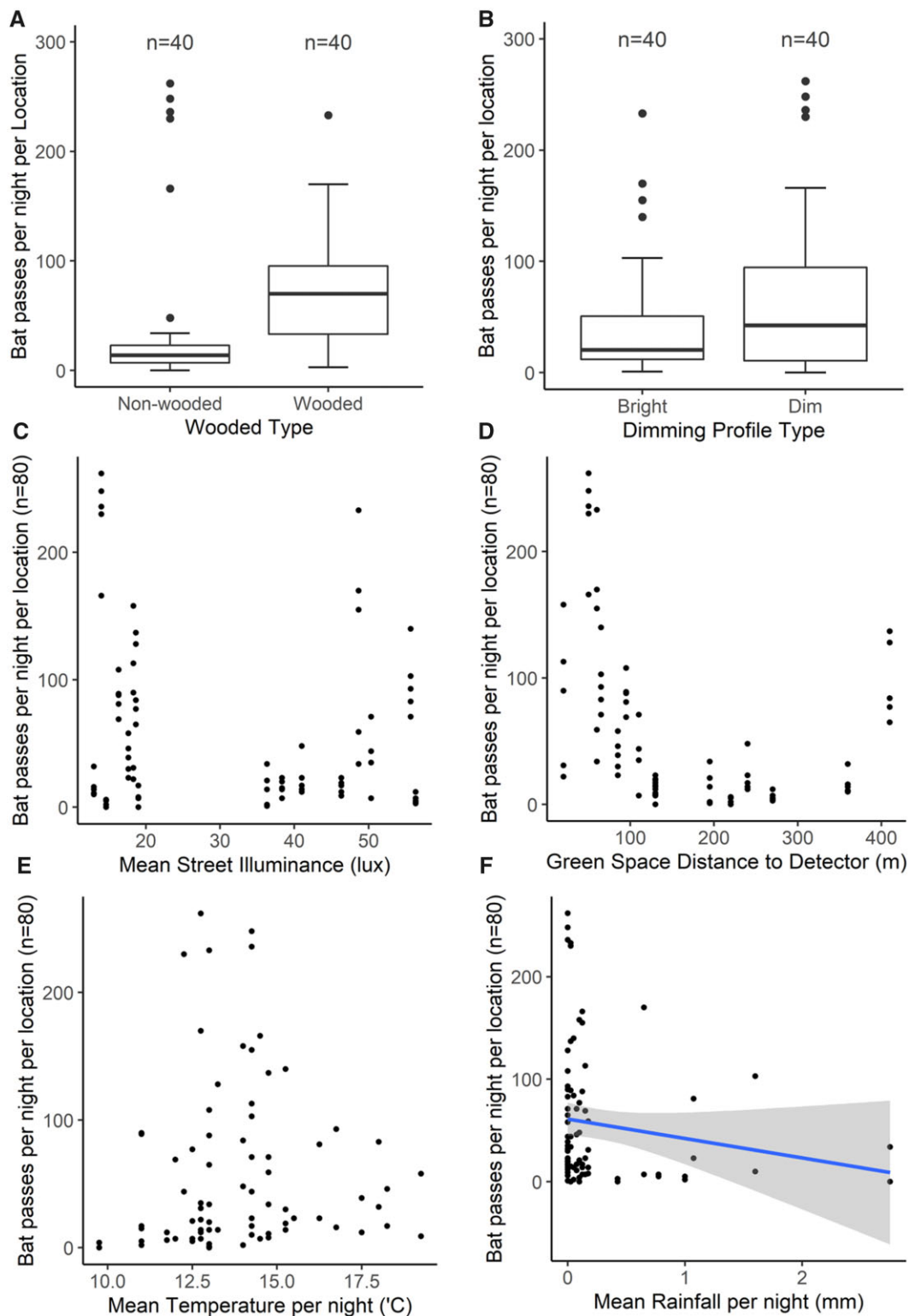


Figure 2: Comparison of common pipistrelle passes per night per location on (A) non-wooded and wooded streets and (B) bright and dim streets. Change in bat passes per night per location with differing (C) mean street illuminance (lux), (D) detector distance to green space (m), (E) nightly mean temperature (°C) and (F) nightly mean rainfall (mm).

high multicollinearity [using ‘check_collinearity’ from the performance package (Lüdtke et al. 2021) with dim type when used in the model (VIF = 19.24)]. Therefore, we decided to only include dim type in the model presented in this manuscript.

However, we also developed a model including mean street illuminance only, which showed no significant effect ($Z = -0.9290$, $df = 71$, $P = 0.3529$). No other instances of high multicollinearity or correlations were found. A backward selection method, based

on the P values calculated, was used to choose the final models, to obtain the most accurate model values.

Coefficients of determination (R^2) for all models were calculated using 'r2_nakagawa' from the performance package (Lüdecke et al. 2021), resulting in marginal and conditional R^2 classifications. The former considers the proportion of variance in the response variable explained by the fixed effects, and the latter considers the proportion of variation in the response variable explained by both the fixed and random effects (Nakagawa and Schielzeth 2013). This allows an estimation of the amount of variation captured by the models.

Results

We recorded 38 416 files across the 16 sites, with 4778 bat calls identified from these. The following six species were detected, ordered by prevalence: common pipistrelle (*Pipistrellus*, 94.11% of calls), common noctule (*Nyctalus noctula*, 2.70%), lesser noctule (*Nyctalus leisleri*, 2.14%), soprano pipistrelle (*Pipistrellus pygmaeus*, 0.02%), Nathusius's pipistrelle (*Pipistrellus nathusii*, <0.01%), and brown long-eared (*Plecotus auritus*, <0.01%). No other species were detected.

Many automated identifications of brown long-eared were false, instead being corrected to common pipistrelle social calls. Many common and lesser noctule calls were corrected as noise, with vehicle noise causing confusion with the auto-identification programme.

Across the 16 streets, between 20:00 and 22:00, the mean street illuminance for bright streets was 49.88 lux (SD 8.80, range 35.67–60.0) and for dim streets 23.25 lux (SD 4.73, range 16.00–29.00). After 22:00, the mean street illuminance for bright streets was 46.63 lux (SD 7.56, range 36.33–56.33) and for dim streets 16.46 lux (SD 2.32, range 13.00–19.00).

The marginal R^2 was 0.368, suggesting that the fixed effects explained a small-to-reasonable amount of the variation observed, with the random effects accounting for much of the variation (conditional $R^2 = 0.878$).

Significantly higher common pipistrelle activity was detected on wooded streets than on non-wooded streets ($P = 0.0174$, Table 1). Figure 2A shows the increased common pipistrelle passes per night on wooded streets. No significant difference was found between common pipistrelle activity on dim and bright streets (Fig. 2B; $P = 0.5159$, Table 1). Green space distance was found to have no significant effect on common pipistrelle activity ($P = 0.1519$, Table 1). However, the removal of Brazil Street (410 m, Fig. 2D), a potential outlier, led to a significant result ($P = 0.0040$). Brazil Street was retained in the final model.

Temperature ($^{\circ}\text{C}$) was found to not have a significant effect (Fig. 2E; $P = 0.0581$, Table 1), while rainfall (mm) was found to

have a negative significant effect on the number of common pipistrelle passes (Fig. 2F; $P = 0.0114$, Table 1).

Discussion

Common pipistrelle activity was significantly higher on wooded than on non-wooded streets, while no difference was found in common pipistrelle activity between dimly and brightly lit streets. Outside of the main hypotheses, rainfall, temperature and green space distance are also discussed.

Wooded type

The significantly increased common pipistrelle activity on wooded streets may be due to their utilization as green corridors, with bats known to follow linear features when commuting (Verboom and Huitema 1997) for three possible purposes: orientation clues, foraging habitat and shelter from wind and/or predators. The predator avoidance hypothesis could explain this behaviour (Lima 1998), with the trees offering cover which decreases the detection of the bats by predators such as the kestrel (*Falco tinnunculus*) at dusk (Mikula et al. 2016) and the tawny owl (*Strix aluco*) during the night (Lima and O'Keefe 2013). Tawny owls have been recorded as recently as 2022 in Leicester, with 103 records since 2016 (NBN Atlas 2023). Common UK bat species, including common pipistrelles, have been found to modify both their timing of foraging (Rydell, Entwistle, and Racey 1996), and movement to reduce their predation risk—preferring to travel along tree lines rather than in the open (Schaub and Schnitzler 2007; Lima and O'Keefe 2013). Both these findings support the suggestion that common pipistrelles would prefer travelling along wooded streets to decrease predation risk. Lesiński, Gryz, and Kowalski (2009) found that tawny owls are more likely to prey on bats in urban areas compared to suburban forests in central Poland. While common pipistrelle were rare compared to other species in their study area, their conclusions indicate that common pipistrelle may be one of the bats tawny owls take most frequently (Lesiński, Gryz, and Kowalski 2009).

Wooded streets could act as foraging habitats, with insect abundances likely higher there than on non-wooded streets. Verboom and Spoelstra (1999) investigated the use of tree lines in common pipistrelles, testing for associations between bat activity, insect abundance and distance from tree lines in rural settings in the Netherlands and Poland, by measuring bat activity and insect abundance at fixed distances from tree lines. They discovered that commuting bats' activity decreased as distance away from tree lines increased, not as insect abundance decreased. Bat activity was only found to decrease with insect abundance on one site (of the three sampled) where a species-rich grassland was present, causing insect abundances to be

Table 1: Results from the GLMM testing the influence of multiple variables on common pipistrelle passes per night

Model	Estimate (b)	SE	Z-value	P-value	Marginal R^2	Conditional R^2
Bat activity					0.368	0.877
Wooded type	1.231600	0.517800	2.378	0.0174*		
Dim type	0.030712	0.479444	2.275	0.5159		
Green space distance	-0.003195	0.002130	-1.433	0.1519		
Mean nightly temperature ($^{\circ}\text{C}$)	0.101000	0.053300	1.895	0.0581		
Mean nightly rainfall (mm)	-0.419300	0.165700	-2.531	0.0114*		

Significant results are in bold: * $P < 0.05$,

higher, with bats visiting the area primarily to forage instead of commuting. In areas of low insect abundance, where bats would mainly be commuting, their results support predator avoidance influencing their association with tree lines instead of insect abundance.

Verboom and Spoelstra's (1999) study also measured the effects of wind speed and direction, finding that high wind speeds and interfering directions influenced bat behaviour, causing them to change the side of the tree line they commuted down, allowing them to shelter from the wind. However, when double parallel rows of trees were present, like on wooded streets, they mainly flew between the tree lines regardless of wind speed or direction. Furthermore, as urban streets are often sheltered by adjacent buildings, it is unlikely that this influenced our results.

Bats could use wooded streets as roosting habitats, with the trees possibly having roosting features. However, the presence of streetlighting, human disturbance and little-to-no surrounding vegetation means it is unlikely that wooded streets are used for roosting (Stone 2013).

Our findings contrast with those of Oprea et al. (2009), who compared bat communities between urban parks, wooded streets and non-wooded streets in the city of Vitória, Brazil. Only a subset of species caught in parks was caught in wooded streets, in small numbers, indicating that wooded streets did not provide connectivity for urban bats. Differences in methodology could explain the contrasting conclusions, with bioacoustics and common pipistrelle activity comparisons used here instead of their mist netting and species richness comparisons. Their study was furthermore conducted in Brazil with a different species assemblage than the UK. Finally, our study was larger with a total of 4778 bat passes across 80 sampling sessions compared to their 174 observations across 12 sampling sessions.

Lewanzik et al. (2022) investigated the effect of landscape canopy cover on bat occurrence in Berlin, Germany, with linear vegetation features, such as wooded streets, included in their analysis. Their findings mirror the discovery here, with common pipistrelle's occurrence probability reacting positively to increased canopy cover, and negatively to increased distance to the nearest linear vegetation structure.

The scope of our study somewhat restricted what data could be recorded. Firstly, no sampling of urban parks was undertaken, like in Oprea et al. (2009), so our results may have only included a subset of Leicester's bat population. Secondly, the wooded and non-wooded street definitions did not consider other non-tree surrounding vegetation, such as vegetation in people's front gardens like hedgerows, which could have led to increased insect abundance or extra cover from predators on both wooded and non-wooded streets.

Dim type and mean street illuminance

The lack of significance found between common pipistrelle activity on bright and dim streets suggests that streetlight dimming does not affect light-opportunistic bat behaviour, despite the presumption that brightly lit streets would have increased activity of light-opportunistic species due to more insect prey. The absence of highly light-averse bats from our results, such as *Myotis* spp. which are known to be present in Leicester (NBN Atlas 2018), suggests they were deterred by the streetlight brightness under both dimming levels. Therefore, streetlight dimming does not appear to mitigate the known negative effects of artificial lighting on light-averse bats. This result

supports what was previously shown by Stone et al. (2009), where *Rhinolophus hipposideros* commuting routes had reduced bat activity following artificial light installation. Predator avoidance likely influences this behaviour, with light-averse bats avoiding light to remain hidden from predators (Rydell and Speakman 1995; Stone et al. 2009).

Rowse et al. (2018) contrastingly found the significantly higher activity of light-opportunistic species, like the common pipistrelle, at less dimmed (50% and 100% brightness) streetlights in comparison to an unlit (0% brightness) treatment, with the observed increased insect abundances at brighter lights possibly influencing this. However, their comparisons involved only three adjacent streetlights, whereas here comparisons involved whole differently dimmed streets. Therefore, while Rowse et al. (2018) showed that light-opportunistic bats will prey on insects accumulating around brighter lights, it did not show whether dimming would affect their overall use of streets, such as for commuting. The latter could be considered more relevant, with councils likely applying streetlight dimming on a street-by-street or area basis, similar to Leicester (Leicester City Council 2021). Furthermore, Rowse et al. (2018) compared bat activity between unlit and three lighting levels (25%, 50% and 100%), whereas this study compared two different dimming programmes, which were at 70% and 30% dimness after 22:00. Therefore, significant differences could have been more likely as they were comparing to an unlit treatment.

Lewanzik et al.'s (2022) found sharp declines in the probability of encountering bats as light radiance increased across an area, differing from the lack of significant difference in common pipistrelle activity between differently dimmed streets discovered in our results. However, this difference may be due to their method of measuring light on a landscape scale rather than on single streets, or more likely due to the dominance of common pipistrelles in our results, which appeared to have a less sharp decline in occurrence with increasing landscape light radiance in their results.

Overall, streetlights may have to be dimmed to below 30% brightness, rendering them unfit for their main purpose, to begin reversing their positive effects on light-opportunistic activity and negative effects on light-averse activity, with the results of the comparison between least dimmed (100% at 18:00, 70% after 22:00) and most dimmed (60% at 18:00, 45% at 19:00, and 30% after 22:00) dimming presented here revealing no difference. The staggered dimming, with less dimming applied earlier in the night, could also have an impact, with bats perhaps deciding on whether to use a street earlier in the night when the street dimming is reduced. Therefore, part-night lighting may be a better approach if aiming to improve the suitability of urban areas for bats, as this may lead to increased use of streets by light-averse bats and thus allow better-connected populations. If this was not possible due to safety concerns, extreme streetlight dimming may be required to reverse the negative effects of ALAN on light-averse species.

One limitation when considering the results was possible variations in the illuminance and frequency of the streetlights on the streets investigated, due to possible minor differences in bulb type, age, and streetlight height. With the recent city-wide installation of LED bulbs between 2012 and 2015 (Leicester City Council 2021), we did not expect this to be a significant factor. Nonetheless with ALAN intensity and frequency known to affect bat foraging rates (Stone, Harris, and Jones 2015; Voigt et al. 2021), light intensity was later collected as 'mean street illuminance'. The data were highly varied, especially on brightly lit streets, showing the potential importance of collecting these

data. However, similarly to the comparison of dim type, a lack of significance was found in common pipistrelle activity based on mean street illuminance, when it was run in a separate model to dim type due to their high correlation. It is worth noting though that light frequency data could not be collected, so any variations in this could have affected our results, although given that the LED bulbs were of similar age and type, the variation is likely to have been minimal.

Other factors

The effect of green space distance on common pipistrelle activity was non-significant; however, this lack of significance may have been due to either a small sample size or an outlier affecting the results. We had a potential outlier in 'Brazil Street', which was the street farthest from a green space (Fig. 2D). The unusually high activity in this street may be caused by a nearby bat roost, with roosting opportunities, including the trees present on the multiple local wooded streets or within roofs of the adjacent older terraced housing. The street also has proximity to the River Soar (approximately 275 m west from the road's end), which could act as foraging habitat, or an ecological corridor, running past both a small woodland (approximately 550 m south-east) and the Aylestone Meadows Local Nature Reserve (approximately 1100 m south-east).

As expected, rainfall had a significant negative effect on activity, aligning with Erickson and West (2002), with raindrops possibly interfering with the bats' echolocation and with insects also avoiding the rain, reducing prey availability. Furthermore, when bats get wet, the metabolic costs of flight can increase twofold (Voigt et al. 2011). Temperature did not have a significant effect, with May to October overnight temperatures being thought to usually be warm enough for common pipistrelle activity. Results on the effects of temperature between May and October in temperate regions vary. Russo and Jones (2003) found only one species, Savi's pipistrelle *Hypsugo savii*, was influenced by temperature during their investigation of foraging habitat use in a Mediterranean region, whereas both Wolbert, Zellner, and Whidden (2014) and Rowse et al. (2018) found significant positive associations between all bats' activity and temperature, in a northern region of Norway and Hertfordshire (UK), respectively.

Future research

From the results and evidence presented here, there is one pressing research question when considering how to make urban areas more suitable for bats. A comparison on a street-by-street basis of how part-night lighting affects bat behaviour, especially light-averse bats, is vital to understanding how artificial lighting in urban areas can be best applied to bats. Stone, Harris, and Jones's (2015) review on artificial lighting and bats aligns with this, stating that further research is required to reveal how variable night lightings, such as streetlight dimming and part-night lighting, may mitigate the negative impacts on some bats. In addition, a study comparing activity on linear and dead-end streets could further reveal if bats were primarily using linear streets as corridors.

Implications for urban bat conservation

Wooded streets have been shown to have value to bats in this study, supporting their installation in urban areas to aid the connectivity of bat populations. Previous documentation from the UK Bat Conservation Trust includes street trees under linear

features which can aid bat commuting and landscape connectivity (Gunnell, Grant, and Williams 2012). The results reported here can now provide evidence for this in temperate regions.

Streetlight dimming has been shown to have no significant effect on bat activity here, answering questions proposed by Stone, Harris, and Jones (2015) on its possible impacts. The results from this and Rowse et al. (2018) can direct future research towards part-night lighting, with this method possibly being able to mitigate the negative effects of ALAN on light-averse bat species.

Conclusion

This study aimed to assess adjustments that could increase the suitability of urban areas for bats. Wooded streets appeared to be used as green corridors, with common pipistrelles likely following them to conceal themselves from predators, such as the tawny owl. Therefore, the proliferation of wooded streets in urban areas could allow better-connected populations to form. Streetlight dimming did not affect the common pipistrelles sampled, but with no light-averse bats detected, even the highly dimmed streets likely deterred them. Therefore, an alternate solution, such as part-night lighting, may be required to increase the suitability of urban areas for those species.

Acknowledgements

We thank Leicester City Council for the data on Leicester's streetlight dimming and permission to set up the bat detectors on their streets, and Grace Deeming for her help in the field and during the preparation of the manuscript. We thank two reviewers for their very helpful recommendations for a previous version of this manuscript.

Author contributions

Chris Stanley [Conceptualization (lead), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Project administration (lead), Visualization (lead), Writing—original draft (lead), Writing—review and editing (equal)], Joanna Bagniewska [Conceptualization (equal), Formal analysis (equal), Methodology (equal), Supervision (equal), Writing—review and editing (equal)], Ada Grabowska-Zhang [Conceptualization (equal), Methodology (equal), Supervision (equal), Writing—review and editing (equal)], and Thomas Hesselberg [Formal analysis (equal), Methodology (equal), Supervision (equal), Writing—review and editing (equal)].

C.S. was the primary contributor to the manuscript, completing it as part of a post-graduate project. C.S. planned and undertook the field research, completed the analysis, and wrote the main manuscript text. A.G.-Z. and J.B. aided the planning phase, guiding the project aims and methods. T.H. aided the planning of the field methods and provided guidance towards the statistical analysis. All authors contributed to the writing and revision of the manuscript with suggestions and critical comments.

Conflict of interest statement. None declared.

Data availability

The data used as input in our statistical tests is available from Figshare - <https://figshare.com/s/31c0c425512f6de67df0>.

References

- Alder, D. C. et al. (2021) 'Irregular Silviculture Positively Influences Multiple Bat Species in a Lowland Temperate Broadleaf Woodland', *Forest Ecology and Management*, **483**: 118786.
- Avila-Flores, R., and Fenton, M. B. (2005) 'Use of Spatial Features by Foraging Insectivorous Bats in a Large Urban Landscape', *Journal of Mammalogy*, **86**: 1193–204.
- Barlow, K. E. et al. (2015) 'Citizen Science Reveals Trends in Bat Populations: The National Bat Monitoring Programme in Great Britain', *Biological Conservation*, **182**: 14–26.
- Benítez-López, A., Alkemade, R., and Verweij, P. A. (2010) 'The Impacts of Roads and Other Infrastructure on Mammal and Bird Populations: A Meta-Analysis', *Biological Conservation*, **143**: 1307–16.
- Blake, D. et al. (1994) 'Use of Lamplit Roads by Foraging Bats in Southern England', *Journal of Zoology*, **234**: 453–62.
- Brooks, M. E. et al. (2017) 'glmmTMB Balances Speed and Flexibility among Packages for Zero-Inflated Generalized Linear Mixed Modeling', *The R Journal*, **9**: 378–400.
- Browning, E. et al. (2021) 'Drivers of European Bat Population Change: A Review Reveals Evidence Gaps', *Mammal Review*, **51**: 353–68.
- Burns, F. et al. (2016) 'Agricultural Management and Climatic Change Are the Major Drivers of Biodiversity Change in the UK', *PLoS One*, **11**: e0151595.
- Carrus, G. et al. (2015) 'Go Greener, Feel Better? The Positive Effects of Biodiversity on the Well-Being of Individuals Visiting Urban and Peri-Urban Green Areas', *Landscape and Urban Planning*, **134**: 221–8.
- Claireau, F. et al. (2019) 'Major Roads Have Important Negative Effects on Insectivorous Bat Activity', *Biological Conservation*, **235**: 53–62.
- Dallimer, M. et al. (2011) 'Temporal Changes in Greenspace in a Highly Urbanized Region', *Biology Letters*, **7**: 763–6.
- Davies, T. W., and Smyth, T. (2018) 'Why Artificial Light at Night Should Be a Focus for Global Change Research in the 21st Century', *Global Change Biology*, **24**: 872–82.
- Erickson, J. L., and West, S. D. (2002) 'The Influence of Regional Climate and Nightly Weather Conditions on Activity Patterns of Insectivorous Bats', *Acta Chiropterologica*, **4**: 17–24.
- Fahrig, L. et al. (1995) 'Effect of Road Traffic on Amphibian Density', *Biological Conservation*, **73**: 177–82.
- Fernández-Juricic, E. (2000) 'Avifaunal Use of Wooded Streets in an Urban Landscape', *Conservation Biology*, **14**: 513–21.
- Gaston, K. J., Visser, M. E., and Hölker, F. (2015) 'The Biological Impacts of Artificial Light at Night: The Research Challenge', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **370**: 20140133.
- Gili, F. et al. (2020) 'Bats in Urbanising Landscapes: Habitat Selection and Recommendations for a Sustainable Future', *Biological Conservation*, **241**: 108343.
- Google Maps (2021). Aerial images of Leicester. Google Maps [online]. Available through: <https://www.google.co.uk/maps> accessed 1 July 2021.
- Grimm, N. B. et al. (2008) 'Global Change and the Ecology of Cities', *Science (New York, N.Y.)*, **319**: 756–60.
- Gunnell, K., Grant, G., and Williams, C. (2012). *Landscape and Urban Design for Bats and Biodiversity*. London: Bat Conservation Trust.
- Hale, J. D. et al. (2012) 'Habitat Composition and Connectivity Predicts Bat Presence and Activity at Foraging Sites in a Large UK Conurbation', *PLoS One*, **7**: e33300.
- Hölker, F. et al. (2010) 'The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy', *Ecology and Society*, **15**:
- Jones, G., and Rydell, J. (1994) 'Foraging Strategy and Predation Risk as Factors Influencing Emergence Time in Echolocating Bats', *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, **346**: 445–55.
- et al. (2009) 'Carpe Noctem: The Importance of Bats as Bioindicators', *Endangered Species Research*, **8**: 93–115.
- Krauss, J. et al. (2010) 'Habitat Fragmentation Causes Immediate and Time-Delayed Biodiversity Loss at Different Trophic Levels', *Ecology Letters*, **13**: 597–605.
- Kunc, H. P., and Schmidt, R. (2019) 'The Effects of Anthropogenic Noise on Animals: A Meta-Analysis', *Biology Letters*, **15**: 20190649.
- Kunz, T. H. et al. (2011) 'Ecosystem Services Provided by Bats', *Annals of the New York Academy of Sciences*, **1223**: 1–38.
- Leicester City Council (2021). *Personal Communication by Email with the Street Lighting Team at Leicester City Council*. Leicester: Leicester City Council.
- Lesiński, G., Gryz, J., and Kowalski, M. (2009) 'Bat Predation by Tawny owls Strix Aluco in Differently Human-Transformed Habitats', *Italian Journal of Zoology*, **76**: 415–21.
- Lewanzik, D. et al. (2022) 'Evaluating the Potential of Urban Areas for Bat Conservation with Citizen Science Data', *Environmental Pollution (Barking, Essex: 1987)*, **297**: 118785.
- Lima, S. L. (1998) 'Stress and Decision-Making under the Risk of Predation: Recent Developments from Behavioral, Reproductive, and Ecological Perspectives', *Advances in the Study of Behaviour*, **27**: 215–90.
- , and O'Keefe, J. M. (2013) 'Do Predators Influence the Behaviour of Bats?', *Biological Reviews of the Cambridge Philosophical Society*, **88**: 626–44.
- Lüdtke, D. et al. (2021) 'Performance: An R Package for Assessment, Comparison and Testing of Statistical Models', *Journal of Open Source Software*, **6**: 3139.
- Mikula, P. et al. (2016) 'Bats as Prey of Diurnal Birds: A Global Perspective', *Mammal Review*, **46**: 160–74.
- Murray, M. H. et al. (2019) 'City Sicker? A Meta-Analysis of Wildlife Health and Urbanization', *Frontiers in Ecology and the Environment*, **17**: 575–83.
- Nakagawa, S., and Schielzeth, H. (2013) 'A General and Simple Method for Obtaining R² from Generalized Linear Mixed-Effects Models', *Methods in Ecology and Evolution*, [online] **4**: 133–42.
- NBN Atlas (2018) Search: Scientific name: "Myotis" OR "Myotis daubentonii" OR "Vespertilio" – within 5 km of point (52.637, -1.14) – since 2016 | Occurrence records | NBN Atlas. Nbnatlas.org. <https://records.nbnatlas.org/occurrences/search?taxa=&q=qid%3A1641460537206&fq=-occurrence_status%3A%22absent%22&fq=%28year%3A%222016%22+OR+year%3A%222017%22+OR+year%3A%222018%22+OR+year%3A%222019%22+OR+year%3A%222021%22+OR+year%3A%222020%22%29&fq=%28taxon_name%3A%22Myotis%22+OR+taxon_name%3A%22Myotis+daubentonii%22+OR+taxon_name%3A%22Vespertilio%22%29&wkt=&lat=&lon=&radius=&dir=&offset=0&max=20&sort=common_name&nbn_loading=true> accessed 6 January 2022.
- (2023) Search: SPECIES: "Strix aluco" – within "City of Leicester (B)" – since 2016 | Occurrence records | NBN Atlas. Nbnatlas.org. <<https://records.nbnatlas.org/occurrences/search?>> accessed 2 February 2023.

- O'Neill, A. (2021) *Urbanization in the United Kingdom 2020*. Statista. <<https://www.statista.com/statistics/270369/urbanization-in-the-united-kingdom/>> accessed 23 August 2021.
- Office for National Statistics (2021) *Overview of the UK population: January 2021*. <<https://www.ons.gov.uk/peoplepopulationandcommunity/populationandmigration/populationestimates/articles/overviewoftheukpopulation/january2021>> accessed 4 January 2022.
- Open Acoustic Devices (2020) *AudioMoth*. Open Acoustic Devices. <<https://www.openacousticdevices.info/audiomoth>> accessed 24 August 2021.
- Oprea, M. et al. (2009) 'Do Wooded Streets Provide Connectivity for Bats in an Urban Landscape?', *Biodiversity and Conservation*, **18**: 2361–71.
- Owens, A. C. et al. (2020) 'Light Pollution is a Driver of Insect Declines', *Biological Conservation*, **241**: 108259.
- Parkins, K. L., and Clark, J. A. (2015) 'Green Roofs Provide Habitat for Urban Bats', *Global Ecology and Conservation*, **4**: 349–57.
- parliament.uk. (2020) *Tree-lined Streets Bill 2019-21* — UK Parliament. <<https://services.parliament.uk/bills/2019-21/treelinedstreets.html>> accessed 5 January 2021.
- QGIS.org (2021) *QGIS Geographic Information System*. QGIS Association. <<http://www.qgis.org>>
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Rowse, E. G., Harris, S., and Jones, G. (2018) 'Effects of Dimming Light-Emitting Diode Street Lights on Light-Oppportunistic and Light-Averse Bats in Suburban Habitats', *Royal Society Open Science*, **5**: 180205.
- Russo, D., and Jones, G. (2003) 'Use of Foraging Habitats by Bats in a Mediterranean Area Determined by Acoustic Surveys: Conservation Implications', *Ecography*, **26**: 197–209.
- et al. (2021) 'Do we Need to Use Bats as Bioindicators?', *Biology*, **10**: 693.
- Rydell, J., Entwistle, A., and Racey, P. A. (1996) 'Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk', *Oikos*, **76**: 243–52.
- , and Speakman, J. R. (1995) 'Evolution of Nocturnality in Bats: Potential Competitors and Predators during Their Early History', *Biological Journal of the Linnean Society*, **54**: 183–91.
- Sanders, D. et al. (2021) 'A Meta-Analysis of Biological Impacts of Artificial Light at Night', *Nature Ecology & Evolution*, **5**: 74–81.
- Salinas-Ramos, V. B. et al. (2021) 'Artificial Illumination Influences Niche Segregation in Bats', *Environmental Pollution (Barking, Essex: 1987)*, **284**: 117187.
- Schaub, A., and Schnitzler, H. U. (2007) 'Flight and Echolocation Behaviour of Three Vespertilionid Bat Species While Commuting on Flyways', *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, **193**: 1185–94.
- Seto, K. C., Güneralp, B., and Hutyra, L. R. (2012) 'Global Forecasts of Urban Expansion to 2030 and Direct Impacts on Biodiversity and Carbon Pools', *Proceedings of the National Academy of Sciences of the United States of America*, **109**: 16083–8.
- Shwartz, A., Turbé, A., Simon, L., and Julliard, R. (2014) 'Enhancing Urban Biodiversity and Its Influence on City-Dwellers: An Experiment', *Biological Conservation*, **171**: 82–90. [10.1016/j.biocon.2014.01.009](https://doi.org/10.1016/j.biocon.2014.01.009)
- Stone, E. L. (2013). *Bats and Lighting: Overview of Current Evidence and Mitigation*. Bristol: University of Bristol.
- , Harris, S., and Jones, G. (2015) 'Impacts of Artificial Lighting on Bats: A Review of Challenges and Solutions', *Mammalian Biology*, **80**: 213–9.
- , Jones, G., and Harris, S. (2009) 'Street lighting disturbs commuting bats', *Current Biology*, **19**: 1123–7.
- , —, and — (2012) 'Conserving Energy at a Cost to Biodiversity? Impacts of LED Lighting on Bats', *Global Change Biology*, **18**: 2458–65.
- Threlfall, C. et al. (2011) 'Ecological Processes in Urban Landscapes: Mechanisms Influencing the Distribution and Activity of Insectivorous Bats', *Ecography*, **34**: 814–26.
- Van der Meij, T. et al. (2015) 'Return of the Bats? A Prototype Indicator of Trends in European Bat Populations in Underground Hibernacula', *Mammalian Biology*, **80**: 170–7.
- Verboom, B., and Huitema, H. (1997) 'The Importance of Linear Landscape Elements for the Pipistrelle *Pipistrellus Pipistrellus* and the Serotine Bat *Eptesicus Serotinus*', *Landscape Ecology*, **12**: 117–25.
- , and Spoelstra, K. (1999) 'Effects of Food Abundance and Wind on the Use of Tree Lines by an Insectivorous Bat, *Pipistrellus Pipistrellus*', *Canadian Journal of Zoology*, **77**: 1393–401.
- Voigt, C. C. et al. (2021) 'The impact of light pollution on bats varies according to foraging guild and habitat context', *BioScience*, **71**: 1103–9.
- et al. (2011) 'Rain Increases the Energy Cost of Bat Flight', *Biology Letters*, **7**: 793–5.
- Wildlife Acoustics. (2021) *Kaleidoscope Pro Analysis Software*. Wildlife Acoustics. <<https://www.wildlifeacoustics.com/products/kaleidoscope-pro>> accessed 6 July 2021.
- Wolbert, S. J., Zellner, A. S., and Whidden, H. P. (2014) 'Bat Activity, Insect Biomass, and Temperature along an Elevational Gradient', *Northeastern Naturalist*, **21**: 72–85.
- Wood, E. et al. (2018) 'Not All Green Space is Created Equal: Biodiversity Predicts Psychological Restorative Benefits from Urban Green Space', *Frontiers in Psychology*, **9**: 2320.
- WorldWeatherOnline. (2021) *Leicester Historical Weather*. WorldWeatherOnline.com. <<https://www.worldweatheronline.com/leicester-weather-history/leicestershire/gb.aspx>> accessed 6 July 2021.