



Cite this article: Rowse EG, Harris S, Jones G. 2018 Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats. *R. Soc. open sci.* **5**: 180205.
<http://dx.doi.org/10.1098/rsos.180205>

Received: 7 February 2018

Accepted: 20 April 2018

Subject Category:

Biology (whole organism)

Subject Areas:

behaviour/ecology

Keywords:

ALAN, bat activity, dimming, light-emitting diode street lights, light-opportunistic species, light-averse species

Author for correspondence:

Elizabeth G. Rowse

e-mail: liz.rowse@bristol.ac.uk

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4106981>.

Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats

Elizabeth G. Rowse, Stephen Harris and Gareth Jones

School of Biological Sciences, Life Sciences Building, University of Bristol,
24 Tyndall Avenue, Bristol BS8 1TQ, UK

EGR, 0000-0003-1065-0587

Emerging lighting technologies provide opportunities for reducing carbon footprints, and for biodiversity conservation. In addition to installing light-emitting diode street lights, many local authorities are also dimming street lights. This might benefit light-averse bat species by creating dark refuges for these bats to forage and commute in human-dominated habitats. We conducted a field experiment to determine how light intensity affects the activity of the light-opportunistic *Pipistrellus pipistrellus* and light-averse bats in the genus *Myotis*. We used four lighting levels controlled under a central management system at existing street lights in a suburban environment (0, 25, 50 and 100% of the original output). Higher light intensities (50 and 100% of original output) increased the activity of light-opportunistic species but reduced the activity of light-averse bats. Compared to the unlit treatment, the 25% lighting level did not significantly affect either *P. pipistrellus* or *Myotis* spp. Our results suggest that it is possible to achieve a light intensity that provides both economic and ecological benefits by providing sufficient light for human requirements while not deterring light-averse bats.

1. Introduction

Over the last 60 years, artificial light at night (ALAN) has increased globally on average by 6% per annum [1]. Although more prevalent in developed countries, ALAN is now considered a global threat because of increasing urbanization and industrialization in many developing countries [2,3]. ALAN is the result of a number of artificially lit sources, but street lights are one of the main contributors as they are installed in most towns and cities across the world [3,4].

Many local authorities across Britain are replacing old lighting stock such as low-pressure sodium (LPS) and high-pressure sodium (HPS) street lights with light-emitting diode (LED) street lights [5]. LED street lights offer a number of advantages over older lighting technologies, including increased energy efficiency, flexibility and longevity [6]. In Britain, LED lights are predicted to contribute up to 70% of the outdoor and residential lighting by 2020 [7]. As well as installing LED lights, many local authorities are implementing strategies to save money and reduce their carbon footprints, such as part-night lighting and dimming. It is relatively easy to employ dimming regimes with LED lights because they have a rapid on/off time [6,8]. Dimming levels can be implemented and adjusted remotely using a central management system (CMS) [3,9]. Dimming LED street lights is typically carried out by pulse-width modulation, which manipulates the duty cycle of a signal, so that the amount of 'on' time is reduced, but the spectral output of the light is unchanged [10,11].

Bats are a useful taxon to study the ecological impacts of light because they are nocturnal and their response to ALAN varies across species. A number of species are considered 'light opportunistic' as they feed on the large numbers of insects attracted to lights [12,13]: the attraction-by-insects hypothesis [14]. In Europe, these species are typically from the genera *Eptesicus*, *Nyctalus* and *Pipistrellus*. However, even light-opportunistic bats such as *Pipistrellus pipistrellus* will avoid lit areas when commuting in urban habitats, preferring to cross gaps in vegetation where there is little artificial light [15]. They also avoid lit areas when drinking at water sources [16].

Conversely, light-averse bats, such as those species from the genera *Myotis*, *Plecotus* and *Rhinolophus*, seem to be negatively affected by all types of street lighting. It is thought that because light-averse bats are often slower flying, more manoeuvrable species [17,18], they avoid light to reduce the risk of predation [19,20]. Many are also of conservation concern because their wing shape limits dispersal and movement [21], and hence they are particularly vulnerable to anthropogenic pressures such as urbanization and the associated ALAN. As dimming reduces both the light intensity of the street light and the amount of light distributed from the light source, it might create dark refuges that light-averse bats could use for commuting and foraging in urban areas [3].

There are many examples of artificial lighting affecting orientation, reproduction, communication and foraging in nocturnal taxa [22–26]. However, few studies have explored the biological impacts of varying light intensities. For example, the reproduction and survival of fruit flies, *Drosophila melanogaster*, are negatively affected by increased light intensity [27]. Increased light intensity also has a detrimental effect on the activity and melatonin level of great tits, *Parus major* [28] and activity patterns of blue tits, *Cyanistes caeruleus* [29], interrupts immune responses of Siberian hamsters, *Phodopus sungorus* [30], and Swiss Webster mice, *Mus musculus* [31], but does not affect sleep in *Parus major* [32].

Studies on the effects of light intensity on bat activity have highlighted that even low levels of ALAN have a detrimental effect on the activity of light-averse species [26,33]. Even when LED street lights were dimmed to a low level (mean 3.6 lux, range 2.90–4.86 lux), there were significantly fewer passes from the light-averse bats *Myotis* spp. and *Rhinolophus hipposideros* than on unlit nights [26]. However, dimming street lights to an intensity below 3.6 lux may not be feasible: street lights exist for human safety and if humans cannot see their surroundings clearly because the light intensity is too low, this nullifies the benefits of having street lights [26,34].

Our aim was to determine whether street light dimming regimes currently used by local authorities can have ecological benefits for bats as well as economic benefits. We tested the following two hypotheses:

- (i) bat activity of the light-opportunistic bat *P. pipistrellus* will decrease at dimmed LED lights compared with undimmed LED lights owing to reduced insect abundance at dimmed street lights; and
- (ii) bat activity of light-averse species from the genus *Myotis* will increase at dimmed LED lights compared with undimmed LED lights because the reduced light distribution will create dark refuges for light-averse bats to forage and commute.

2. Methods

2.1. Experimental design

Fieldwork took place between May and August 2015 at 21 sites using existing street lights in Hertfordshire, southeast England. Each site consisted of three lighting columns (lamp posts), which ran

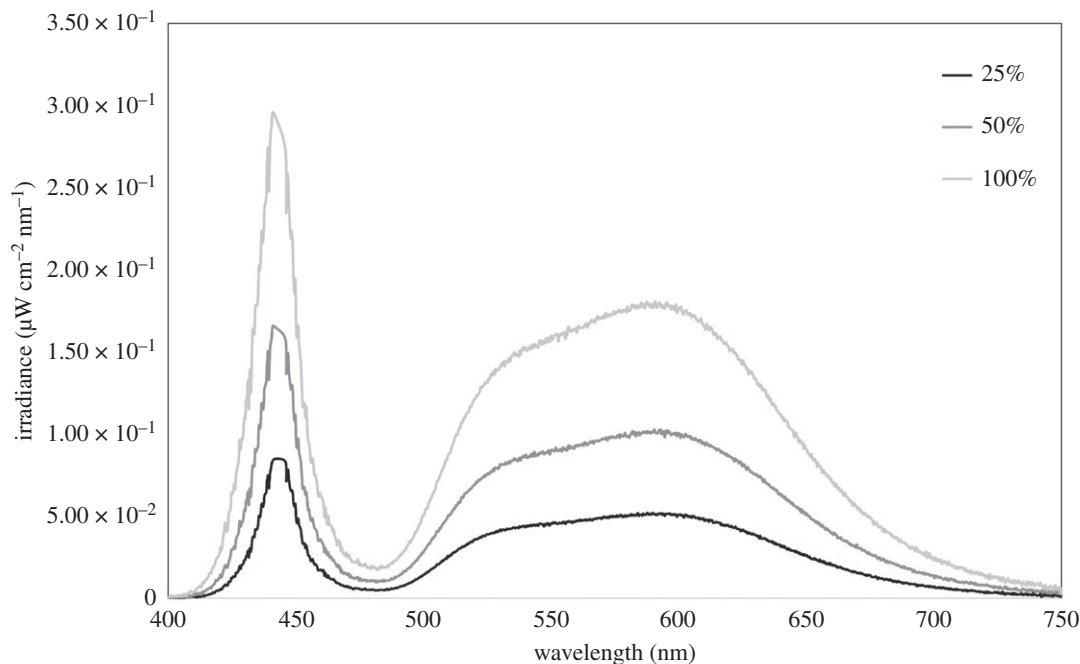


Figure 1. The spectral output of LED street lights at the three lighting levels (25%, 50% and 100%) from one of the 21 sites chosen at random.

a series of lighting levels: 0%, 25%, 50% and 100% of the original output. These lighting levels refer to changes in duty cycle as described in the Introduction. Illuminance values for the four lighting levels are provided in the Results. As our aim was to assess the impacts of different street lighting levels, we used three adjacent lighting columns per site to ensure that a stretch of road (at least 60 m) was subjected to the same lighting level. The experiment ran for eight nights at each site, with the lighting level switching every two nights, i.e. each lighting level ran for two consecutive nights. The lighting schedules were randomized across sites to prevent any order effects, and sites were separated by at least 1 km to ensure the collection of independent samples. The lighting levels we used were representative of differing light intensities being employed by local authorities. Light levels were controlled using pulse width modulation by a sub-contractor of Hertfordshire County Council using a CMS.

All the street lights used in this study were neutral LED lights (MIDI, 97 W, 4250 K, Urbis Schreder, Basingstoke, RG24 8GG, UK) that were 10 m in height. We selected street lights along tree lines that contained trees more than 4 m in height, and each site was at least 20 m from the beginning of the tree line [15,35]. All sites were also close to other linear features such as hedgerows, and typical bat foraging habitats, such as woodland and grassland, were at least 35 m from a building, and were located on A (major) roads in suburban areas that experienced similar traffic intensity. To ensure that lighting levels were comparable across sites, both illuminance (lux) and irradiance ($\mu\text{W cm}^{-2} \text{nm}^{-1}$) were measured. We used a TES 1330 lux meter (ATP Instrumentation Ltd, Ashby-de-la-Zouch, LE65 2UU, UK) at 1.8 m from the ground, directly underneath the lantern of the street light to measure illuminance, and a calibrated Ocean Optics USB 2000 spectrometer (Largo, FL 33777, USA), a 7 m P400-5-UV/VIS patch cord and a CC-3 cosine corrector, all positioned 5 m directly underneath the lantern, to measure irradiance. Irradiance readings also allowed us to ensure that the spectral output of the street light remained unchanged and that only intensity varied with each light level (figure 1).

We measured bat activity by monitoring echolocation calls using SM3 bat detectors (Wildlife Acoustics, Inc., Maynard, MA, USA). Three sites ran concurrently. Bat detectors were set to record activity using triggers from 30 min before sunset on the first night until 30 min after sunrise on the ninth morning. At each site, one bat detector was attached to the middle experimental lighting column 1 m below the lantern, using street sign and Tamtorque sign-fixing clamps, with the microphone on the detector pointing slightly downwards and positioned on the same side of the column as the lantern. Bat detectors were randomized across sites. Files were stored as wavefile audio (WAV) files. The settings on the detectors were: high-pass filter 16 kHz; sample frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 s; trigger level 12 dB.

Bat activity for each lighting level was measured as the number of passes over each two-night period. Each 15 s file containing echolocation calls was considered as one bat pass [36]. At sites 19, 20 and 21 the sub-contractor failed to change the lighting level according to the agreed schedule, so bat passes were only counted for one night per treatment, which was selected at random. To compare bat feeding rates at different light levels, we calculated the buzz ratio, i.e. the proportion of passes that contained a feeding buzz [37] at each lighting level.

At seven sites (one from each of the three recording periods), a 12 megapixel 1080 HD Hunting Trail Infra-Red Camera (SpyCameraCCTV, Bristol, BS5 9PQ, UK) was attached to the lighting column to estimate the number of insects attracted to each lighting level. Infrared cameras were used so that the number of insects could be estimated when the street lights were dimmed to low light levels (25%) or switched off (0%). The camera takes high-resolution still images (12 megapixels) meaning that even small flies appeared on the images. The camera was attached to the lighting column immediately below the lantern, so its focus was within the light cone. A burst of three still images were taken once an hour throughout the night (sunset until sunrise). These data were used to compare the attractiveness of the LED lights at different lighting levels to aerial insects.

Nightly temperature and humidity were recorded at each site with a Tinytag TGP-4017 Plus 2 Internal Temperature data logger (Gemini Data Loggers UK Ltd., Chichester, PO19 8UJ, UK). Mean nightly rainfall (mm) and wind speed (km hr^{-1}) were obtained from Met Office weather stations within 35 km of each site (www.metoffice.gov.uk/).

2.2. Data processing

All bat calls were analysed using KALEIDOSCOPE PRO (v. 3.1.1, Wildlife Acoustics, Inc.) with British Bat Classifiers (v. 3.0.0). The auto-identification of *P. pipistrellus* and *P. pygmaeus* was accepted [36]. However, all other calls were manually identified to either species (*Eptesicus serotinus*, *Nyctalus noctula*, *Pipistrellus nathusii* and *Plecotus auritus*) or group (*Myotis* spp.); *Myotis* spp. are usually grouped because of the difficulty of separating the echolocation calls of the different species [38–40]. We also manually identified files that had a margin factor of zero (either KALEIDOSCOPE PRO was unable to identify the call or classified the call as a noise file). Margin scores in KALEIDOSCOPE PRO are uncalibrated confidence scores, whereby higher values are more likely to be correctly identified than lower values. Species identification was verified for 0.5% of the bat echolocation call files (676 files) to ensure that the auto-identification software was working effectively. These files were randomly selected across all sites to account for any differences between sites and included noise files to ensure that all files that contained a bat pass were being included in the analysis.

As we did not manually verify species from every file, we calculated the feeding buzz from a representative sample of files. For each site, we separated calls for each lighting level, then randomly selected 5% of files to check if a feeding buzz was present (mean number of files per lighting level were 35, 44, 51 and 48 for 0%, 25%, 50% and 100% lighting levels, respectively). We identified all feeding buzzes from all species, but they were mostly from *P. pipistrellus*. All noise files were excluded as a bat pass had to occur for a feeding buzz to be present. We calculated the buzz ratio to determine how the proportion of feeding buzzes compared with the number of echolocation calls changed with light intensity.

Insect activity was determined for one night of each lighting level, when there was no rain; this was owing to the difficulty in identifying the presence of an insect from an image when raining. Each visible white dot on the image was counted as an insect [12]. Only insects that were within the light cone, i.e. directly underneath the light were counted and we excluded non-volant invertebrates, i.e. we did not include spiders, many of which make their webs on street lights [41]. It was only possible to estimate total insect abundance and not to identify species. The number of insects counted in each image was carried out blind, i.e. the scorer was unaware of the lighting level when counting the number of insects. The number of insects from the three images for each hour was averaged and the hourly totals then averaged over the night for each lighting level. This reduced ‘noise’ that might be introduced if any of the three images were unclear.

2.3. Statistical analyses

Data were analysed in R STUDIO using R v. 3.3.3 (R Core Team 2017). We used generalized linear mixed models (GLMMs) to determine potential drivers of bat activity, insect counts and buzz ratios using the lme4 package [42]. Models for bat activity and insect counts followed a negative binomial distribution with a log-link function, and the model for buzz ratio followed a binomial distribution with a logit-link

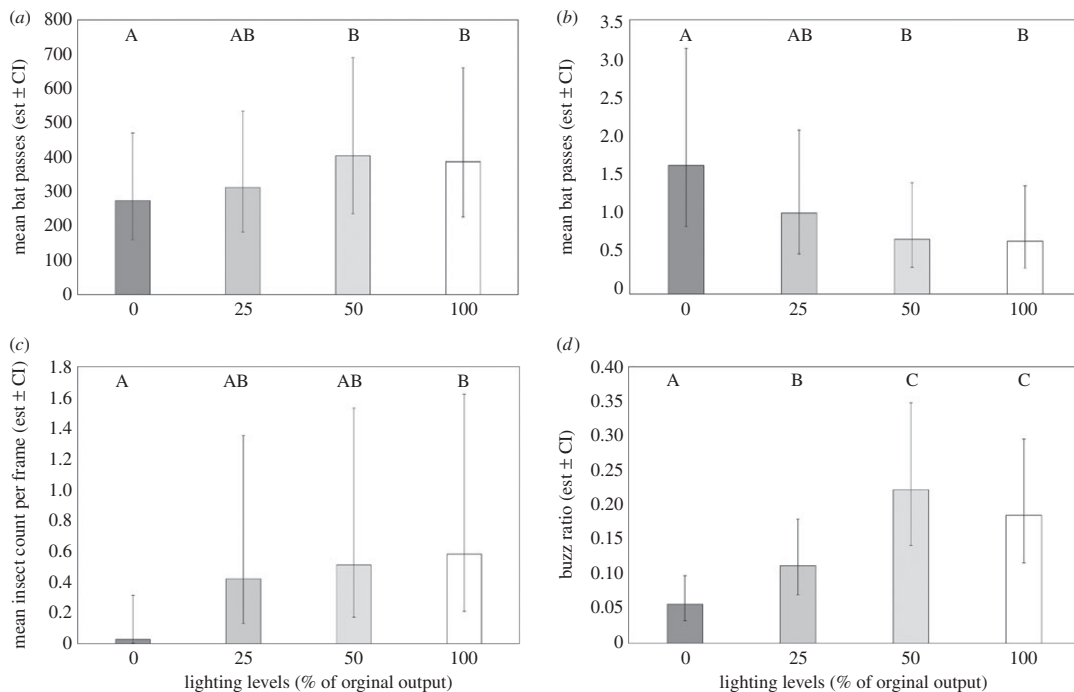


Figure 2. Mean predicted bat activity (number of bat passes) back-transformed across all sites ($n = 21$) for each lighting level for (a) *Pipistrellus pipistrellus* and (b) *Myotis* spp. (c) Mean predicted insect counts back-transformed across selected sites ($n = 7$) for each lighting level. (d) Mean predicted buzz ratios back-transformed across all sites ($n = 21$) for each lighting level. For all graphs letters identify groups that were significantly different from each other and vertical lines denote 95% confidence intervals (CIs).

function. Model choice was based on backward selection based on the second-order information criterion (AICc) using the *bbmle* package [43]. If the Δ AICc was less than 2 between models, we chose the model with the fewest number of parameters [44]. Model fit was validated using the *Dharma* package [45] to ensure that data were not overdispersed and to provide plots of residuals. Before fitting the GLMMs, we checked to see that the predictors, particularly the weather variables, were not correlated i.e. Spearman's rank correlation coefficient less than 0.5 [46].

For bat activity (bat passes), we used three models; all species, *P. pipistrellus* and *Myotis* spp. For all three models, the fixed factors included lighting level (0%, 25%, 50% and 100%) as well as standardized weather variables (centred around a mean of 0 and a standard deviation of 1), mean nightly temperature ($^{\circ}\text{C}$), mean nightly wind speed (km hr^{-1}) and mean nightly rainfall (mm). Site was included as a random effect to account for repeated measurements within each lighting column. Date was also included as a random effect to account for recording at multiple sites (three sites concurrently). Post hoc comparisons between intermediate lighting levels (i.e. 25% versus 50%, 25% versus 100% and 50% versus 100%) were carried out using the *multcomp* package [47] with single-step corrected probabilities.

The coefficient of determination (R^2) was calculated to compare the goodness-of-fit across the models for different bat species [48]. In mixed-effect models, R^2 has two classifications: marginal, which is the proportion of variance in the response variable explained by the fixed effects, and conditional, which is the proportion of variance in the response variable explained by both the fixed and random effects [49]. R^2 values for the buzz ratio model were calculated using the *MuMIn* package [50], and the R^2 values for the bat activity and insect count models were calculated as proposed by Nakagawa *et al.* [51].

3. Results

Across 21 sites, we recorded 135228 files that included 74965 bat passes from seven species/species groups. Most passes (76.7%) were from *P. pipistrellus*, followed by *P. pygmaeus* (20.9%), *N. noctula* (1.9%), *Myotis* spp. (0.2%), *Eptesicus serotinus* (0.08%), *Plecotus auritus* (0.08%) and *P. nathusii* (0.08%) (electronic supplementary material, tables S1–S4). No other species were recorded. From the 676 files that were manually verified, there was 87% agreement between the manual and automatic classifications, with 100% agreement with the automatic classifications of *P. pipistrellus* and *P. pygmaeus*. KALEIDOSCOPE

Table 1. Results from GLMMs for the bat passes of (a) all species, (b) *Pipistrellus pipistrellus* and (c) *Myotis* spp., (d) buzz ratios for all species (based on a 5% sample) and (e) mean insect counts. (All estimates were compared against the unlit treatment (0%). Significant results are in bold. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.)

model	estimate	s.e.	Z-value	p-value	marginal R^2	conditional R^2
(a) all species					0.183	0.832
25%	0.174	0.164	1.059	0.289		
50%	0.391	0.161	2.433	0.015*		
100%	0.290	0.160	1.810	0.070		
temperature (°C)	0.473	0.093	5.084	< 0.001***		
wind speed (km hr⁻¹)	-0.191	0.074	-2.572	0.010*		
(b) <i>P. pipistrellus</i>					0.203	0.851
25%	0.130	0.169	0.767	0.443		
50%	0.386	0.168	2.304	0.021*		
100%	0.343	0.167	2.054	0.040*		
temperature (°C)	0.531	0.097	5.452	< 0.001***		
wind speed (km hr⁻¹)	-0.252	0.079	-3.207	0.001**		
(c) <i>Myotis</i> spp.					0.126	0.797
25%	-0.408	0.231	-1.771	0.077		
50%	-0.828	0.237	-3.501	< 0.001***		
100%	-0.740	0.242	-3.057	0.002***		
rain (mm)	-0.340	0.184	-1.844	0.065		
wind speed (km hr ⁻¹)	-0.201	0.111	-1.861	0.063		
(d) buzz ratio					0.061	0.196
25%	0.689	0.217	3.170	0.001**		
50%	1.371	0.218	6.292	< 0.001***		
100%	1.190	0.220	5.406	< 0.001***		
temperature (°C)	0.427	0.168	2.540	0.011*		
(e) insect counts					0.188	0.227
25%	2.686	1.422	1.888	0.059		
50%	2.729	1.423	1.917	0.055		
100%	2.905	1.415	2.053	0.040*		

occasionally classified a file as a noise file or was unable to determine a classification, even when a call was present. As all files that were not classified as *P. pipistrellus* or *P. pygmaeus* were manually identified, we feel that our method was appropriate, given the large amount of data collected and the time needed to analyse all the data manually.

Across the 21 sites, mean light intensities for each lighting level were 11.35 lux (s.d. 3.23, range 8.68–14.9 lux) for 25%, 20.23 lux (s.d. 3.23, range 16.77–23.9 lux) for 50% and 35.46 lux (s.d. 5.94, range 29.4–44.0 lux) for 100%.

Statistical analyses were carried out on the number of bat passes for all species, *P. pipistrellus*, *Myotis* spp., feeding behaviour (buzz ratio) and mean insect counts, with standardized weather variables included as fixed factors in the GLMMs. The best models, determined by the lowest AICc values, generally included temperature (°C) and wind speed (km hr⁻¹) but not mean nightly rainfall (mm). Temperature had a positive significant effect on the number of bat passes, i.e. there were more bat passes as the nightly temperature increased, whereas wind speed had a significant negative effect on the number of bat passes, i.e. there were fewer bat passes as the nightly wind speed increased. So, it was important that both variables were included as fixed effects in the model.

Table 2. Results of the post-hoc comparisons applied to GLMMs for the bat passes of (a) all species, (b) *Pipistrellus pipistrellus* and (c) *Myotis* spp., (d) buzz ratios for all species (based on a 5% sample) and (e) mean insect counts. (Lighting levels were 25 (25%), 50 (50%) and 100 (100%). Significant results are in bold. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.)

model	estimate	s.e.	Z-value	p-value
<i>(a) all species</i>				
50–25	0.217	0.161	1.343	0.536
100–25	0.116	0.159	0.727	0.886
100–50	−0.101	0.157	−0.641	0.919
<i>(b) P. pipistrellus</i>				
50–25	0.257	0.167	1.535	0.416
100–25	0.213	0.164	1.298	0.564
100–50	−0.043	0.163	−0.265	0.994
<i>(c) Myotis spp.</i>				
50–25	−0.420	0.257	−1.635	0.358
100–25	−0.332	0.265	−1.253	0.592
100–50	0.088	0.271	0.325	0.988
<i>(d) buzz ratio</i>				
50–25	0.682	0.163	4.192	< 0.001***
100–25	0.501	0.161	3.116	0.010**
100–50	−0.181	0.161	−1.125	0.670
<i>(e) insect counts</i>				
50–25	0.043	0.723	0.059	1.000
100–25	0.219	0.696	0.315	0.988
100–50	0.177	0.689	0.257	0.994

When considering all bat species, there were significantly more bat passes at 50% compared to 0% lighting levels, but not between 25% or 100% and 0% levels (table 1). For light-opportunistic *P. pipistrellus*, the results were broadly similar: there were significantly more passes at 50% and 100%, compared with the 0% lighting level, but there was no difference in the number of bat passes between the 0% and 25% lighting levels (table 1 and figure 2a). Conversely, higher light intensities had a negative effect on the light-averse *Myotis* spp. There were significantly fewer *Myotis* passes at 50% and 100% lighting levels, compared with the unlit treatment, but there was no significant difference between the 0% and 25% lighting levels (table 1 and figure 2b).

The insect count data also showed significantly higher insect activity at the 100% lighting level compared with the unlit treatment, but there was no difference between 0% and 25% or 50% lighting levels (table 1 and figure 2c). There were significantly more feeding buzzes at 25%, 50% and 100% lighting levels, compared with the unlit treatment (table 1 and figure 2d).

While there were no significant differences between intermediate light levels, i.e. 25% compared to 50% or 100%, or 50% compared to 100% (table 2) for the bat activity data for any of the species or insect counts, there were significantly more feeding buzzes at 50% and 100%, compared with the 25% lighting level (table 2).

4. Discussion

Our results are broadly consistent with our hypotheses, that higher light levels (50% and 100%) increased the activity of light-opportunistic species such as *P. pipistrellus*, but reduced the activity of light-averse species such as *Myotis* spp. However, lower light levels (25%) do not affect activity levels of either light-opportunistic or light-averse species of bats compared to the unlit treatment (0%).

The increase in the number of bat passes of the light-opportunistic *P. pipistrellus* at 50% and 100%, compared to the unlit treatment, is most probably owing to the greater number of insects being attracted to the street lights at higher lighting levels. This supports the attraction-by-insects hypothesis, as opposed to the attraction-by-artificial-light hypothesis, which argues that bats are attracted to the lights for other reasons [14]. Foraging benefits can also be inferred from the buzz ratio data. The proportion of feeding buzzes compared to the number of bat passes was significantly higher at the 25%, 50% and 100% lighting levels than the unlit treatment. Also, there were significantly more buzzes relative to echolocation calls at the 50% and 100% lighting levels compared to the 25% level. Our feeding buzz data suggest that the main benefit for some species of bats flying close to street lights is to prey on the insects attracted to the light source. Even though the number of light-opportunistic bat passes did not increase significantly at the 25% lighting level, compared to the unlit treatment, nor between intermediate lighting levels (i.e. 25% and 50% or 25% and 100%), the buzz ratios increased, suggesting that these species of bats increase their feeding efficiency at street lights. This could be owing to the reduced anti-predator behaviour of moths [52] or because around street lights bats may possibly feed on large numbers of relatively small insects that have a lower energy content than larger insects.

Furthermore, there were significantly more insects at the 100% compared to the unlit treatment and the differences between the 25% and 50% lighting levels and the unlit treatment were almost significant (table 2). While there were not significantly more insects at the 25% or 50% lighting levels compared to the unlit treatment, there were more feeding buzzes relative to the number of bat passes. This could be owing to the absence of a linear relationship between the number of insects attracted to a light source and its illuminance [53]. Although the light intensity at the 50% level (mean 20.23 lux) was double that of the 25% level (mean 11.35 lux), this does not mean that double the number of insects should be attracted to the 50% lighting level. To determine the attractiveness of a light source, it is necessary to consider the spectral sensitivities of the insects [3] and calculate either the square root of the ratio between the illuminance of the light source and its surrounding background [54] or use a function of the luminance of the light source [55]. The difference between the insect and buzz ratio data could also be owing to the smaller sample sizes for the insect counts.

Lighting level appeared to have a stronger effect at 50% than 100% for both bat activity and feeding behaviour, possibly because when the LED street lights are at 50% of their original output, there is an increase in insect numbers and hence feeding opportunities but fewer risks from potential predators. Alternatively, when light intensities increase above 50% of the original output, the illuminance may disturb bats [56] or, at light intensities above 50%, more bats may be attracted to the higher insect numbers, and hence be affected by echolocation interference from the calls of other bats. This makes it more difficult for a bat to differentiate its own returning echoes from those of conspecifics [57].

It is unsurprising that we found significantly fewer bat passes of *Myotis* spp. at 50% and 100% lighting levels compared to the unlit treatment [26,33]. However, it is encouraging that the low lighting level (25%) did not have a detrimental effect on the number of *Myotis* spp. passes. From a conservation perspective, this is a positive outcome as it means there is scope to work with local authorities to determine if it is possible to find a light intensity that is acceptable for humans but does not adversely affect bat activity, particularly for light-averse species.

At the low lighting level (25%), as less light was distributed from the light source, it is likely that dark corridors were created that light-averse species, such as *Myotis* spp., could fly along, either as a more efficient commuting route or even to forage. However, once the street light intensities exceeded 11.35 lux, the perceived threat of predation becomes too great, significantly reducing the number of *Myotis* spp. passes near the street lights. This contrasts with an earlier study, which found that LED light intensities as low as 3.6 lux negatively affected the number of bat passes from light-averse bats such as *Myotis* spp. and *Rhinolophus hipposideros* [26]. This could be owing to differences in experimental design: our study took place in suburban areas, where street lights have existed for decades, and hence the bats may have adapted to the presence of artificial lights, whereas the earlier study set up street lights in unlit areas [26], and hence the novelty of lighting may have affected the bats differently. Differences could also be because fewer *Myotis* spp. are found in suburban areas compared to rural areas (figure 2*a,b*). As *Myotis* spp. are light-averse, they tend to avoid suburban areas when commuting and foraging, preferring more cluttered habitats [17,19]. Our results are consistent with an earlier study which also found that light intensity had a significant positive effect on light-opportunistic species such as *P. pipistrellus*, but a significant negative effect on light-averse species such as *Myotis* spp. [33].

Reducing the light intensities of street lights could also benefit invertebrates by decreasing flight-to-light behaviour, thereby lowering the risk of mortality from exhaustion and predation, as well as

preventing disruptions to biological cycles [58,59]. To reduce the ecological impact on invertebrates, it has been advised that LED street lights should be dimmed to 50% of their original output (less than 14 lux) and adhere to a part-night lighting scheme, i.e. switched off between midnight and 04.00 [60].

In conclusion, our results support dimming as an effective strategy to mitigate the ecological impacts of street lights as it seems possible to achieve a light intensity that could benefit both light-opportunistic and light-averse species of bats [56], potentially realigning the balance that existed before street lighting dominated our landscapes. It is worth mentioning that ideally the installation of street lights should be avoided, but as this is not feasible in many areas owing to safety and security reasons, dimming seems to be the most suitable alternative.

We believe further studies are required to investigate the impacts of dimming in different locations to include other light-averse species, such as *Plecotus* and *Rhinolophus* species. It would also be useful to repeat this study, using residential areas, instead of A roads where street lights are typically 5 m as opposed to 10 m high, and have a lower power and illuminance. It might be possible to reduce light intensities even further, while still striking the balance between maintaining biodiversity, economic benefits and human safety [61].

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. Conceived and designed the experiments: E.G.R., S.H. and G.J. Performed the experiments and analysed the data: E.G.R. Contributed reagents/materials/analysis tools: E.G.R. and G.J. Wrote the paper: E.G.R., S.H. and G.J. Supervised the study: S.H. and G.J.

Competing interests. We declare that we have no competing interests.

Funding. The project was funded by a studentship from the Natural Environment Research Council, grant no. NE/K500823/1. The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

Acknowledgements. We thank Shelby Temple for loaning the spectrometer, Hertfordshire County Council and Ringway (Eurovia Vinci, UK) for their invaluable help with the experiments, particularly Jon Watt and Graham Black, and Neil Rowse and Pauline Smith for their assistance in the field.

References

- Hölker F *et al.* 2010 The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecol. Soc.* **15**, 13. (doi:10.5751/ES-03685-150413)
- Cinzano P, Falchi F, Elvidge CD. 2001 The first world atlas of the artificial night sky brightness. *Mon. Not. R. Astron. Soc.* **328**, 689–707. (doi:10.1046/j.1365-8711.2001.04882.x)
- Gaston KJ, Davies TW, Bennie J, Hopkins J. 2012 Reducing the ecological consequences of night-time light pollution: options and developments. *J. Appl. Ecol.* **49**, 1256–1266. (doi:10.1111/j.1365-2664.2012.02212.x)
- Navara KJ, Nelson RJ. 2007 The dark side of light at night: physiological, epidemiological, and ecological consequences. *J. Pineal Res.* **43**, 215–224. (doi:10.1111/j.1600-079X.2007.00473.x)
- Jägerbrand AK. 2016 LED (light-emitting diode) road lighting in practice: an evaluation of compliance with regulations and improvements for further energy savings. *Energies* **9**, 357. (doi:10.3390/en9050357)
- De Almeida A, Santos B, Paolo B, Quicheron M. 2014 Solid state lighting review: potential and challenges in Europe. *Renew. Sust. Energy. Rev.* **34**, 30–48. (doi:10.1016/j.rser.2014.02.029)
- Baumgartner T, Wunderlich F, Jaunich A, Sato T, Bundy G, Griebmann N, Kowalski J, Burghardt S, Hanebrink J. 2012 *Lighting the way: perspectives on the global lighting market*, 2nd edn. New York, NY: McKinsey & Co.
- Beccali M, Lo Brano V, Bonomolo M, Cicero P, Corvisieri G, Caruso M, Gamberale F. 2017 A multifunctional public lighting infrastructure, design and experimental test. *J. Sustain. Dev. Energy Water Environ. Syst.* **5**, 608–625. (doi:10.13044/j.sdwes.d5.0164)
- Stone EL, Harris S, Jones G. 2015 Impacts of artificial lighting on bats: a review of challenges and solutions. *Mammal. Biol.* **80**, 213–219. (doi:10.1016/j.mambio.2015.02.004)
- Barroso A, Haifig I, Janei V, da Silva I, Dietrich C, Costa-Leonardo AM. 2017 Effects of flickering light on the attraction of nocturnal insects. *Lighting Res. Technol.* **49**, 100–110. (doi:10.1177/1477153515602143)
- Wakefield A. 2016 Insects and lighting: how green is white light? PhD thesis, University of Bristol, Bristol, UK.
- Rydell J. 1992 Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* **6**, 744–750. (doi:10.2307/2389972)
- Blake D, Hutson AM, Racey PA, Rydell J, Speakman JR. 1994 Use of lamplit roads by foraging bats in southern England. *J. Zool.* **234**, 453–462. (doi:10.1111/j.1469-7998.1994.tb04859.x)
- Voigt CC, Roeleke M, Marggraf L, Petersons G, Voigt-Heucke SL. 2017 Migratory bats respond to artificial green light with positive phototaxis. *PLoS ONE* **12**, e0177748. (doi:10.1371/journal.pone.0177748)
- Hale JD, Fairbrass AJ, Matthews TJ, Davies G, Sadler JP. 2015 The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Glob. Change Biol.* **21**, 2467–2478. (doi:10.1111/gcb.12884)
- Russo D, Cistrone L, Libralato N, Korine C, Jones G, Ancilotto L. 2013 Adverse effects of artificial illumination on bat drinking activity. *Anim. Conserv.* **20**, 492–501.
- Norberg UM, Rayner JMW. 1987 Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond. B* **316**, 335–427. (doi:10.1098/rstb.1987.0030)
- Jennings NV, Parsons S, Barlow KE, Gannon MR. 2004 Echolocation calls and wing morphology of bats from the West Indies. *Acta Chiropterol.* **6**, 75–90. (doi:10.3161/1508110042176644)
- Jones G, Rydell J. 1994 Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* **346**, 445–455. (doi:10.1098/rstb.1994.0161)
- Rydell J, Entwistle A, Racey PA. 1996 Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* **76**, 243–252. (doi:10.2307/3546196)
- Jones KE, Purvis A, Gittleman JL. 2003 Biological correlates of extinction risk in bats. *Am. Nat.* **161**, 601–614. (doi:10.1086/368289)
- Rand AS, Bridaroli ME, Dries L, Ryan MJ. 1997 Light levels influence female choice in Túngara frogs: predation risk assessment? *Copeia* **1997**, 447–450. (doi:10.2307/1447770)
- Salmon M, Tolbert MG, Painter DP, Goff M, Reiners R. 1995 Behavior of loggerhead sea turtles on an urban beach. II. Hatching orientation. *J. Herpetol.* **29**, 568–576. (doi:10.2307/1564740)

24. Lloyd JE. 1994 Where are the lightningbugs? Fireflyer Companion 1, 1, 2, 5, 10.
25. Stone EL, Jones G, Harris S. 2009 Street lighting disturbs commuting bats. *Curr. Biol.* **19**, 1123–1127. (doi:10.1016/j.cub.2009.05.058)
26. Stone EL, Jones G, Harris S. 2012 Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Glob. Change Biol.* **18**, 2458–2465. (doi:10.1111/j.1365-2486.2012.02705.x)
27. McLay LK, Green MP, Jones TM. 2017 Chronic exposure to dim artificial light at night decreases fecundity and adult survival in *Drosophila melanogaster*. *J. Insect Physiol.* **100**, 15–20. (doi:10.1016/j.jinsphys.2017.04.009)
28. de Jong M, Ouyang JQ, van Grunsven RHA, Visser ME, Spoelstra K. 2016 Do wild great tits avoid exposure to light at night? *PLoS ONE* **11**, e0157357. (doi:10.1371/journal.pone.0157357)
29. de Jong M, Caro SP, Gienapp P, Spoelstra K, Visser ME. 2017 Early birds by light at night: effects of light color and intensity on daily activity patterns in blue tits. *J. Biol. Rhythms* **32**, 323–333. (doi:10.1177/0748730417719168)
30. Aubrecht TG, Weil ZM, Nelson RJ. 2014 Dim light at night interferes with the development of the short-day phenotype and impairs cell-mediated immunity in Siberian hamsters (*Phodopus sungorus*). *J. Exp. Zool.* **321A**, 450–456. (doi:10.1002/jez.1877)
31. Fonken LK, Weil ZM, Nelson RJ. 2013 Mice exposed to dim light at night exaggerate inflammatory responses to lipopolysaccharide. *Brain Behav. Immun.* **34**, 159–163. (doi:10.1016/j.bbi.2013.08.011)
32. Raap T, Sun J, Pinxten R, Eens M. 2017 Disruptive effects of light pollution on sleep in free-living birds: season and/or light intensity-dependent? *Behav. Process.* **144**, 13–19. (doi:10.1016/j.beproc.2017.08.011)
33. Lacoëuilhe A, Machon N, Julien J-F, Le Bocq A, Kerbiriou C. 2014 The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLoS ONE* **9**, e103042. (doi:10.1371/journal.pone.0103042)
34. Lyytimäki J, Rinne J. 2013 Voices for the darkness: online survey on public perceptions on light pollution as an environmental problem. *J. Integr. Environ. Sci.* **10**, 127–139. (doi:10.1080/1943815X.2013.824487)
35. Verboom B, Spoelstra K. 1999 Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Can. J. Zool.* **77**, 1393–1401. (doi:10.1139/z99-116)
36. Mathews F, Roche N, Aughney T, Jones N, Day J, Baker J, Langton S. 2015 Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Phil. Trans. R. Soc. B* **370**, 20140124. (doi:10.1098/rstb.2014.0124)
37. Vaughan N, Jones G, Harris S. 1997 Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. Appl. Ecol.* **34**, 716–730. (doi:10.2307/2404918)
38. Russ J. 2012 *British bat calls: a guide to species identification*. Exeter, UK: Pelagic Publishing.
39. Walters CL *et al.* 2012 A continental-scale tool for acoustic identification of European bats. *J. Appl. Ecol.* **49**, 1064–1074. (doi:10.1111/j.1365-2664.2012.02182.x)
40. Rydell J, Nyman S, Eklöf J, Jones G, Russo D. 2017 Testing the performances of automated identification of bat echolocation calls: a request for prudence. *Ecol. Indic.* **78**, 416–420. (doi:10.1016/j.ecolind.2017.03.023)
41. Heiling AM. 1999 Why do nocturnal orb-webs spiders (Araneidae) search for light? *Behav. Ecol. Sociobiol.* **46**, 43–49. (doi:10.1007/s002650050590)
42. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
43. Bolker B, R Development Core Team. 2017 *bbmle: tools for general maximum likelihood estimation*. R package version 1.0.20. See <https://CRAN.R-project.org/package=bbmle>.
44. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
45. Hartig F. 2017 DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. See <https://cran.r-project.org/web/packages/DHARMA/vignettes/DHARMA.html>.
46. Freckleton RP. 2002 On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J. Anim. Ecol.* **71**, 542–545. (doi:10.1046/j.1365-2656.2002.00618.x)
47. Hothorn T, Bretz F, Westfall P. 2008 Simultaneous inference in general parametric models. *Biometrical J.* **50**, 346–363. (doi:10.1002/bimj.200810425)
48. Johnson PCD. 2014 Extension of Nakagawa & Schielzeth's R^2_{GLMM} to random slopes models. *Methods Ecol. Evol.* **5**, 944–946. (doi:10.1111/2041-210X.12225)
49. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
50. Barton K. 2018 MuMIn: multi-model inference. R package version 1.40.4. See <https://CRAN.R-project.org/package=MuMIn>.
51. Nakagawa S, Johnson PCD, Schielzeth H. 2017 The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *J. R. Soc. Interface* **14**, 20170213. (doi:10.1098/rsif.2017.0213)
52. Wakefield A, Stone EL, Jones G, Harris S. 2015 Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls. *R. Soc. open sci.* **2**, 150291. (doi:10.1098/rsos.150291)
53. Longcore T, Aldern HL, Eggers JF, Flores S, Franco L, Hirshfield-Yamanishi E, Petrinec LN, Yan WA, Barroso AM. 2015 Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. *Phil. Trans. R. Soc. B* **370**, 20140125. (doi:10.1098/rstb.2014.0125)
54. Bowden J. 1982 An analysis of factors affecting catches of insects in light-traps. *Bull. Entomol. Res.* **72**, 535–556. (doi:10.1017/S0007485300008579)
55. Stevens SS. 1961 To honor Fechner and repeal his law: a power function, not a log function, describes operating characteristic of a sensory system. *Science* **133**, 80–86. (doi:10.1126/science.133.3446.80)
56. Lewanzik D, Voigt CC. 2017 Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *J. Appl. Ecol.* **54**, 264–271. (doi:10.1111/1365-2664.12758)
57. Amichai E, Blumrosen G, Yovel Y. 2015 Calling louder and longer: how bats use biosonar under severe acoustic interference from other bats. *Proc. R. Soc. B* **282**, 20152064. (doi:10.1098/rspb.2015.2064)
58. Macgregor CJ, Pocock MJO, Fox R, Evans DM. 2015 Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecol. Entomol.* **40**, 187–198. (doi:10.1111/een.12174)
59. de Medeiros BAS, Barghini A, Vanin SA. 2017 Streetlights attract a broad array of beetle species. *Rev. Bras. Entomol.* **61**, 74–79. (doi:10.1016/j.rbe.2016.11.004)
60. Davies TW, Bennie J, Cruse D, Blumgart D, Inger R, Gaston KJ. 2017 Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. *Glob. Change Biol.* **23**, 2641–2648. (doi:10.1111/gcb.13615)
61. Azam C, Le Viol I, Bas Y, Zissis G, Vernet A, Julien J-F, Kerbiriou C. 2018 Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landsch. Urban Plan.* **175**, 123–135. (doi:10.1016/j.landurbplan.2018.02.011)