

Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats

EMMA L. STONE, GARETH JONES and STEPHEN HARRIS

School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK

Abstract

Artificial lighting is a key biodiversity threat and produces 1900 million tonnes of CO₂ emissions globally, more than three times that produced by aviation. The need to meet climate change targets has led to a global increase in energy-efficient light sources such as high-brightness light-emitting diodes (LEDs). Despite the energetic benefits of LEDs, their ecological impacts have not been tested. Using an experimental approach, we show that LED street lights caused a reduction in activity of slow-flying bats (*Rhinolophus hipposideros* and *Myotis* spp.). Both *R. hipposideros* and *Myotis* spp. activities were significantly reduced even during low light levels of 3.6 lux. There was no effect of LED lighting on the relatively fast-flying *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *Nyctalus/Eptesicus* spp. We provide the first evidence of the effects of LED lights on bats. Despite having considerable energy-saving benefits, LED lights can potentially fragment commuting routes for bats with associated negative conservation consequences. Our results add to the growing evidence of negative impacts of lighting on a wide range of taxa. We highlight the complexities involved in simultaneously meeting targets for reduction of greenhouse gas emissions and biodiversity loss. New lighting strategies should integrate climate change targets with the cultural, social and ecological impacts of emerging lighting technologies.

Keywords: anthropogenic impacts, biodiversity conservation, climate change targets, LED street lights, light pollution, light-emitting diodes

Received 13 January 2012 and accepted 3 March 2012

Introduction

Biodiversity is declining globally, whereas the drivers of biodiversity loss (including resource consumption, invasive alien species, overexploitation and climate change impacts) are increasing (Butchart *et al.*, 2010). Artificial lighting is increasing globally by 6% per annum and has been identified as a key biodiversity threat, ranked within the top 10 emerging issues in biodiversity conservation (Hölker *et al.*, 2010a). Artificial lighting consumes 19% of total global electricity, equivalent to 1900 Mt of CO₂ per year (Hölker *et al.*, 2010b), resulting in a worldwide shift of lighting policies towards energy efficiency and reduction of greenhouse gas emissions in line with Kyoto targets for tackling climate change (Anon, 2006; Hölker *et al.*, 2010b). Policy shifts have catalyzed a global increase in demand for energy-efficient lighting sources, such as high-brightness light-emitting diodes (LEDs), which had an estimated 31% growth in market share in 2010 (Steele, 2010). The global LED market is expected to grow from

€7 billion in 2010 to €65 billion in 2020, representing almost 60% of the total lighting market (Peters, 2011). LEDs are replacing traditional street lighting sources such as high pressure sodium (HPS) and incandescent lamps, due to their increased energy efficiency, increased design flexibility, the ability to change the colour of the light (Peters, 2011), longer lifespan (and therefore lower maintenance costs) and improved light quality (Hölker *et al.*, 2010b; Steele, 2010). Awareness of the ecological impacts of artificial light pollution is increasing (Navara & Nelson, 2007; Horváth *et al.*, 2009; Smith, 2009; Hölker *et al.*, 2010a). Light pollution can affect ecological interactions across a range of taxa, including critical animal behaviours such as foraging, reproduction and communication (Rich & Longcore, 2006).

Artificial lighting affects bat roosting and foraging behaviour. Lighting around bat roosts can delay nightly emergence time (Downs *et al.*, 2003). Delayed emergence causes bats to miss the peak abundance in insects that occurs at dusk (Jones & Rydell, 1994) and hence a significant loss of foraging opportunities. Some bat species forage actively under street lights, taking advantage of the high densities of insects attracted to light (Eisenbeis, 2006). In such cases, bat densities can be much higher at street lights than the surrounding dark

Correspondence: Emma Louise Stone, tel. + 00 44 0117 954 5953, fax + 00 44 0117 3317985, e-mail: emma.stone@bristol.ac.uk; Gareth Jones, tel. + 00 44 0117 954 5953, fax + 00 44 0117 331 7985, e-mail: gareth.jones@bristol.ac.uk

landscape. For example, activity levels of *Pipistrellus pipistrellus* were at least 10 times higher in lit areas in England than at unlit sites (Rydell & Racey, 1995). The highest levels of bat activity have been recorded at white lights (Blake *et al.*, 1994; Rydell & Racey, 1995; Avila-Flores & Fenton, 2005), which is the consequence of five times more insects being attracted to white lights than sodium lights (Rydell, 1992). Bats feeding on tympanate moths may have improved foraging success under lit conditions as the moths' evasive behaviours are reduced under mercury vapour lights, increasing their vulnerability to predation (Svensson & Rydell, 1998).

In contrast some species appear to be averse to lights. In Canada and Sweden, *Myotis* spp. and *Plecotus auritus* were only recorded away from street lights (Furlonger *et al.*, 1987; Rydell, 1992), and activity of *R. hipposideros* was significantly reduced along commuting routes illuminated with HPS street lights (Stone *et al.*, 2009). Acoustic tracking experiments demonstrated that *Eptesicus bottae* failed to forage under lit conditions (Polak *et al.*, 2011).

The increased awareness of the ecological impacts of artificial light pollution, combined with the pressure to reduce greenhouse gas emissions and energy consumption, highlights the need to identify lighting technologies that can simultaneously satisfy potentially conflicting demands. Although white LEDs are considered a 'green' technology because of their energy-saving benefits, their ecological impacts have not been tested. Being nocturnal, bats are one of the taxa most likely to be affected by light pollution, making them ideal subjects to test the effects of new lighting technologies. All bats, their resting and breeding sites are strictly protected in Europe under the European Habitats Directive (Conservation of Natural Habitats of Wild Flora and Fauna 1992/42/EEC). Under regulation 41, it is an offence to disturb a bat deliberately, where disturbance is defined as anything that impairs a bat's ability to survive, breed or reproduce, or affect significantly the local distribution or abundance of a species. Disturbance caused by artificial lighting may potentially constitute an offence under European law and therefore must be considered during environmental impact assessments.

Our previous research identified a negative effect of HPS street lights on the commuting behaviour of a relatively slow-flying threatened bat (*R. hipposideros*) (Stone *et al.*, 2009), confirming predictions that slower-flying bats avoid light due to light-dependent predation risk (Rydell, 1992). Slow-flying bats such as *Rhinolophus*, *Myotis* and *Plecotus* species have echolocation and wing morphology adapted for cluttered environments (Norberg & Rayner, 1987), and emerge from roosts relatively late when light levels are low, probably to

avoid predation by diurnal birds of prey (Jones & Rydell, 1994). To better understand the consequences of future changes in the lighting market, we used an experimental approach to test the effect of LED street lights, new to the market in 2009, on the activity of bats flying along hedgerows. We tested the impact on five bat species/groups (*Myotis* spp., *Nyctalus/Eptesicus* spp., *P. pipistrellus*, *Pipistrellus pygmaeus* and *R. hipposideros*) with different flight morphologies and hence different expected light tolerances. We predicted that slower-flying species (*R. hipposideros* and *Myotis* spp.) would be affected negatively by LED lights and that impacts would be comparable to those recorded for HPS lights (Stone *et al.*, 2009; Stone, 2011). We also tested the effect of varying light intensities on bat activity to determine whether dimming lights may reduce impacts on those species affected negatively. This is the first empirical attempt to investigate the effects of white LED lighting on wildlife, taking a proactive approach to the future management of the ecological impacts of emerging artificial light technologies.

Materials and methods

Lighting experiments were conducted along hedgerows used as flight routes by bats near 10 *R. hipposideros* maternity roosts in southwest England and Wales between May and August 2009. Hedges were illuminated with two portable cool white Monaro LED street lights obtained from DW Windsor UK (Hoddesdon, Hertfordshire, UK), under guidance from the Institution of Lighting Professionals (Rugby, Warwickshire, UK). Monaro LEDs are commercially available street lights at the forefront of emerging street lighting technology (Fig. 1). Lamps contained 24 × 2.4 watt high-power LEDs which were programmed remotely from a laptop to enable dimming and were powered by a Honda EU26i portable silenced generator [Honda (UK), Slough, Berkshire, UK] located an average of 59.7 m (SD = 25.5 m, range = 34.2–110) from experimental hedges (Stone *et al.*, 2009). Lights were dimmed using the pulse-width modulation method which alters the pulse current width to control light intensity (Manninen & Orreveläinen, 2007). A low switching frequency (duty cycle) corresponds to low power and therefore low light levels. We selected a generator with the lowest noise output available at the time of study. The generator contained sound proofing insulation inside the housing which resulted in a noise output of 49 dB at 7 m. Light units were placed 30 m apart to replicate the spacing of standard street lights (Stone *et al.*, 2009) and lamps directed towards the ground (Fig. 1).

Experiments lasted six nights per site (Table 1) and comprised a control treatment on night one, a noise treatment on night two and three different lit treatments comprising low (mean 3.6 lux, SD = 0.48, *n* = 20, range = 2.90–4.86), medium (mean 6.6 lux, SD = 0.93, *n* = 15, range = 4.95–8.60) and high light intensity (mean 49.8 lux, SD = 4.50, *n* = 14, range = 38.10–55.60). One of the lit treatments was conducted on either night three, four or five, and a repeat of the noise treatment



Fig. 1 Experimental LED lights along a hedgerow used as a commuting route by *Rhinolophus hipposideros* during the field study.

was performed on night six. The order of lit treatments on nights three to five was randomized between sites to control for order effects. The light level (lux) used during the high light intensity treatment was within the range of our previous experiments using HPS to enable direct comparisons between light types (Stone *et al.*, 2009). Illuminance (in lux) was measured using a T-10 illuminance metre (Konica Minolta Sensing Inc, Osaka, Japan) held horizontally 1.7 m high at the hedge below the lights. Mean hedgerow height across sites was 7.34 m (SD = 4.45 m) on the lit side and 7.55 m (SD = 4.91) on the unlit opposite side. Mean nightly temperature using a TinyTag TGP-1500 Datalogger (Gemini Dataloggers UK Ltd, Chichester, West Sussex, UK) was recorded at four sites only due to equipment failures at the remaining six sites. Mean daily rainfall (mm) and mean nightly temperature (degrees Celsius) for the remaining six sites were obtained from the Met Office (<http://www.metoffice.gov.uk>) from the weather station closest to each site (mean distance 17.5 km, SD = 15.5 km).

Bat activity (number of bat passes) was recorded using two AnaBat SD1 acoustic detectors (Titley Electronics, Ballina,

New South Wales, Australia), with one placed on average 1.7 m high on each side of the experimental hedge. AnaBat detectors supply a readily accessible and noninvasive means to access information pertaining to bat ecology, and frequently record species that fly outside the usual range of bat traps such as mist nets or harp traps (O'Farrell *et al.*, 1999). Echolocation call analysis was conducted using AnalookW 3.7o 2009 (Titley Electronics). Since it is not possible to identify individual bats from echolocation calls, mean number of bat passes was used as an index of relative bat activity (Stone *et al.*, 2009). A single bat pass was classified when the time between call pulses exceeded four times the pulse interval (as quantified in Parsons & Jones, 2000). Individual bat passes which were overlapping were distinguished using abrupt changes in the pulse interval and peak frequency. Bats were identified to the three species (*P. pipistrellus*, *P. pygmaeus*, *R. hipposideros*) and two species groups (*Myotis* spp. and *Nyctalus/Eptesicus* spp.) according to characteristic call parameters (Russ, 1999; Collins & Jones, 2009).

Feeding activity was also recorded. As bats approach insects they produce 'terminal phase' calls during which pulse

Table 1 Experimental treatment regime conducted at 10 sites. Treatments on nights two and six were the same at each site. The sequence of light treatments (low, medium or high) was randomized among nights three to five across sites to control for the potential cumulative effect of light on bats

Night	Treatment	Description
1	Control	Detectors installed at hedge, no lighting treatment or generator
2	Noise	Detectors installed, lighting units installed but switched off, generator running all night
3	LED	Detectors installed, lighting units (and generator) installed and illuminated all night using either the low (3.6 lux), medium (6.6 lux) or high (49.8 lux) light treatment. Sequence of lit treatments randomly selected at each site
4	LED	As night 3 with second randomized light treatment
5	LED	As night 3 with remaining light treatment
6	Noise	Repeat of noise as in night 2

duration and interval between pulses shortens producing a diagnostic feeding buzz (Griffin *et al.*, 1960). Relative feeding activity was measured using a 'buzz ratio', calculated as the ratio of feeding buzzes to total number of passes per species per night (Vaughan *et al.*, 1997). A 'buzz ratio' of one indicates that on average every bat pass contains a feeding buzz.

Observations of *R. hipposideros* were conducted during lit experimental nights ($n = 29$, mean 2.9 per site) at all sites to determine whether bats were flying wide of, or high above the detectors and evading detection. Behavioural responses and number of bats were recorded and categorized as either having passed through or avoided the light. The responses of bats that avoided the light were further classified as turned around; flew through the hedge; flew over the hedge or flew under the hedge. In view of logistical constraints, it was not possible to record behavioural observations of other species during lit nights.

Repeated measures general linear models (RMGLMs) were used to test for differences in temperature and rainfall among treatment nights using SPSS for Windows 16 (SPSS Inc., Chicago, IL, USA). As there was no significant difference in mean nightly temperature ($F_{5,45} = 0.73$, $n = 10$ sites, $P = 0.61$) and mean nightly rainfall ($F_{5,45} = 1.79$, $n = 10$ sites, $P = 0.13$) among treatment nights, these variables were excluded from further analyses to achieve model simplification (Crawley, 2007). RMGLMs were used to test the effect of treatment type on bat activity. Data were log transformed to meet assumptions of homoscedasticity and normality (Altman, 1991).

Bat activity (number of bat passes per night per species) among lit nights was compared using a RMGLM where species were recorded at less than seven sites. Where there was no significant difference among lit nights (low, medium and high), data were pooled and tested using RMGLM with four within-subject effects (control, noise, lit and noise 2) to increase residual degrees of freedom. Where significant treatment effects were found, activity data for the unlit side of the treatment hedge were analysed using a RMGLM to assess whether bats switched to the unlit side of the hedge during lit nights. Sufficient feeding activity data were only available for *P. pipistrellus* ($n = 8$ sites) and *P. pygmaeus* ($n = 7$ sites). The effect of treatment on *P. pipistrellus* feeding activity (buzz ratio) was tested using a Friedman's nonparametric ANOVA using R version 2.10.1.

Results

LED street lights have a negative effect on the activity of some bat species (specifically *R. hipposideros* and *Myotis* spp.). Treatment type had a significant effect on *R. hipposideros* activity levels ($F_{2,9,26.3} = 24.9$, $n = 10$, $P = <0.001$). The difference in mean activity between the control (conducted on night one) and the first noise treatment (conducted on night two) was not significant (Fig. 2a; Table 2). For *R. hipposideros*, there was a significant reduction in activity between the control (conducted on night one) and the second noise treatment (conducted on night six), and no significant difference in activity between both noise treatments

(Table 2). Activity during all lit treatments was lower than control values, and the first noise treatment (Table 2), demonstrating that LED lights had a significant negative effect on bat activity. There was a significant difference in bat activity levels between the high and medium light treatments ($P = 0.002$), and no significant difference between the medium and low light treatments ($P = 0.251$).

Behavioural observations of *R. hipposideros* were recorded at ten sites over 29 nights. On 56% of observations bats flew through the lights, and on the remaining 44% avoided the lights. The majority of those bats that avoided the lights flew over the hedge and then out of sight (53%), turned around before the lights (43%), flew through the hedge (3%) or possibly avoided detection by flying high above or wide of the lights (1%). There was no significant effect of treatment on *R. hipposideros* activity on the unlit side of the hedge ($F_{5,30} = 1.202$, $n = 7$, $P = 0.332$), indicating that bats did not avoid the lit side of the hedge by flying down the unlit side. Mean light levels recorded on the unlit side of the hedge opposite the lights were 0.59 lux (SD = 0.58, $n = 42$, range = 0.07–2.30) on lit treatment nights and 0.55 lux (SD = 0.56, $n = 42$, range = 0.00–1.90) on control and noise nights.

Treatment type had a significant effect on *Myotis* spp. activity ($F_{5,30} = 6.28$, $n = 7$, $P = 0.004$). There was no significant difference in *Myotis* spp. activity between the control and the first noise treatment (Fig. 2b; Table 2), or between the control and the second noise treatment (Table 2), i.e. the presence of the unlit lighting units and noise from the generator had no effect on *Myotis* spp. activity. Activity recorded during all lit nights was significantly lower than control nights (Table 2), demonstrating that LED lights had a negative effect on *Myotis* spp. activity. There was no significant difference in *Myotis* spp. activity recorded between low light and the first noise treatments ($F_{1,6} = 9.64$, $n = 7$, $P = 0.210$, $r = 0.79$) and the high light and the first noise treatment ($F_{1,9} = 0.21$, $n = 7$, $P = 0.663$, $r = 0.18$). *Myotis* spp. activity was significantly lower during the medium light treatment than the first noise treatment ($F_{1,6} = 13.89$, $n = 7$, $P = 0.041$, $r = 0.84$), and there was no significant effect of treatment ($F_{5,25} = 0.431$, $n = 6$, $P = 0.823$) on *Myotis* spp. activity on the unlit side of the hedge.

In contrast, there was no effect of treatment type on the activity of *P. pipistrellus* ($F_{5,45} = 0.821$, $n = 10$, $P = 0.542$, Fig. 2c), *P. pygmaeus* ($F_{1,45} = 0.375$, $n = 10$, $P = 0.863$, Fig. 2d) or *Nyctalus/Eptesicus* spp. ($F_{5,40} = 1.121$, $n = 9$, $P = 0.365$, Fig. 2e). Light treatment had no significant effect on feeding activity for *P. pipistrellus* ($\chi^2_5 = 9.12$, $n = 8$, $P = 0.105$) or *P. pygmaeus* ($\chi^2_5 = 5.77$, $n = 7$, $P = 0.329$).

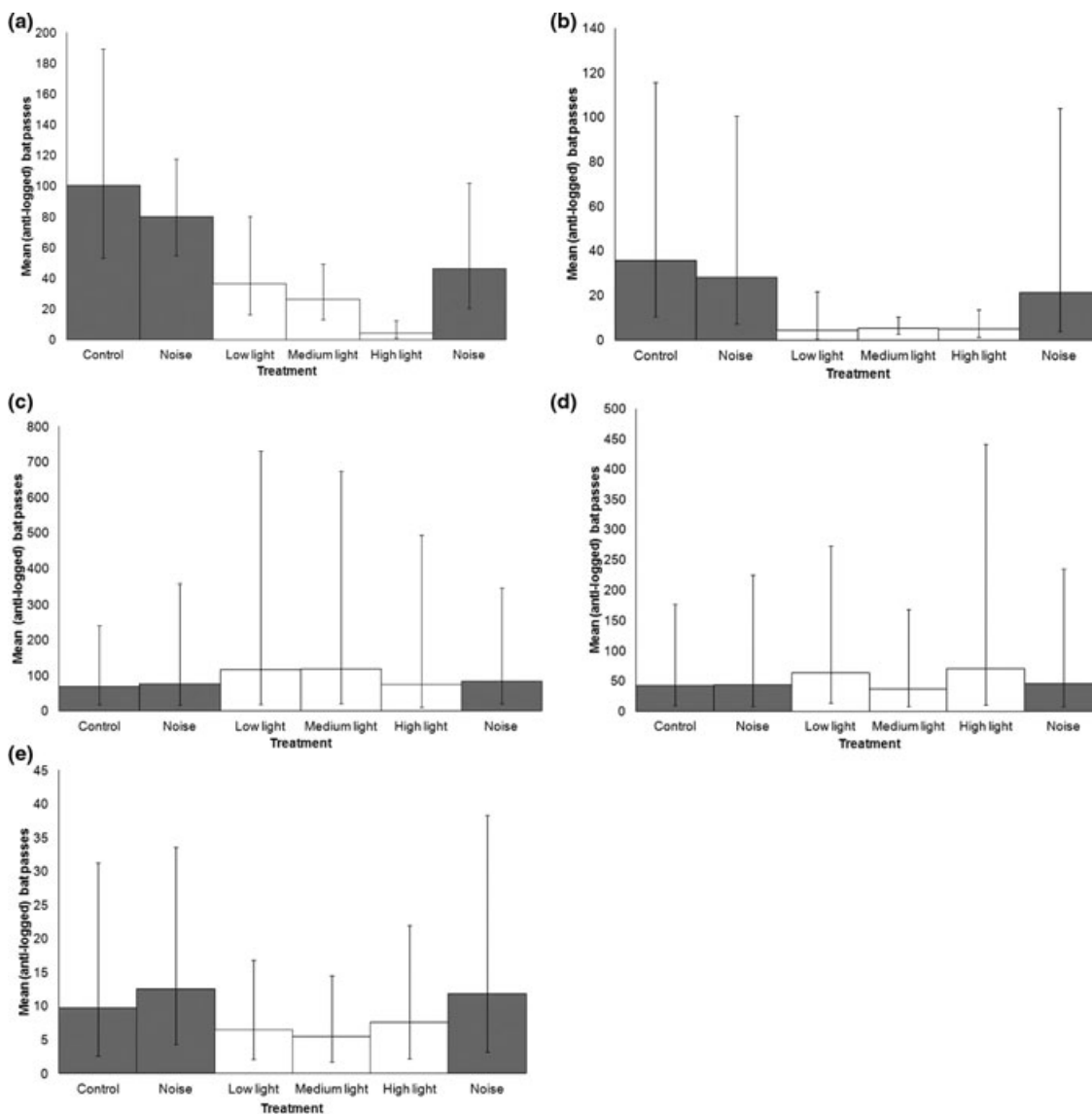


Fig. 2 Geometric mean and confidence intervals of bat passes along the treatment hedge across treatments for (a) *Rhinolophus hipposideros*, (b) *Myotis* spp., (c) *Pipistrellus pipistrellus*, (d) *Pipistrellus pygmaeus* and (e) *Nyctalus/Eptesicus* spp. White bars indicate lit treatments.

Discussion

Light-emitting diode lights had no significant effect on *P. pipistrellus*, *P. pygmaeus* and *Nyctalus/Eptesicus* spp. activity, consistent with our previous research with HPS lights (Stone, 2011). Light treatments had no significant effect on feeding activity of both *P. pipistrellus* and *P. pygmaeus*. Previous studies have found that white street lights such as High Pressure Mercury Vapour (HMPV) lamps which emit short wavelength UV light and attract high insect densities, in turn attract some bat species, including *P. pipistrellus* (Rydell, 1992; Blake *et al.*, 1994; Rydell & Racey, 1995). In comparison, HPS lights, which emit both shorter

and longer wavelength light (Rydell, 2005), were of medium attractiveness to insects, attracting 57% fewer insects than HMPV (Eisenbeis, 2006) and, therefore, fewer bats (Blake *et al.*, 1994). Foraging on swarming insects at street lights is more profitable for some bat species (Rydell, 2005), which benefit from a higher food intake when feeding around street lights than in other habitats (Rydell, 1992). White light in particular interferes with moth behaviour by disabling their acoustic defences, increasing their vulnerability, giving bats a competitive advantage (Svensson & Rydell, 1998).

Although they emit white light, LEDs are comparable with HPS in terms of spectral content, as they emit very little short wavelength light, i.e. the ultraviolet end of

Table 2 Within subjects contrasts for *Rhinolophus hipposideros* and *Myotis* spp

Contrast	<i>Rhinolophus hipposideros</i>			<i>Myotis</i> spp.		
	F	r	P	F	r	P
Control vs. noise 1	1.2	0.34	0.308	0.61	0.30	0.466
Control vs. noise 2	23.8	0.85	0.001*	2.17	0.52	0.191
Noise 1 vs. noise 2	3.9	0.55	0.081	0.21	0.18	0.663
Control vs. low LED	15.6	0.80	0.003*	12.72	0.82	0.012*
Control vs. med LED	11.6	0.75	0.008*	15.32	0.85	0.008*
Control vs. high LED	70.3	0.94	0.000*	12.37	0.82	0.013*
Low LED vs. med LED	1.5	0.38	0.251	0.14	0.15	0.723
Med LED vs. high LED	17.4	0.81	0.002*	0.06	0.10	0.819
Low LED vs. high LED	30.2	0.88	0.000*	0.03	0.07	0.868
Low LED vs. noise 1	9.0	0.71	0.015*	9.64	0.79	0.210
Med LED vs. noise 1	19.8	0.83	0.002*	13.89	0.84	0.041*
High LED vs. noise 1	80.6	0.95	0.000*	0.21	0.18	0.663

*Significant at $P = 0.05$.

the spectrum. Therefore, the lack of increased feeding activity recorded during lit treatment nights may be a function of the spectral content of LED lights, with low UV resulting in a lower attractiveness for bats. However, the attractiveness of light to insects is also dependent on insect species, with higher densities of some moths (e.g. *Idaea dimidiata*) recorded at HPS than at white lights (Kolligs, 2000). During this study, insects were observed swarming at the lights during the high LED treatments, and at some sites, bats were observed foraging around the lights for many hours. So the low feeding rates of *P. pipistrellus* and *P. pygmaeus* recorded in this study may be due to the short-term experimental nature of the study. Bats may need some time to locate and identify newly installed lights as an attractive foraging source. However, attractiveness of street lights to insects may also be a function of street light intensity, street light location and weather (Eisenbeis, 2006), all of which may have contributed to the lack of increased feeding activity of both *P. pipistrellus* and *P. pygmaeus*.

In contrast LED lights reduced commuting activity for *R. hipposideros* and activity (and probably commuting activity) for *Myotis* spp. Behavioural observations confirmed that *R. hipposideros* were avoiding the lights, with only 1% of bats observed flying high above or wide of the lights and possibly avoiding detection. Activity levels recorded on the opposite side of the hedge during lit treatments demonstrate that both *R. hipposideros* and *Myotis* spp. did not avoid the lit side of the hedge by flying along the unlit side.

Myotis spp. warrant further investigation as, despite no difference between control and the first noise

treatment, activity levels during the medium light treatment were significantly different from the first noise treatment. There may be species-specific differences in the responses of bat species in the *Myotis* genus to light: further work is needed to test this.

The light levels recorded during the high light treatment (range = 38.1–55.6 lux) were mostly within the range of those recorded during our HPS experiments (Stone *et al.*, 2009) (range = 47.3–60.2 lux). Light levels recorded on the high light treatment fell outside the range of the HPS experiments at only one site, and therefore, direct comparison of light types is possible. The magnitude of the effect of the high light treatment ($r = 0.94$) on *R. hipposideros* activity was similar to that recorded during the HPS light treatments (Lit 1 $r = 0.95$, Lit 2 $r = 0.90$, Lit 3 $r = 0.91$). Our results suggest that at similar light intensities, there is little difference in the magnitude of effects from HPS and LED lights for this species.

Light-emitting diode lights are very energy efficient (Hölker *et al.*, 2010b) and, therefore, have a lower environmental impact than other light sources. Because they emit very little or no ultraviolet light, it has been argued that they are less ecologically disruptive as fewer insects are attracted to LED lights (Anon, 2009a). However, our results clearly show that there is little difference in both the magnitude and nature of the impact of both HPS and LED on *R. hipposideros* and *Myotis* spp., with both light types causing a significant reduction in activity along lit hedgerows. It is likely, therefore, that the impacts of LED light disturbance on *R. hipposideros* and *Myotis* spp. will be similar to those caused by HPS lights, i.e. LED lights can fragment commuting routes, causing bats to alter their behaviour with potentially negative conservation consequences (see discussion in Stone *et al.*, 2009).

Myotis spp. showed no significant difference in response to changes in light intensity, whereas *R. hipposideros* activity was significantly lower during the high than during the medium light intensity treatment (Table 2). Despite the differences in activity in relation to intensity, *R. hipposideros* and *Myotis* spp. activity levels for all light treatments were significantly lower than control levels even at very low light levels (3.6 lux, low light treatment). Avoidance of light at very low levels has important implications, since reducing light intensity has often been advocated as a potential mitigation strategy for lighting schemes affecting bats (Anon, 2009b); this assumes that there is a critical light threshold below which there are no negative effects on bat activity. However, for these species, we have shown that light levels would have to be lower than at least 3.6 lux before a potential threshold is found. In reality,

achieving such low levels may not be practical: public perception of safety (Anon, 2009b), combined with the practicality of achieving these levels, often precludes dimming to very low light levels.

The potential long-term impacts of artificial lighting on the conservation status of bats are unknown. Boldogh *et al.* (2007) found that juvenile *M. emarginatus* and *M. oxygnathus* were smaller and weighed less in illuminated compared with nonilluminated roosts, suggesting delayed parturition or slower growth rates. This may have long-term consequences as smaller bats have lower over-winter survival rates (Ransome, 1989). The negative impacts of lighting on bats reported here add to the growing evidence that artificial light pollution can have detrimental behavioural effects on a wide range of taxa, e.g. birds (Le Corre *et al.*, 2002; Poot *et al.*, 2008; Kempenaers *et al.*, 2010), amphibians and reptiles (Wang *et al.*, 2007; Perry *et al.*, 2008), small mammals (Bird *et al.*, 2004) and insects (Svensson & Rydell, 1998; Eisenbeis, 2006). The nature and extent of the impacts of lighting on hibernation will depend on many factors including the thermoregulatory flexibility of the species in question, with more flexible species able to adapt to artificial stressors such as lighting, and therefore less likely to be affected negatively (Boyles *et al.*, 2011).

The fitness consequences of reduced foraging and commuting by bats caused by artificial lighting are difficult to quantify and unknown at present. Avoidance of lit areas may cause increased energetic costs and reduced foraging time, which could affect individual fitness and reproduction. Bats are slow to reproduce, with most temperate bat species rearing one single offspring per year (Dietz *et al.*, 2009) and are therefore more sensitive to changes at the population level. Further long-term experimental research is required to investigate the potential impacts of lighting on population dynamics of bats. Species-specific effects of light pollution can also have negative effects at the community level. Studies of the effect of anthropogenic noise pollution on birds have found community-level effects through disruption of interactions between predators and prey (Francis *et al.*, 2009). The reduction in activity of some bat species at the expense of others may result in competitive exclusion of less tolerant species, as more light tolerant species may out-compete them for aerial insect prey (Polak *et al.*, 2011).

Our results demonstrate that disturbance from LED street lights along commuting routes produces complex and species-specific responses in bats and has wider implications for the potential mitigation of the ecological impacts of emerging 'green' lighting technologies. Our results highlight the need for research into the impacts of LEDs and other new lighting technologies on other taxonomic groups. Technological innovations

and changes in lighting strategies should consider benefits for reductions in greenhouse gases and energy consumption in parallel with their potential ecological impacts, an approach being adopted with wind energy. Although climate change benefits of wind energy are considerable, wind turbines kill substantial numbers of bats and approaches which maximize climate change benefits while minimizing bat fatalities are being sought (Curry, 2009; Arnett *et al.*, 2011). We argue for a holistic multidisciplinary approach to the development of lighting strategies and technologies, which is not driven solely by economic, energetic and climate change targets. To be effective, policy objectives need to consider the cultural, social, energetic, economic and ecological impacts of future lighting technologies.

Acknowledgements

We thank A. Wakefield for field assistance; T. Webster and T. Walker from DW Windsor UK; C. Williams from the Bat Conservation Trust; A. Crook for electrical expertise; site owners and bat group members across southwest England and Wales; SITA Trust, Mammals Trust UK, ARUP, Bat Conservation International, Natural England, One World Wildlife, Countryside Council for Wales, RGS-IBG, Dulverton Trust, DW Windsor UK and CSa Environmental for funding; DW Windsor UK for technical expertise and LED lights; and Jacobs Engineering Group Inc. for loan of detectors.

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