

Street Lighting Disturbs Commuting Bats

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Summary

Anthropogenic disturbance is a major cause of worldwide declines in biodiversity [1]. Understanding the implications of this disturbance for species and populations is crucial for conservation biologists wishing to mitigate negative effects. Anthropogenic light pollution is an increasing global problem [2], affecting ecological interactions across a range of taxa and impacting negatively upon critical animal behaviors including foraging, reproduction, and communication (for review see [2, 3]). Almost all bats are nocturnal [4], making them ideal subjects for testing the effects of light pollution. Previous studies have shown that bat species adapted to foraging in open environments feed on insects attracted to mercury vapor lamps. Here, we use an experimental approach to provide the first evidence of a negative effect of artificial light pollution on the commuting behavior of a threatened bat species. We installed high-pressure sodium lights that mimic the intensity and light spectra of streetlights along commuting routes of lesser horseshoe bats (*Rhinolophus hipposideros*). Bat activity was reduced dramatically and the onset of commuting behavior was delayed in the presence of lighting, with no evidence of habituation. These results demonstrate that light pollution may have significant negative impacts upon the selection of flight routes by bats.

Results and Discussion

Anthropogenic disturbance can negatively affect wildlife by causing alterations to behaviors necessary for survival, such as foraging or reproduction [5]. Disturbance can result in reduced use of foraging areas [6], alterations in movement patterns, reduced breeding success, or increased predation rates [2]. Despite increasing light pollution, few studies have experimentally assessed the impact of artificial lighting on the commuting and foraging behavior of bats. We chose *Rhinolophus hipposideros* as a study species because its global populations are decreasing (www.iucnredlist.org/, accessed March 17, 2009) and the species is now endangered in many industrialized countries in central Europe. Avian predation risk is a major factor explaining chiropteran nocturnality [7], with predatory birds accounting for 11% of annual mortality in British bats [8]. *R. hipposideros* is slow flying, travels a maximum of 4.17 km from the roost per night [9], and has echolocation adapted for cluttered environments [10, 11]. Slow flight renders *R. hipposideros* vulnerable to predation by diurnal birds of prey and also unlikely to exploit insects attracted to street lamps [10]. Indeed, the species is

predicted to avoid artificially illuminated areas because of light-dependent predation risk [4, 11]. We therefore hypothesized that artificial illumination would have a negative effect on the commuting activity of *R. hipposideros*. This was tested via artificial light experiments at hedgerows in eight sites in southern Britain between April and July 2008.

Streetlight Surveys

We conducted streetlight surveys in 2 km × 2 km squares during August 2007 to determine light levels for use in field experiments. We recorded an average of 51.67 lux (confidence interval ± 11.68, n = 26) along hedgerows illuminated with high-pressure sodium (HPS) streetlights. Experimental hedges were therefore illuminated to an average of 53.09 lux (SD = 2.73, range = 47.3–60.2, n = 36). A mean of 4.17 lux (SD = 7.77, range = 0.07–24.28, n = 16) was recorded during lit treatment nights on the unlit side of the hedge, which was significantly higher than the mean light level recorded at the same locations on unlit nights (Mann-Whitney U test, W = 230.5, p < 0.01, mean 0.03, SD = 0.03, n = 62). The mean ambient light level in the middle of the fields on lit treatment nights was 0.04 lux (SD = 1.3, range = 0.02–5.46, n = 23).

Bat Activity

Hedges were subject to the following treatments: control (no lights), noise (generator on, lights installed but switched off), lit (full illumination all night, repeated over four consecutive nights), and noise (see Table 1). Treatment type had a significant effect on *R. hipposideros* activity levels ($F_{2,54, 17.74} = 9.51$, n = 8, p < 0.02). The difference in mean activity between the control and the first noise treatment was not significant ($F_{1,7} = 5.5$, n = 8, p > 0.05). There was no difference between activity during the control and the second noise treatment ($F_{1,7} = 2.58$, n = 8, p > 0.05), or between both noise treatments ($F_{1,7} = 0.63$, n = 8, p > 0.05). Thus, there was no statistical effect of generator noise or the presence of unlit lighting units on bat activity. Activity during all lit treatments was different from control levels (p < 0.05; Figure 1), demonstrating that HPS lights had a significant negative effect on bat activity. To assess whether bats switched to the unlit side of the hedge during lit nights, activity data were analyzed using four within-factor levels (control, noise, lit, and noise; see Experimental Procedures). There was no significant effect of treatment on activity on the unlit side of the hedge ($F_{3,12} = 2.71$, n = 5, p > 0.05; Figure 2). Within-factor effects were also nonsignificant ($F_{1,4} = 2.71$, n = 5, p > 0.05), indicating that bats did not avoid the lit side of the hedge by flying down the darker unlit side. The median time of emergence was 32 min after sunset (n = 8 exit counts). During our experiments, there was no evidence of short-term habituation during lit nights.

Commencement of Activity

We tested the effect of light disturbance on the time of commencement of bat activity at the experimental hedgerows. Although there was no overall effect of treatment on commencement of bat activity ($F_{3,5} = 2.48$, n = 8, p > 0.05), within-factor effects were significant ($F_{3,21} = 4.78$, n = 8, p < 0.02). Contrasts revealed that activity commenced

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Table 1. Experimental Treatment Regime

Night	Treatment	Description
1	Control	Detectors installed at hedge, no lighting treatment or generator
2	Noise	Detectors installed at hedge, lighting units installed but switched off, generator running all night
3	Lit 1	Detectors installed at hedge, lighting units installed and switched on, generator running all night
4	Lit 2	As Lit 1
5	Lit 3	As Lit 1
6	Lit 4	As Lit 1
7	Noise	Repeat of noise treatment as in night 2

significantly earlier on the first noise treatment (mean 23.0 min after sunset) compared to control nights (mean 29.9 min after sunset, $F_{1,7} = 5.90$, $n = 8$, $p < 0.05$; Figure 3). However, activity commenced significantly later on lit nights (mean 78.6 min after sunset) compared to both control ($F_{1,7} = 6.73$, $n = 8$, $p < 0.04$) and the first noise treatments ($F_{1,7} = 9.23$, $n = 8$, $p < 0.02$). Initiation of activity during the second noise treatment was not significantly different from the control value ($F_{1,7} = 0.24$, $n = 8$, $p > 0.05$).

Linear habitat features are important for many bat species at the landscape scale (for overview see [12]). *R. hipposideros* and many other slow-flying bat species avoid open areas, typically flying within vegetation cover, commuting along hedgerows or tree lines between roosts and foraging areas [13]. Bats use linear landscape features for increased insect abundance, shelter from wind and rain, acoustic orientation, and predator avoidance [14, 15]. Reliance on linear habitat features makes bats vulnerable to habitat fragmentation. Our results imply that light pollution may fragment the network of *R. hipposideros* commuting routes, causing bats to alter their commuting behavior, which could have significant conservation consequences. Disruption of animal spatial behavior can decrease energetic gains and increase costs by increasing flight time and stress and cortisol levels, which may in turn reduce survival and reproductive success [16]. For bats, such effects are likely to be more pronounced during periods of high energetic demand such as lactation.

To predict the effects of light disturbance on fitness and ultimately survival, we need to identify the nature of behavioral responses. Commuting bats may respond to light disturbance

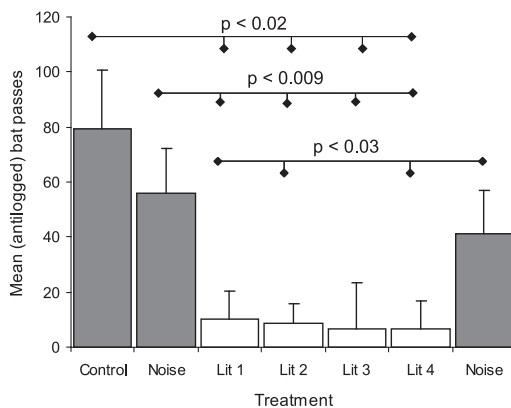


Figure 1. *R. hipposideros* Mean Activity in Relation to Treatment Type
Data are presented as mean \pm SEM. Significant within-subject differences are shown with p values.

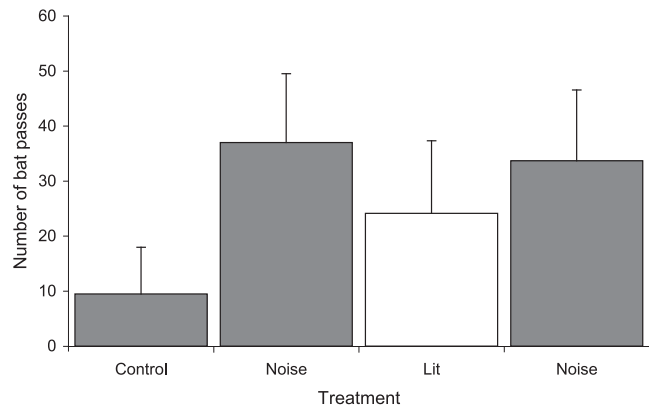


Figure 2. *R. hipposideros* Mean Activity on Opposite Unlit Side of the Experimental Hedge across Treatment Types

Data are presented as mean \pm SEM.

in four ways: (1) flying high above or around the lights, (2) flying on the unlit side of the hedge, (3) choosing an alternative route, and/or (4) returning to the roost. Bats flew through the lights on 42 percent of observations during lit nights, turned around before reaching the lights on 30 percent of observations, flew over the hedge on 17 percent, flew through the hedge on 9 percent, and flew wide or high around the lights on only 2 percent of observations.

It is unsurprising that few bats flew along the unlit side of the hedge, given that light levels on the unlit side on lit nights (mean 4.17 lux) were significantly higher than those along dark hedges (mean 0.45 lux); even these relatively low light levels may make established routes unsuitable for commuting. During experiments, it was not possible to assess whether bats returned to the roost. Returning to the roost would have significant energetic costs because bats would fail to feed. However, at each site, some bats were observed flying along alternative routes during lit nights, and it seems probable that the majority of bats selected an alternative route in response to disruption of their preferred commuting route.

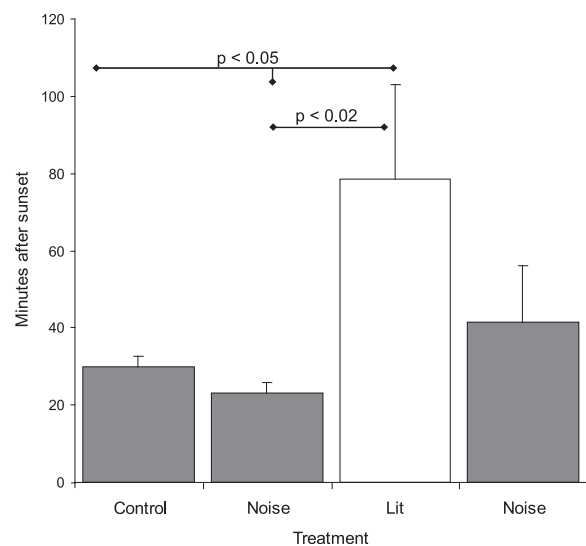


Figure 3. Mean Commencement of Activity
Data are presented as mean minutes after sunset of emergence of first bat at hedge, \pm SEM.

The fitness consequences of route switching will depend on the availability, length, and quality of alternative routes at each site. If alternative routes are suboptimal in terms of quality or distance to foraging habitats, this may have significant conservation consequences—e.g., if alternative routes provide reduced shelter, bats may be forced to fly along exposed routes, thereby increasing predation risk, particularly for juvenile bats, which fly especially slowly [17]. Such routes may also increase exposure to elements such as wind and rain, which would increase flight costs [14].

Alternative routes with longer flight distances to foraging areas might also affect individual fitness and therefore reproduction because of increased energetic costs—for example, in *Myotis grisescens*, increased travel distances to foraging areas for lactating females suppress juvenile growth rates [18]. Commuting costs become prohibitive for *Pipistrellus pipistrellus* when foraging areas are more than 5 km from the roost [19]. If the energetic costs of alternative routes exceed the threshold for energetic benefit, bats may become isolated from their foraging habitat. As bats select roosts according to the quality of surrounding habitat features, including linear connectivity [20, 21], in extreme cases such disruption may result in roost abandonment.

The timing of activity recorded during control and noise nights here was similar to previous studies in which *R. hipposideros* commenced activity 19 min after sunset [22]. Activity commenced earlier on the first noise night than on the control night, whereas it did not on the second noise night. It is therefore possible that some bats emerged early to investigate the noise on the first noise treatment. Commencement of activity during lit nights was significantly later than during unlit nights, consistent with a previous study using white light at a *Pipistrellus pygmaeus* roost [23]. *R. hipposideros* foraging activity peaks at dusk, in line with the peak abundance of key prey (small dipteran flies) [11]. Delayed activity as a result of light disturbance may therefore result in missed foraging opportunities.

Here we have shown that light pollution can have significant conservation consequences for a threatened bat species as a result of changes in the use of established flight routes and delaying commuting behavior. In contrast, other studies have shown some fast-flying bat species are attracted to white lights because of the high insect concentrations found near such light sources [10, 24, 25]. Our study highlights the importance of adopting a species-specific approach to understanding the ecological consequences of artificial light pollution. Conservation consequences are likely to depend on factors such as predation risk and will vary according to light type and environmental and site-specific characteristics. Yet light pollution is rarely considered in habitat management plans, and street lighting is excluded from English and Welsh light-pollution legislation [26]. Our study provides evidence that light pollution may force bats to use suboptimal flight routes, potentially causes isolation of preferred foraging sites, and therefore must be considered when developing conservation policy.

Experimental Procedures

Streetlight Surveys

Three tetrads (2 km × 2 km squares) in North Somerset, southwest Britain, were selected via a random numbers table and traveled along by car at night. Urban areas were excluded, but suburban areas on the edges of villages were included. All roads in each tetrad were traveled once commencing 1 hr after dark, starting from a randomly chosen point. Lux levels were recorded on hedgerows illuminated with HPS lights. Lux was

measured along hedgerows with a Konica Minolta T-10 illuminance meter held horizontally at a height of 1.7 m. Lux was measured at four sampling points from each streetlight, one below the light and then at three subsequent 7.5 m intervals along the hedge.

Emergence Surveys

A total of eight emergence surveys were randomly conducted at seven sites (mean one per site) over four lit nights, three noise nights, and one control night. Two observers stood on average 10–15 m from the roost and counted bats as they emerged from the roost, recording time after sunset for each observation.

Lighting Experiments

Experiments were conducted along hedgerows in the vicinity of eight *R. hipposideros* maternity roosts. Active flight paths along hedgerows were identified with AnaBat II and SD1 ultrasonic remote detectors (Tittle Electronics, Ballina, NSW, Australia) on stands approximately 1.2 m high. Detectors were set to a sensitivity of 8 and a division ratio of 16 and were started manually 30 min before sunset. At each site, the hedge with the highest relative bat activity on the first night was chosen for the experiment. Experiments were conducted over a period of seven nights at each site (Table 1). Hedges were illuminated to a mean of 53.09 lux with two portable HPS streetlights located 30 m apart powered by a Honda EU portable generator (Figure 4). The generator was located an average of 58 m from experimental hedges. The generator and lights were switched on 30 min before sunset. Illumination was measured at the hedge at a height of 1.75 m behind the light units at an average of 58 min after sunset. Lights and luminaires were standard UK streetlights obtained from DW Windsor Ltd., under guidance from the Institute of Lighting Engineers. Lights were placed on average 269 m (range 91–791 m) from the roost sites. Detectors were rotated between treatments to control for potential biases in sensitivity. To determine whether bats were flying wide or high above the detectors and evading detection, observations of bats were conducted during lit experimental nights (n = 14). Behavioral responses and number of bats were recorded.

Mean nightly rainfall (mm) and wind speed (knots/hr) were obtained from weather stations in the locality of each site from the Met Office (www.metoffice.gov.uk/). Nightly temperature was recorded at each site with a TinyTag TGP-1500 data logger (Gemini Data Loggers UK Ltd.).

Bat Echolocation Call Analysis

Echolocation call analysis was conducted in AnalookW 3.3g 2006 (Tittle Electronics). Relative bat activity was measured using the mean number of bat passes per treatment night, because it is impossible to count individual bats from recordings of their echolocation calls. A single bat pass was counted when the time between calls exceeded four times the inter-pulse interval [27]. The calls of *R. hipposideros* are diagnostic, dominated by a constant frequency component between 106 and 114 kHz.

Statistical Analysis

Bat Activity

Data from lit experimental hedges were log transformed to meet the assumptions of normality and homoscedasticity [28]. Activity data were analyzed via a repeated-measures general linear model (RMGLM) with SPSS for Windows 16 (SPSS Inc.). Light treatment was fitted as the within-factor effect with seven levels. Data for the unlit sides of hedges were collected at five sites. All lit nights were compared via a RMGLM to increase residual degrees of freedom. Because there was no significant difference between lit nights ($F_{3,12} = 0.390$, $n = 5$, $p > 0.05$), data were pooled and tested via RMGLM with four within-factor effects (control, noise, lit, and noise). Antilog-transformed means ± standard error of the mean are presented in all relevant figures.

Our experimental design should take into account any variation in weather in relation to treatment, because unfavorable weather was assumed to be equally likely on any night. Because RMGLM tests revealed no significant differences in temperature ($F_{1,6} = 2.80$, $p > 0.05$), wind speed ($F_{1,6} = 0.30$, $p > 0.05$), or rainfall ($F_{2,6} = 2.32$, $p > 0.05$) according to treatment type, weather variables were excluded from further analyses.

Commencement of Activity

The effect of treatment on commencement of bat activity was assessed via a RMGLM. Differences in the time that the first bat was observed (minutes after sunset) were analyzed using seven within-factor effects (treatment nights).



Figure 4. Experimental Lights along a Hedgerow Used as a Commuting Route by *R. hipposideros*

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References

1. Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., et al. (2005). Global consequences of land use. *Science* 309, 570–574.
2. Rich, C., and Longcore, T. (2006). *Ecological Consequences of Artificial Night Lighting* (Washington, DC: Island Press).
3. Longcore, T., and Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment* 2, 191–198.
4. Speakman, J.R. (1991). Why do insectivorous bats in Britain not fly in daylight more frequently? *Funct. Ecol.* 5, 518–524.
5. Le Corre, M., Ollivier, A., Ribes, S., and Jouventin, P. (2002). Light-induced mortality of petrels: A 4-year study from Réunion Island (Indian Ocean). *Biol. Conserv.* 105, 93–102.
6. Bird, B.L., Branch, L.C., and Miller, D.L. (2004). Effects of coastal lighting on foraging behavior of beach mice. *Conserv. Biol.* 18, 1435–1439.
7. Speakman, J.R. (1995). Chiropteran nocturnality. *Symp. Zool. Soc. Lond.* 67, 187–201.
8. Speakman, J.R. (1991). The impact of predation by birds on bat populations in the British Isles. *Mammal Rev.* 21, 123–142.
9. Bontadina, F., Schofield, H., and Naef-Daenzer, B. (2002). Radio-tracking reveals that lesser horseshoe bats (*Rhinolophus hipposideros*) forage in woodland. *J. Zool.* 258, 281–290.
10. Rydell, J., and Racey, P.A. (1995). Streetlamps and the feeding ecology of insectivorous bats. *Symp. Zool. Soc. Lond.* 67, 291–307.
11. 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, 243–252.
12. Rydell, J. (1992). Exploitation of insects around streetlights by bats in Sweden. *Funct. Ecol.* 6, 744–750.
13. Ekman, M., and De Jong, J. (1996). Local patterns of distribution and resource utilization of four bat species (*Myotis brandtii*, *Eptesicus nilssonii*, *Plecotus auritus* and *Pipistrellus pipistrellus*) in patchy and continuous environments. *J. Zool.* 238, 571–580.
14. Verboom, B., and 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, 1393–1404.
15. Verboom, B., Boonman, A.M., and Limpens, H.J.G.A. (1999). Acoustic perception of landscape elements by the pond bat (*Myotis dasycneme*). *J. Zool.* 248, 59–66.
16. Papouchis, C.M., Singer, F.J., and Sloan, W.B. (2001). Responses of desert bighorn sheep to increased human recreation. *J. Wildl. Manage.* 65, 573–582.
17. Racey, P.A., and Swift, S.M. (1985). Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging Behaviour. *J. Anim. Ecol.* 54, 205–215.
18. Tuttle, M.D. (1976). Population ecology of the gray bat (*Myotis grisescens*): Factors influencing growth and survival of newly volant young. *Ecology* 57, 587–595.
19. Speakman, J.R., Racey, P.A., Catto, C.M.C., Webb, P.I., Swift, S.M., and Burnett, A.M. (1991). Minimum summer populations and densities of bats in NE Scotland, near the northern borders of their distributions. *J. Zool.* 225, 327–345.
20. Oakeley, S.F., and Jones, G. (1998). Habitat around maternity roosts of the 55 kHz phonic type of pipistrelle bats (*Pipistrellus pipistrellus*). *J. Zool.* 245, 222–228.
21. Jenkins, E.V., Laine, T., Morgan, S.E., Cole, K.R., and Speakman, J.R. (1998). Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Anim. Behav.* 56, 909–917.
22. Jones, G., and Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 346B, 445–455.
23. Downs, N.C., Beaton, V., Guest, J., Polanski, J., Robinson, S.L., and Racey, P.A. (2003). The effects of illuminating the roost entrance on

- the emergence behaviour of *Pipistrellus pygmaeus*. *Biol. Conserv.* *111*, 247–252.
24. Blake, D., Hutson, A.M., Racey, P.A., Rydell, J., and Speakman, J.R. (1994). Use of lamplit roads by foraging bats in southern England. *J. Zool.* *234*, 453–462.
 25. Rydell, J. (1991). Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssonii*. *Holarctic Ecology* *14*, 203–207.
 26. Coatham, D. (2005). Light pollution and new legislation. *The Lighting Journal* *70*, 12.
 27. Parsons, S., and Jones, G. (2000). Acoustic identification of 12 species of echolocating bat by discriminant function analysis and artificial neural networks. *J. Exp. Biol.* *2003*, 2641–2656.
 28. Altman, D.G. (1991). *Practical Statistics for Medical Research* (London: Chapman & Hall).