The effect of artificial lighting on bats: a landscape study

Introduction

Large areas of the world are artificially illuminated at night [1] and the annual rate of increase is approximately 6 % [2]. Many aspects of behaviour are influenced by artificial lighting, including communication, foraging and reproduction (for overview see [3]). Lighting can create advantages to predators through the concentration of prey items [4,5] and extended hours of activity for diurnal and crepuscular species [6]. Artificial lighting may both benefit and compromise an individual in different ways, making cost-benefit analyses complex [6]. For example, lighting may delay roost emergence in *Pipistrellus pygmaeus* [7] but increased foraging opportunities are sometimes recorded for this species [8]. Bats are largely nocturnal [9], and as such are acutely exposed to the influence rendered by artificial lighting, including at or near roosts and within the wider landscape where they forage. Previous studies have experimented with the effects of artificial lighting within or close to roosts and found delayed emergence, reduced activity and change of flight paths [7,10].

In this study we investigated the effects of artificial lighting on common pipistrelle (*Pipistrellus pipistrellus*), greater horseshoe (*Rhinolophus ferrumequinum*) and lesser horseshoe (*Rhinolophus hipposideros*) bats at a broad landscape scale. In contrast to previous experimental work, the study investigated impacts on animals that had been given the opportunity, over many years, to habituate to the lighting regime. The genera *Pipistrellus* and *Rhinolophus* were hypothesised to have contrasting tolerance to artificial light. Pipistrelle bats appear to be relatively light-tolerant [9,11–15], whereas artificial lighting is known to disrupt the flight paths of *R. hipposideros* [10]. *P. pipistrellus* and both *Rhinolophus* spp. are sympatric in the south west of England and feed on similar prey; mainly moths and *Diptera* [16–18]. We assessed the hypothesis that the two genera (*Pipistrellus* and *Rhinolophus*) can be categorized as light tolerant and light shy, respectively. A 2km radius landscape level approach was used to record bat abundance in artificially light and naturally
dark areas that were known to be *Rhinolophus* strongholds. For *P. pipistrellus* we also assessed whether the rate of feeding was higher in artificially light areas compared to dark. Finally, we assessed whether there is any evidence that changes in relative abundance is due to inter-specific competition related to artificial light tolerance.

**Methods**

We studied how bats use the landscape around eight *R. hipposideros* maternity sites across the south west region of England between 8 May and 2 July 2012. At each maternity roost we surveyed bat activity within a 2km radius, but excluded the immediate 200m radius of the roost since bats may be unable to express avoidance behaviours in this region because of the very limited area available. Activity was monitored for an average of 5 nights using full spectrum acoustic recorders (Song Meter 2 (SM2), Wildlife Acoustics, Maynard, USA). Recorders were positioned within linear features, such as tree lines and hedges, which are known to facilitate movement between resource patches for both genera [19–22] and were programmed to start recording 30 min before sunset and finish 30 min after sunset. Each recording was automatically tagged with a date and time-stamp. The recorders were placed at the nearest locations to 50 randomly generated points that had suitable tree or hedge cover and were adjacent to roads, footpaths and bridleways. Each location was classified in the field by one of three light levels (light, semi-light and dark) based on the distance the recorder was from sources of artificial light; light (less than 20m from streetlight), semi-light (less than 50m from other artificial light source e.g. housing, security or flood lighting) and dark (more than 50m from artificial lighting). At each recorder site, adjacent habitat was observed, recorded and later used to assign each site as having the presence or absence of fields containing pasture (here defined as enclosed grassland including unimproved, semi-improved and improved pasture, whether used for grazing or cut for hay or silage) and grazing livestock (horses, sheep or cattle).
Omni-directional SMX-US microphones were coupled with the recorders and positioned within hedgerows, tree lines and other linear features (walls and fence lines). Acoustic data were saved hourly as Wildlife Acoustics Compression (WAC) files. Recordings were triggered by a signal to noise ratio exceeding a pre-determined threshold (here: 18db to 48db) and continuing until the threshold was not sustained for a period of at least two seconds.

The WAC files were subsequently converted to Waveform Audio Format (WAV) files using Kaleidoscope Pro (KPro) software (v. 1.1.20, Wildlife Acoustics, Maynard, USA). This extracted the triggered events from the hour-long recordings and filtered out noise files. Triggered events had a minimum of two pulses with signals between 16 and 120kHz of duration ranging between 2 and 500 ms. The advanced signal enhancement option within the software was also selected, as per the manufacturer default, for filtering UK bat species (see Wildlife Acoustics http://www.wildlifeacoustics.com/ for further details of settings and operation).

The KPro software classifies each WAV file using British classifiers (v.1.0.5). To restrict the data to a manageable size and add further detail, all files classified as *P. pipistrellus* occurring within 2 hours after sunset were manually verified. Additionally, all files across the whole night classified as a *Rhinolophus* spp. or as an unidentified bat were manually verified to pull out the *Rhinolophus* spp. and additional *P. pipistrellus* calls. During this analysis, the number of passes for each species was counted, defined as a continuous run of pulses for a single individual where pulses were not separated by a gap of more than one second [23]. The numbers of feeding buzzes were counted for the *P. pipistrellus* calls, though not for the *Rhinolophus* spp. because of the difficulty of distinguishing feeding calls in this genus. Parameters taken from [24] were used to identify bat species during manual verification. However, due to the lower detectability yet distinctive call shape, a minimum of one pulse for *Rhinolophus* spp. was used to define a pass. In some cases (where the frequency modulated portion of the call and fundamental frequency of 55.5kHz for *R. hipposideros* and 40.5kHz
for *R. ferrumequinum* [23] were not visible within the sonogram) it was not possible to distinguish between *R. hipposideros* and *R. ferrumequinum* calls. This is because of an artefact of the recording system and software. Due to the low numbers of *Rhinolophus* spp. calls recorded and the inability to distinguish some calls apart, as explained above, analysis was conducted on all *Rhinolophus* spp. activity pooled together, as well as *R. hipposideros* activity modelled independently.

Roost locations and recorders were digitised in a geographical information system (GIS) using ArcGIS (ESRI ArcMap 10.0). Ordinance Survey vector Mastermap data were used within a 2km buffer of each roost. The distance from each recorder to the nearest woodland (coniferous, deciduous and mixed as classified by OS Mastermap within and beyond the 2km radius) and the percentage building cover within a 100m buffer of the recorder were calculated.

**Statistical Analysis**

A generalized liner-mixed effects model with a negative binomial error structure was used to model the total number of *P. pipistrellus* passes in the first two hours after sunset per night. We included light level (factor three levels: light, semi-light and dark), pasture (yes, no), grazing (yes, no), percentage building cover and distance to woodland as predictor variables. The two-way interactions between light level and each habitat variable were assessed. Roost was included as a random effect to account for the temporal and spatial autocorrelation in the dataset. The same model structure and fixed and random effects was used to model the total number of all *Rhinolophus* spp. passes per night. We used a Tukey post-hoc test to assess which paired combinations differed significantly within the factor light level.

We modelled *Rhinolophus* spp. passes within the first two hours to assess if *P. pipistrellus* activity within the same time period was a significant predictor, in order to assess if there is any evidence of inter-specific competition. We used GLMMs with a negative binomial error structure and night
nested within detector nested within roost fitted as a random effect. We assessed this for only detectors located in dark locations, due to the very low *Rhinolophus* spp. activity at semi-light and light locations. *P. pipistrellus* total nightly passes was predicted as a predictor for *Rhinolophus* spp. activity. Model selection was conducted using likelihood ratio tests until the most parsimonious model was derived. All statistical analyses were carried out using R (v.3.1.1), using the glmmADMB package (v. 0.8.0) for GLMMs. Graphs were produced using ggplot2 (v.1.0.0). All confidence intervals were expressed as 95%.

**Results**

*All species summary*

Bat activity was monitored using a mean of 24 recorders (±SD 5.6) per roost in dark locations, 10 recorders per roost (±SD 4.1) in semi-light locations and 10 per roost (±SE 5.2) in light locations. There were 1619 recorder nights available for analysis: 881 dark, 381 semi-light and 351 light. For *P. pipistrellus*, 81,246 passes were recorded within the first two hours after sunset across the study. Based on initial assessments of call distributions using automated identification (which we have previously found to classify calls assigned as pipistrelles in the same way as manual assignment 97% of the time), 78% of pipistrelle calls were identified as *P. pipistrellus*. Further analyses therefore focused on this representative of the *Pipistrellus* genus, and all calls were manually verified.

For *Rhinolophus* spp. there were a total of 1,499 passes (*R. hipposideros* 624) recorded over the full night, across the study (see summary Table 1.0). *P. pipistrellus* activity was a positive significant predictor of *Rhinolophus* spp. activity (*z* = 3.46, *P* < 0.001), however, the effect size was small (estimate: 0.003293, SE 0.000952), and so other variables, in particular detector location, and hence habitat, within site which had the highest variance component of the random effects (*z* = 2.908 SD 1.705) is perhaps a more important predictor of *Rhinolophus* spp. activity.
The interaction between the percentage building cover and lighting was a significant predictor of *P. pipistrellus* activity ($\chi^2 = 10.00, P = 0.007$). Predictions from the model show that in dark and semi-light locations the number of *P. pipistrelle* passes increase as percentage building cover increases from 0-10-20, whereas in light locations passes decrease over the same range. In reality there were no dark locations where building cover was greater than 11% and the maximum recorded was 47% in a semi-light location and 45% in a light location.

The interaction between the presence of pasture and lighting was also a significant predictor of *P. pipistrellus* activity ($\chi^2 = 9.22, P = 0.01$). Predictions from the model show that in dark and semi-light locations the number of *P. pipistrelle* passes increase where pasture was present compared to when there was no pasture, whereas for light locations the relationship was reversed. See Table 1.1. When considering both factors together, the greatest number of passes predicted is at dark locations when percentage building cover is high (20%) with adjacent pasture 248 (46-1329) (Figure 1).

*P. pipistrellus feeding activity*

The interaction between distance to woodland and lighting ($\chi^2 = 13.14, P = 0.001$) and the interaction between the presence of livestock grazing and lighting ($\chi^2 = 21.02, P = <0.001$) were significant in predicting the *P. pipistrellus* feeding buzzes. The models were similar for both measures of feeding (ratio of feeding buzz to search call and absolute measure of feeding buzzes). Feeding is highest in semi-light and light locations where livestock grazing is present, and increases with increasing percentage building cover and distance to woodland (Figure 2). This pattern of increasing feeding with increasing building cover and distance to woodland was consistent across all light levels. However, with the additional influence of livestock grazing, feeding is approximately doubled at semi-light and quadrupled at light locations, while at dark locations feeding remains virtually unchanged.
Rhinolophus spp.

The interactions between distance to woodland and lighting ($\chi^2 = 5.82, P = 0.054$) and the interaction between presence of pasture and lighting ($\chi^2 = 6.84, P = 0.033$) significantly predicted Rhinolophus spp. activity. Predictions from the model show that in all categories of light, the number of Rhinolophus spp. passes decreases with increasing distance to woodland with the lowest pass rates predicted in light locations furthest from woodland. For pasture, predictions from the model show that in both dark and light locations passes increase with the presence of pasture, but in semi-light locations this relationship is reversed (Figure 3). When considering both pasture and distance to woodland together, the greatest number of passes predicted is at dark locations, next to woodland with adjacent pasture 1.27 (0.55-2.93).

R. hipposideros

R hipposideros activity was predicted by light level ($\chi^2 = 42.24, P < 0.001$), distance to woodland ($\chi^2 = 5.04, P = 0.025$) and the presence of pasture ($\chi^2 = 5.77, P = 0.016$). Similar to the Rhinolophus spp. model predictions, passes were highest in dark locations, next to woodland and with adjacent pasture 0.6 (0.23-1.24).

Discussion

For both genera, the locations with the highest average pass rates were dark. The presence of pasture and increased building cover were positively linked with P. pipistrellus activity, whilst the presence of and reduced distance to woodland were positively linked with the activity of all Rhinolophus spp. combined and R. hipposideros individually. The positive association with building cover for P. pipistrellus is most likely attributed to an increase in roosting, and possibly foraging, opportunities. The built environment has added value for some species of bat [25] and P. pipistrelle are one of several species in Europe that have adapted to the human built environment [26] as natural roosts have become scarcer. This adaptation to urban environments has been recently
highlighted in Italian populations of *Pipistrellus kuhlii* where an increase in skull size has been recorded since World War II [27]. This rapid evolution is thought to be an adaptation to the rapid increase in artificial light linked to urban expansion, facilitating a change to larger prey items (*Lepidoptera* rather than *Diptera*) attracted to street lights. Other studies on *P. kuhlii* have also found a preference for street light foraging [12,28]. However, our results indicate that *P. pipistrellus* activity is higher in dark environments. It also appears that lighting modifies the response of bats to building cover: in dark locations there is a marked increase in pipistrelle bat activity as building density increases from 0 to 40%, whereas this trend is much less steep in semi-light locations, and is slightly negative in lit areas. This provides strong evidence that *P. pipistrellus* make use of the built environment but prefer it when it is dark. This species was found by [11] to be more abundant in the dark (100m from a street light) than at street lamps. In Sweden, [13] found that *P. pipistrellus* were not present at street lights, although this was attributed to possible competitive exclusion by the larger *Eptesicus nilssonii* present in the study area. More recently, [29] recorded *P. pipistrellus* flying in an urban environment, between vegetation gaps and found a preference for darker gaps and lower lighting thresholds for larger gaps.

Periods of foraging activity for an insectivorous bat have been calculated to account for only 15-17% of the daily time budget but are the largest component of the average daily energy budget, at above 60% [30]. Bats have a very high energy requirement compared to terrestrial mammals [31] and take advantage of concentrated resource patches [32–34] important for survival. Artificial lighting is known to attract insects in large numbers [4,35,36] and as such provides a somewhat reliable opportunity for bats to relinquish the high energy demands of foraging. Our data show that *P. pipistrellus* feeding (both measures) is higher in light locations compared to dark in areas with livestock grazing, whereas there was more foraging in dark areas where no livestock grazing were present. In both cases, feeding also increases sharply with greater building density. These results suggest that livestock grazing may generate increased numbers of insects around streetlights either
by acting as a direct attractant [37] or by increasing primary productivity, whereas the insect congregations may be less marked in other habitats. Further work to sample invertebrate abundance at streetlights is required to verify this hypothesis. The highest feeding activity occurred in semi-light locations with adjacent livestock grazing, possibly reflecting an optimal combination of resources available to bats. It should be noted that a variety of light types were included in this category, which may explain the large confidence intervals around the predictions.

The raw data from this study show a negative association with percentage building cover and passes recorded for *Rhinolophus* spp., although numbers recorded were low. Hence, the models showed that percentage building cover was not significant at predicting passes. It would be easy to attribute the low numbers recorded to reduced, suitable insect abundance in relation to increased building density. However, *P. pipistrellus*, which feeds on similar prey [16–18] were shown to be feeding at an increased rate as building cover increased. In a study by [38], insect biomass and bat foraging were found to be lowest in high density housing areas which was attributed to an increase in large impermeable surface area rather than low vegetation cover, leading to low primary productivity of insects. This is understandable in highly urbanized locations but is not the case in the rural and semi urban sites for our study. When buffering around recorder locations using GIS at a 50m radius and around the roost at a 2km radius, across all sites, only 10.7% (±SE 0.7%) and 4.9% (±SE 1.0%) of surface was classified as 'manmade' respectively, hence, insect generating habitat was not considered to be in short supply across the study areas. The higher numbers of *Rhinolophus* spp. bats we recorded in less urbanized areas can explained by their foraging ecology and preference for woodland clutter environments [39]. With increasing distance to woodland, the number of *Rhinolophus* spp. passes at dark and semi light locations declines, and passes in light locations remain unchanging at near zero. *Rhinolophus* spp. are commonly associated with woodland environments [30] and are rarely found in highly urbanized areas. In part, this is likely due to their wing morphology and echolocation call design which constrains open site foraging, but aversion to
light is also a major factor. From our data set, we found interactions between light level and distance to woodland and light level and the presence of pasture. Our models show that passes for *Rhinolophus* spp. will be highest when close to woodland, when pasture is close by and in the absence of artificial light. This may be attributed to the increased number of invertebrates generated by pasture habitat (c.f. arable and non-natural surfaces) which are not subsequently attracted to street lighting in a vacuum-like effect and the benefits of hedge networks associated with pasture fields facilitating commuting routes.

This study shows that *Rhinolophus* spp. avoid artificially light environments. We investigated behaviour at a wide spatial scale, using scenarios where bats had been given long-term opportunities to habituate to lighting. Avoidance of artificial lighting is not only found near their roosts and the immediate commuting routes but across the wider landscape. Even for the more anthropogenically-robust *P. pipistrellus*, artificial lighting was associated with reduced activity. While they have adapted to an increasing human built environment by utilizing roosting opportunities, the increasing artificial lit environment may be a more difficult adaptation. Feeding was shown to be higher in light and semi light locations, adjacent to grazing, but lower in the absence of grazing, which suggest that *P. pipistrellus* may be drawn to artificial lights where insects are attracted in larger densities.

These results highlight the complex interactions between habitat, lighting and movement of bats in the landscape. We have clearly demonstrated that *Rhinolophus* spp. are light phobic and are closely associated with woodland and pasture. For *P. pipistrellus*, there is a more complex relationship with artificial light and feeding. This species shows an adaptability to foraging at light locations where habitat generates light-attracted insects. This may be a problematic scenario for light phobic bat species where the vacuum effect of artificial light attracts insects into a 'no go' area. In more natural
habitats, adjacent to artificial lighting, a food resource disparity between bat species with similar diets but extreme differences in tolerances to light may be created.

Whilst bat roosts within the European Union are legally protected under the EU Habitats Directive (1992/43/EEC), the level of protection afforded to commuting routes is less clear [40]. Maintaining or increasing important habitats in eroding dark landscapes is key, yet light pollution is seldom considered in habitat management plans. The negative effects of artificial light shown here and in other studies should be considered when increasing the amount of artificial light in the environment.
Literature


Table 1. The average number of passes recorded for each species at light, semi-light and dark locations across all sites. For *P. pipistrellus* we report results for the first two hours after sunset, and for *Rhinolophus* spp. the total number of passes across the full night.

<table>
<thead>
<tr>
<th></th>
<th>Dark (±SE)</th>
<th>Semi Light (±SE)</th>
<th>Light (±SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. pipistrellus</em></td>
<td>52 (3.62)</td>
<td>32 (2.88)</td>
<td>32 (2.88)</td>
</tr>
<tr>
<td><em>Rhinolophus Spp.</em></td>
<td>1.26 (0.18)</td>
<td>0.78 (0.20)</td>
<td>0.25 (0.05)</td>
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<tr>
<td><em>Rhinolophus hipposideros</em></td>
<td>0.58 (0.12)</td>
<td>0.24 (0.04)</td>
<td>0.05 (0.01)</td>
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</table>
Table 2. The number of *P. pipistrellus* feeding buzzes recorded at detectors located in different habitats and at three measures of light. Confidence intervals are given in parentheses.

<table>
<thead>
<tr>
<th>Distance to woodland</th>
<th>% Building cover</th>
<th>Dark</th>
<th>Semi-light</th>
<th>Light</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>27 (19-37)</td>
<td>13 (8-22)</td>
<td>13 (8-21)</td>
</tr>
<tr>
<td>40</td>
<td>40</td>
<td>97 (46-206)</td>
<td>48 (22-107)</td>
<td>47 (20-111)</td>
</tr>
<tr>
<td>400</td>
<td>0</td>
<td>17 (10-27)</td>
<td>34 (13-87)</td>
<td>12 (5-28)</td>
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<tr>
<td>40</td>
<td>40</td>
<td>60 (26-142)</td>
<td>124 (39-395)</td>
<td>43 (14-134)</td>
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<td>0</td>
<td>29 (19-45)</td>
<td>29 (13-62)</td>
<td>50 (24-106)</td>
</tr>
<tr>
<td>40</td>
<td>40</td>
<td>105 (46-243)</td>
<td>105 (38-288)</td>
<td>182 (60-549)</td>
</tr>
<tr>
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<td>18 (11-31)</td>
<td>74 (25-219)</td>
<td>46 (16-132)</td>
</tr>
<tr>
<td>40</td>
<td>40</td>
<td>66 (26-164)</td>
<td>269 (74-980)</td>
<td>166 (43-640)</td>
</tr>
<tr>
<td></td>
<td>Pasture</td>
<td>No Pasture</td>
<td>Woodland 0m</td>
<td>Woodland 100m</td>
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<tr>
<td>--------------------</td>
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<td>------------</td>
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<td>---------------</td>
</tr>
<tr>
<td><strong>Rhinolophus spp.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>1.08</td>
<td>0.47</td>
<td>0.91</td>
<td>0.74</td>
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<td></td>
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<td>(0.22-1.01)</td>
<td>(0.4-2.05)</td>
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<tr>
<td>S</td>
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<td>0.61</td>
<td>0.90</td>
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<td>0.12</td>
<td>0.18</td>
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<td>(0.04-0.36)</td>
<td>(0.05-0.59)</td>
<td>(0.04-0.48)</td>
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<tr>
<td><strong>R. hipposideros</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>0.29</td>
<td>0.47</td>
<td>0.38</td>
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<td>(0.16-0.54)</td>
<td>(0.24-0.93)</td>
<td>(0.19-0.77)</td>
</tr>
<tr>
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<td>0.30</td>
<td>0.17</td>
<td>0.28</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
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<td>(0.08-0.36)</td>
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</tr>
<tr>
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<td>0.06</td>
<td>0.04</td>
<td>0.06</td>
<td>0.05</td>
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<tr>
<td></td>
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<td>(0.01-0.09)</td>
<td>(0.02-0.16)</td>
<td>(0.02-0.13)</td>
</tr>
</tbody>
</table>
Fig. 1 Relationship between *P. pipistrellus* activity and building cover, depending on lighting regime and the presence of pasture.
Fig. 2. Relationship between feeding buzz ratio for *P. pipistrellus* and building cover, depending on distance to woodland, livestock grazing, and lighting regime.
Fig. 3. Relationship between Rhinolophid activity and distance to woodland, depending on the presence of pasture and lighting regime.