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Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland

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Artificial lighting is a particular problem for animals active at night. Approximately 69% of mammal species are nocturnal, and one-third of these are bats. Due to their extensive movements—both on a nightly basis to exploit ephemeral food supplies, and during migration between roosts—bats have an unusually high probability of encountering artificial light in the landscape. This paper reviews the impacts of lighting on bats and their prey, exploring the direct and indirect consequences of lighting intensity and spectral composition. In addition, new data from large-scale surveys involving more than 265 000 bat calls at more than 600 locations in two countries are presented, showing that prevalent street-lighting types are not generally linked with increased activity of common and widespread bat species. Such bats, which are important to ecosystem function, are generally considered 'light-attracted' and likely to benefit from the insect congregations that form at lights. Leisler's bat (*Nyctalus leisleri*) may be an exception, being more frequent in lit than dark transects. For common pipistrelle bats (*Pipistrellus pipistrellus*), lighting is negatively associated with their distribution on a landscape scale, but there may be local increases in habitats with good tree cover. Research is now needed on the impacts of sky glow and glare for bat navigation, and to explore the implications of lighting for habitat matrix permeability.

1. Introduction

Light pollution is a rapidly growing global problem that can profoundly affect the behaviour of animals active at night [1]. Approximately 69% of mammals are nocturnal and one-third of these are bats. This taxon has a perilous conservation status—17% of species are listed as endangered or near threatened by the International Union for Conservation of Nature [2]. Given their importance as ecosystem service providers [3–5], and the potential for artificial lighting at night to exacerbate other conservation threats such as habitat fragmentation and climate change [1], serious consideration must be given to the potential positive and negative consequences of artificial lighting at night.

As the only mammals capable of true flight, bats are able to exploit widely dispersed ephemeral food supplies. Their nightly foraging movements exceed those of many other mammals, and lactating females will make multiple trips, returning at intervals to suckle their young. Long-distance movements are also undertaken, particularly when the animals switch between breeding, mating and hibernation sites. Avoidance of lit areas could therefore result in the effective division of habitat available to bats, with all of the potential consequences for migration, colonization, inbreeding and population extinction associated with other forms of habitat fragmentation [6]. Conversely, if insect prey are concentrated into smaller areas as a result of their attraction to light [7,8], then foraging efficiency could be increased with potentially positive implications for

those bat species able to exploit this resource. In the UK at least, lighting has therefore been considered a positive form of habitat management for some bats [9]. This paper will review the evidence for lighting affecting bat behaviour and movements, considering both ultimate and proximate mechanisms. It will also present the largest scale surveys to date on the impacts of lighting on the activity of common bat species in both the immediate vicinity of artificial illumination and across large areas subjected to different amounts of light.

(a) Attraction and repulsion

Few aerial predators are active at night, and therefore nocturnal behaviour offers bats considerable protection [10,11]. However, trade-offs between emergence time (and consequent risk of predation) and the need to fulfil energetic demands are likely [12]: in many species, lactating females, which have very high energy requirements, emerge earlier than other age/sex classes [13–16]. Emergence times also appear to be linked to both flight speed and diet, with later emergence being observed among slow-flying species (those with a low wing loading, that is, mass/wing area) and pregnant bats (which are less able to escape predators due to being less manoeuvrable) [13,15,17]. On overcast evenings, and where roost entrances are shaded, bats emerge earlier, presumably taking advantage of the protection from predators [13,17]. For aerial hawking bats such as *Pipistrellus* spp. and *Nyctalus* spp. that feed predominantly on insects with crepuscular activity peaks, prey availability rather than light levels will be a key constraint on their activity patterns. By contrast, gleaners and moth specialists (e.g. *Barbastella barbastellus*, *Myotis nattereri*, *M. bechsteini*) would be expected to be particularly sensitive to lighting as they experience less selective pressure to emerge before complete darkness [12,17]. Nonetheless, even *Pipistrellus* bats appear reluctant to fly in lit conditions in the laboratory [10].

Information on the responses of bats to natural light allows predictions to be made about the potential effects of artificial night lighting. For example, as expected, the illumination of buildings delays roost exit times [18,19], and also appears to have negative consequences for reproductive success [20]. It would also be predicted that the most extreme aversive responses to light would occur in animals that naturally emerge late to forage (slow flyers that are not dependent on crepuscular prey). These bats often conduct ‘light sampling’ behaviour prior to emergence. This is thought to have evolved to minimize the risk of predation by ensuring that they remain within the roost until diurnal predators are no longer a threat [21], and to enable the animals to constrain their endogenous circadian rhythm to a 24 h cycle [22]. Conversely, less sensitive species could exploit the high density of insects that accumulate around lights [23]. The available evidence supports these predictions. *Lasiurus* spp., *Eptesicus* spp., *Nyctalus* spp. and *Pipistrellus* spp.—all bats with high or medium wing-loading and fast flight—have been observed catching insects at street lights [24–32], whereas gleaners and flutter-detectors, such as *Rhinolophus* spp., *Plecotus* spp. and *Myotis* spp., rarely if ever forage at street lights [33]. The ability of bats to exploit these concentrated feeding resources may also be limited by other factors. These range from the lack of suitable commuting routes to provide access to potential foraging patches, particularly in urban and suburban landscapes [34,35], to unexpected effects such as an increased risk of collision with stationary

objects for bats flying in light compared with dark conditions [36,37]. Finally, animals under energy stress (e.g. lactating females) may be expected to be more likely to forage beneath street lights, given that they are known to be more tolerant of natural light and have high prey requirements [13,17]. Observations made on the behaviour of *Eptesicus nilssonii* are consistent with this hypothesis [31]. It has also been noted that although reduced activity in the open is generally observed under bright moonlight [38], bats attending swarming sites do not show the expected lunar-phobic responses [39]. Further work is warranted to explore within-species variation in light tolerance and identify whether aversive responses are constrained during periods when particular activities, such as mating or lactation, occur.

The presence of artificial lighting may act as a barrier to the movement of some species. Experimental work in southern England has demonstrated that the activity of *Rhinolophus hipposideros* was reduced approximately fivefold when high-pressure sodium lamps were introduced on hedgerows close to roosts [40]. The timing of activity was also delayed by approximately 50 min on nights with lighting treatment compared with controls. Similar results were obtained with light emitting diode (LED) lights, with reductions in activity being seen between high and medium light intensities, but not between low and medium intensities [41]. Neither lighting type had a significant effect on the activity of *Pipistrellus* spp. or *Nyctalus/Eptesicus* spp. The effects of halogen lighting on *Myotis dasycneme* behaviour has also been investigated experimentally at four sites in The Netherlands [42]. Here, lights had no clear effects on the number of passing bats, and nor did bats make increased use of an alternative commuting route when just one of two possible routes was lit. However, light did reduce the percentage of feeding buzzes by more than 60%, despite a general increase in prey abundance. In addition, between 28 and 42% of pond bats altered their flight trajectory when they approached a light; and if the bats were obliged to fly straight into the beam of light because of the presence of other barriers, virtually all (96%) turned around. It is therefore clear that lighting has the potential to alter the commuting behaviour of at least some bat species. However, the responses may be complex depending on the availability of alternative routes in the landscape, and the extent to which lights actually prevent bats accessing otherwise suitable (dark) foraging areas remains unclear.

(b) Changing lightscapes and spectral perception by insects and bats

The amount of lighting in the environment, as well as the intensity of individual lamps, is changing rapidly. In the UK, illumination is estimated to be increasing at approximately 3% per annum [43], while across the globe, the spread is approximately 6% per year [44]. Much of this is attributable to urbanization, the expansion of the road network, and increases in the amount and brightness of carriageway lighting. The spectral composition of artificial lighting is also shifting, driven by the need to improve energy efficiency, together with a desire for broad-spectrum white lighting that closely mimics daylight in its colour rendering abilities. Orange and yellow sodium lights, which currently predominate, are therefore being replaced by metal halide, incandescent lights (including halogen), compact fluorescent and other types of new technologies

that emit white light; or with LEDs which can be designed to produce light of any colour (frequently white) [45].

Most lighting in the UK is yellow high-pressure sodium: traditional white mercury vapour lamps are no longer legal, and inefficient orange low-pressure sodium lamps are being phased out. Nevertheless, orange low-pressure sodium remains a major type of lighting in Ireland and also in rural districts of the UK. On highways, new and replacement lighting is usually lower wattage high-pressure sodium lighting or metal halide, with LEDs and other new technologies, e.g. compact fluorescent lights, tending to be too expensive except in special circumstances. However, these new technology lights are increasingly used in town centres where pedestrian safety is paramount, and in residential areas where the installation costs are frequently borne by developers.

The attractiveness of lighting to insects, and therefore to bats that exploit these congregations of prey, is linked to the amount of short-wavelength light produced, particularly ultraviolet (UV). Traditional mercury vapour lamps produced large amounts of UV light and had high attractiveness [7,25,29,33,46,47]. There is also evidence that the acoustic defences of tympanate (hearing) moths, which allow them to evade hunting bats, are compromised at mercury vapour lights [48]. By contrast, the replacement orange low-pressure sodium lamps are effectively monochromatic, producing no UV, and are therefore much less attractive to insects or bats [25]. The newer pinkish-yellow high-pressure sodium lights have a broader spectral composition, but still relatively little short-wavelength emissions. Like low-pressure sodium, they are therefore much less attractive to insects than mercury vapour: several studies report that insect abundance is around 50% lower, and moths 75% lower [7] at high-pressure sodium compared with mercury vapour lights. Therefore, it is possible that the ecological implications of night lighting have been limited by chance over recent decades due to the replacement of short-wavelength mercury vapour lamps by sodium lighting. The effects of modern lighting technologies that are superseding mercury and sodium lamps are also likely to vary according to their spectral composition [46,49]. For example, metal halide luminaires, which are currently replacing sodium ones along many British motorways, produce more short-wavelengths than do LEDs [45]; and even LEDs, despite having little UV, contain variable amounts of short-wavelength emissions. Unfortunately, current models of the effects of lighting on invertebrates have poor predictive power [50] and more work is urgently required to resolve conflicting evidence on the effects of LEDs [51,52]. Nevertheless, negative ecological impacts have been reported for some species [46,50,51].

In addition to affecting bats indirectly through impacts on prey distribution, spectral composition may also directly affect bat behaviour. A wide range of species are now considered highly likely to perceive colour, possessing both retinal cone cells [53–55] and a functional long-wave *M/LWS* gene [56]. This corresponds to ecological evidence of disturbed emergence patterns from bat roosts illuminated by red [18] or blue light [19]. Recognizing the potential disorientating effects of night lighting on migratory birds, green LED lighting which has fewer adverse effects [57,58] (e.g. the Philips ‘Clear Sky’ bulb) is now being deployed at some oil rigs [59] and highway junctions in The Netherlands. However, different solutions may be required for bats as they can readily perceive green light. A number of other LED lamps, including Philips ‘Clear

Field’ and the ‘Bat-lamp’ patented by the Dutch Roads Agency, have therefore been designed to produce narrow band-width amber light (*ca* 600 nm), and their impacts on bats are currently being tested.

Perhaps surprisingly, recent evidence from behavioural and physiological investigations shows that bats also have high sensitivity to ultraviolet light. This characteristic appears to be widespread, though absent from *Rhinolophus* bats and cave-dwelling fruit bats [60–62]. Molecular evidence based on the presence of a functional short-wave *SWS1* opsin gene supports these findings [56]. Lighting types which include UV, such as metal halide, are likely, therefore, to be more disturbing to light-shy non-horseshoe than to horseshoe bats. There is also the possibility that prolonged exposure to short-wavelength light may cause retinal damage [63,64]. This is a cause for concern given the longevity of bats, particularly for groups such as *Nyctalus* which regularly forage close to lamps and also fly long-distances in the open. Such species are likely to rely extensively on vision for navigation due to the short effective range of echolocation in identifying objects such as trees and woodland edge in the landscape [65,66].

(c) Landscape-scale effects

The potential impact of lighting is modulated by its position within the landscape. For example, the lighting of woodland edge may be more damaging than comparable lighting in open areas due to the enhancement of ‘edge effects’ [67] that limit the movement and foraging of light-shy species. At some times of the year, large congregations of animals can form at swarming, hibernation and maternity sites. Lighting adjacent to such sites therefore has the capacity to influence large numbers of individuals. However, bats also disperse very rapidly, so that encounter rates can diminish to close to zero even within 0.5 km of a major roost. Therefore, if negative effects are local (e.g. aversion to travelling close to a light), then provided most of the landscape remains unlit, the ecological impacts may be limited. Conversely, if the functionality of key commuting routes or mating/swarming sites is destroyed by lighting, then there may be important population effects from even small amounts of lighting. Theoretical predictions have been made about the resistance generated by lighting to movement through a habitat matrix [68]. These now need to be tested empirically, informed by species-specific work that establishes the minimum sizes required for the ecological function of dark foraging patches and commuting corridors.

Given that bat guilds respond differently to lighting, alterations in community composition might be expected when light is introduced into a dark landscape. There is tentative evidence that competitive exclusion from Swiss valleys of light-shy *R. hipposideros* by potentially more light-tolerant *P. pipistrellus* has already taken place [69]. Even in the absence of competitive exclusion, lights undoubtedly create accumulations of insect prey species, which are presumably matched by corresponding reductions in availability in dark areas (the ‘vacuum effect’). The effects of such decreases in prey availability on bats have not been explored. There could also be a change in invertebrate community composition due to differences between species in response to lighting. For example, larger moths such as noctuids are particularly attracted by short-wavelength light [46,70], and insects which emerge from aquatic environments seem to be drawn to lights over longer distances than are terrestrial species [71]. It may be that some bats are able to exploit this

change: for example, it has recently been suggested that *P. kuhlii*, the commonest bat at streetlamps throughout southern Europe, has undergone an alteration in its cranial morphology over the last century, developing larger mouthparts that would be adaptive for a dietary switch from soft-bodied dipterans to hard-bodied moths [72]. In addition to the changes in predation, the high fatality rates of insects at lights, and the diversion from other vital activities such as foraging and mating, would be expected to affect population and community structure in invertebrates. Such changes have been demonstrated in other groups (e.g. [73]) but not yet specifically in bat prey species.

The implications of street lighting for bat conservation could be considerable. However, most research pre-dates the use of high-pressure sodium and other modern lighting types. Much recent work has also focused on rare species, yet, as in other taxa [74–77], common and widespread bats such as *Pipistrellus*, *Nyctalus* and *Eptesicus* have important roles in ecosystem function. The two most abundant bats in Europe are *P. pipistrellus* and *Pipistrellus pygmaeus* [78]: in Britain and Ireland, they are estimated to be an order of magnitude more abundant than the next most common species (current best estimates of populations for *P. pipistrellus* is 2 430 000 and *P. pygmaeus* is 1 300 000 in UK [79]). Along with *Nyctalus* and *Eptesicus* bats, they are likely to have high encounter rates with lighting due to their use of edge and open habitats. We therefore set out to test whether there was evidence for the common assumption, based largely on observations of feeding activity at street lights [23,25], that *Pipistrellus*, *Nyctalus* and *Eptesicus* bats are light-attracted rather than light-neutral or light-shy [9]. At a broad spatial scale relevant to many conservation policy decisions, we investigated whether bat activity and species composition varied in landscapes with different lighting profiles. Then at a finer spatial scale, we investigated whether bat activity depended on local lighting conditions and whether habitat modulated the effects of lighting.

2. Material and methods

Our studies were conducted at three spatial scales. These were multiple 1.6 km transects distributed across Ireland, short sections within transects of approximately 16 km in one English region, and localized point effects monitored using static passive acoustic recorders at multiple sites in southwest England. The analyses focused on *P. pipistrellus*, *P. pygmaeus*, *Nyctalus noctula*, *N. leisleri* and *Eptesicus serotinus*, which were the species most commonly recorded.

(a) Transect surveys

In Ireland, the transect surveys were conducted by car as part of an ongoing project to survey population trends at a wide spatial scale [80]. In each of twenty-eight 30-km grid squares (i.e. $28 \times 900 \text{ km}^2$), volunteer surveyors drove a predetermined route. Each route included 15×1 mile (1.6 km) transects. Two replicate surveys of each route were made each year from 2010 to 2013, the first between mid-late July (Survey 1) and the second in early-mid August (Survey 2). Each survey began 45 min after sunset and was driven as closely as possible to a constant speed of 24 km h^{-1} . A time-expansion detector (Tranquility Transect, Courtpan Electronics) was linked to a recording device such as a minidisc, digital recorder or android smartphone. The time-expansion detector was set to record for 320 ms then replay the sound at $\times 10$ time expansion. The weather conditions were recorded at the start of the survey, and volunteers were instructed

to avoid beginning surveys under conditions likely to be unsuitable for bats (heavy rain, temperature less than 8°C or high wind).

Data on street-light types were collected every year by surveyors. To enable identification of the various types of lamp, illustrations of high-pressure sodium (yellow) and low-pressure sodium (orange) lights were provided with the survey information pack so that survey teams could distinguish the two types. White street lights were recorded simply as 'white' with no attempt being made to distinguish the various potential forms either by surveyors (because of the difficulties of distinguishing types from a moving vehicle), or retrospectively (no information is available on the relative abundance or distribution of the different types in use in Ireland; until relatively recently the main type of white light used for street lighting was mercury vapour). Because of the use of volunteer surveyors, there were some inconsistencies in the numbers of lights reported. Analyses are therefore based on the median count for each transect. Percentage cover of built environment habitat types were extracted for each transect from the Corine Land Cover map for Ireland 2006, which employs remotely sensed data (variables: urban (classes 112 and 113); other built environment (classes 121, 131 and 142)).

The English survey used 22 bicycle transects, with one survey per night being conducted in May–June 2007 during periods of good weather (more than or equal to 10°C at dusk; wind less than Beaufort 4 and no heavy rain). An Anabat SD2 detector (Titley Electronics, Australia), which recorded zero-crossing signals in real time was linked to an eTrex GPS Personal Navigator (Global Positioning System: Garmin, KS, USA) that recorded location every second. The detector was carried at an angle of 45° from vertical during the survey and was triggered automatically during the recording period. Sound files were saved onto a compact flash card and were later analysed using ANALOOK (Titley Scientific, Australia). All transects began at sunset, and surveyors rode at a speed as close as possible to 16 km h^{-1} for approximately 1 h (precise durations and distances differed slightly between transects). A different transect was used on each night, and although transects occasionally crossed because of road configurations, care was taken to ensure that transects sampled different areas and were at least 0.5 km apart for the majority of their length. Daytime surveys were conducted to record the habitat characteristics of the transects (table 1). Lighting type was assessed by inspections during both daylight and nighttime, with judgements being based on the shape of bulb and housing, the colour of the light and information from the local council (note that no LEDs were in use at the time of this survey). Transect sections were defined in the field on the basis of representing stretches of broadly consistent habitat. For example, a new section started where the street-light type changed; if urbanization changed from none to low-density rural; or if habitat changed from arable to broad-leaved woodland. The presence or absence of water within a 100 m radius of any point on the transect section was then recorded. We cannot exclude the possibility that the same bats were occasionally sampled in transect sections that were close to each other. However, given that the surveyor passed through the transect section at a moderate speed, it is unlikely that this problem would be sufficient to materially alter the results. The 12 transect sections that had different types of lighting on the opposite side of the road or were lit with metal halide were excluded from the analysis, due to small sample sizes (7 and 5, respectively), leaving 350 transect sections for analysis.

(b) Static detector surveys

For the static detector survey, data were collected using SM2 BAT full-spectrum bat detectors (Wildlife Acoustics, USA) at eight study areas (each of radius 4 km) in the southwest of England. The study was conducted from late April to June 2013. A total of 188 detector locations were used, with between 16 and 30 detectors (median 24) being deployed simultaneously within each study

Table 1. Categorization of habitat features along transect, and scoring scheme (where applicable).

feature	classification (score)
habitat (class of land adjacent to transect section) ^a	built environment
	arable
	broad-leaved woodland
	broad-leaved woodland and wetland
	unimproved grassland
	unimproved grass and broad-leaved woodland
scale of urbanization ^b	none (rural with no buildings) (0)
	rural low-density (scattered buildings, less than 15% land covered by buildings) (1)
	urban low-density (scattered buildings, including industrial estates, large houses, less than 15% land covered by buildings) (2)
	rural higher density rural (village streets, etc. more than or equal to 15% land covered by buildings) (3)
	urban/suburban higher density ($\geq 15\%$ land covered by buildings) (4)
tree cover	absent
	scattered
	dense cover on one or both sides of the road
	dense cover both sides of road including closed canopy
road type	'A' (ordnance survey map class for major road)
	'B' (ordnance survey map class for more minor road)
	unclassified (minor road) and cycle paths
lighting type	high-pressure sodium
	low-pressure sodium
	metal halide
	mixed

^aDefined using standardized methods of Phase 1 Habitat Survey [81].

^bDefined following classification of urbanization used previously for work on habitat selection in *P. pipistrellus* and *P. pygmaeus* [82].

area. In order to maximize the opportunity to separate out the effects of lighting from those of habitat, all of the detectors were positioned in treelines or along overgrown hedgerows considered to provide good habitat for foraging and commuting bats. The detectors were therefore predominantly positioned in rural areas (e.g. lights at road junctions) and at the urban–rural interface. A paired study design was used, with a 'light' detector being placed beneath a high-pressure sodium light, and a 'dark' detector being placed in an unlit position at least 100 m from the nearest street light but otherwise as close as possible to the 'light' detector and within the same habitat type. The variations in the number of pairs used at each site resulted from differences in the numbers of street lights adjacent to suitable hedgerows or treelines, and occasionally also the lack of suitable habitat pairings. The omni-directional microphones (SMX-US, Wildlife Acoustics) were fixed in a horizontal position at 1.5–2.0 m above ground level, and the detectors were programmed to record automatically from 30 min before sunset until 30 min after sunrise each day. The detectors were left in place for four to eight nights (median 5; one site each had deployments of two and 10 nights), providing a total of 1050 detector-nights for analysis. Despite the paired structure, there was some residual variability in the amount of built environment adjacent to the 'light' and 'dark' detectors, as street lights are generally placed in areas with greater amounts of built environment.

(c) Acoustic analysis

All sound analyses were conducted using relevant reference guides for species found in the UK and Republic of Ireland [83–85], and

were based on the maximum and minimum frequencies, repetition rate, slope, pattern of call type (e.g. alternating constant frequency/frequency modulated calls) and call duration. In the case of time-expansion and real-time recordings, the peak energy frequency was also recorded. In cases of doubt about the species identity, judgements were made after discussion with experienced users of sound analysis from outside the research team, and where necessary the bat was recorded to genus or classified as unidentified. Verification of the species identification was conducted by a second assessor for a subset of the data (*ca* 1% for the transect surveys, 0.1% passive acoustic surveys using static detectors). Data recorded using Anabat detectors were analysed using ANALOOK (Titley Electronics, Australia), and time-expansion data were analysed using BATSOUND (Pettersson Elektronik, Sweden). *Pipistrellus* spp. calls that exhibited a maximum energy peak in the quasi-constant frequency component at 48–51 kHz (or in the case of frequency-division calls a peak in cycles between these frequencies) were recorded as 'unknown pipistrelle' because they could not be identified with certainty to be either *P. pipistrellus* or *P. pygmaeus*; other pipistrelle calls were identified to species.

The data collected using static SM2 detectors were processed using KALEIDOSCOPE Pro (v. 0.1.1.20, Wildlife Acoustics) with British bat classifiers (v. 1.0.5). We have previously manually verified the ability of this system to classify calls in the same way as assignment by human observers using a separate sample of 190 631 calls [86]. Taking human classification as 'the gold standard', 97% of species identified as common and soprano pipistrelles are given the same classification using the automated identification. In addition, we manually verified 778 files from the present study and found

that 99.5% of automatically classified calls were assigned in the same way when human classification was used; we therefore accepted the automated classifications for these species in this project. Given that the automated identification system does not distinguish bat passes (as conventionally defined as a continuous run of pulses not separated by a time gap of more than 1 s [87]), we here consider a file to be the equivalent of a pass. Our previous work indicates that multiple passes of the same species in relatively low activity areas (away from roosts and swarming areas) occurs in approximately 4% of files and that the nightly estimates of bat activity obtained from 'files' and 'bat passes' are not significantly different. The main constraint of using automated identification is that where two bats of different species are present in the same file, only a single classification is given. Some under-recording of species diversity is therefore possible. However, given the extensive sampling frame used in the project, together with the fact that the finding of multiple species within a file was rare among the pipistrelle data checked manually, it is unlikely that such under-recording will have materially altered the results. All files containing *Nyctalus* spp., *E. serotinus* and *P. nathusii* calls, together with all those that were not allocated a species identification, were manually checked following the procedures previously described for the other acoustic analyses.

(d) Statistical analysis

The bicycle and car transect surveys conducted in England and Ireland, respectively, were analysed separately due to their different survey designs. In both cases, activity was summarized for illustration as passes per minute.

In the Irish study, data were analysed at the transect level because the speed of the survey meant that there were a low number of passes within any given subsection. Activity was defined as the overall number of passes per transect divided by the survey time, with data being \log_{10} transformed ($\log(\text{rate} + 0.1)$) prior to analysis. Initial explorations were conducted using the overall mean pass rate for each transect, averaged across repeats and years. The link between bat activity and the amount of street lighting ($\log(\text{total number of lights per transect} + 1)$) was assessed using restricted maximum-likelihood models, adjusting for the degree of urbanization ($\log(\% \text{ urban})$ and $\log(\% \text{ other built environment})$). Colour differences in the effects of street lights were then modelled by including separate terms to represent the amount of street lighting of each colour ($\log(\text{number of lights} + 1)$). More complex models were built to account more fully for the structure of the survey. Repeat (first or second survey) was treated as a fixed effect and, to account for the spatial autocorrelation in the data, grid square was included as a random effect, along with the interactions between grid square and transect, year and repeat. To help visualize the results, numbers of passes per minute were predicted when no lights were present, or when there were 20 lights per transect of the appropriate colour. Predictions were averaged on the log-scale over other terms in the model; their absolute value is not necessarily realistic, but their values provide an impression of the relative magnitude of effects. The links between weather conditions and bat activity at the level of the survey square (i.e. combining the 15 surveys completed in one night) are reported elsewhere [80]: there were no significant links with *P. pipistrellus* or *P. pygmaeus* activity, though there is a consistent link across years between temperature and *N. leisleri* activity. However, even for the latter species, given that each transect was repeatedly surveyed under variable weather conditions over years, and each survey square contained multiple transects surveyed on the same night, it is highly unlikely that any effect of lighting would be confounded by weather, and therefore this variable is not considered further. All of the analyses were conducted in GENSTAT v. 17 [88].

In the English transect study, the links between the presence or absence of bats and street lighting were investigated using

generalized linear mixed effects models (GLMERs) with binomial error structures and a logit-link. The varying duration of each transect section was accounted for using an offset ($\log(\text{transect duration})$), and transect identity was specified as a random effect to allow for non-independence of sections within transects. The amount of activity was investigated similarly but used a Poisson error structure and a log-link, and the standard errors were corrected to account for over-dispersion by adding a random variable with a distinct level for each observation in the dataset [89].

Prior to fitting the models, we explored the correlations between potential predictor variables. The variables 'urban' and 'habitat' were highly correlated—both included a measure of built environment (Spearman's rank correlation coefficient $\rho = -0.831$). 'Urban' was therefore selected for inclusion in subsequent models as this variable had the greatest influence on the Akaike information criterion (AIC) value. In addition, because of the relatively high number of potential predictors with multiple levels in relation to the numbers of degrees of freedom, we conducted an initial screening and included only those variables that showed some association with the outcomes (using a relaxed inclusion criterion of $p < 0.1$). Road type was therefore excluded. Model selection then used a backwards manual process until the minimum adequate model was obtained (the random effects were retained in all models as they were part of the study design). First-order interactions between lighting and other fixed effects were considered, but other interactions were not used due to sample size constraints. Model comparisons were based on inspection of AIC values, and tests of significance between alternative models were based on likelihood ratio tests of change in deviance (indicated here as χ^2). For the purposes of illustration, raw data were plotted, with standard errors being computed for proportions using the Wilson method (the results were similar to the predicted values from the models with random effects set to zero).

For the static detector survey, nightly bat activity at 'light' and 'dark' detectors was compared using GLMERs, with either Poisson or negative binomial error structures and log-links. Where appropriate, an observer-level random effect was also included in the model to correct for over-dispersion. Pair identity and site were specified as random effects to account for the spatial structuring of the data. The fit of the models was assessed by inspection of the residuals, examination of AIC values and consideration of the dispersion parameter.

The analyses of both the English studies were conducted using R (v. 3.0.2) [90] with the packages LME4 v. 1.1–7 [91] and glmmADMB v. 3.1.0 [92]. Post hoc comparisons between levels of a predictor were made using Tukey's Honestly Significantly Different test and by computing confidence limits for estimates using the packages 'Multcomp' v. 1.3.6 [93] (for explorations of simple models without interactions) and with Horn pairwise distances in 'phia' 0.1–5 [94] (for models with interactions).

3. Results

(a) Comparison of study designs

All of the studies had sodium lamps as the dominant lighting type. Both the Irish and English transect surveys both had a roughly equal split between low- and high-pressure sodium lighting. In the English study, there were 93 yellow high-pressure sodium transect sections; 115 orange low-pressure sodium transect sections; and 142 were dark. In Ireland, 67 transects had yellow lights (18 had more than or equal to 10 yellow lamps); 111 had orange lights (16 had more than or equal to 10 orange lamps); and 55 had white light (two had more than or equal to 10 white lamps). The landscape was sampled at a very broad scale in the Irish study, and therefore the transects were relatively dark and the distribution of streetlamp

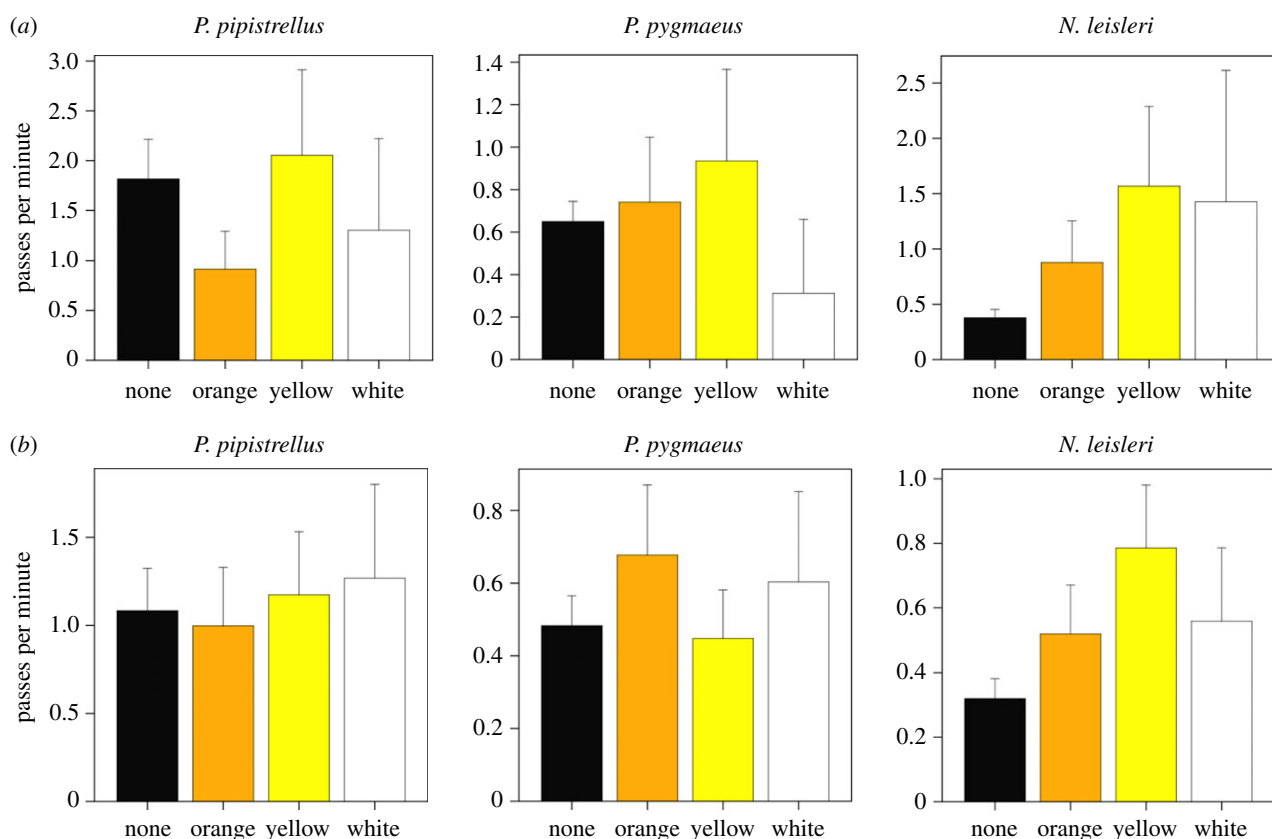


Figure 1. Mean predicted bat activity level (back transformed) per 20 street lights in Irish transect survey from (a) models based on data averaged across surveys; and (b) models allowing for the variation in bat activity between surveys and years. Bars indicate standard errors. (Online version in colour.)

numbers was skewed: over 95% of them had fewer than 20 lamps per 1.6 km, 60% were completely dark, while small numbers were highly illuminated. By contrast, the English transect study deliberately over-represented suburban and urban areas in comparison to their availability in the landscape overall, and the 'lit' transect sections were illuminated throughout their length. The English static survey set out specifically to separate the effect of habitat from that of roadside lighting in areas of apparently good quality for bats. It therefore focused on rural areas and the interface between built and rural environments, and over-sampled lit areas in these habitats compared with their availability. All the lights in this study were high-pressure sodium.

All three studies recorded similar bat activity levels (0.6–2.0 total passes per minute). However, the static surveys recorded throughout the night, rather than just for a short period close to sunset when the activity of common bat species tends to peak. The similarity in average activity levels compared with transect surveys, despite the inclusion of these low activity periods, implies that the static detector sites had higher activity than the transect sites in the early part of the night, reflecting the deliberate selection of favourable habitat for this study. The great majority of recordings were *Pipistrellus* spp. The ratio of common : soprano pipistrelles was approximately 2 : 1 in the Irish study compared with 11 : 1 in the English transect study and 4 : 1 in the static survey. The Irish study also recorded a substantial number of *N. leisleri* (24% of all passes; $n = 1685$), a species rare in England. In comparison, the next most abundant species in the English static survey contributed a very small proportion of total calls (1.6%; $n = 4133$ of the total were *Nyctalus/Eptesicus* spp. combined). *Nyctalus noctula* and *E. serotinus* (species absent in Ireland) were found at all eight study sites,

whereas *N. leisleri* were identified at six of the eight sites and formed just 0.02% of the total calls.

(b) Transect surveys

The Irish study recorded 2950 *P. pipistrellus*, 1563 *P. pygmaeus* and 1685 *N. leisleri*. Results are also presented for all pipistrelles combined, which includes 627 pipistrelle passes that could not be identified to species.

The activity of common and soprano pipistrelle bats did not vary with the density of street lights (all colours combined), although there was a significant positive association for *N. leisleri*. These patterns remained unaltered by adjusting for the amount of built-up habitat within the transect (*P. pipistrellus* $F_{1,391} = 1.11$, $p = 0.292$; *P. pygmaeus* $F_{1,388} = 0.10$, $p = 0.758$; all *Pipistrellus* spp. combined $F_{1,397} = 0.96$, $p = 0.327$; *N. leisleri* $F_{1,399} = 31.0$, $p < 0.001$).

The positive association of *N. leisleri* activity and lighting levels was present for each colour of lighting individually (orange $F_{1,392} = 3.98$, $p = 0.047$; yellow $F_{1,396} = 10.28$, $p = 0.001$; white $F_{1,397} = 3.13$, $p = 0.078$ in model adjusted for habitat), whereas pipistrelle activity was not associated with lighting of any colour (figure 1a). In the more complex models that allowed for the potential temporal variation in bat activity between surveys, the same general patterns were found, with minor differences in the relative effect sizes for the different lighting colours (figure 1b).

The English study considered 350 transect sections. Most (86%) of the 275 bat passes recorded were pipistrelles (*P. pipistrellus* $n = 165$; *P. pygmaeus* $n = 15$; unknown *Pipistrellus* spp. $n = 56$). The probability of bats being present or absent in a transect section varied according to lighting

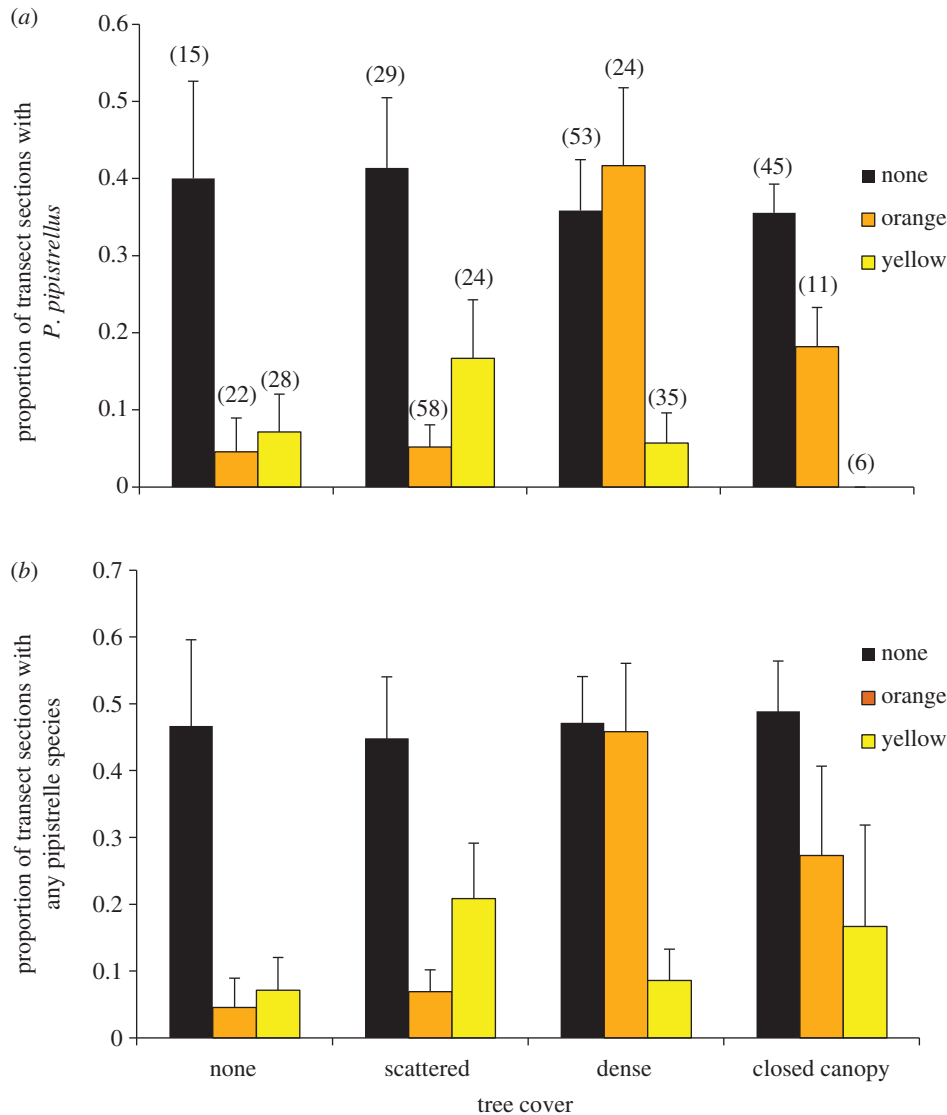


Figure 2. Raw data from English transect survey showing (a) proportion of transects where common pipistrelles (*P. pipistrellus*) were recorded; (b) proportion of transects where any pipistrelle bat was recorded. Bars indicate standard errors, and numbers in parentheses indicate numbers of transects in each combination of lighting and tree cover. (Online version in colour.)

conditions. Dark transect sections were more likely to have bat passes than lit sections: of the sections where pipistrelles were recorded, 69% were dark environments compared with 21% in low-pressure sodium and 10% in high-pressure sodium. In GLMERs without any other habitat variables, lighting was significantly associated with both *P. pipistrellus* and total *Pipistrellus* bat presence (*P. pipistrellus* $\chi^2 = 21.61$, d.f. = 2, $p < 0.001$; total *Pipistrellus* bat $\chi^2 = 33.0$, d.f. = 2, $p < 0.0001$). Sections lit by low-pressure sodium had a 3.3 times lower (95% CI 3.32, 3.26; Tukey $p < 0.001$) probability of *P. pipistrellus* presence than did dark sections, and high-pressure sodium had a 6.7 times lower probability (95% CI 6.68, 6.74; Tukey $p < 0.001$). The minimum adequate GLMER model indicated that urbanization, tree cover and lighting type were all predictors of bat presence and that there was an interaction between lighting type and tree cover (*P. pipistrellus* interaction $\chi^2 = 18.82$, d.f. = 2, $p < 0.04$; total *Pipistrellus* bat interaction $\chi^2 = 17.45$, d.f. = 2, $p = 0.008$). This effect is illustrated by the raw data shown in figure 2a: *Pipistrellus* presence showed little relationship with tree availability in dark areas, whereas it increased with tree shelter in lit areas.

Similar patterns were obtained when the amount of bat activity, rather than the presence or absence of bats, was used as the outcome measure. Activity was lower in lit than dark transects (overall effect of lighting type on *P. pipistrellus* in simple GLMER excluding other habitat variables, $\chi^2 = 23.43$, d.f. = 2, $p < 0.001$; for total *Pipistrellus* bat $\chi^2 = 35.89$, d.f. = 2, $p < 0.001$); the estimated activity was 3.4 (95% CI 1.36, 8.47) times lower in low-pressure sodium-lit areas, and 7.2 (95% CI 2.43, 21.12) times lower in high-pressure sodium-lit areas. The minimum adequate GLMER, which included lighting, urbanization and tree cover, showed there was an interaction between lighting type and the amount of tree cover (illustrated by raw data in figure 1b; lighting–tree interaction for *P. pipistrellus*, $\chi^2 = 16.40$, d.f. = 6, $p = 0.012$; for total *Pipistrellus* bat, $\chi^2 = 18.71$, d.f. = 6, $p < 0.004$).

(c) Static study

A total of 264 648 bat passes were recorded: these were identified as *P. pipistrellus* ($n = 201\ 625$); *P. pygmaeus* ($n = 57\ 620$), *N. noctula* ($n = 2263$), *E. serotinus* ($n = 1128$) and *N. leisleri* ($n = 65$). In addition to single-species models, we also

explored the effects of lighting on all *Pipistrellus* spp. combined (including *P. nathusii* and *Pipistrellus* of unknown species); all *Nyctalus* spp. combined (including 648 files identified to genus only); and *Nyctalus* and *Eptesicus* combined (including 29 files identified only as belonging to one of these genera). Best-fit GLMER models for pipistrelles were obtained using negative binomial error distribution. For all other species, optimum models were obtained using a Poisson distribution (in the case of *N. noctula*; all *Nyctalus* spp. combined; and *Nyctalus/Eptesicus* combined, the models also included an observer-level random effect).

The minimum adequate model for *P. pipistrellus* indicated a negative link with the amount of built environment ($\chi^2 = 4.3$, d.f. = 1, 1043, $p = 0.024$) and a marginally significant positive link with lighting ($\chi^2 = 4.3$, d.f. = 1, 1043, $p = 0.0381$). Based on fixed effects only and adjusting for the amount of built environment, activity was 1.87 (95% CI 1.04, 3.38) times greater under street lights compared with darkness. No other species individually, and no larger grouping of species, showed any relationship with lighting, and there were no interactive effects between lighting and the amount of built environment.

4. Discussion and recommendations

We have investigated the implications of lighting for abundant and widespread bats with important ecosystem functions. *Pipistrellus pipistrellus*, *P. pygmaeus*, *N. noctula*, *N. leisleri* and *E. serotinus* are all generally considered light-attracted, potentially using the insect congregations that accumulate at street lamps [9,23,25,95]. However, in the largest investigation to date, we show that their activity is not increased, except possibly for *N. leisleri* and for *P. pipistrellus* under certain habitat conditions. The reasons are uncertain, but bats appear to rely on vision in lit conditions despite their limited capability for fine spatial resolution in bright light: experiments have shown bats to have an increased propensity to collide with stationary objects in light compared with dark conditions, even though there was no change to their echolocation patterns [37]. Similar mechanisms may compromise the ability of bats to achieve feeding benefits from insects congregated at lights [41].

For *P. pipistrellus*, activity was actually lower in the lit habitats studied in the English transect study except for where dense tree cover was available, and in the widest scale study (Irish transect study) we found no evidence for increased activity of pipistrelles in transects with lights. This observation was explored further in our large-scale static detector survey, using paired sites with good cover and similar habitat. Here, *P. pipistrellus* activity was approximately twice as high in lit than dark areas. This may be because the cover provided by trees offset the increased predation risk associated with light conditions, or because lamps adjacent to trees were particularly insect rich. Alternatively, there could be other benefits from flying close to trees, such as favourable microclimate, which outweigh any disadvantages associated with lighting. *Nyctalus leisleri* activity was positively associated with street lighting in the Irish study (our only project which had a reasonable sample size for this species). This contrasts with a recent report where no difference was observed at orange low-pressure sodium or white mercury vapour lights [95], possibly reflecting the large sample size in our study, and confirms earlier reports from Ireland of this species being light-attracted [26].

The lightscape is rapidly changing, and most of the white mercury vapour lamps associated with increased bat activity in previous surveys (e.g. [25,30,33,95]) have already been replaced. Similarly, energy-inefficient orange low-pressure sodium lights which have low insect attractiveness [7,25] and are generally considered neutral for bats (e.g. [25] though see [95] for a report of positive effects on both *P. pipistrellus* and *P. pygmaeus*) are being replaced, frequently with yellow or white lighting which has greater impacts on insects. In our work, yellow high-pressure sodium lighting was not linked with increased abundance of *N. noctula*, *E. serotinus* or *P. pygmaeus*, and it is now important to test the impacts of replacement white lighting types on common bat species. Further exploration of the effects of high-pressure sodium lighting in open habitats, rather than those with good tree cover, would also be helpful.

Our studies have the advantage, compared with short-term experiments, of exploring the effects of lighting on animals that have been given the opportunity to habituate to their environment. We used a combination of transect and static detector methods. The transects enabled us to study activity over a gradient of habitats, with their representation reflecting their availability in the sampled landscapes. They therefore give the best available impression of the overall effect of lighting at the landscape level relevant to populations. By contrast, the intensive monitoring of a large sample of closely paired sites provided the best opportunity for disentangling the effects of lighting from those of local habitat variations, using sites that provided favourable habitats for bats.

With the exception of *N. leisleri* which is common in Ireland, and possibly for *P. pipistrellus* under certain localized habitat conditions, our work suggests no positive effect of lighting on the most abundant bat species found across Europe. Lighting is therefore likely to contribute to biotic homogenization not by providing more favourable conditions for common species, such as pipistrelles, as previously proposed [69], but by being differentially worse for light-sensitive bats (e.g. *Plecotus* spp., *Myotis* spp. and *Rhinolophus* spp.). Such species are likely to be excluded by lighting from otherwise suitable habitat such as roadside treelines. It is therefore vital that large-scale studies are now conducted for these species, for example on roads adjacent to woodlands, and that use is made of recent evidence on the sensitivities of different genera to lighting spectra. While some information can be gathered from focal studies and local experimentation, these studies must be accompanied by assessments over wider spatial scales. In addition, detailed work is needed to assess the size and connectivity of dark patches necessary for them to retain their ecological function as corridors or foraging areas. For example, if lighting affects only a small proportion of all potentially suitable areas for bats, then even marked local effects in the immediate vicinity of street lights may have little effect on the total distribution of foraging bats in the landscape unless they happen to coincide with key commuting routes.

To date, research has focused on the local effects of point illumination, such as delayed emergence or altered flight paths. However, other equally important aspects of lighting have not been explored. Sky glow, the illuminance caused when lighting is reflected from clouds, results not only in the 'glow' in the sky, but also a wide-scale increase in ambient light sufficient to obscure the stars. Under these conditions, bats are readily visible to the human eye, with consequences for predation risk and bat behaviour. In

addition, there may be impacts on navigation. The afterglow from sunset is used for orientation after roost emergence in *E. fuscus* [96], and sky glow reduces the visibility of sunset.

Good lighting design can help to reduce sky glow, by restricting the upward spillage of light (though some bounce from reflective surfaces such as roads and waterbodies is inevitable). However, even with downward-facing lights, the glare from street lights, and even from car headlights, is visible in the horizontal plane over a distance of many kilometres. This issue is exacerbated where the lights are in elevated positions such as hillsides. At least two consequences are possible. First, the lights may signal the general unsuitability of an area to bats (or possibly act as an attractant for large fast-flying species such as *N. leisleri*), leading to altered habitat use over a large spatial scale. Second, the high contrast between lights and the surrounding dark landscape might make it difficult or impossible for animals to see adjacent features used for foraging or roosting such as hedgerows, woodlands, buildings or lakes. The rod cells in the mammalian eye operate best at low light intensities, and over-stimulation, caused by viewing a bright light, results in the rods becoming unresponsive for periods of more than 10 min [97,98]. The greater the contrast with the surrounding environment, the worse this problem becomes. Security lights in an otherwise dark environment may therefore have profound adverse effects, whereas visual acuity may be less affected where there is also sky glow or moonlight. Given the short range over which echolocation is effective [99], even 'light-shy' species such as the *Pl. auritus* use sight to help identify tree holes, while homing and long-distance navigation are dependent on visual cues in the landscape [100–102].

The disruption of vision by lighting may even affect bat migration. The technological difficulties of tracking long-range movements in small animals mean that bat migration is poorly understood, but it is likely to involve a magnetic compass [103–105]. This may be calibrated by celestial references such as the sun or stars, or alternatively by reference to landscape features. The implications of different forms of light pollution are likely to depend on which mechanism dominates. For example, more migratory activity of *P. nathusii* has been recorded on clear compared with cloudy nights [106], which suggests that interfering with the ability of bats to see the stars—whether by confusion with point light sources or by sky glow which obscures them—could affect navigation. Conversely, if navigation during migration largely relies on landscape 'map cues', then the effects of glare would be more important than sky glow. It is unclear whether bats, like birds and many other organisms, also use polarized light to aid long-distance navigation and to identify water bodies at night [107,108]. However, it has recently been shown that polarization cues at sunset were used by *M. myotis* to calibrate

a magnetic compass which was subsequently used for orientation during a homing experiment [109]. Given the recent increases in polarized light pollution, due to reflectance from shiny surfaces such as glass and solar panels, this area should be a priority for research.

The potential implications of light pollution for the conservation of bats are considerable, particularly for many of our rarer, specialist bats. Our own research shows that even common species formerly considered to use street lighting may in fact show unexpected avoidance, depending on the extent of vegetation cover. For bats such as *N. leisleri*, which in this study demonstrated a preference for lit areas of roadside, it is important to assess the risk of retinal damage through sustained exposure to short-wavelength light. The cumulative effects of lighting must therefore be considered alongside those of other current threats such as habitat loss, mortality at wind farms and agricultural intensification, and mitigated for appropriately. Lighting technology is evolving rapidly, and as well as presenting threats—in the form of more intense and cheaper lighting—it also offers opportunities. These range from reducing the absolute amount of light released into the environment, through 'smart' lighting controls, to altering spectral compositions by removing the most damaging wavelengths. For example, the UV component of artificial lighting is non-functional for humans and so could be removed without loss, while delivering potential benefits to a wide range of invertebrates and bats. Close collaboration between ecologists and lighting engineers is now required if these opportunities are to be realized.

Data accessibility. Records for the Car-based Bat Monitoring Scheme for the Republic of Ireland are provided to the National Biodiversity Data Centre (www.biodiversityireland.ie) and can be viewed on its mapping facility at a 1-km resolution. Data for Northern Ireland are submitted to CEDaR of the National Museums Northern Ireland (www.nmni.com/cedar). The relevant data for the English surveys are deposited in the Open Research Exeter archive <https://ore.exeter.ac.uk/repository/>. The R and Genstat scripts used to generate the analyses can be requested from the authors.

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Authors contributions. F.M., N.R., T.A., N.J., J.D. and J.B. carried out the fieldwork, and N.R., N.J., J.B. and J.D. conducted the data abstraction and interpretation. F.M. and S.L. conducted the statistical analyses. F.M., N.R., T.A. and S.L. conceived and designed the study. All authors helped to interpret the data, draft the manuscript and gave final approval for publication.

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References

- Gaston KJ, Duffy JP, Gaston S, Bennie J, Davies TW. 2014 Human alteration of natural light cycles: causes and ecological consequences. *Oecologia* **176**, 917–931. (doi:10.1007/s00442-014-3088-2)
- IUCN. 2014 *The IUCN Red List of Threatened Species*, v. 2014.2. <http://www.iucnredlist.org>.
- Boyles JG, Cryan PM, McCracken GF, Kunz TH. 2011 Economic importance of bats in agriculture. *Science* **332**, 41–42. (doi:10.1126/science.1201366)
- Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH. 2011 Ecosystem services provided by bats. *Ann. NY Acad. Sci.* **1223**, 1–38. (doi:10.1111/j.1749-6632.2011.06004.x)
- Lewanzik D, Voigt CC. 2014 Artificial light puts ecosystem services of frugivorous bats at risk. *J. Appl. Ecol.* **51**, 388–394. (doi:10.1111/1365-2664.12206)

6. Hanski I. 1998 Metapopulation dynamics. *Nature* **396**, 41–49. (doi:10.1038/23876)
7. Eisenbeis G. 2006 Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In *Ecological consequences of artificial night lighting* (eds C Rich, T Longcore), pp. 281–304. Washington, DC: Island Press.
8. Longcore T, Rich C. 2004 Ecological light pollution. *Front. Ecol. Environ.* **2**, 191–198. (doi:10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2)
9. Entwistle A, Harris S, Hutson A, Racey P, Walsh A, Gibson S, Hepburn I, Johnston J. 2001 *Habitat management for bats*. Peterborough, Canada: Joint Nature Conservation Committee.
10. Speakman J. 1991 Why do insectivorous bats in Britain not fly in daylight more frequently? *Funct. Ecol.* **5**, 518–524. (doi:10.2307/2389634)
11. Fenton M, Rautenbach I, Smith S, Swanepoel C, Grosell J, Van Jaarsveld J. 1994 Raptors and bats: threats and opportunities. *Anim. Behav.* **48**, 9–18. (doi:10.1006/anbe.1994.1207)
12. 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)
13. Duvergé PL, Jones G, Rydell J, Ransome RD. 2000 Functional significance of emergence timing in bats. *Ecography* **23**, 32–40. (doi:10.1111/j.1600-0587.2000.tb00258.x)
14. Jones G. 1995 Flight performance, echolocation and foraging behaviour in noctule bats *Nyctalus noctula*. *J. Zool.* **237**, 303–312. (doi:10.1111/j.1469-7998.1995.tb02764.x)
15. Russo D, Cistrone L, Jones G. 2007 Emergence time in forest bats: the influence of canopy closure. *Acta Oecol.* **31**, 119–126. (doi:10.1016/j.actao.2006.11.001)
16. Shiel CB, Fairley JS. 1999 Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland. *J. Zool.* **247**, 439–447. (doi:10.1111/j.1469-7998.1999.tb01007.x)
17. 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)
18. Downs N, Beaton V, Guest J, Polanski J, Robinson S, Racey P. 2003 The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus*. *Biol. Conserv.* **111**, 247–252. (doi:10.1016/S0006-3207(02)00298-7)
19. Zagmaster M. 2014 Changing the external illumination of churches to reduce disturbance for bats - examples from Slovenia. In *X111th European Bat Research Symposium* (eds AM Hutson, PCH Lina), pp. 186. Sibenik, Croatia: Croatian Biospeleological Society.
20. Boldogh S, Dobrosi D, Samu P. 2007 The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterol.* **9**, 527–534. (doi:10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
21. Erkert HG. 1982 Ecological aspects of bat activity rhythms. In *Ecology of bats* (ed. TH Kunz), pp. 201–242. New York, NY: Springer.
22. DeCoursey G, DeCoursey PJ. 1964 Adaptive aspects of activity rhythms in bats. *Biol. Bull.* **126**, 14–27. (doi:10.2307/1539413)
23. Rydell J. 2006 Bats and their insect prey at streetlights. In *Ecological consequences of artificial night lighting* (eds T Longcore, C Rich), pp. 43–60. Washington, DC: Island Press.
24. Catto CMC, Hutson AM, Racey PA, Stephenson PJ. 1996 Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool.* **238**, 623–633. (doi:10.1111/j.1469-7998.1996.tb05419.x)
25. Blake D, Hutson A, Racey P, Rydell J, Speakman J. 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)
26. Shiel CB, Fairley JS. 1998 Activity of Leisler's bat *Nyctalus leisleri* (Kuhl) in the field in south-east county Wexford, as revealed by a bat detector. *Biol. Environ.: Proc. R. Irish Acad.* **98B**, 105–112.
27. Haffner M, Stutz H. 1985 Abundance of *Pipistrellus pipistrellus* and *Pipistrellus kuhlii* foraging at street-lamps. *Myotis* **23**, 167–172.
28. Geggie J, Fenton M. 1985 A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Can. J. Zool.* **63**, 263–266. (doi:10.1139/z85-040)
29. Rydell J. 1992 Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* **6**, 744–750. (doi:10.2307/2389972)
30. Kronwittter F. 1988 Population structure, habitat use and activity patterns of the noctule bat *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertilionidae) revealed by radio-tracking. *Myotis* **26**, 23–85.
31. Rydell J. 1991 Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssonii*. *Ecography* **14**, 203–207. (doi:10.1111/j.1600-0587.1991.tb00653.x)
32. Furlonger C, Dewar H, Fenton M. 1987 Habitat use by foraging insectivorous bats. *Can. J. Zool.* **65**, 284–288. (doi:10.1139/z87-044)
33. Rydell J, Racey P. 1995 Street lamps and the feeding ecology of insectivorous bats. In *Symposia of the Zoological Society of London* (eds PA Racey, SM Swift), pp. 291–307. London, UK: The Society.
34. Threlfall CG, Law B, Banks PB. 2012 Influence of landscape structure and human modifications on insect biomass and bat foraging activity in an urban landscape. *PLoS ONE* **7**, e38800. (doi:10.1371/journal.pone.0038800)
35. Hale JD, Fairbrass AJ, Matthews TJ, Sadler JP. 2012 Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. *PLoS ONE* **7**, e33300. (doi:10.1371/journal.pone.0033300)
36. McGuire LP, Fenton MB. 2010 Hitting the wall: light affects the obstacle avoidance ability of free-flying little brown bats (*Myotis lucifugus*). *Acta Chiropterol.* **12**, 247–250. (doi:10.3161/150811010X504734)
37. Orbach DN, Fenton B. 2010 Vision impairs the abilities of bats to avoid colliding with stationary obstacles. *PLoS ONE* **5**, e13912. (doi:10.1371/journal.pone.0013912)
38. Saldaña-Vázquez RA, Munguía-Rosas MA. 2013 Lunar phobia in bats and its ecological correlates: a meta-analysis. *Mammal. Biol. Z. Säugetierkunde* **78**, 216–219. (doi:10.1016/j.mambio.2012.08.004)
39. Karlsson B-L, Eklöf J, Rydell J. 2002 No lunar phobia in swarming insectivorous bats (family Vespertilionidae). *J. Zool.* **256**, 473–477. (doi:10.1017/S0952836902000511)
40. 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)
41. 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)
42. Kuijper DP, Schut J, van Dulleman D, Toorman H, Goossens N, Ouwehand J, Limpens H. 2008 Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). *Lutra* **51**, 37.
43. Royal Commission. 2009 *Artificial light in the environment*. London, UK: HMSO.
44. Hölker F et al. 2010 The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecol. Soc.* **15**, 13. <http://www.ecologyandsociety.org/vol15/iss4/art13/>.
45. Elvidge CD, Keith DM, Tuttle BT, Baugh KE. 2010 Spectral identification of lighting type and character. *Sensors* **10**, 3961–3988. (doi:10.3390/s100403961)
46. van Langevelde F, Etema JA, Donners M, WallisDeVries MF, Groenendijk D. 2011 Effect of spectral composition of artificial light on the attraction of moths. *Biol. Conserv.* **144**, 2274–2281. (doi:10.1016/j.biocon.2011.06.004)
47. Avila-Flores R, Fenton MB. 2005 Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* **86**, 1193–1204. (doi:10.1644/04-MAMM-A-085R1.1)
48. Svensson A, Rydell J. 1998 Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera* spp.; Geometridae). *Anim. Behav.* **55**, 223–226. (doi:10.1006/anbe.1997.0590)
49. Gaston KJ, Bennie J, Davies TW, Hopkins J. 2013 The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev.* **88**, 912–927. (doi:10.1111/brv.12036)
50. van Grunsven RH, Donners M, Boeke K, Tichelaar I, van Geffen K, Groenendijk D, Berendse F, Veenendaal E. 2014 Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *J. Insect Conserv.* **18**, 225–231. (doi:10.1007/s10841-014-9633-9)
51. Pawson S, Bader M-F. 2014 LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecol. Appl.* **24**, 1561–1568. (doi:10.1890/14-0468.1)
52. Eisenbeis G, Eick K. 2011 Studie zur Anziehung nachtaktiver Insekten an die Straßenbeleuchtung

- unter Einbeziehung von LEDs. *Nat. Landschaft* **86**, 298–306.
53. Kim T-J, Jeon Y-K, Lee J-Y, Lee E-S, Jeon C-J. 2008 The photoreceptor populations in the retina of the greater horseshoe bat *Rhinolophus ferrumequinum*. *Mol. Cells* **26**, 373–379.
54. Müller B, Glösmann M, Peichl L, Knop GC, Hagemann C, Ammermüller J. 2009 Bat eyes have ultraviolet-sensitive cone photoreceptors. *PLoS ONE* **4**, e6390. (doi:10.1371/journal.pone.0006390)
55. Peichl L. 2005 Diversity of mammalian photoreceptor properties: adaptations to habitat and lifestyle? *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **287**, 1001–1012. (doi:10.1002/ar.a.20262)
56. Zhao H, Rossiter SJ, Teeling EC, Li C, Cotton JA, Zhang S. 2009 The evolution of color vision in nocturnal mammals. *Proc. Natl Acad. Sci. USA* **106**, 8980–8985. (doi:10.1073/pnas.0813201106)
57. Poot H, Ens BJ, de Vries H, Donners MA, Wernand MR, Marquenie JM. 2008 Green light for nocturnally migrating birds. *Ecol. Soc.* **13**, 47.
58. Gauthreaux Jr SA, Belsler CG, Rich C, Longcore T. 2006 Effects of artificial night lighting on migrating birds. In *Ecological consequences of artificial night lighting* (eds C Rich, T Longcore), pp. 67–93. Washington, DC: Island Press.
59. Davies TW, Duffy JP, Bennie J, Gaston KJ. 2014 The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* **12**, 347–355. (doi:10.1890/130281)
60. Fujun X, Kailiang H, Tengzeng Z, Paul R, Xuzhong W, Yi S. 2012 Behavioral evidence for cone-based ultraviolet vision in divergent bat species and implications for its evolution. *Zoologia* **29**, 109–114.
61. Xuan F, Hu K, Zhu T, Racey P, Wang X, Zhang S, Sun Y. 2012 Immunohistochemical evidence of cone-based ultraviolet vision in divergent bat species and implications for its evolution. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **161**, 398–403. (doi:10.1016/j.cbpb.2012.01.005)
62. Douglas R, Jeffery G. 2014 The spectral transmission of ocular media suggests ultraviolet sensitivity is widespread among mammals. *Proc. R. Soc. B* **281**, 20132995. (doi:10.1098/rspb.2013.2995)
63. Douglas R, Marshall N. 1999 A review of vertebrate and invertebrate ocular filters. In *Adaptive mechanisms in the ecology of vision* (ed. SN Archer), pp. 95–162. New York, NY: Springer.
64. van Norren D, Gorgels TG. 2011 The action spectrum of photochemical damage to the retina: a review of monochromatic threshold data. *Photochem. Photobiol.* **87**, 747–753. (doi:10.1111/j.1751-1097.2011.00921.x)
65. Stilz W-P, Schnitzler H-U. 2012 Estimation of the acoustic range of bat echolocation for extended targets. *J. Acoust. Soc. Am.* **132**, 1765–1775. (doi:10.1121/1.4733537)
66. Schnitzler H-U, Moss CF, Denzinger A. 2003 From spatial orientation to food acquisition in echolocating bats. *Trends Ecol. Evol.* **18**, 386–394. (doi:10.1016/S0169-5347(03)00185-X)
67. Laurance WF, Yensen E. 1991 Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* **55**, 77–92. (doi:10.1016/0006-3207(91)90006-U)
68. Bennie J, Davies TW, Inger R, Gaston KJ. 2014 Mapping artificial lightscapes for ecological studies. *Methods Ecol. Evol.* **5**, 534–540. (doi:10.1111/2041-210X.12182)
69. Arlettaz R, Godat S, Meyer H. 2000 Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biol. Conserv.* **93**, 55–60. (doi:10.1016/S0006-3207(99)00112-3)
70. Somers-Yeates R, Hodgson D, McGregor PK, Spalding A. 2013 Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biol. Lett.* **9**, 20130376. (doi:10.1098/rsbl.2013.0376)
71. Perkin EK, Hölker F, Tockner K. 2014 The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshw. Biol.* **59**, 368–377. (doi:10.1111/fwb.12270)
72. Tomassini A, Colangelo P, Agnelli P, Jones G, Russo D. 2014 Cranial size has increased over 133 years in a common bat, *Pipistrellus kuhlii*: a response to changing climate or urbanization? *J. Biogeogr.* **41**, 944–953. (doi:10.1111/jbi.12248)
73. Davies TW, Bennie J, Gaston KJ. 2012 Street lighting changes the composition of invertebrate communities. *Biol. Lett.* **8**, 764–767. (doi:10.1098/rsbl.2012.0216)
74. Inger R, Gregory R, Duffy JP, Stott I, Voříšek P, Gaston KJ. 2014 Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecol. Lett.* **18**, 28–36. (doi:10.1111/ele.12387)
75. Schwartz M, Brigham C, Hoeksema J, Lyons K, Mills M, Van Mantgem P. 2000 Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**, 297–305. (doi:10.1007/s004420050035)
76. Gaston KJ, Fuller RA. 2008 Commonness, population depletion and conservation biology. *Trends Ecol. Evol.* **23**, 14–19. (doi:10.1016/j.tree.2007.11.001)
77. Conrad KF, Warren MS, Fox R, Parsons MS, Woivod IP. 2006 Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* **132**, 279–291. (doi:10.1016/j.biocon.2006.04.020)
78. Hutson AM, Spitzenberger F, Aulagnier S, Coroiu I, Karataş A, Juste J, Paunovic M, Palmeirim J, Benda P. 2008 *The IUCN Red List of Threatened Species*, v. 2014.3. *Pipistrellus pipistrellus*. <http://www.iucnredlist.org/details/17317/0>.
79. The Tracking Mammals Partnership. 2005 *UK mammals species status and population trends. First report by the tracking mammals partnership*. Peterborough, UK: JNCC/Tracking Mammals Partnership.
80. Roche N, Langton S, Aughney T, Russ J, Marnell F, Lynn D, Catto C. 2011 A car-based monitoring method reveals new information on bat populations and distributions in Ireland. *Anim. Conserv.* **14**, 642–651. (doi:10.1111/j.1469-1795.2011.00470.x)
81. Joint Nature Conservancy Council. 2004 *Handbook for Phase 1 habitat survey - a technique for environmental audit*. Peterborough, Canada: Nature Conservancy Council.
82. Davidson-Watts I, Walls S, Jones G. 2006 Differential habitat selection by *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus* identifies distinct conservation needs for cryptic species of echolocating bats. *Biol. Conserv.* **133**, 118–127. (doi:10.1016/j.biocon.2006.05.027)
83. Russ J. 2012 *British bat calls: a guide to species identification*. Exeter, UK: Pelagic Publishing Ltd.
84. Russ J. 1999 *The bats of Britain and Ireland. Echolocation calls, sound analysis and species identification*. Powys, UK: Alana Books.
85. Vaughan N, Jones G, Harris S. 1997 Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics* **7**, 189–207. (doi:10.1080/09524622.1997.9753331)
86. Richardson SM, Hosken DJ, Mathews F. Submitted. Acoustic monitoring for bats: solving current problems.
87. Fenton M, Jacobson S, Stone R. 1973 An automatic ultrasonic sensing system for monitoring the activity of some bats. *Can. J. Zool.* **51**, 291–299. (doi:10.1139/z73-041)
88. VSN International. 2014 *Genstat for Windows, V17*. Hemel Hempstead, UK: VSN International.
89. Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS. 2009 Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**, 127–135. (doi:10.1016/j.tree.2008.10.008)
90. R Development Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
91. Bates D, Maechler M, Bolker B. 2011 *lme4: Linear mixed-effects models using Eigen and S4. R package, v. 0.999375–42*. <http://cran.r-project.org/web/packages/lme4/lme4.pdf>.
92. Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B. 2012 *glmmADMB: generalized linear mixed models using AD Model Builder*. <http://glmmadmb.r-forge.r-project.org>.
93. Hothorn T, Bretz F, Westfall P. 2012 *Multcomp: simultaneous inference in general parametric models, v. 1.2–12*. <http://cran.r-project.org/web/packages/multcomp/multcomp.pdf>.
94. de Rosario-Martinez H, Fox J, R Core Team. 2014 *Phia*. (0.1–5 edn). Vienna, Austria: R Core Development Team.
95. Lacoëuilhe A, Machon N, Julien J-F, Le Bocq A, Kerbirou 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)
96. Buchler ER, Childs SB. 1982 Use of the post-sunset glow as an orientation cue by big brown bats

- (*Eptesicus fuscus*). *J. Mammal.* **63**, 243–247. (doi:10.2307/1380633)
97. Hulburt E. 1951 Time of dark adaptation after stimulation by various brightnesses and colors. *J. Ophthalmol. Soc. Am.* **41**, 402–403. (doi:10.1364/JOSA.41.000402)
98. Rowland WM, Sloan LL. 1944 The relative merits of red and white light of low intensity for adapting the eyes to darkness. *J. Opt. Soc. Am.* **34**, 601. (doi:10.1364/JOSA.34.000601)
99. Lawrence B, Simmons J. 1982 Echolocation in bats: the external ear and perception of the vertical positions of targets. *Science* **218**, 481–483. (doi:10.1126/science.7123247)
100. Masterson FA, Ellins SR. 1974 The role of vision in the orientation of the echolocating bat, *Myotis lucifugus*. *Behaviour* **51**, 88–98. (doi:10.1163/156853974X00156)
101. Barbour RW, Davis WH, Hassell MD. 1966 The need of vision in homing by *Myotis sodalis*. *J. Mammal.* **47**, 356–357. (doi:10.2307/1378156)
102. Jensen ME, Moss CF, Surlykke A. 2005 Echolocating bats can use acoustic landmarks for spatial orientation. *J. Exp. Biol.* **208**, 4399–4410. (doi:10.1242/jeb.01901)
103. Holland RA, Thorup K, Vonhof MJ, Cochran WW, Wikelski M. 2006 Navigation: bat orientation using Earth's magnetic field. *Nature* **444**, 7022. (doi:10.1038/444702a)
104. Holland RA. 2007 Orientation and navigation in bats: known unknowns or unknown unknowns? *Behav. Ecol. Sociobiol.* **61**, 653–660. (doi:10.1007/s00265-006-0297-7)
105. Wang Y, Pan Y, Parsons S, Walker M, Zhang S. 2007 Bats respond to polarity of a magnetic field. *Proc. R. Soc. B* **274**, 2901–2905. (doi:10.1098/rspb.2007.0904)
106. Eklöf J, Šuba J, Petersons G, Rydell J. 2014 Visual acuity and eye size in five European bat species in relation to foraging and migration strategies. *Environ. Exp. Biol.* **12**, 1–6.
107. Holland RA, Borissov I, Siemers BM. 2010 A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. *Proc. Natl Acad. Sci. USA* **107**, 6941–6945. (doi:10.1073/pnas.0912477107)
108. Horváth G, Kriska G, Malik P, Robertson B. 2009 Polarized light pollution: a new kind of ecological photopollution. *Front. Ecol. Environ.* **7**, 317–325. (doi:10.1890/080129)
109. Greif S, Borissov I, Yovel Y, Holland RA. 2014 A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. *Nat. Commun.* **5**, 4488. (doi:10.1038/ncomms5488)