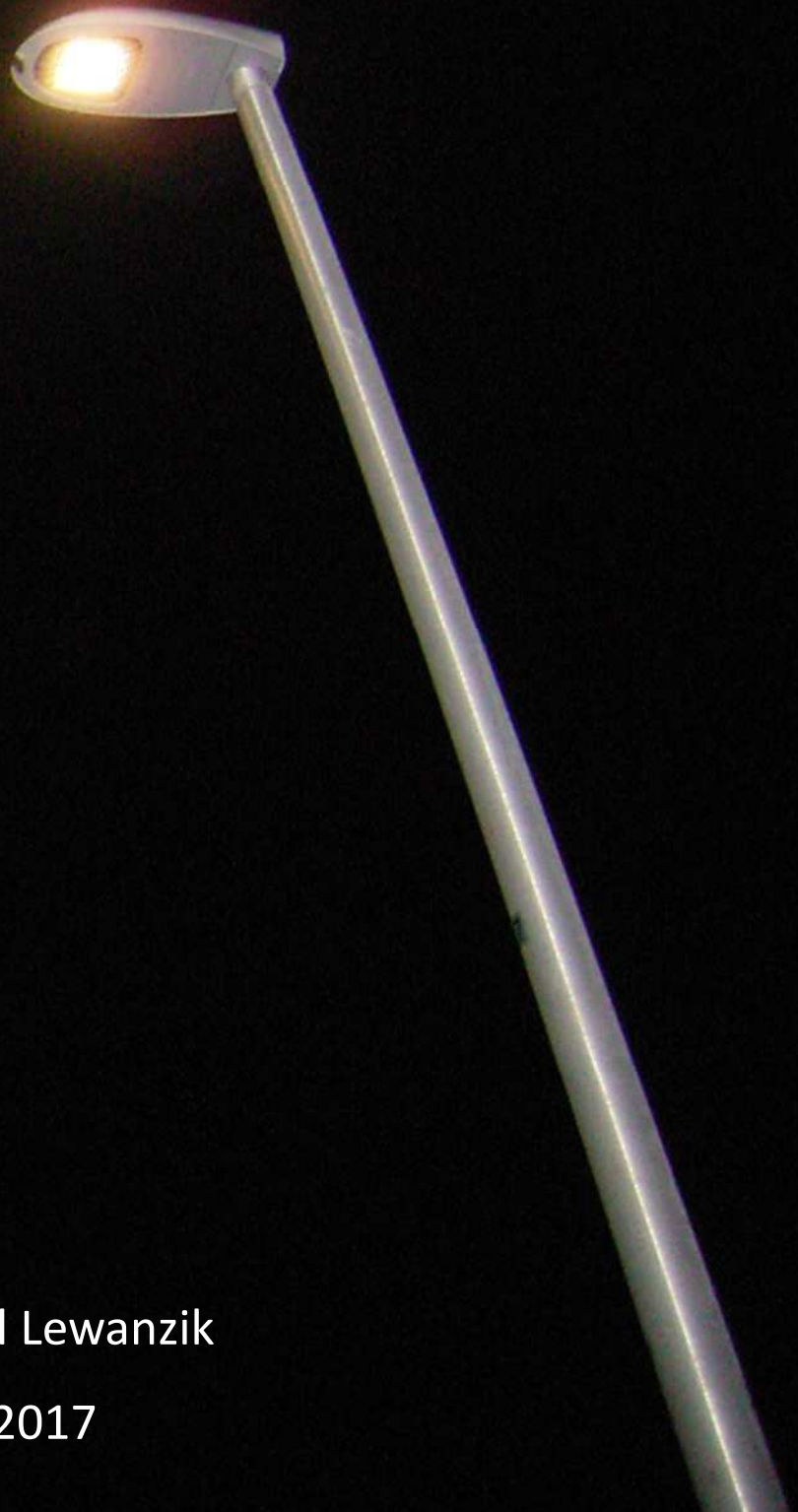




Artificial light affects bats

across climatic zones and feeding guilds



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Artificial light affects bats across climatic zones and feeding guilds

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1. Gutachter: PD Dr. Christian C. Voigt

2. Gutachter: Prof. Dr. Jonathan Jeschke

Disputation am 27. September 2017

“What if we woke up one morning only to realize that all of the conservation planning [...] told only half of the story – the daytime story?”

(Rich & Longcore 2006)

This thesis is based on the following manuscripts:

1. **Lewanzik D^{1,2}, Voigt CC^{1,2} (2017) Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology*, **54**, 264–271.**

C. C. Voigt and I planned the experiment under the framework of the “Loss of the Night” project. I carried out the field work and analysed the data. I wrote the manuscript with input from C. C. Voigt.

2. **Rowse EG³, Lewanzik D^{1,2}, Stone EL³, Harris S³, Jones G³ (2016) Dark matters: the effects of artificial lighting on bats. In: Voigt CC & Kingston T (eds.) *Bats in the Anthropocene: Conservation of Bats in a Changing World*, Springer International Publishing AG, Cham, Switzerland, pp 187-213.**

E.G. Rowse and D. Lewanzik: Equal contributors.

I wrote the first draft of sections 7.5 (The biological effects of light pollution), 7.7 (Observational studies on bats at street lights), 7.9 (Winners and losers: light-tolerant and light-averse bats) and 7.10 (Effects of light pollution on ecosystem services provided by bats). I then worked on these sections in collaboration with all authors.

3. **Lewanzik D^{1,2}, Voigt CC^{1,2} (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology*, **51**, 388-394.**

I conceived the experiment in collaboration with C. C. Voigt. I conducted the experiments and statistical analyses. I wrote the manuscript with input from C. C. Voigt.

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1. ZUSAMMENFASSUNG

Künstliches Licht, insbesondere Straßenbeleuchtung, wird weltweit in schnell zunehmendem Maße genutzt und dringt in vormals unberührte Gegenden vor. Besorgniserregend ist dabei, dass es Wildtiere beeinträchtigen und sich nachteilig auf die Biodiversität und ganze Ökosysteme auswirken kann. Daher wird künstliches Licht, das den natürlichen Rhythmus zwischen Licht und Dunkelheit verändert und auf diese Weise die Umwelt ‚verschmutzt‘, mittlerweile als schädlich angesehen. Insbesondere Fledermäuse leiden unter Lichtverschmutzung, da ihre Sinne an das Jagen und Orientieren in Dunkelheit angepasst sind. Zum Beispiel verzögert künstliches Licht den abendlichen Ausflug aus dem Quartier, beeinflusst ihr Jagdverhalten, beeinträchtigt ihre Orientierung und verlangsamt das Wachstum der Nachkommen.

In chapter 1 gebe ich einen Überblick über den derzeitigen Stand der Wissenschaft und fasse die Auswirkungen von künstlichem Lichts auf Physiologie und Verhalten von Fledermäusen zusammen. Zudem diskutiere ich den Zusammenhang zwischen Phototropismus von Insekten und der Aktivität lichttoleranter Fledermäuse und beantworte die Frage, warum lichtscheue Fledermäuse diesem Muster nicht folgen. Im Anschluss betrachte ich die Auswirkungen künstlichen Lichts auf der Ebene des Ökosystems und schlage Maßnahmen vor, die geeignet sind, die schädlichen Effekte zu verringern.

Eine wichtige Erkenntnis aus chapter 1 ist, dass die meisten Studien bisher Insekten fressende Fledermausarten der gemäßigten Breiten untersucht haben, obwohl die Diversität in tropischen Gegenden bedeutend höher ist. Tropische Fledermäuse besetzen zentrale Positionen im Ökosystem und vollbringen entscheidende Ökosystem-Dienstleistungen. So bestäuben Nektar trinkende Fledermäuse die Blüten einer Vielzahl ökologisch und wirtschaftlich wichtiger Pflanzen und Früchte fressende Arten verbreiten deren Samen.

Um herauszufinden, wie sich Straßenbeleuchtung auf die Nahrungssuche fruchtfressender Fledermäuse auswirkt, habe ich Verhaltensexperimente mit *Carollia sowelli* sowohl im Flugraum als auch im Freiland durchgeführt (chapter 2). *Carollia sowelli* stellt in vielen Gegenden der Neuwelt-Tropen einen wichtigen Samenverbreiter von Pionierpflanzen dar. Ich konnte zeigen, dass *C. sowelli* in beleuchteten Arealen weniger Früchte erntet als von unbeleuchteten Kontrollpflanzen. Wenn dadurch auch die

Samenverbreitung vermindert wird, könnte künstliches Licht weitreichende Folgen für die Regeneration von Wäldern haben und Neotropische Ökosysteme gefährden.

So wie *C. sowellii* vermeiden es auch einige Insekten fressende Fledermausarten in beleuchteten Gegenden zu jagen. Andere Insekten fressende Arten hingegen reduzieren sogar ihren Jagdaufwand, indem sie gezielt Jagd auf Insekten machen, die von Straßenlampen angezogen wurden. Daher können Straßenlampen die lokale Artenzusammensetzung und folglich die Konkurrenz zwischen den Arten verändern. Allerdings unterscheiden sich die verschiedenen Lichtarten bezüglich ihres Einflusses auf Fledermäuse, abhängig von der spektralen Zusammensetzung ihres Lichts. In Europa und vielen außereuropäischen Ländern ist die Neuinstallation von Quecksilberdampf- (MV, *Mercury Vapour*) und anderen ineffizienten Leuchtmitteln bereits verboten und es wird erwartet, dass sie schrittweise vor allem durch LEDs (*Light Emitting Diodes*) ersetzt werden. Diese großflächige Umrüstung wird das Wellenlängen-Spektrum von Nachtlandschaften erheblich verändern. Daher ist es besonders für den Arten- und Naturschutz entscheidend zu verstehen, wie sich moderne LEDs bezüglich ihrer Auswirkungen auf Fledermäuse von herkömmlichen Leuchtmitteln unterscheiden.

Um die Folgen einer solchen Umrüstung für Fledermäuse in urbanen Habitaten abschätzen zu können, habe ich die Fledermausaktivität an MV-Straßenlaternen, die durch LEDs ersetzt wurden, mit der Fledermausaktivität an Kontrolllaternen verglichen, die über den Zeitraum des Experiments durchgängig mit MV-Leuchtmitteln bestückt waren. In chapter 3 zeige ich, dass *Pipistrellus pipistrellus*, die häufigste Fledermausart an meinen Untersuchungsstandorten, ihre Aktivität in Folge der Umstellung auf LEDs um 45% verringert hat. Die Aktivität von *Myotis* spp., die Licht im Allgemeinen meiden, nahm hingegen an LED-Laternen um den Faktor 4,5 zu. Diese Ergebnisse deuten darauf hin, dass der großflächige Wechsel von herkömmlichen MV-Leuchtmitteln hin zu LEDs den anthropogenen Einfluss auf Fledermäuse verringert. Kurzfristig könnten manche Arten jedoch einen Nachteil durch eine geringere Jagdeffizienz an LEDs haben.

Fazit: In meiner Doktorarbeit konnte ich demonstrieren, dass sich künstliches Licht nicht nur auf Insekten fressende sondern auch auf Früchte fressende Fledermäuse auswirkt. Zudem zeigen meine Untersuchungen, dass verschiedene Leuchtmittel Fledermäuse in unterschiedlichem Maße beeinflussen. Die Ergebnisse legen nahe, dass negative Auswirkungen künstlichen Lichts verringert werden können, indem konventionelle durch moderne, weniger schädliche Leuchtmittel ersetzt werden.

2. SUMMARY

Artificial light at night, in particular street lighting, is rapidly increasing globally and sprawls into formerly pristine areas. Worryingly, it can have detrimental effects on wildlife and eventually on biodiversity and ecosystem functioning. Therefore, artificial light is considered a pollutant changing the natural light-dark regime. Light pollution particularly impairs bats, the second most diverse mammal taxon. Bats have evolved traits well-adapted for nocturnal activity but which make them vulnerable to the prevailing high levels of artificial light at night. Indeed, over the past decades an increasing number of studies has demonstrated deleterious effects of artificial light on bats: it delays emergence of bats and reduces the number of emerging individuals, affects their commuting and foraging behaviour, interferes with navigation and slows down juvenile growth.

In chapter 1 I review the existing literature, summarising the physiological and behavioural consequences that artificial light has for bats. I discuss the correlation between phototropism of insects and activity of light-tolerant bats and expound upon reasons for why and how this relation is very different for light-averse species. I then widen the scope to cascading effects at the ecosystem level. Finally, I suggest mitigation measures and conclude by pointing out remaining questions.

A key finding of chapter 1 is that, to date, most studies have focused on insectivorous species in the temperate climate zone, although bat diversity is much higher in tropical regions. Tropical bats occupy central positions in the ecosystem and provide key ecosystem services. For instance, nectarivorous and frugivorous bats pollinate flowers and disperse seeds of numerous ecologically and economically important plants. To test how street lighting affects the foraging behaviour of frugivorous bats, I carried out experiments in both the field and a flight room using *Carollia sowelli* (chapter 2). *Carollia sowelli* is an abundant bat species in many Neotropical regions and constitutes a crucial seed disperser of pioneer plants. In chapter 2 I demonstrate that *C. sowelli* avoids lit areas in both space and time; specifically, it harvested less fruits in the vicinity of lit street lights, compared with unlit control lights. It stands to reason that if reduced harvesting translates into reduced seed dispersal, artificial light not only deteriorates food availability for light-averse bats, but could have far-reaching consequences for forest regeneration and compromise ecosystem functioning in Neotropical regions.

Similarly, several insectivorous bats also reduce commuting and foraging when their habitat becomes lit. Other insectivorous species, however, exploit insect aggregations around street lights and reduce foraging efforts in that way. Thus, street lights can change local bat species composition and affect inter-specific competition. Yet, the impact of street lights differs between light types and strongly depends on their spectral signature. Across Europe and many non-European countries conventional mercury vapour (MV) street lights and other inefficient illuminants are being phased out and a widespread replacement by light-emitting diodes (LEDs) is expected. This change-over will tremendously alter the wavelengths spectrum of lightscapes at night. From a conservation perspective it is thus crucial to understand how modern LEDs differ from conventional illuminants concerning their impacts on wildlife. In order to predict the consequences of the anticipated changeover on urban bats, I conducted a large-scale field experiment across Germany where I compared bat activity at municipal MV street lamps that were replaced by LEDs with control lamps that remained with MV illuminants throughout the study. In chapter 3, I show that *Pipistrellus pipistrellus*, the most abundant species at my study sites, decreases its activity by 45% at LEDs compared with MV lights, probably in response to a reduction in insect numbers. In contrast, generally light-averse *Myotis* spp. increase their activity 4.5-fold when MV street lights are replaced by LEDs. These findings suggest that the transition from conventional MV lights to LEDs decreases the anthropogenic impact on bats in urban habitats. In the short-term, however, some species might suffer from a reduced foraging efficiency at LEDs.

In conclusion, chapter 1 through 3 of my doctoral thesis demonstrate that the effects of artificial light are not restricted to insectivorous bats, but are also relevant for fruit-eating species. Further, my findings show that illuminants differ concerning their impact on bats and suggest that the negative effects of artificial light can be mitigated to some extent by replacing conventional illuminants with modern, less pernicious light types.

3. GENERAL INTRODUCTION

3.1 The spread of artificial light

Since electric light became common in the early twentieth century, artificial light at night has increasingly transformed the naturally dark night into illuminated habitats in many parts of the world. Artificial light allows humans to work beyond dusk and thus has long been a symbol of technological progress, modern life, and wealth. Also, lighted surroundings increase the sense of security at night (Nasar & Jones 1997). Accordingly, the trend towards more outdoor lighting is unbowed: artificial lighting is increasing at unprecedented rates, particularly in less developed parts of the world. Yet, even in highly developed countries, in which one might assume the ‘light scape’ to be saturated, artificial lighting is still growing (OECD/IEA 2006; Hölker et al. 2010). In Europe, already 88% of the land surface is affected by light pollution at night and, globally, 80% of humanity lives under light-polluted skies (Falchi et al. 2016; Fig. 1). As the human population increases and the world continues to urbanise rapidly, cities grow and encroach into formerly pristine habitats. Artificial light is intrinsically associated with urban sprawl and thus spreads as well (Cinzano, Falchi & Elvidge 2001; UN 2014; UNPFA 2015).

Over the past few decades it has become more and more evident that artificial light at night has detrimental effects on wildlife and humans, and poses a severe threat to biodiversity (Rich & Longcore 2006; Hölker et al. 2010b; Gaston et al. 2015). To account for these negative effects, the term ‘ecological light pollution’ was established: too much or improperly used artificial light that pollutes the environment by altering the natural light regimes in ecosystems (Longcore & Rich 2004). A widely visible phenomenon resulting from light pollution is the so-called ‘sky glow’: when light propagates into the sky either indirectly via reflection from surfaces or directly from upward-directed lamps, the light is partially scattered back by atmospheric particles towards the ground. At night, this scattering causes the sky to ‘glow’. Particularly during cloudy nights when the air is full of water particles, the light dome emerging from cities and towns increases night sky brightness over large distances (Kyba et al. 2011). Even protected areas designated for biological conservation suffer from light pollution nowadays (Aubrecht, Jaiteh & de Sherbinin 2010).

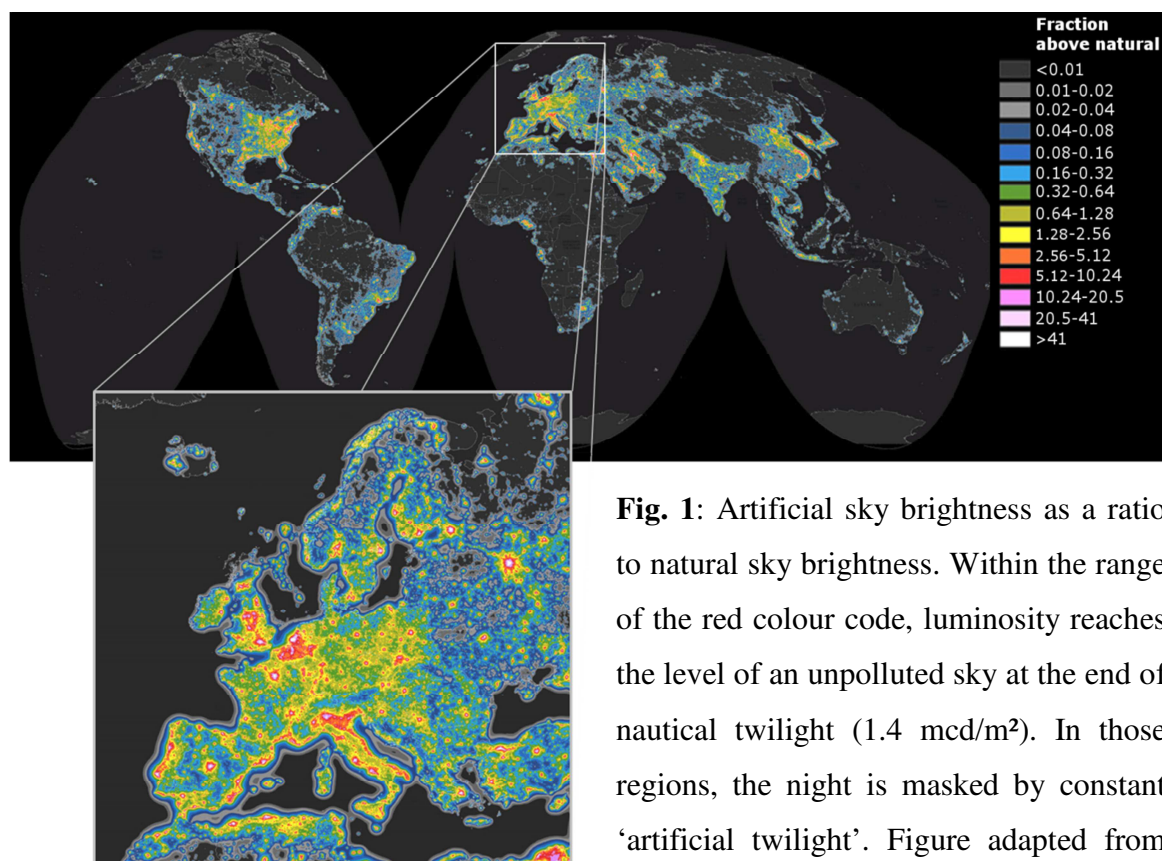


Fig. 1: Artificial sky brightness as a ratio to natural sky brightness. Within the range of the red colour code, luminosity reaches the level of an unpolluted sky at the end of nautical twilight (1.4 mcd/m^2). In those regions, the night is masked by constant ‘artificial twilight’. Figure adapted from Falchi et al. (2016)

3.2 Light pollution from street lights

Light pollution can originate from a multitude of sources. Often, facades of buildings and monuments are illuminated with strong lights for aesthetical reasons. Similarly, brightly lit or self-illuminated advertisements can cause light pollution during the entire dark phase. Frequently, the lights in shops and office buildings are not switched off at night, illuminating the surroundings. Vehicles also use bright headlamps with a long reach. Yet on a global scale, the most important sources of light pollution are street and car park lighting, which together account for 93% of all stationary outdoor lighting (53% and 40%, respectively; OECD/IEA 2006). Given that the world’s estimated 600 million street lights are rarely installed and managed in an optimal way to minimise light pollution, they emit an enormous amount of waste light (Gaston et al. 2015; Brazil 2016). Besides being employed ubiquitously, the illuminance level of street lights is usually high not only during busy times but during the entire dark phase. Their contribution to light pollution is further increased because their light is usually very poorly directed (OECD/IEA 2006). In the worst case, street light luminaires are glass balls that emit light in every direction,

even vertically into the sky. However, even most fully shielded ‘cut-off’ luminaires, which direct light downwards only, add to light pollution when illuminance levels are higher than actually needed or when lights are used at unnecessary times and sites. Importantly, also the type of illuminant used is a key determinant of the degree to which street lights contribute to ecological light pollution and affect wildlife.

3.3 Illuminants used for street lights

Global street lighting is dominated by low- and high-pressure sodium and mercury vapour lamps, which together made up about 92% of total outdoor lighting in 2006; another 6% were metal halide lamps (OECD/IEA 2006). These technologies differ drastically with respect to luminous efficacy, i.e. the ratio between light output and input power, and colour rendering index, which describes how well colours can be distinguished when using that light source. The trend goes towards broad spectrum ‘white’ illuminants with good colour rendering (Davies et al. 2013). However, in many regions orange sodium vapour lamps are still retained due to their high luminous efficacy, but also for cultural reasons (Fig. 2).

Low-pressure sodium vapour (LPS) lamps emit virtually monochromatic orange light and produce an extremely narrow emission spectrum which peaks at 589.3 nm (Fig. 7.1 in chapter 1). Accordingly, LPS lamps only possess the potential to pollute the environment and stimulate photoreceptors with single wavelengths. For this reason, low pressure sodium vapour light hardly allows any colour discrimination, and objects that reflect light mainly outside the narrow LPS wavelengths range appear dim (Davies et al. 2013). Yet, it is among the illuminants with the highest luminous efficacy, because the wavelengths emitted are very close to the peak photopic light sensitivity for human vision.

High-pressure sodium vapour (HPS) illuminants are high-intensity discharge lamps, which produce yellow-orange light and – as LPS lamps – do not emit UV radiation. The luminous efficacy of HPS illuminants is almost as high as LPS lights but, in contrast to LPS lamps, they emit a range of wavelengths (Fig. 7.1 in chapter 1) and thus enable humans to distinguish colours to some degree. HPS lamps are therefore much more commonly used for street lighting than LPS lights (OECD/IEA 2006).

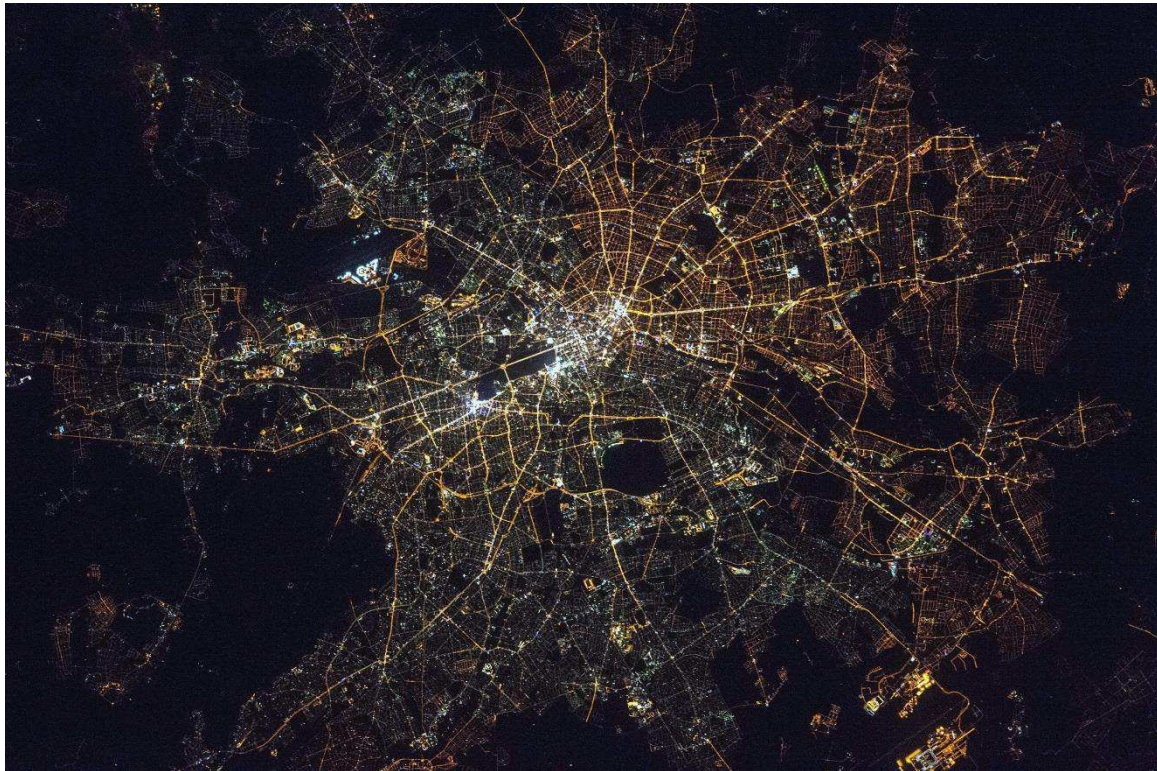


Fig. 2: Bird's eye view of Berlin, Germany, at night. It becomes obvious that a large portion of artificial light originates from streets; in Berlin about a third of all upward directed light pollution (Kuechly et al. 2012). Also, the photo illustrates that the dominance of a particular illuminant can be rooted in culture: even 26 years after the German reunification (picture taken in 2016) former East Berlin is mainly illuminated by orange sodium vapour lamps while former West Berlin chose mainly white lights. Image courtesy of the Earth Science and Remote Sensing Unit, NASA Johnson Space Center.

High-pressure mercury vapour (MV) lights emit a multitude of wavelength across the visible spectrum (Fig. 7.1 in chapter 1). Accordingly, they have a high colour rendering index and humans perceive their light as white. MV lights have been widely used around the world, particularly in areas where good colour discrimination is requested (OECD/IEA 2006). They emit a relatively high proportion of their energy in the UV range, which is not visible for humans, and consequently is waste light. MV lighting is a superseded technology that has much lower efficacies than all other commonly used street light technologies and is therefore phased out in Europe, for example (EU 2009).

Metal-halide (MH) illuminants also emit ‘white’ light of which a significant fraction is UV (Fig. 7.1 in chapter 1). However, their light contains less UV than MV illuminants. Their luminous efficacy is lower than that of LPS and HPS but higher than that of MV lamps (OECD/IEA 2006).

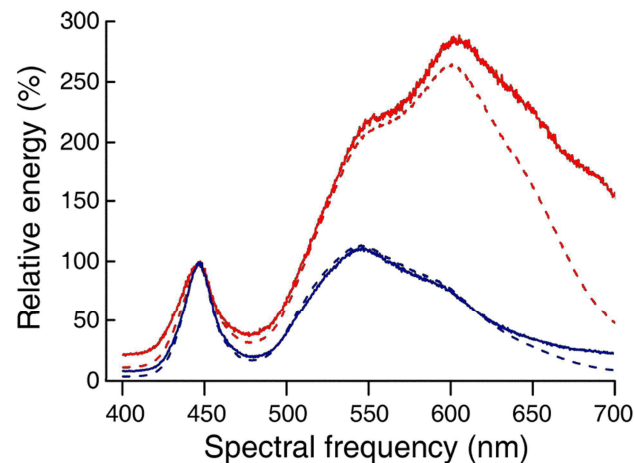


Fig. 3: Power spectra of ‘cold white’ (6500 K; blue lines) and ‘warm white’ (2700 K; red lines) LEDs. Emission spectra are normalised to the peak intensity in the 400-500 nm range. Multiple intermediate colour temperature LEDs can be manufactured that mainly differ in the ratio between energy emitted below and above 500 nm. Solid lines: naked LEDs. Dashed lines: operational LEDs (behind Perspex and Tanglefoot-coated Mylar). Figure adapted from Pawson & Bader (2014).

Since the early 1990s white light can also be produced using light-emitting diodes (LEDs). Since then LEDs are increasingly employed in street lighting. LEDs provide several advantages compared with conventional lighting techniques: while emitting white light they can be manufactured to have a very high luminous efficacy. Furthermore, their colour-temperature can be modified, i.e. their spectrum can be customised to emit either warm-white or cold-white light, while not emitting waste UV light (Pawson & Bader 2014; Longcore et al. 2015; Fig. 3). Another important advantage is the option to dim LEDs down to about 10% of their maximum luminance level and to increase light intensity instantaneously when needed (Kyba, Hänel & Hölker 2014). Finally, the light of LEDs can be directed more precisely than the light of conventional illuminants. Thus, LEDs offer extensive flexibility in the way they can be used.

Electric lighting is one of the largest electrical end-users and, accordingly, one of the biggest contributors to energy-related greenhouse gas emissions (OECD/IEA 2006). Yet, LEDs consume comparably little energy. In an attempt to reduce energy consumption and carbon dioxide emissions, government initiatives and legislation in many countries foster the replacement of conventional inefficient street lights by LEDs. To date, LED lamps are rather expensive and have not yet reached a competitive cost position. However, their price is dropping rapidly and their share among outdoor lighting applications is predicted to increase tremendously to about 70% in 2020 (Baumgartner et al. 2011). Low electricity consumption and hence low running costs of LEDs could boost the employment of more high intensity lights (Jenkins, Nordhaus & Shellenberger 2011). The consequences such a global change-over will have on wildlife are difficult to predict, since the global spread of LEDs has just begun and studies investigating its effects are still rare.

3.4 Effects of artificial light on wildlife

For millions of years, periodic changes between bright days and dark nights, as well as seasonal changes in photoperiod, have been the most reliable time cues. Accordingly, it is first and foremost light that has evolved as *Zeitgeber* and organizes biological systems, from unicellular organisms to ecosystems (Gaston, Visser & Hölker 2015). On cloudless full-moon nights, illuminance levels are about 0.1 lx while levels drop three orders of magnitude during overcast nights (Rich & Longcore 2006). Illuminance levels under street lights, in contrast, are often in the range of 40 lx and can go beyond 200 lx, i.e. about 400 to 2000 times full moon levels (chapter 3). Even in tens of kilometres distance, street lights can significantly increase night sky brightness via sky glow (Kyba et al. 2011). Consequently, artificial light at night has an enormous potential to adversely affect both humans and wildlife. Indeed, it has already been demonstrated that artificial light can disrupt behaviour and physiology of a wide range of taxa (Rich & Longcore 2006). Furthermore, by altering interactions between species and their environment, artificial light affects entire ecosystems and is today regarded as a key threat to biodiversity (Hölker et al. 2010b).

Since artificial light is usually employed at night, it particularly disturbs nocturnal species, which make up a large part of faunal biodiversity; 30% of all vertebrates and more than 60% of all invertebrates are nocturnal (Hölker et al. 2010b). Nocturnal

animals, such as bats, are potentially exposed to artificial light during their entire active phase, yet they are adapted to roam and forage in darkness (Voigt & Lewanzik 2011). Their photoreceptors are generally very sensitive to low light intensities as an adaptation to low light levels at night (e.g. Eklöf 2003). In contrast to diurnal vertebrates, which sleep at night and strongly reduce or eliminate photic input in the visual system during sleep or inactivity, the eyes of nocturnal species are open and accordingly not shielded from surrounding light by an eye-cover when being active at night (Kavanau 1997). Thus, even very low levels of light pollution can impact behaviour and physiology of nocturnal mammals, of which more than 1300 species - almost a fifth of all mammal species - are bats (Fenton & Simmons 2014).

3.5 Bats: high potential to be affected by light pollution

Bats are the only mammals capable of active flight, which enables them to cover large distances and to forage over extended areas. In contrast to other mammals whose home-ranges are comparably small, such as shrews, the large-scale movements of bats could potentially allow them to evade small illuminated areas if adjacent dark habitats are sufficiently available. Yet, lighted areas sprawl and the coverage of suitable, naturally dark habitats shrinks rapidly (Hölker et al. 2010; Falchi et al. 2016).

However, some insectivorous bat species tolerate artificial light when foraging and can even benefit from urbanisation. *Pipistrellus kuhlii*, for instance, favours urban habitats where it forages on insect aggregations at street lights and has a higher reproductive success compared to rural areas (Barak & Yom-Tov 1989; Ancillotto, Tomassini & Russo 2015). ‘Light-tolerant’ aerial-hawking species that forage around street lights benefit, at least in the short-term, from local insect accumulations (chapter 1). In the long-term, however, artificial lighting might contribute to insect populations’ declines and would then be disadvantageous even for ‘light-tolerant’ species (Macgregor et al. 2015). Notably, even ‘light-tolerant’ species can behave as light-averse when roosting or commuting (Downs et al. 2003; Hale et al. 2015). Many species are behaviourally not very flexible but rather show considerable fidelity to established commuting routes and roosting sites (Veilleux & Veilleux 2004; Hillen, Kiefer & Veith 2010; Rodhouse & Hyde 2014). Therefore, light pollution can affect bats adversely even when only a small part of their habitat becomes lit, if the lit area comprises commuting routes or roosts.

In contrast to ‘light-tolerant’ bats, many light-averse bats avoid lit habitats not only when roosting or commuting, but also when foraging. The species-specific level of light avoidance appears to be a function of habitat-related flight style, morphology, and echolocation: light-averse species are typically rather slow-flying but highly manoeuvrable forest-dwelling bats, whose low-intensity biosonar is well-adapted for cluttered habitats, but not far reaching (for details see chapter 1). Ultimately, a general avoidance of light by bats likely evolved in response to a higher predation pressure under naturally strong light conditions, such as on full moon nights or at dusk. In the vicinity of artificial lights the better visibility to predators might increase the perceived predation risk, especially for slowly flying species (Mathews et al. 2015; Stone, Harris & Jones 2015). Proximately, bats’ vision can be impaired in brighter compared to darker surroundings (Bradbury & Nottebohm 1969; Eklöf 2003; McGuire & Fenton 2010).

3.6 Bat vision

Bats have functional eyes and use vision in addition to their biosonar for navigation, foraging, predator surveillance, and social activities, for instance. In accordance with the nocturnal lifestyle of bats, their retinas are mainly composed of rods, which are organised in relatively large receptor fields (Neuweiler 2000; Kim et al. 2008; Müller et al. 2009). As a consequence, the bat visual system generally trades off spatial acuity for high light-gathering power. The system is adapted to work best under very low light conditions and performance usually decreases tremendously at photopic light levels (Bradbury & Nottebohm 1969; Ellins & Masterson 1974; Müller et al. 2009; Gutierrez et al. 2014). Yet, light tolerance of bats seems to be dependent on the species’ average exposure to daylight; species roosting in the foliage of trees and emerging early have higher tolerances than species occupying dark roosts and emerging after dusk (Hope & Bhatnagar 1979).

Since the bat’s visual system works well beyond the range of biosonar and bats even seem to be farsighted, vision is believed to be the primary sense for long-range orientation (Eklöf 2003; Boonman et al. 2013). Even though bats predominantly use their biosonar for orientation in the short-range, several bats complement echolocation with vision to locate prey and even give precedence to visual stimuli under certain circumstances (Bell 1985; Eklöf, Svennson & Rydell 2002; Altringham & Fenton 2003; Eklöf & Jones 2003; Winter, López & von Helversen 2003; Gutierrez et al. 2014). When

biosonar and vision provide contradictory information, bats rely more heavily on vision (Davis & Barbour 1965; Eklöf, Tranefors & Vazquez 2002).

Frugivorous and nectarivorous bats generally have larger eyes than insectivorous bats, presumably reflecting the extent to which they make use of vision (Eklöf 2003; Eklöf et al. 2014; Gutierrez et al. 2014). Brain structures associated with vision are usually larger and more developed in frugivorous (and gleaning) bats than in species that catch insects on the wing (Eklöf 2003). Consequently, frugivorous bats might be particularly vulnerable to the spread of artificial light at night when the associated increasing ambient light levels impair the use of vision. Yet, research on the effects of artificial light on frugivorous and nectarivorous bats is largely lacking.

Recent evidence suggests that many bats possess dichromatic colour vision (Zhao et al. 2009). Their retinas contain a significant number of cone photoreceptors (Müller, Goodman & Peichl 2007; Kim et al. 2008). In these cone photoreceptors, two opsins – a middle-to-long wave and a short wave sensitive opsin (M/LWS and SWS, respectively) – are present or the coding genes identified in these species (Wang et al. 2004; Müller, Goodman & Peichl 2007; Feller et al. 2009; Zhao et al. 2009). Specifically, the M/LWS opsin gene is functional in all species investigated. The SWS opsin gene has been retained in all species using low-duty-cycle echolocation (i.e. in all Yangochiroptera and *Megaderma spasma*) as well as in obligate tree-roosters among the Pteropodidae (Old World fruit bats). Only high-duty-cycle echolocators and cave-roosting Pteropodidae lost the SWS opsin gene functionality and, thus, do not possess dichromatic colour vision (Zhao et al. 2009).

The spectral sensitivity of the M/LWS opsin peaks between 500 nm and 570 nm ('green') while the ancestral vertebrate SWS opsin sensitivity peaked at around 360 nm (Dieterich & Dodt 1970; Hope & Bhatnagar 1979b; Zhao et al. 2009). Hence, already the ancestral SWS opsin was UV sensitive. Also among extant bat species, the existence of UV colour vision is increasingly gaining support and seems to be widespread (Zhao et al. 2009; Fujun et al. 2012; Gorresen et al. 2015). Possibly, bats with UV sensitive eyes perceive UV-emitting lights as brighter than non-UV-emitting lights of the same illuminance level. This could explain why lights that emit energy in the UV wavelength range, for instance MV lamps, are generally more repulsive to light-averse bats than lights that do not (Stone, Jones & Harris 2009 & 2012).

3.7 Aims of this thesis

The overall aim of my dissertation is to increase our understanding and fill existing knowledge gaps concerning the effects of artificial light on bats. Research on light pollution is heavily biased towards species in the temperate climate zone. The vast majority of bat species, on the contrary, live in tropical regions where they occupy central positions in the ecosystem and provide key ecosystem services.

Similarly, many studies have investigated different aspects of the impact of conventional mercury vapour light on bats, but the question of how bats react to state-of-the-art LEDs has thus far received little attention. Notably, no research has addressed how the anticipated widespread replacement of mercury vapour street lights by LEDs may affect bat communities. Consequently, the three main aims of my dissertation are:

- **Reviewing the existing literature concerning the effects of artificial light on bats (chapter 1)**

Artificial light affects bats in various aspects of their behaviour, physiology and life history and responses to artificial light are species-specific. In the review chapter 1, I first describe the past, current, and anticipated future changes in light pollution quantity and quality, summarise what is known about how artificial light impacts bats, and discuss the correlation between phototropism of insects and activity of light-tolerant bats. I then contrast this positive relationship between insect aggregations and bat activity at lights with experimental studies highlighting detrimental effects of artificial light on bats, before eventually widening the scope to cascading effects on the ecosystem level. I close chapter 1 by suggesting mitigation measures and emphasizing future challenges.

- **Investigating the impact of street lights on harvesting activity of frugivorous bats (chapter 2)**

In contrast to insectivores, which might benefit from insect aggregations at lights, fruit- and nectar-eating bats do not have any apparent advantage that could compensate for the disadvantages of foraging in the sphere of artificial light. Thus, artificial light should be particularly pernicious and avoided by frugivorous and nectarivorous bats. These bats provide numerous ecosystem services, which are pivotal for ecosystem functioning in tropical regions. They pollinate large numbers of flowers and disperse the seeds of a wide variety of plant species (Kunz et al.

2011; Ghanem & Voigt 2012). Aside from birds, bats constitute the main long-distance seed dispersers; they even outperform birds with respect to seed dispersal into open areas and therefore are crucial for efficient forest regeneration (Fleming 1988; Medellín & Gaona 1999). Despite the importance of frugivorous bats to tropical ecosystems, information about the influence of light pollution on these species is largely missing. Thus, I set out to experimentally test how street lighting alters foraging activity of a frugivorous bat species that constitutes an important seed disperser of successional plants in the Neotropics.

- **Studying the effects of a large-scale replacement of MV street lights by LEDs on bats in urban areas (chapter 3)**

Across Europe and several non-European countries conventional MV street lights are phased out; a large-scale replacement of these lights by energy-efficient LEDs is expected (Baumgartner et al. 2011). Yet, it is unknown if the anticipated widespread replacement of MV street lights by LEDs will alter activity of urban insectivorous bats and, if so, in which way and to what extent bat activity will change. Understanding the consequences of that changeover for bats is important since all bats are protected in countries of the European Union by the EU Habitat Directive. A widespread change of street light illuminants could directly affect individual fitness and eventually populations' resilience. Populations of many European bat species have stabilized recently. However, many species underwent severe population declines in the second half of the twentieth century, so that populations are at comparably low levels nowadays (Hutson, Mickleburgh & Racey 2001; Barlow et al. 2015; Van der Meij et al. 2015). Therefore, any further population decrease due to artificial lighting, for instance, might jeopardize species persistence, at least at the local level. To predict the species-specific consequences of the expected changeover from MV to LED street lighting on bats in urban areas, I conducted a large-scale field experiment in multiple towns across Germany. Applying a before-after-control-impact design, I compared bat activity at municipal MV street lamps that were replaced by LEDs with control sites that were not changed.

3.8 References

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CHAPTER 1

Dark matters: the effects of artificial
lighting on bats

Chapter 7

Dark Matters: The Effects of Artificial Lighting on Bats

E.G. Rowse, D. Lewanzik, E.L. Stone, S. Harris and G. Jones

Abstract While artificial lighting is a major component of global change, its biological impacts have only recently been recognised. Artificial lighting attracts and repels animals in taxon-specific ways and affects physiological processes. Being nocturnal, bats are likely to be strongly affected by artificial lighting. Moreover, many species of bats are insectivorous, and insects are also strongly influenced by lighting. Lighting technologies are changing rapidly, with the use of light-emitting diode (LED) lamps increasing. Impacts on bats and their prey depend on the light spectra produced by street lights; ultraviolet (UV) wavelengths attract more insects and consequently insectivorous bats. Bat responses to lighting are species-specific and reflect differences in flight morphology and performance; fast-flying aerial hawking species frequently feed around street lights, whereas relatively slow-flying bats that forage in more confined spaces are often light-averse. Both high-pressure sodium and LED lights reduce commuting activity by clutter-tolerant bats of the genera *Myotis* and *Rhinolophus*, and these bats still avoided LED lights when dimmed. Light-induced reductions in the activity of frugivorous bats may affect ecosystem services by reducing dispersal of the seeds of pioneer plants and hence reforestation. Rapid changes in street lighting offer the potential to explore

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mitigation methods such as part-night lighting (PNL), dimming, directed lighting, and motion-sensitive lighting that may have beneficial consequences for light-averse bat species.

7.1 Introduction

Anthropogenic change is altering ecosystems at unprecedented rates and humans now dominate most ecosystems (Vitousek et al. 1997; McDonald 2008). Urbanisation in particular has major impacts on bat activity and abundance (Jung and Threlfall 2016), and one aspect of global change that occurs predominately, but not exclusively, in urban areas is increased artificial light at night. Almost a fifth of the global land area was affected by light pollution in 2001 (Cinzano et al. 2001). Although night-time brightness generally increased in Europe between 1995 and 2010, regional patterns are complex, with some localised declines (Bennie et al. 2014). However, the biological impacts of light pollution have only recently been recognised (Longcore and Rich 2004).

Being nocturnal, bats are likely to be affected by light pollution. In this chapter, we review the types of artificial light that bats experience, describe how light pollution has become more widespread in recent years, show how technological changes may lead to significant reductions in light pollution and describe some of the physiological consequences of light pollution that may be relevant to bats. We then discuss how artificial lighting affects the insect prey of bats, and why some bats may benefit from the growth in artificial lighting, whereas others are affected detrimentally. After highlighting some aspects of bat vision, we describe the shift from observational to experimental studies of how bats respond to lighting. Finally, we identify some of the major knowledge gaps and suggest priorities for future research on the effects of artificial lighting on bats.

7.2 Types of Artificial Light

The electromagnetic spectrum encompasses radiation with wavelengths ranging from less than a nanometre (gamma rays) to a kilometre (radio waves) (Campbell 2011). While humans perceive wavelengths between 400 and 700 nm as ‘visible light’ (Purves and Lotto 2003), birds, fish and invertebrates can detect light in the ultraviolet (UV) range (10–400 nm). Recent work suggests that UV sensitivity may be widespread among mammals (Douglas and Jeffery 2014), and snakes and beetles can detect spectral emissions in the infrared range (700–1000 nm) (Schmitz and Bleckmann 1998; Land and Nilsson 2012).

Artificial lighting has infiltrated all aspects of human life both indoors and outside (Gaston et al. 2012). Here, we focus on street lighting because of its universal use and potential for ecological impacts (Gaston et al. 2012). Different types of street light have distinct spectral signatures (Fig. 7.1); their primary emissions

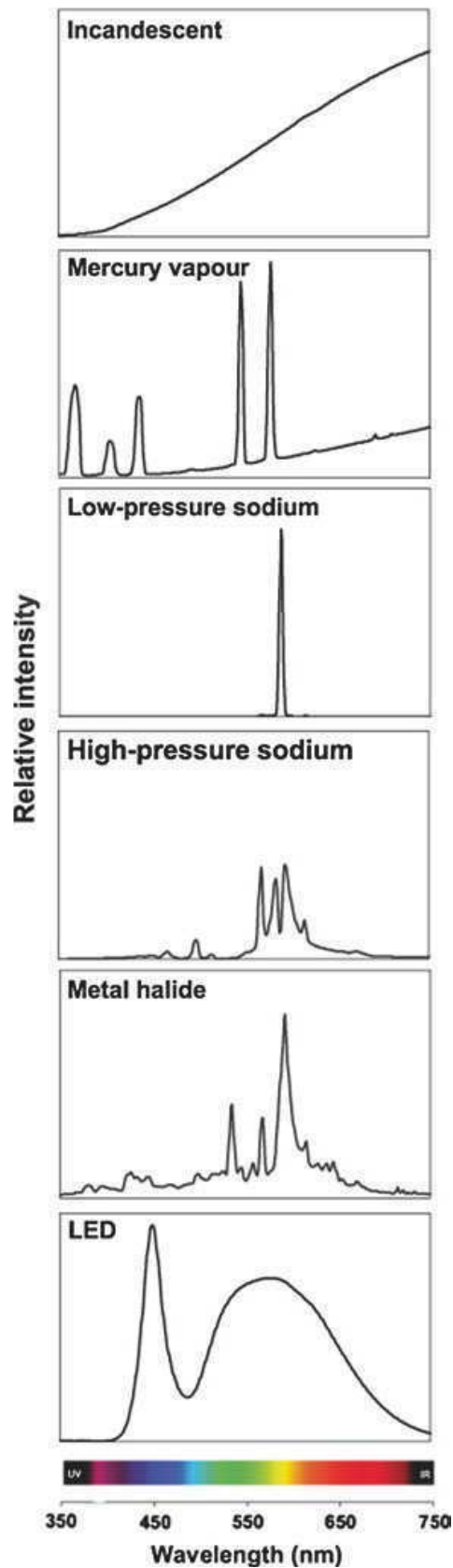


Fig. 7.1 The spectral content of different light types varies considerably. The spectral composition of common lighting technologies is shown. From Gaston et al. (2013)

depend on the type of reactive material or coating in the lamps (Buchanan 2006). Incandescent lamps, developed by Thomas Edison in 1880, mainly emit long wavelengths with a maximum intensity between 900 and 1050 nm (Elvidge et al. 2010). Despite improvements such as the quartz halogen lamp, which uses an inert gas to preserve the tungsten filament, incandescent lamps are still relatively inefficient because their emissions are predominantly near the infrared spectrum and so largely invisible to humans (Elvidge et al. 2010).

Gas discharge lamps, developed by the mid-twentieth century, produce light by passing electric arcs through gas-filled bulbs (Elvidge et al. 2010). These are further classified as low-pressure discharge and high-intensity discharge (HID) lamps (Elvidge et al. 2010). Low-pressure discharge lamps include the compact fluorescent lamp (CFL) and low-pressure sodium (LPS) lamps. Fluorescent lamps produce distinct emission peaks, which combine to emit a 'white' light (Royal Commission on Environmental Pollution 2009; Elvidge et al. 2010), whereas LPS lamps have a narrow spectral signature, emitting monochromatic orange light with a peak intensity of 589 nm (Fig. 7.1) (Rydell 2006; Elvidge et al. 2010).

HID lamps include high-pressure mercury vapour (HPMV) lamps, which produce a bluish-white light, and high-pressure sodium (HPS) and metal halide lamps that have broader spectral emissions (Fig. 7.1) (Davies et al. 2013). Emissions from HPMV lamps extend into the UV range (Rydell 2006; Elvidge et al. 2010), whereas HPS lamps emit yellow-orange light and metal halide lamps 'white' light (Royal Commission on Environmental Pollution 2009; Davies et al. 2013; Gaston et al. 2013). The colour rendering index (CRI) compares how accurately a light source replicates the full range of colours of an object viewed in natural light on a scale of 0–100, where 100 is equivalent to natural light (Schubert and Kim 2005; Elvidge et al. 2010; Davies et al. 2013). HPS lamps typically have a CRI between 7 and 32, whereas metal halide lamps have a CRI ranging from 64 to 100, reflecting their ability to render colour more suited for human vision (Elvidge et al. 2010; Gaston et al. 2012).

Gas discharge lamps replaced incandescent lamps because of their energy efficiency and improved longevity (Schubert and Kim 2005), and LPS (44 %) and HPS (41 %) lamps came to dominate street lighting in the UK (Royal Commission on Environmental Pollution 2009) and elsewhere. The luminous efficacy (LE) (amount of light produced per watt of electricity) of gas discharge lamps is five times higher than incandescent lamps (Schubert and Kim 2005; Elvidge et al. 2010). However, with pressure to reduce energy use and CO₂ emissions, the lighting industry is now turning to light-emitting diodes (LEDs) (Elvidge et al. 2010; Gaston et al. 2012). LEDs have broad spectral signatures, typically 400–700 nm, with very few emissions in the UV range (Elvidge et al. 2010). This is achieved mainly through the use of cerium-doped yttrium aluminium garnet (YAG:Ce) phosphors with a gallium nitride (GaN) which converts monochromatic blue to 'white' light. However, more recently LEDs are able to produce light by combining multiple monochromatic sources (red, green and blue), which allows for greater control over spectral emissions (Narendran et al. 2004; Gaston et al. 2012, 2013; Davies et al. 2013). LED lamps have comparable CRI scores to metal

halide lamps (65–100) (Elvidge et al. 2010) but benefit from lower running costs (Gaston et al. 2012); low energy consumption (Elvidge et al. 2010); controllability of spectral, temporal and intensity of emissions; reduced CO₂ emissions (Hölker et al. 2010a); and smart lighting capabilities that enable dimming in response to weather, traffic and lunar conditions (Bennie et al. 2014).

7.3 The Growth of Light Pollution

Light pollution is defined as the changing of natural light levels in nocturnal landscapes (nightscape) through artificial lighting sources (Falchi et al. 2011; Kyba and Hölker 2013). Here, we focus on ecological light pollution, i.e. the direct ecological effects of light as opposed to astronomical light pollution, which describes the light that disrupts viewing of stars and other celestial matter (Longcore and Rich 2004). Ecological light pollution can be caused by glare (extreme contrasts between bright and dark areas), over-illumination, light clutter (unnecessary numbers of light sources), light trespass (unwanted light) and skyglow, where artificial light is directed towards the sky, scattered by atmospheric molecules and reflected back to earth (Royal Commission on Environmental Pollution 2009; Gaston et al. 2012; Kyba and Hölker 2013).

Artificial lighting has increased as a result of urbanisation, population growth, economic development and advances in lighting technologies and provides numerous economic, commercial, recreational and security benefits (Riegel 1973; Hölker et al. 2010a; Davies et al. 2012). However, light pollution is now of global concern: the accelerated use of electric lighting, growing at 6 % per year, has escalated light pollution to threat status (Hölker et al. 2010a, b). Satellite images suggest that 19 % of the global land surface surpassed the threshold for acceptable lighting levels (Cinzano et al. 2001). However, satellites are unable to capture all illumination from light sources (Bennie et al. 2014). While light pollution is currently more apparent in developed nations (Fig. 7.2), projected increases in industrial and urban growth suggest that light pollution will become more spatially heterogeneous both locally and regionally (Cinzano et al. 2001; Gaston et al. 2012; Hölker et al. 2010b; Bennie et al. 2014).

In the UK, street lighting consumes approximately 114 Twh of energy annually (International Energy Agency 2006) and is growing at 3 % per annum (Royal Commission on Environmental Pollution 2009). The number of lighting installations is increasing (Gaston et al. 2012), and the change in emissions due to increased use of broad spectrum technologies is also likely to affect light pollution as these sources emit higher levels of blue light. This scatters more into the atmosphere than green or red light, ultimately making a bigger contribution to skyglow (Benenson et al. 2002; Falchi et al. 2011; Kyba and Hölker 2013). The growth in light pollution will be further exacerbated because, as LEDs become cheaper, non-essential uses, such as advertising and architectural lighting, may increase (Schubert and Kim 2005).



Fig. 7.2 Artificial lighting is currently most widespread in the developed world. Global use of lighting at night in 2000. From NASA Earth Observatory/NOAA NGDC (2012)

7.4 Projected Changes in Technology

International lighting policies are prioritising energy-efficient technologies to reduce costs and CO₂ emissions. The European Ecodesign Directive, for instance, encourages moves from energy-intensive technologies such as incandescent, LPS and HPMV lamps (Hölker et al. 2010a) to ‘whiter’ lighting with higher colour rendering capabilities (Gaston et al. 2012). This may reduce CO₂ emissions in the EU by as much as 42 Mt per year. A number of pilot studies in cities around the world (including Adelaide, Hong Kong, London, Mumbai, New York, Sydney and Toronto) have compared LED lamps against existing lighting technologies. After a three-year trial, the City of Sydney Council agreed to switch to LEDs on 6500 outdoor lights due to their reduced energy consumption, cost-effectiveness and improved illuminance (The Climate Group 2014).

Future research will focus on increasing the efficiencies of LEDs: the LE of a LED is 60–90 lm/W, compared to 80–120 lm/W for HPS lamps (California Lighting Technology Center 2010). More effective ways of producing light are also being investigated, such as combining multiple monochromatic sources as opposed to using phosphors: this will increase control over spectral emissions (Schubert and Kim 2005; Gaston et al. 2012).

7.5 The Biological Effects of Light Pollution

The number of studies revealing negative consequences of artificial night lighting on a multitude of both diurnal and nocturnal vertebrates and invertebrates is increasing rapidly (reviewed in Rich and Longcore 2006). Most negative effects

are due to the disruption of natural circadian and circannual cycles, which in turn can affect a whole range of species interactions, physiological processes and behaviours.

7.5.1 Impacts of Light Pollution on Intra- and Inter-specific Competition

Light-induced changes in circadian activity patterns can alter competition both within species (e.g. for mates) and between species (e.g. interference and exploitation competition). These are best documented for birds. For instance, early singing may be a signal of male quality in songbirds and increases the rate of extra-pair copulations, which are usually higher in older males. In territories affected by artificial light, males of several songbird species start singing earlier at dawn and thereby gain access to about twice as many extra-pair mates (Kempnaers et al. 2010; Nordt and Klenke 2013; Dominoni et al. 2014). The effect of artificial light on paternity gain is even stronger in yearlings than in adults, and so street lights might result in maladaptive mate choice of females by artificially increasing the extra-pair success of yearlings (Kempnaers et al. 2010). Whether similar maladaptive effects occur with nocturnal species is less clear.

Artificial light can affect niche partitioning by extending the activity of diurnal species, bringing them into inter-specific competition with nocturnal species (Longcore and Rich 2004; Rich and Longcore 2006). The scissor-tailed flycatcher *Tyrannus forficatus*, for example, will catch insects at street lights until at least 3 h after sunset (Frey 1993); this may increase exploitation and interference competition with insectivorous bats. Light pollution may also cause inter-specific competition between bats, with light-sensitive bat species excluded from illuminated resources exploited by light-tolerant species (Arlettaz et al. 2000).

7.5.2 Effects of Artificial Light on Physiological Homeostasis

Light-induced changes in circadian rhythms may induce physiological aberrations. For instance, exposure of captive mice to light at night disrupts metabolic signals, leading to increased body mass and decreased glucose tolerance (Fonken et al. 2010). Dim night-time light can also impair learning and memory, affect stress hormone levels, compromise immune function and cause depressive-like behaviour in rodents (Bedrosian et al. 2011, 2013; Fonken et al. 2012). In humans, depression, obesity and cancer risk relate to light pollution and associated disruptions of the circadian system (Fonken and Nelson 2011; Kronfeld-Schor and Einat 2012; Haim and Portnov 2013).

Light pollution can also result in a decoupling of seasonal behaviours and physiological adaptations from the optimal time of year. So, for instance, reproduction might be desynchronised from peak food availability; even very low light levels at night advance avian reproduction (Dominoni et al. 2013) so that birds breed earlier close to street lights than in darker territories (Kempnaers et al. 2010). Light-induced decoupling can even reverse an animal's seasonal phenotype, so that it exhibits a long-day phenotype in winter and vice versa. In sheep, 1 h of light during the dark phase is enough to mimic a long-day during short-day conditions (Chemineau et al. 1992). Also in primates, artificial light at night can induce a long-day phenotype; these animals had higher core body temperatures, showed less locomotor activity during the nocturnal activity period and had fainter torpor bouts compared with short-day photoperiod acclimated animals (Le Tallec et al. 2013). Voles that experienced light interference at night showed reduced winter acclimatisation of their thermoregulatory system to such a degree that they reduced heat production and died under winter field conditions (Haim et al. 2004, 2005). Thus, light pollution may have deleterious impacts on survival when animals expend too much energy during winter (Haim et al. 2004): this may be relevant for hibernating bats.

7.5.3 Interference of Light Pollution with Nocturnal Navigation

A well-documented effect of light pollution not mediated through circadian rhythms is the impact on movement decisions of visually orienting animals. Nesting attempts of female sea turtles are disrupted by artificial light, and light attracts or confuses the hatchlings, rendering them more vulnerable to predation, exhaustion and dehydration (Salmon 2006; Perry et al. 2008; Berry et al. 2013).

Birds migrating at night often approach bright lights instead of following their normal migration route, possibly because the light interferes with their magnetic compass (Poot et al. 2008). Birds may also be trapped within the sphere of light, milling around illuminated objects until they die through collisions or exhaustion (Gauthreaux and Belser 2006; Montevecchi 2006; Spoelstra and Visser 2014). This may have relevance to bats, which also use magnetic compasses for navigation (Holland et al. 2006).

Similarly many insects, particularly moths (Lepidoptera), use artificial lights rather than the moon for orientation and die of exhaustion when circling a lamp or following a collision with the hot cover. Artificial light also provokes a 'dazzling effect': many insects become immobilised when approaching a lamp and rest on the ground or in vegetation, becoming easy prey (Eisenbeis 2006). Light pollution may even be a driver of an insect biodiversity crisis (Conrad et al. 2006). The 'vacuum cleaner' effect, i.e. the long-distance attraction of light-susceptible species to lamps, removes large numbers of insects from the ecosystem, even

resulting in local extinctions. This flight-to-light behaviour strongly depends on spectral output of the lighting: white HPMV lamps have a high UV proportion of their spectrum, and so four times as many moths are captured at HPMV lights compared to yellow/orange HPS lights (Eisenbeis 2006). Warm-white and cool-white LED lights induce less flight-to-light behaviour than HPS lights (Huemer et al. 2010; Eisenbeis and Eick 2011), and the virtually monochromatic deep-orange LPS lights are least attractive to insects (Rydell 1992; Blake et al. 1994; Eisenbeis 2006; Frank 2006).

Several spiders, amphibians, reptiles, birds and bats focus their foraging on insects accumulated at street lights (Rich and Longcore 2006). For bats, this can also be advantageous because artificial light disrupts the evasive behaviour of most nocturnal Lepidoptera, rendering them more vulnerable to bat attacks (Svensson and Rydell 1998; Acharya and Fenton 1999).

7.6 Bat Vision

Vision is important in the lives of many bats; see reviews in Suthers (1970), Altringham and Fenton (2003) and Eklöf (2003). A number of species rely on vision to a large extent (Altringham 2011). Since vision is important to both bats and their predators, we briefly summarise some key recent findings relevant to bats' perception of artificial lighting.

Most pteropodids do not echolocate and use vision to locate fruit and flowers. Some echolocating bats use vision to complement auditory information when hunting (Eklöf and Jones 2003) and, if vision and echolocation provide conflicting information, visual information is used in preference (Orbach and Fenton 2010). Vision can also be more effective than echolocation over long distances (Boonman et al. 2013), and the California leaf-nosed bat *Macrotus californicus* relies more on vision when hunting prey under low levels of illumination equivalent to a moonlit night (Bell 1985).

Recent research on bat vision has focussed on the molecular evolution of light-sensitive pigments (Jones et al. 2013). As for most nocturnal mammals, bat retinas are dominated by rods: they are highly sensitive under low light and confer monochromatic vision. The opsin DNA sequences of rhodopsin (the opsin in rods) were intact in 15 bat species (Zhao et al. 2009a) and wavelengths of maximum absorbance were 497–501 nm.

Colour vision in mammals results in part from opsins in the cones that are sensitive to short and medium wavelengths. Zhao et al. (2009b) sequenced a short-wavelength sensitive opsin gene (*Sws1*) that is most sensitive to blue-violet wavelengths, and a medium-to-long-wavelength sensitive opsin gene (*M/lws*) in a range of bat species; maximum absorbance of red light wavelengths by the *M/lws* opsin was at 545–553 nm. Although many bats resemble diurnal mammals in having the potential for dichromatic vision, with both genes being intact, *Sws-1* was pseudogenised in all the rhinolophid and hipposiderid bats studied and in some pteropodids, especially cave-roosting taxa. Immunohistochemistry suggests that

the primary visual cortex may not respond to stimulation by UV light in these taxa (Xuan et al. 2012a), and behavioural responses to UV were also lacking (Xuan et al. 2012b). The lesser Asiatic yellow bat *Scotophilus kuhlii* and Leschenault's rousette *Rousettus leschenaultii* showed behavioural (Xuan et al. 2012b) and immunohistochemical responses in the primary visual cortex (Xuan et al. 2012a) to UV light at 365 nm. Two phyllostomid species (Pallas's long-tongued bat *Glossophaga soricina* and Seba's short-tailed bat *Carollia perspicillata*) possess significant cone populations and express opsins that are sensitive to short and long wavelengths. The short-wavelength opsin is sensitive to UV and may be advantageous for the detections of UV-reflecting flowers (Winter et al. 2003; Müller et al. 2009). Other bat species with intact *Sws1* genes may be UV sensitive, as ancestral reconstructions suggest UV sensitivity, with maximal sensitivity close to 360 nm (Zhao et al. 2009b).

Whether differences in UV sensitivity among bat taxa affect how species with intact and pseudogenised *Sws1* genes respond to different types of lighting remains unknown. Nevertheless the findings are of interest given that the wavelengths of maximum absorbance in bat opsins lie close to some of the peak emissions of wavelengths in a range of light types (Davies et al. 2013). Moreover emerging LED lighting technologies do not emit UV wavelengths, whereas older technologies, especially HPMV lamps, emit wavelengths that extend into the UV range and so HPMV lights may have been particularly conspicuous to horseshoe bats.

7.7 Observational Studies on Bats at Street Lights

Bats have been observed foraging around lights ever since artificial lighting became pervasive (Shields and Bildstein 1979; Belwood and Fullard 1984; Barak and Yom-Tov 1989; Acharya and Fenton 1999). Artificial light attracts many positively phototactic insects (Rydell 1992; Eisenbeis 2006), and most insectivorous bats are probably opportunistic feeders. Thus, they quickly identify and exploit insect accumulations such as swarming termites (Gould 1978) and insect clusters at artificial lights (Fenton and Morris 1976; Bell 1980; de Jong and Ahlén 1991). So some insectivorous bats probably profit from street lights because resource predictability and high insect densities increase foraging efficiency (Rydell 1992, 2006). For instance, 18 of 25 Neotropical insectivorous bat species which could be detected by acoustic monitoring were observed foraging around street lights in a small settlement. While more species were recorded in mature forest, total bat activity was lowest in forest but highest around street lights (Jung and Kalko 2010).

Bats prey on relatively large insects at street lights, mostly moths (Fenton and Morris 1976; Belwood and Fullard 1984; Acharya and Fenton 1992; Acharya 1995; Hickey et al. 1996; Acharya and Fenton 1999; Jacobs 1999; Pavey 1999; Fullard 2001). While moths are the most numerous insects around artificial lights (Huemer et al. 2010; Eisenbeis and Eick 2011), their contribution to a bat's diet can be much higher than expected from their relative abundance at street lights

(Belwood and Fullard 1984). This implies that bats focus on larger moths rather than smaller prey at street lights. Although moths were only captured in 36 % of attacks, northern bats *Eptesicus nilssonii* probably gain more than twice as much energy when feeding on moths at street lights than smaller dipterans in woodlands (Rydell 1992).

Aggregations of large insects around lamps enable bats to reduce foraging time and hence energy costs while maximising energy returns (Acharya and Fenton 1999; Jung and Kalko 2010). Big brown bats *Eptesicus fuscus*, for instance, spend less than half as much time outside the roost where in habitats where they forage at street lights than where they do not use lamps for hunting (Geggie and Fenton 1985). Hence, foraging at lights might be beneficial when a high foraging efficiency compensates for the potentially higher predation risk.

Bat activity and foraging efficiency at street lights are mainly determined by the number and size of prey insects available, both of which are strongly affected by the spectral characteristics of the light (Blake et al. 1994). Thus, the type of light indirectly influences bat activity. The light's attractiveness for insects increases with its UV spectral content. Aerial-hunting long-legged myotis *Myotis volans* and California myotis *M. californicus* consistently preyed on insects clustered in the cone of experimental black (UV) lights in North America (Bell 1980). While black light is not used for street lighting, similar results are seen with street lights that produce UV emissions. Thus, bat density can be an order of magnitude higher in towns illuminated by HPMV compared with those illuminated by HPS lights and road sections illuminated by HPMV rather than deep-orange LPS lights (Rydell 1992). In Britain, mean bat activity, likely to be mainly common pipistrelles *Pipistrellus pipistrellus*, is usually equal to or lower along roads lit by LPS lights than in dark sections, whereas bat activity is higher under HPMV than LPS lights or sections with no light (Fig. 7.3; Blake et al. 1994).

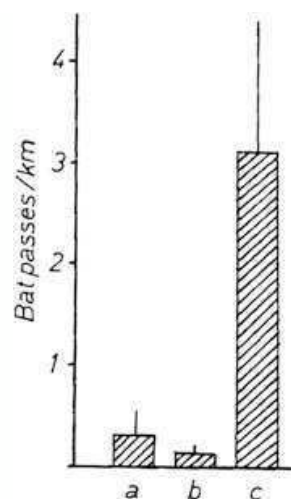


Fig. 7.3 Bat activity varies according to the type of artificial lighting. Activity of pipistrelle *Pipistrellus* spp. bats (mean and SD) along a 28 km stretch of road near Aberdeen, Scotland. *a* rural sections of the road without streetlamps, *b* village sections with sodium (orange) lamps and *c* a village with high-pressure mercury vapour lamps. From Rydell and Racey (1995)

7.8 Experimental Studies on Bats at Street Lights

Drawing conclusions from observational studies can be difficult, especially since confounding factors other than the presence of street lights can affect bat activity. Experimental field studies have demonstrated species-specific impacts of street lighting. Two 70 W HPS (DW Windsor Ltd, UK) lights, spaced and orientated to replicate street lights, were installed along preferred commuting routes of lesser horseshoe bats *Rhinolophus hipposideros*. The commuting activity of *R. hipposideros* (Fig. 7.4) and *Myotis* spp. was significantly reduced, and the onset of commuting delayed, on lit nights (Stone et al. 2009; Stone 2011). The following year the experiment was repeated on the same routes using white LED lights (Monaro LED, DW Windsor Ltd), at low (3.6 lux), medium (6.6 lux) and high (49.8 lux) light intensities. Activity of both *R. hipposideros* and *Myotis* spp. was significantly reduced during all lit treatments, and for *R. hipposideros*, the effect size at 49.8 lux was the same as that under HPS illumination. So both HPS and LED light disturbance caused spatial avoidance of preferred commuting routes by *R. hipposideros* and *Myotis* spp. (Stone et al. 2009), with no evidence of short-term habituation. Further work is needed to test for long-term habituation. In contrast, there was no significant change in bat activity under HPS and LED light treatments for *P. pipistrellus*, and for bats in the genera *Eptesicus* and *Nyctalus* (Fig. 7.5).

R. hipposideros and many other slow-flying species rely on linear habitat features for shelter from wind, rain and predators; acoustic orientation; and foraging

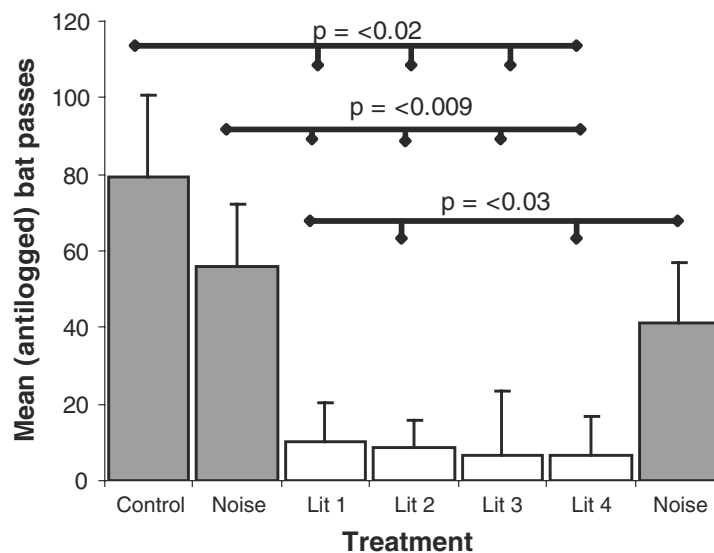


Fig. 7.4 Light-averse bat species show reduced activity along commuting routes subjected to high-pressure sodium (HPS) lighting. Activity of lesser horseshoe bats *Rhinolophus hipposideros* (mean passes and SE) in relation to lighting treatment. Significant within-subject differences with p values are shown. Treatments were control nights (no lighting treatment or generator), noise controls (HPS light units installed but switched off, generator running at night), 4 nights where lighting was switched on and powered by the generator (Lit 1 to Lit 4) and a final noise control. From Stone et al. (2009)

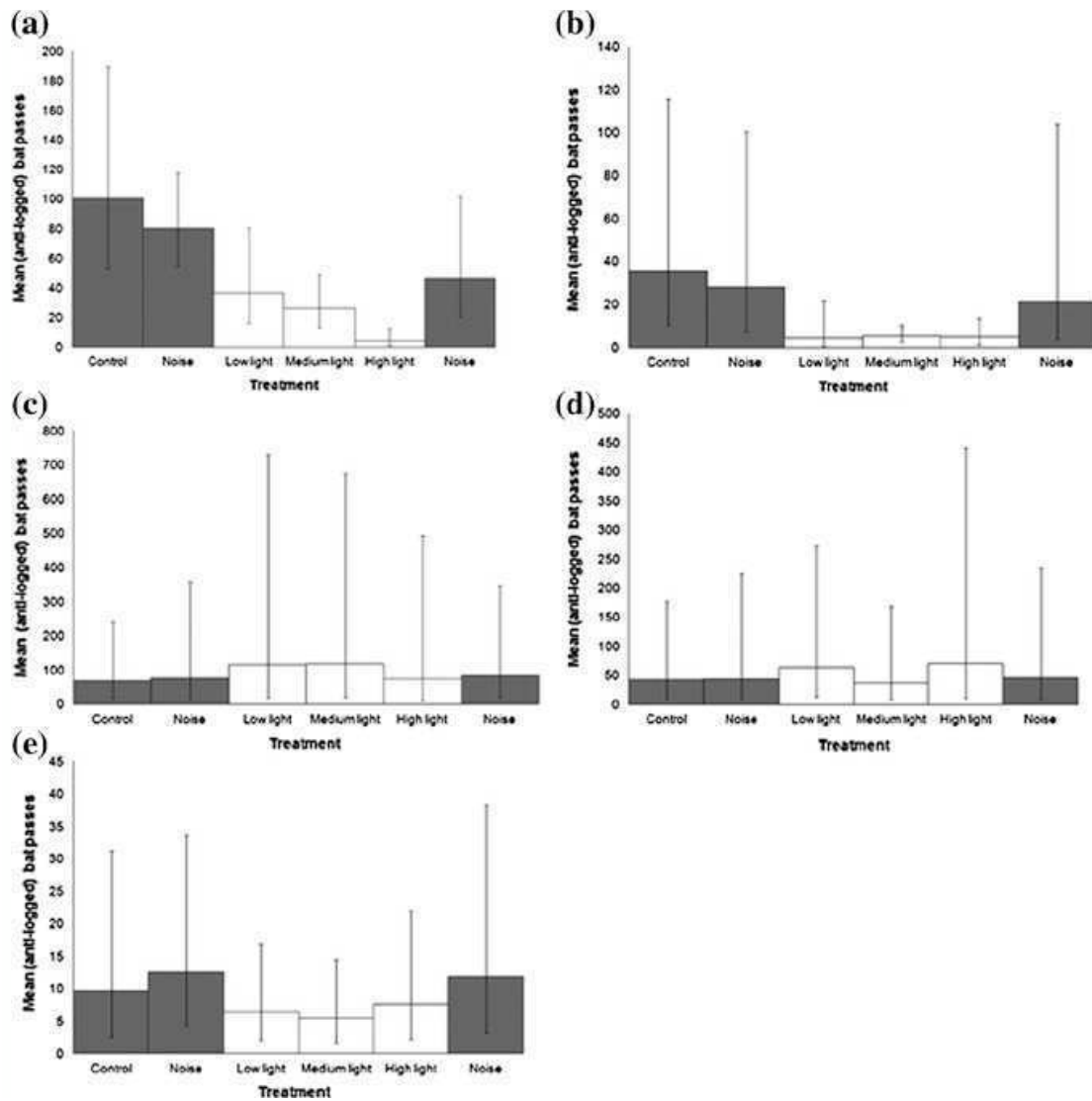


Fig. 7.5 Bats respond in different ways to LED lighting. Although the light-averse *Rhinolophus hipposideros* showed higher activity under more dimmed treatments compared with less dimmed ones, activity was still less than under unlit conditions. *Myotis* spp. showed negligible activity under all dimmed treatments. Geometric mean and confidence limits for bat passes along treatment hedges subjected to LED illumination at different light intensities are illustrated. Treatments were control nights (no lighting treatment or generator), noise controls (LED light units installed but switched off, generator running at night), 3 nights where illumination levels were modified (low light mean = 3.6 lux; medium light mean = 6.6 lux; and high light mean = 49.8 lux), and a final noise control. Bat passes were monitored on Anabat bat detectors and are shown for **a** *Rhinolophus hipposideros*, **b** *Myotis* spp., **c** common pipistrelle *Pipistrellus pipistrellus*, **d** soprano pipistrelle *Pipistrellus pygmaeus* and **e** *Nyctalus/Eptesicus*. From Stone et al. (2012)

(Verboom and Spoelstra 1999; Verboom et al. 1999). Using suboptimal routes with reduced cover to avoid artificial lighting may increase vulnerability to aerial predators and energetic costs due to increased exposure to wind and rain. So bats may have to travel further to reach foraging areas, reducing foraging time and increasing energetic losses, with consequential negative effects on reproduction rates and fitness. For example, juvenile growth rates were suppressed in the grey bat

Myotis grisescens with increased travel distance to foraging grounds (Tuttle 1976). Compensating for energetic losses by increasing foraging time may not be possible if, for instance, emergence and/or commuting is delayed by light pollution (Stone et al. 2009). Such delays also increase the risk that bats will miss the dusk peak in insect abundance, reducing the quality of foraging time. Delayed emergence could therefore affect the fitness of both individuals and the roost as whole.

Light disturbance along the commuting routes may isolate bats from their foraging grounds if the energetic costs of using alternative routes exceed the benefits. The commuting costs for *P. pipistrellus* become prohibitive when foraging areas are more than 5 km from the roost (Speakman 1991). Since bats select roosts based on the quality of surrounding habitat features, including linear connectivity (Jenkins et al. 1998; Oakeley and Jones 1998), maintaining optimal commuting routes is paramount. Whether fitness, or likely proxies of fitness, is affected by lighting needs further evaluation.

7.9 Winners and Losers: Light-Tolerant and Light-Averse Bats

Bats show variable responses to light pollution. Insectivorous bats that hunt in open spaces above the canopy (open-space foragers) or along vegetation edges such as forest edges, tree lines or hedgerows (edge foragers) are the species most tolerant of artificial lighting. They have evolved traits advantageous for foraging in sparsely structured habitats (Norberg and Rayner 1987; Neuweiler 1989) and so are preadapted to foraging in urban habitats (Rydell 2006; Jung and Kalko 2010; Jung and Threlfall 2016). Open-space foragers, such as the noctule *Nyctalus noctula*, typically have long narrow wings with a high aspect ratio, often combined with a high wing loading (weight/wing area). They have to fly fast to remain airborne and so use high-intensity, low-frequency narrowband echolocation calls that facilitate long-range detection of insects (Norberg and Rayner 1987; Rydell 2006; Kalko et al. 2008). When foraging at street lights, open-space foragers typically fly above the lamps, diving into the light cone to catch insects (Jung and Kalko 2010).

Edge foragers generally use echolocation calls with a conspicuous narrowband component, but usually also include a frequency-modulated ‘broadband’ component during the search phase, which is advantageous for ranging when flying close to obstacles. They comprise relatively fast-flying species with above-average aspect ratio and wing loading (e.g. *P. pipistrellus*), and species with an average aspect ratio and wing loading (e.g. *E. nilssonii*). Edge foragers tend to be more manoeuvrable than open-space foragers (Norberg and Rayner 1987; Kalko et al. 2008), and some can even conduct circuits inside the light cone when hunting insects at street lights (Jung and Kalko 2010).

Though most edge foragers fly with agility and speed (Norberg and Rayner 1987), they differ in their degree of synanthropism. While Kuhl’s pipistelle

Pipistrellus kuhlii is recorded almost exclusively at street lights in southern Switzerland, *P. pipistrellus* forage to a similar extent both at lights and at least 100 m from lights (Haffner and Stutz 1985). Even within a species, foraging activity at lamps can be highly variable depending on the quantity of insects available: Geggie and Fenton (1985) never observed *E. fuscus* foraging around street lights in an urban environment, whereas in rural habitats feeding activity was greater at lights than in areas without lights. In spring and autumn, when artificial lights attract numerous insects in Sweden, *E. nilssonii* activity is about 20-fold higher in towns with street lighting than in non-illuminated towns, forest and farmland (de Jong and Ahlén 1991; Rydell 1991), with the bats flying back and forth above the street lights, regularly diving to within 1 m of the ground to catch insects.

Although fast-flying species adapted to forage in open areas, particularly bats of the genera *Eptesicus*, *Nyctalus* and *Pipistrellus*, may benefit from the increased foraging opportunities provided at lamps that attract high densities of insects, Stone et al. (2009, 2012) found no significant increases in bat activity for these ‘light-tolerant’ species during lit treatments. This could be due to two factors. First, HPS lights are less attractive to insects than white lights because their spectral content has less UV (Blake et al. 1994); for example, HPS street lights attracted fewer insects than white lights in Germany (Eisenbeis and Eick 2011). Second, the experimental nature of the study may have affected the results, since bats may need time to find and recognise newly installed lights as an attractive foraging source.

Though a relatively high proportion of aerial insectivorous bats may forage in suburban habitats, bat activity and the number of bat species decrease significantly towards highly urbanised areas. This is probably because both roosts and appropriate insect habitats are lacking, and those insects which are present might not aggregate at street lamps because the pervasive artificial lighting in city centres causes a dilution effect, rendering the lights less attractive for bats (Gaisler et al. 1998; Avila-Flores and Fenton 2005; Frank 2006; Rydell 2006; Jung and Kalko 2011; Jung and Threlfall 2016). In Panama, 18 of 25 insectivorous bat species frequently foraged around street lamps in a settlement bordering mature forest; the reduced vegetation cover in town constrained strictly forest-dwelling species from hunting at lamps (Jung and Kalko 2010). Yet, even some closely related and ecologically similar species may differ in their tolerance of urban habitats, and their potential to adapt to anthropologically altered habitats is best viewed from a species-specific perspective.

As compared to open-space foragers, bats at the other end of the wing shape spectrum, such as many horseshoe bats (Rhinolophidae) with their low aspect ratio wings and a low wing loading, rarely forage near artificial lights (Rydell 2006; Stone et al. 2009, 2012). They are mostly forest-dwelling and their short broad wings facilitate the high manoeuvrability needed for hawking insects in a cluttered environment (Norberg and Rayner 1987). However, their morphology only allows slow flight speeds, which might render them more vulnerable to predators when flying in a sphere of light away from protective vegetation cover (Jones and Rydell 1994; Rydell et al. 1996). Most forest-dwelling bat species emerge from

their roosts relatively late in the evening, presumably to minimise predation risk from diurnal birds of prey (Jones and Rydell 1994) and so may be ‘hard-wired’ to be light-averse. Furthermore, slow-hawking bats use echolocation calls that are adapted for short-range prey detection among clutter (Norberg and Rayner 1987), and so these may not be suitable for orientation in semi-open habitats where most street lights are positioned.

Myotis spp. in Canada and Sweden and brown long-eared bats *Plecotus auritus* in Sweden were only recorded away from street lights (Furlonger et al. 1987; Rydell 1992). In Australia, the chocolate wattled bat *Chalinolobus morio* avoided parks when lights were switched on (Scanlon and Petit 2008). Despite having street-lit areas in their home range, they were never utilised by greater horseshoe bats *Rhinolophus ferrumequinum* (Jones and Morton 1992; Jones et al. 1995). Artificial light reduced the foraging activity of pond bats *Myotis dasycneme* over rivers in the Netherlands (Kuijper et al. 2008), and commuting activity of *R. hipposideros* and *Myotis* spp. was reduced under LED and HPS street lights (Stone et al. 2009, 2012). It is likely that the *Myotis* spp. in Stone et al.’s studies were Natterer’s bats *Myotis nattereri* (Stone 2011). *M. nattereri* emerges from roosts relatively late (Jones and Rydell 1994), at median light levels (3.5 lux, Swift 1997), lower than those recorded for *R. hipposideros* (Stone et al. 2009). *M. nattereri* and *R. hipposideros* use different echolocation strategies (Parsons and Jones 2000) but have similar flight and foraging patterns. *M. nattereri* has broad wings, prefers foraging in woodlands and is slow-flying and manoeuvrable, often foraging close to vegetation to glean prey (Arlettaz 1996; Swift 1997). This suggests that light-dependent predation risk limits the ability of these bats to take advantage of illuminated areas. Nevertheless, one large-eared horseshoe bat *Rhinolophus philippinensis* was repeatedly observed traversing 200 m of open grassland to forage extensively around artificial lights in Australia. The same lights were also used by eastern horseshoe bats *Rhinolophus megaphyllus* (Pavey 1999).

Extinction risk is highest in bat species with low aspect ratios (Jones et al. 2003; Safi and Kerth 2004), which are the species that show aversion to artificial lighting. Thus, species that may suffer most from light pollution are likely to be already threatened taxa.

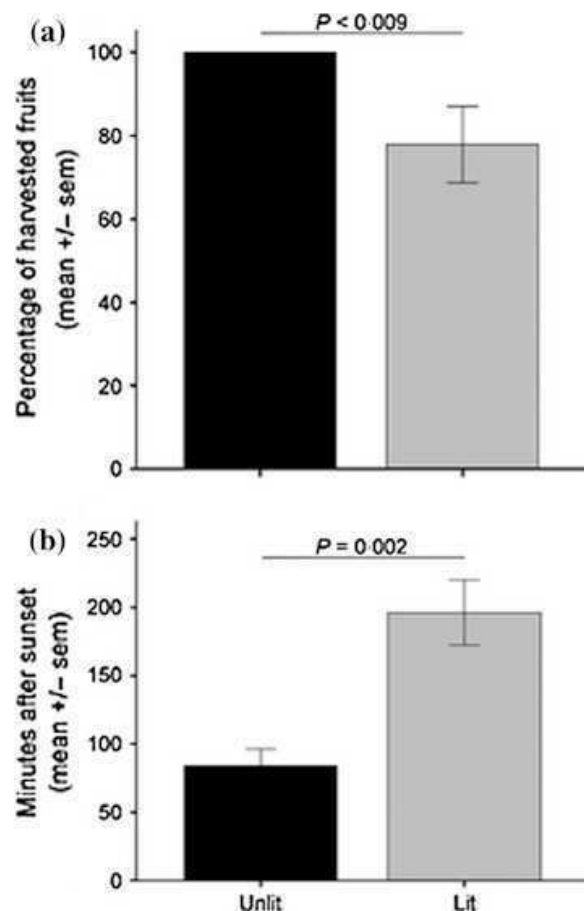
7.10 Effects of Light Pollution on Ecosystem Services Provided by Bats

The impacts of lighting go far beyond changing the physiology, behaviour and/or distribution of individual species. Since congeners interact with each other as well as their prey and predators, light pollution is likely to have far-reaching consequences for the entire biome and the ecosystem services that bats provide. Insectivorous bats, for instance, significantly reduce the number of insects that cause damage to flora and fauna (Ghanem and Voigt 2012). The value of

insectivorous bats to the US agricultural industry by reducing insect populations was estimated to be \$23 billion/year (Boyles et al. 2011).

Most studies to date have been on temperate-zone insectivorous bats. However, many tropical bats feed on nectar and fruits, thereby pollinating flowers and dispersing seeds of several hundred species of plants (Ghanem and Voigt 2012). Consequently, frugivorous bats are key for succession and maintaining plant diversity, especially in fragmented Neotropical landscapes (Medellin and Gaona 1999; Muscarella and Fleming 2007). However, very little is known about the impact of light pollution on this feeding guild. Southern long-nosed bats *Leptonycteris yerbabuena*, a nectar- and fruit-eating species, used areas of relatively low light intensity when commuting (Lowery et al. 2009) and Oprea et al. (2009) rarely captured frugivorous bats along roads, although some were present in municipal parks. However, neither study could disentangle the influence of lighting from other factors related to urbanisation, such as altered vegetation cover or increased noise levels. Lewanzik and Voigt (2014) provided the first experimental evidence for light avoidance by frugivorous bats. They found that Sowell's short-tailed bat *Carollia sowelli*, a specialist on fruits of the genus *Piper*, harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour street light than in a dark compartment, and free-ranging bats neglected ripe fruits that were experimentally illuminated (Fig. 7.6). Lewanzik and Voigt (2014) concluded that artificial light might reduce nocturnal dispersal of pioneer plant seeds. Since

Fig. 7.6 Artificial lighting reduces and delays feeding behaviour on pepper plants by a frugivorous bat. **a** Percentage of harvested infructescences of *Piper sancti-felices* among 14 marked plants harvested by Sowell's short-tailed bats *Carollia sowelli* in non-illuminated conditions (*black*) and under conditions where plants were illuminated by a street lamp (*grey*) in the field, **b** time after sunset when infructescences were harvested. From Lewanzik and Voigt (2014)



bat-mediated seed intake is particularly important during the early stages of succession (Medellin and Gaona 1999; Muscarella and Fleming 2007), light pollution might slow down the reforestation of cleared rainforests (Lewanzik and Voigt 2014).

7.11 Knowledge Gaps, Future Challenges and Mitigation Strategies

7.11.1 Knowledge Gaps

Light pollution has only recently been acknowledged as a threat to biodiversity (Hölker et al. 2010b), and there are still many unknowns about the interactions between bat species and artificial lighting sources (Hölker et al. 2010a). Most studies have focused on specific ecological behaviours such as foraging (Rydell 1992; Blake et al. 1994), predator–prey interactions, particularly with moths (Rydell et al. 1995; Svensson and Rydell 1998), commuting routes (Stone et al. 2009, 2012) and roost emergence (Downs et al. 2003). No long-term studies have been carried out to determine whether any of these behavioural changes have fitness consequences (Beier 2006; Stone et al. 2012). The only indication of potential population-level responses has been shown in Hungary on *Myotis* species, where juveniles roosting in illuminated buildings had a lower body mass than their counterparts in unlit roosts (Boldogh et al. 2007). However, this study did not establish whether a lower body mass in these juveniles reduced their survival rate after hibernation. It is particularly important to understand higher level responses for bat species because they have low fecundity rates, usually only producing one pup per year (Dietz et al. 2009), and so populations are sensitive to sudden changes (Stone et al. 2012).

Further studies are needed to address the impact of artificial lighting at the community level (Davies et al. 2012). The current literature highlights that artificial lighting causes species-specific responses (Rydell 1992; Stone et al. 2009, 2012; Jung and Kalko 2010), which could cause light-tolerant species to exclude light-averse species (Polak et al. 2011; Stone et al. 2012). Such competitive interactions have been proposed as the driving force behind changes in bat populations in Switzerland, where decreases in photosensitive *R. hipposideros* have been linked to increases in light-tolerant *P. pipistrellus* (Stutz and Haffner 1984; Arlettaz et al. 2000). It is believed that by avoiding street lights, *R. hipposideros* are foregoing profitable prey sources exploited by *P. pipistrellus* (Arlettaz et al. 1999, 2000).

So far research has focussed largely on insectivorous bats in temperate zones. Further research in tropical ecosystems is needed. For example, the forested areas of South-east Asia contain a high diversity and abundance of horseshoe bat species that are likely to be negatively affected by light pollution, and the impact of light

pollution on pollination and seed dispersal in the tropics and subtropics needs further investigation.

Research on the impacts of different light spectra in emerging technologies on bat activity and reproduction will be valuable; this is currently being investigated in the Netherlands as part of a large-scale investigation exposing a wide range of taxa to white, red and green LED lighting (see <http://www.lichtopnatuur.org>). With the current plans to switch to broader spectrum lighting sources, it is important to understand more about the spectral sensitivities of bats (Davies et al. 2012, 2013), especially given the recent findings on opsin genes highlighted above. Determining if there are spectral and intensity thresholds for different species would aid mitigation strategies and improve conservation initiatives (Stone et al. 2012; Gaston et al. 2013).

7.11.2 Mitigation Strategies

The most effective approach to reduce the detrimental effects of artificial lighting is to limit the growth of lighting by restricting unnecessary installations or removing them from areas already saturated with artificial lighting sources. This has the greatest potential to reduce light pollution and minimise ecological effects (Gaston et al. 2012). Turning off lights in areas commonly used by light-averse bats to forage, commute or roost during key times such as reproduction (Jones 2000) may be effective. Bats are faithful to maternity roosts due to the specific conditions they provide, and so conserving them is important for maintaining bat populations (Lewis 1995; Mann et al. 2002). However, some photosensitive bats may be disrupted even if areas were only lit for a short period of time (Boldogh et al. 2007), and switching off lighting may be challenged if it is perceived to jeopardise public safety (Lyytimäki and Rinne 2013).

Reducing the duration of illumination through part-night lighting (PNL) schemes could also help limit the adverse effects of light on nocturnal animals (Gaston et al. 2012). This has already been adopted by a number of local authorities in the UK, which switch off lights in specified areas between midnight and 05.30 to reduce CO₂ emissions and save money (Lockwood 2011). Since April 2009, lights along sections of motorways have also been switched off between these hours (Royal Commission on Environmental Pollution 2009). While this may help to reduce light pollution, it is unlikely to have significant ecological benefits since the lights remain switched on in the early part of the night, when bats and other nocturnal species undertake key activities such as foraging and commuting (Gaston et al. 2012). Intelligent lighting schemes, such as the use of motion sensors, have already been implemented in Portugal and may have more ecological benefits. The lights remain switched off unless needed and so still provide all the perceived public safety benefits (Royal Commission on Environmental Pollution 2009). However, these fluctuations in lighting levels may also be damaging to bats (Longcore and Rich 2004).

It is also important to reduce the trespass of artificial lighting to minimise the impact on bats. Newer technologies such as LEDs produce more directional light (Gaston et al. 2012), preventing the horizontal or upward emissions which contribute most to light pollution (Falchi et al. 2011). Effective luminaire design, installation of shielding fixtures and correct column height can also help focus light and avoid wasteful emissions (Royal Commission on Environmental Pollution 2009). In Lombardia, Italy, for example, 75 % of light pollution was due to poorly designed luminaires; the other 25 % was unavoidable reflection from road surfaces (Falchi 2011). Vegetation canopies such as hedgerows can also help decrease light trespass, which is crucial for many bat species that use linear features as commuting routes (Rydell 1992; Fure 2006). Diminishing trespass could create dark refuges, providing corridors for bats to forage in fragmented habitats (Longcore and Rich 2004; Stone et al. 2012; Gaston et al. 2012).

Light intensity has a significant effect on bat activity (Stone et al. 2012) and delays roost emergence (Downs et al. 2003). If bats delay foraging, they risk missing the peak abundance in insects that occurs shortly after dusk, so may not meet their energy requirements, which in turn could reduce fitness (Jones and Rydell 1994; Stone et al. 2012). In addition to implementing PNL, many local authorities are also dimming lights in specified areas (Gaston et al. 2012). This relies on local authorities already having lights such as LEDs that have the necessary centralised management system (International Energy Agency 2006). These schemes are more environmentally friendly and cost-effective (Gaston et al. 2012). However, dimming lights may not be beneficial to all bat species; Daubenton's bats *Myotis daubentonii*, for instance, only emerge from their roosts at very low light levels (less than 1 lux) (Fure 2006) and *R. hipposideros* and *Myotis* spp. avoid commuting routes illuminated to 3.6 lux (Stone et al. 2012). Since illumination levels of street lights are usually between 10 and 60 lux (Gaston et al. 2012), it may not be feasible to dim lighting to such low intensities without compromising public perceptions of safety (Stone et al. 2012; Lyytimäki and Rinne 2013).

7.11.3 Future Challenges

With a number of changes to street lighting planned in the coming years, including dimming, PNL and modifications to luminaire design to reduce light pollution, energy expenditure and greenhouse gas emissions, nightscapes could increase in heterogeneity, making it even more challenging to understand the impacts of artificial lighting on biodiversity (Gaston et al. 2012).

This is further complicated because current metrics for measuring emissions from light sources omit key biological information (Longcore and Rich 2004; Gaston et al. 2012). Illumination is measured in lux, which is defined as the brightness of a light according to human spectral sensitivities; spectral sensitivities of other taxa are often very different from ours (Peitsch et al. 1992; Briscoe and Chittka 2001). In bats, for example, many species can detect wavelengths in

the UV range (Winter et al. 2003; Wang et al. 2004; Müller et al. 2009). So HPS and LPS lamps could have the same intensity of light, e.g. 50 lux, but HPS lamps emit UV wavelengths, whereas LPS lamps do not, thereby affecting both bats and their insect prey in different ways (Longcore and Rich 2004). Since lux is commonly used as a metric by lighting engineers, designers and environmental regulators, migrating from this measure may thwart interdisciplinary communication (Longcore and Rich 2004).

Another challenge is to find more effective ways of quantifying the impact of artificial lighting on bat species. Current methods use acoustic survey methods to quantify bat activity; this underestimates the activity of bats that use low-intensity echolocation calls (O'Farrell and Gannon 1999). Crucially, we also need to determine whether artificial lighting has fitness consequences (Stone et al. 2012). A decrease in bat activity may have no relevance for fitness if, for example, the bats are able to utilise equally suitable alternative sites nearby.

A transdisciplinary approach needs to be adopted to minimise the impact of light on biodiversity, reduce CO₂ emissions, increase energy efficiency and reduce costs (Hölker et al. 2010a; Gaston et al. 2012). Scientists, policymakers and engineers need to work together to implement successful strategies (Stone et al. 2012). Moreover, it is vital to find ways to broaden awareness of light pollution and its ecological impacts. Since the public plays an integral part in agreeing mitigation schemes such as dimming lights, their support is pivotal in moving forward (Hölker et al. 2010a).

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CHAPTER 2

Artificial light puts ecosystem services
of frugivorous bats at risk

Artificial light puts ecosystem services of frugivorous bats at risk

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Summary

1. Currently, tropical forests are transformed into pasture and agricultural areas at an unprecedented rate, yet converted areas are often abandoned by farmers because depleting soil fertility renders unprofitable any agricultural land use. Natural succession of abandoned land could counter the loss of biodiversity, but the rate of natural reforestation is slow.

2. Neotropical frugivorous bats facilitate natural succession because they seem to tolerate habitat disturbance when dispersing seeds of pioneer plants. Under naturally dark conditions, bats produce a copious seed rain even in deforested habitats and connect distant forest fragments. Yet, artificial light at night may compromise bat-mediated seed dispersal if bats avoid lit areas. This may delay or jeopardize natural forest succession in fragmented tropical landscapes.

3. We asked whether the foraging behaviour of Sowell's short-tailed bats *Carollia sowelli*, a specialist on infructescences of pepper plants (Piperaceae), is negatively affected by artificial light at night.

4. First, in a dual choice experiment with captive bats, we demonstrate that food was less often explored and consumed in the dimly illuminated than in the dark compartment, indicating that artificial light alters the foraging behaviour of fruit-eating bats. Secondly, using observations in free-ranging bats, we found that infructescences were less likely to be harvested when plants were illuminated by a street lamp than under natural darkness.

5. *Synthesis and applications.* Natural succession of deforested areas and connectivity of remaining forest patches may suffer due to artificial light at night through a reduction in nocturnal seed disperser activity in lit areas. This could have negative impacts on biodiversity and consequent effects on land erosion, particularly in developing countries of the tropics where light pollution increases rapidly with growing economies and human populations. Mitigation requires that the use of artificial light should be limited in space, time and intensity to the minimum necessary. The effectiveness of 'darkness corridors' to enhance fragment connectivity and to reduce species loss should be evaluated. Policy-makers of tropical countries should become aware of the potential detrimental effects of artificial lighting on wildlife and ecosystem functioning.

Key-words: bat-facilitated succession, *Carollia sowelli*, fragmentation, frugivory, habitat connectivity, light pollution, Phyllostomidae, reforestation, seed dispersal

Introduction

Ecological light pollution, the alteration of the natural light and dark cycle by artificial light at night (Longcore & Rich 2004), has received increasing attention since it became evident that artificial light at night may be detrimental for many animals and ecosystem processes (reviewed in Rich & Longcore 2006) but continues to

spread at unprecedented rates (Hölker *et al.* 2010). Obligatorily nocturnal animals such as bats are particularly prone to night lighting, since they may be exposed to artificial light during their entire activity period. Yet, light intensities as low as moon light can potentially reduce the foraging behaviour of bats (e.g. Morrison 1978; Fleming 1988).

So far, only a few experimental studies have addressed the effects of light pollution on bats and all of those dealt with insectivorous bats mainly in the temperate zone.

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These studies have shown that some species abandon traditional commuting routes when illuminated by either high-pressure sodium (orange) or light emitting diode ('LED'; white) street lights, which potentially deterred bats from reaching their preferred foraging habitat (Stone, Jones & Harris 2009, 2012). *Eptesicus bottae* flew faster and ceased hunting insects when exposed to artificial light (Polak, Korine & Holderied 2011) and obstacle avoidance capabilities of free-ranging *Myotis lucifugus* were altered by experimental illumination (Orbach & Fenton 2010). Only a very few insectivorous species were shown to make use of insect accumulations at artificial lights (e.g. Rydell 1991) though, in these instances, their foraging effort could be reduced significantly.

In the tropics, feeding habits of bats are much more diverse than in the temperate zone. Many tropical bats consume nectar and fruits, thus offering pollination and seed dispersal services to several hundreds of plant species (Ghanem & Voigt 2012). Next to birds, frugivorous bats constitute the most numerous seed-dispersing agent in the Neotropics where they are particularly important for the dispersal of seeds during the early stages of succession (Medellin & Gaona 1999; Muscarella & Fleming 2007). Due to this important role for ecosystem functioning, bats may represent a keystone taxon in the tropics (Willig *et al.* 2007).

In contrast to insectivorous bats, fruit-eating species do not benefit from foraging at lights and therefore should preferentially stay in dark areas to avoid being visibly exposed to predators (e.g. Fleming 1988). Accordingly, indirect evidence suggests that, for example, nectar and fruit-eating lesser long-nosed bats *Leptonycteris curasoae* avoid lit areas (Lowery, Blackman & Abbate 2009). Yet, since artificial light conditions were not experimentally altered in that study, it was not possible to determine whether this effect is due to artificial light at night or to some confounding factor of urbanization, such as altered vegetation cover and/or increased noise levels. Thus far, experimental evidence for light avoidance behaviour of frugivorous bats is lacking, even though this feeding guild plays an essential role in the succession and maintenance of plant diversity especially in fragmented landscapes of the Neotropics (Muscarella & Fleming 2007). When human populations encroach in natural habitats, areas that were previously dark at night might become artificially illuminated, which may repel frugivorous bats. If these effective dispersal agents refrain from foraging in illuminated areas, artificial light at night may not only disrupt the habitats of light-sensitive species but also jeopardize the ecosystem services fruit-eating bats provide. This problem may become increasingly urgent in tropical countries with a prospering economy and an exponential growth of their human populations (CIA World Factbook 2011; UNPF state of world population 2011). Both growing economy and increased urbanization are known to correlate strongly with the degree of light pollution by street lamps (e.g. Elvidge *et al.* 2001).

We asked whether artificial light at night diminishes the harvesting activity of frugivorous bats at food plants and thus reduces the likelihood of seeds to be dispersed by bats. We focused on the effects of the widespread high-pressure sodium vapour light because high-intensity discharge lamps such as sodium lamps accounted for more than 80% of the global outdoor lighting market in 2010 (Baumgartner *et al.* 2011). Though the penetration rate of LED lights might increase, for example in Europe and North America during the forthcoming decades due to government initiatives, we believe that sodium lights will remain predominant in many developing countries of the tropics because they are cost efficient. Sodium lights have both low initial and low operating costs (Rea, Bullough & Akashi 2009), and LEDs have not yet reached a competitive cost position (Baumgartner *et al.* 2011). Further, LED street lights have been shown to repel several insectivorous bat species to a similar degree as high-pressure sodium lights (Stone, Jones & Harris 2012). To test the effect of artificial light on the harvesting activity of bats, we conducted a binary choice experiment during which we simultaneously offered fruits to Sowell's short-tailed bats *Carollia sowelli* in a dark and in a dimly illuminated compartment of a flight cage. We used Sowell's short-tailed bats because they are the primary disperser of pepper seeds (genus *Piper*), a key plant group during early succession in the Neotropics (Muscarella & Fleming 2007). We expected *C. sowelli* to evade artificial light and consequently to use the dimly illuminated compartment less often and to harvest fewer fruits from it than from the dark compartment. To ascertain the relevance of our experiment for free-living populations, we also video-recorded the feeding activity of bats at individual ripe *Piper* infructescences under dark and illuminated conditions in the wild in order to test whether the light treatment reduced the removal rate of ripe infructescences.

Materials and methods

Experiments were conducted at 'La Selva' Biological Station (Heredia Province, Costa Rica, 10°26'N, 83°59'W) in November–December 2011 and in March 2012. Monitoring of wild *Piper* plants was also conducted in November–December 2012. For both experiments, we used a custom-made street lamp to illuminate either one choice compartment or free-living *Piper* plants (see below). The lamp consisted of a high-pressure sodium light bulb ('Master SON PIA 50°W', Koninklijke Philips Electronics N.V., Eindhoven, the Netherlands) which was covered by a translucent beaker glass (Duran Group GmbH, Wertheim/Main, Germany) and operated by an electronic control gear (electronic ballast 'Ecolum EC4-70'; aplicaciones electrónicas industriales, s.l., Zaragoza, Spain). The lamp was mounted at a height of 3.5 m on a pole and powered via a wall socket. The necessary voltage of 220 V was produced by a series transformer (Votcraft AT-400 NV; Votcraft, Hirschau, Germany). High-intensity discharge lamps such as high-pressure sodium lamps accounted for more than 80% of the global outdoor lighting market (Baumgartner *et al.* 2011) and are commonly used as street lamps across the

world (Country Lighting Assessment). The particular light bulb used was manufactured for the use in street lamps.

CHOICE EXPERIMENT

We captured bats in a Costa Rican lowland rain forest reserve ('La Selva') by setting up 6-m and 9-m mist nets (height: 2.5 m, mesh: 16 × 16 mm; Ecotone, Gdynia, Poland) from dusk until at latest 2300 h. Bat species were identified according to Timm and LaVal (1998), and all other than adult *C. sowelli* were released immediately after capture. We transferred *C. sowelli* into a shared keeping cage (6.1 × 3.4 × 2.5 m) that was situated at a distance of about 50 m from the closest clearing and surrounded by mature forest such that bats in the keeping cage were not exposed to any artificial light but to the natural light/dark cycles. Captive bats were supplied with banana, papaya and water *ad libitum* and kept together in captivity for a maximum of 5 days before being transferred to the choice experiment.

For the choice experiment, we released individuals singly in a flight cage (Fig. 1) that was situated at a linear distance of about 250 m from the keeping cage. The experimental flight cage consisted of three compartments, the release area (5 × 3 × 2 m) and two choice compartments of equal size (2 × 1.5 × 2 m) which were separated from the release area by a retractable mesh curtain. One choice compartment was dimly illuminated by our custom-made street lamp. Since the lamp could not be dimmed sufficiently to have only low light intensities inside the choice compartment when fixing the lamp inside the choice compartment, we set up the street light outside of the flight cage at a distance of about 3 m from the rear end of the choice area (Fig. 1). Except for the front (the 'entrance'), the other choice compartment was shielded from the light by black plastic foil. To produce the same echo-acoustic environment for both choice compartments, we covered the illuminated compartment with transparent plastic foil. Between experiments, we randomly switched between illuminating the right and the left choice compartment. We set up two infrared-sensitive cameras (HDR-SR10E; Sony Corporation, Tokyo, Japan) and three infrared lights (TV6700; ABUS KG, Wetter, Germany; 24 LEDs, 2.5 W, 850 nm) to record the behaviour of bats (Fig. 1).

Depending on fruit availability, we equipped the choice compartments with ripe infructescences or fruits that local *C. sowelli* are known to forage on, namely *Piper sancti-felices*, *Solanum*

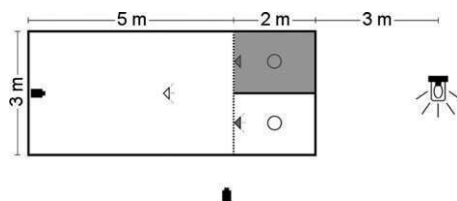


Fig. 1. Scheme of the flight cage set-up. Bats could enter two choice compartments in which fruits were offered on a platform (circle). We randomly chose one of the two choice compartments to be shielded from the experimental light. We used two infrared-sensitive cameras (one in the back of the flight cage and one in line with the removable mesh (dotted line)) to observe bat behaviour. Infrared lights were installed on the ground of the release area pointing towards the choice compartments (open triangles) and one each on the ceiling of each choice compartment directed downwards (filled triangles).

rugosum or *Ficus colubrinae*. For a given dual choice experiment, we always used same numbers of fruits of the same plant species in both compartments, in most trials this was four *Piper* infructescences. *Piper* infructescences were put with their basal part in a small plastic bowl filled with silica gel and placed centrally in the choice compartments on a platform around 80 cm in height such that bats could harvest them in flight. Branches of *Solanum* and *Ficus* with an equal number of fruits (5–15) were fixed at the ceiling of the choice compartments when we did not find enough ripe *Piper* infructescences. During some trials, we also offered banana on the central platform because we either lacked other ripe fruits or bats were not motivated to forage on fruits other than banana. Light intensity at the *Piper* infructescence was below the threshold of the luxmeter (0.01 lux; luxmeter LX-1108; Voltcraft) in the dark compartment and 4.5 ± 0.4 lux (mean \pm SD) in the illuminated compartment, measured horizontally towards the lamp. This light intensity (4.5 lux) corresponds to a distance of approximately 8 m from the lamp if the light was not dimmed, assuming an isotropic light source and optimal conditions.

Experimental trials were conducted between 1830 and 0200 h. The entrance to the choice compartments was closed when we released a bat in the release area, yet the fruit scent could pass through the dividing mesh. Bats were habituated to the flight cage until they either clearly switched from flying in circles to flying back and forth in front of the choice compartments or until they stopped flying and continuously clang to the mesh for at least 30 s. We then lifted the curtain that separated the choice compartments from the release area and recorded the bat's behaviour for at least 15 min with the video cameras. After experiments, all bats were released at the site of capture.

Based on the video recordings, we counted the number of explorative flights, that is, the number of entries in each choice compartment, within 15 min after opening the choice area. To account for differences in total numbers of flights between individuals, we used a weighted regression (generalized linear model with family = binomial and link = logit) on the number of explorative flights in either choice compartment. For the regression, we incorporated the independent variables 'gender' and 'side-of-light', indicating which of the two choice compartments was illuminated, as well as the interaction between 'gender' and 'side-of-light'. The weighing was achieved in R using a two-vector object combining the number of flights in both left and right choice compartment as dependent variable for the GLM fit.

Further, we determined from the video recordings whether bats harvested fruits/infructescences in either the dark or the lit compartment. Usually, bats harvested only one infructescence and became torpid afterwards for the remaining of the recording period. In a few trials, however, bats fed on more than one fruit. For those individuals, we only included the compartment of the first feeding activity in the analysis. To evaluate whether bats harvested fruits less often under illuminated than under dark conditions, we conducted a generalized linear model for a binary response variable (family = binomial, link = logit) also incorporating 'gender', 'side-of-light' and the interaction between the two factors as predictor variables.

HARVEST OF WILD *PIPER* INFRUCTESCENCES

To verify the relevance of the flight cage experiment for free-ranging populations of bats, we also conducted a field-based light experiment. We regularly checked 14 *P. sancti-felices* plants for

ripe infructescences. Thirteen of these plants grew at the edge between secondary forest/abandoned agroforestry and the clearing (c. 2 ha) of the biological station (at a maximal distance of 25 m from the forest edge). One additional plant was monitored at the edge between a smaller clearing (c. 150 m²) and secondary forest. Plants were chosen according to the site's accessibility to electric power to run the high-pressure sodium light. However, due to numerous wall sockets at the buildings on the clearing, most *Piper* plants at the forest edge were within the range of our extension cable (c. 25 m), but we focused only on those that were more than 25 m apart. There is a potential lack of spatial independence in these samples due to the proximity of the *Piper* plants to each other or the identity of the foraging bats. Ideally, we would have worked on replicate study plots that are at several kilometres apart or even in different countries, but unfortunately, this approach was not feasible. Our choice of monitored plants aimed at minimizing spatial dependence given the constraints for setting up experimental lights, yet we cannot rule out the possibility that our data may suffer to some extent from a lack of independence. However, due to the high abundance of *C. sowelli* at our study site (Rex *et al.* 2008) and the overall distance of monitored *Piper* plants, we suggest that harvest events were almost independent.

At smaller plants, we were able to mark every ripe infructescence when monitoring the respective plant since *Piper* plants produce only a few ripe infructescences each night over extended periods of time. At large plants with many ripe infructescences, we randomly chose a subset of the ripe ones. Every *Piper* plant was used at least twice, once under naturally dark conditions and once when it was illuminated by the experimental street light. At most plants, however, we increased the number of infructescences monitored by marking ripe infructescences on more than one dark and one illuminated night ($n = 63$ marked infructescences for dark and light condition, respectively). On average, we marked 5 ± 4 and 5 ± 3 (mean \pm SD) infructescences per plant during dark and illuminated conditions, respectively (min to max = 1–14 and 1–10), shortly before sunset by knotting a short piece (c. 5 cm) of thin orange thread to the branch at a distance of about 5 cm from the respective ripe infructescence. Due to the orange colour of the sodium vapour light, the thread was only distinguishable from the plant by its colour during daylight but not during dark or artificially lit conditions. Three hours following sunset, we counted the number of marked infructescences that were harvested.

The light was placed at a mean (\pm SD) distance of 2.5 ± 0.7 m from the observed infructescences. It was switched on before sunset and ran until midnight. The mean light intensity (\pm SD) was 57.0 ± 19.1 lux at the monitored *Piper* infructescences under illuminated conditions which is comparable to light intensities measured underneath or in proximity to high-pressure sodium street lights (e.g. Stone, Jones & Harris 2009: 52 lux). During the dark treatment, light intensity was below the threshold of the luxmeter (0.01 lux). Light intensities were measured horizontally at a height of 1.8 m towards the lamp using the luxmeter LX-1108 (Voltcraft). The nature of the first treatment (either dark or light) was assigned randomly to experimental plants. After each illuminated monitoring, we waited at least three nights before using the same plant again under dark conditions to avoid any sequential effects on the outcome of the experiments.

We used a logistic regression framework to analyse the influence of light on the probability of fruits to be harvested by bats.

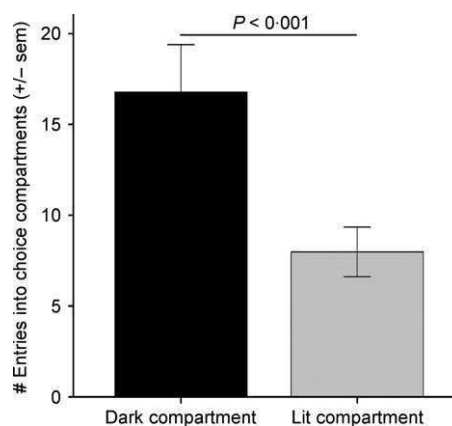


Fig. 2. Observed mean number of entries per bat from 56 *Carolinia sowelli* bats in either the dark or the dimly illuminated ('lit') choice compartment.

The dependent variable y of the model was a binary variable, indicating whether a given fruit had been harvested ($y = 1$) or not ($y = 0$). We considered the light treatment as a binary variable (defined by: 0 = dark, 1 = light) modelled as a fixed effect, and we modelled the plant identity as a random effect to account for the lack of independence of fruits marked at the same bush. As such, the model corresponds to a generalized linear mixed effect model (GLMM) that we fitted using the function 'glmer' from the packages LME4 v. 0.999999-2 (Bates, Maechler & Bolker 2013). We tested the effect of the light treatment by comparing the observed likelihood ratio test statistic measured for this covariate to its distribution under the null hypothesis obtained by parametric bootstrap (referred as PBtest in the results). This was done using the function 'PBmodcomp' from the package PBKRTEST v.0.3-5 (Halekoh & Højsgaard 2013) that we used through the wrapper package AFEX v. 0.5-71 (Singmann 2013).

At a subset of 12 plants, we also video-recorded a randomly chosen ripe infructescence under both dark and illuminated conditions from sunset until midnight. From those recordings, we determined the time (minutes after sunset) at which the respective infructescence was harvested. We then tested for significant differences between the two treatments using the paired-samples t -test in PASW statistics 18.0 (SPSS Inc., Chicago, IL, USA).

If not mentioned otherwise, all analyses were conducted in R (R Core Team 2012). We used an alpha value of 5%.

Results

In our dual choice experiment, we conducted 56 experimental trials using 39 male and 17 female *C. sowelli*. The number of explorative flights in either choice compartment was affected by light treatment ($Z = 8.87$, $P < 0.001$) but not by gender ($Z = -0.84$, $P = 0.402$) nor by the interaction between gender and light treatment ($Z = 0.94$, $P = 0.349$). Bats performed less explorative flights in the dimly illuminated than in the dark compartment (Fig. 2). On average, bats entered the dimly illuminated compartment four times (median; min/max = 0 and 41, respectively) and the dark compartment eight times (median; 0–88). The light treatment also affected in which

compartment bats harvested food ($Z = -2.29$, $P = 0.022$), but neither gender ($Z = -0.48$, $P = 0.35$) nor the interaction between gender and light treatment ($Z = 1.16$, $P = 0.247$) had an effect on this decision. Bats harvested food almost twice as often in the dark than in the dimly illuminated compartment ($N_{\text{dark}} = 36$, $N_{\text{light}} = 20$).

In the free-ranging population, our camera recordings ($N = 40$) revealed that after sunset no other vertebrates besides bats harvested infructescences of *P. sancti-felices* at our study site.

We found that the light treatment exerted a significant influence on the probability of a fruit being harvested (PBtest: likelihood ratio test statistics = 19.2, 666 simulations reaching convergence, $P < 0.009$, Fig. 3a). In the naturally dark environment, 100% ($N = 63$) of fruits were harvested within 3 h after sunset, while the model predicts that only 89.5% of fruits were harvested on each plant under illumination. This estimate deviates slightly from the 77.8% (49 of 63) of infructescences that were harvested across all plants during the experiment because the removal rates differed between plants (variance of the random effect expressed in the logit scale = 4.77) and the data collection was not balanced with respect to plants, while model estimates are.

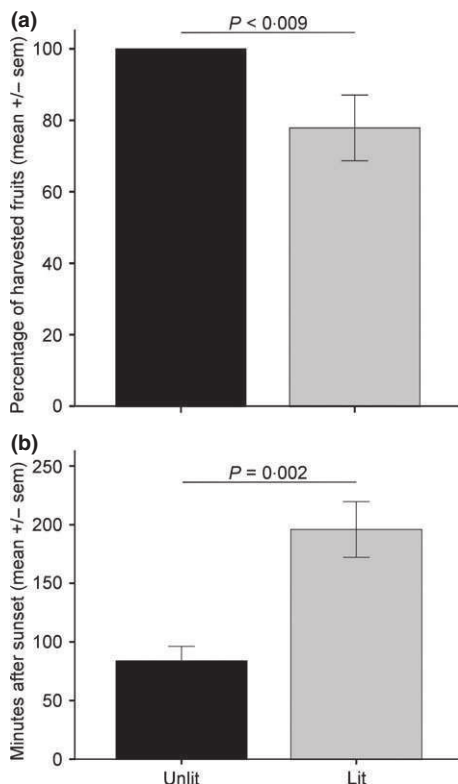


Fig. 3. (a) Observed percentage of harvested *Piper sancti-felices* infructescences among all marked ones ($n = 14$ plants) and (b) for infructescences that were harvested, the minutes after sunset when infructescences were harvested by free-ranging bats from plants in either a naturally dark surrounding ('unlit') or from the same plants under illumination of a street lamp ($n = 12$ infructescences each from a different *P. sancti-felices* plant for dark and illuminated conditions, respectively).

If harvested at all, infructescences under illumination were harvested about 2 h later than infructescences from the same plants but in a dark surrounding (mean \pm SD = 84 ± 42 min and 196 ± 82 min after sunset, respectively; paired-samples $T = -4.1$, $N = 12$, $P = 0.002$; Fig. 3b).

Discussion

Our study provides first evidence that frugivorous bats are repelled by artificial light at night, indicating that light pollution interferes with valuable ecosystem services provided by nocturnal seed dispersers. In particular, experiments with captive *C. sowelli* highlighted that bats performed more explorative flights and harvested fruits more often in a dark than in an illuminated environment. Given the low light intensities used in the experiment, we infer that *C. sowelli* was repelled by intensities even lower than those measured underneath street lights. We therefore suggest that the rapid spread of light pollution might severely affect the spatial foraging behaviour of frugivorous bats. Nocturnal seed dispersers may visit fruiting plants or entire feeding areas less often when these are illuminated by artificial light. Particularly frugivorous bats such as *C. sowelli* depend on many fruiting plants because each plant individual produces only a few ripe infructescences per night. Consequently, bats of the genus *Carollia* search ripe infructescences at numerous plants each night and switch frequently between distant feeding areas when foraging (Fleming 1988).

Our findings with captive bats were consistent with those obtained from free-ranging bats. Wild bats harvested fewer *Piper* infructescences from illuminated *Piper* plants and, when foraging did occur, they removed infructescences from illuminated plants about 2 h later than from plants in complete darkness. This delay in foraging activity may drastically reduce the likelihood of seed dispersal for a plant, particularly when additional adverse conditions reduce the activity of bats later at night, for example during tropical rainfalls (Voigt *et al.* 2011). Further, if a *Piper* infructescence is not harvested during the first night after ripening, it may not be removed and may fall to the ground (Thies & Kalko 2004). Irrespective of whether an illuminated infructescence is harvested later at night or whether it is completely neglected and not removed at all, in both circumstances, the avoidance behaviour of frugivorous bats towards artificial light at night reduces the probability of successful seed dispersal. This has major implications for ecosystem functioning when tropical habitats are increasingly exposed to artificial light. Bat-dispersed successional plants in particular, such as Piperaceae and Solanaceae, might suffer from a reduced visitation rate in an illuminated environment. Due to their preference for disturbed areas, pioneer plants are more likely exposed to artificial light, for example, when street lights are established along roads or when lights at buildings illuminate the surroundings at night.

Anthropogenic disturbance *per se* may not necessarily reduce bat abundance and the associated ecosystem services, because some bat species are relatively resistant to fragmentation. Many frugivorous bat species fly up to 2.5 km across open areas in the Neotropics (Bernard & Fenton 2003) and some species which are specialized on pioneer plants might even be more abundant in disturbed habitats (Willig *et al.* 2007). These bats are important for the rapid succession in clearings because they produce a copious seed rain even in deforested areas such as abandoned pastures (Medellin & Gaona 1999). In the Neotropics, the majority of cleared lowland forest becomes pasture but more than 50% of the clearings in the Amazon are abandoned within 10 years because of the poor fertility of tropical soils (Hecht 1993). Here, bat-mediated seed intake could promote reforestation and reduce the many negative outcomes associated with abandonment such as pronounced land erosion which may cause landslides, runoff, water loss, leaching and siltation of streams and rivers. However, the ability of a species to resist anthropogenic disturbance depends on the nature and the level of disturbance. Although frugivorous bats might easily traverse open areas between forest fragments in naturally dark nights, our results suggest that they are less likely to use habitats which are 'polluted' by artificial light at night. It appears that artificial light constitutes a severe anthropogenic disruptive factor which affects even species that are tolerant to fragmentation or other anthropogenic changes to ecosystems. Accordingly, succession with pioneer plants may slow down in areas with artificial light and habitat loss may be aggravated for light-sensitive species. This may result in cascading effects that could prove expensive for landowners and communities.

Artificial light from villages and street lamps may serve as a 'light barrier' that inhibits light-sensitive bats from conducting long-distance seed dispersal and pollination services between remaining forest fragments and therefore increases the degree of isolation. The light-barrier argument goes beyond what can be directly inferred from our experiment, but it seems plausible given the fact that street lights are usually brighter than the 4.5 lux used in our experiment. Also, bats of the genus *Carollia* usually fly at low heights above-ground (Rex *et al.* 2011) and may therefore be unwilling to cross illuminated streets above the glare of lamps. Some support for a light-barrier effect comes from a study which showed that the few frugivorous bat species which do occur in urban areas can rarely be captured along roads (Oprea *et al.* 2009). Further, even some insectivorous bats that could potentially benefit from feeding on insects attracted to street lights avoid roads more than other urban land cover classes when commuting (Davies, Hale & Sadler 2012) or do not commute in the catchment area of street lights at all (Stone, Jones & Harris 2009, 2012). If commuting of frugivorous bats is affected in a similar way by light barriers, then artificial light at night might not only lead to genetic isolation of illuminated plants and to a loss of

suitable habitats for light-sensitive species but could also hinder seed exchange and genetic connectivity between whole forest fragments (Jordano *et al.* 2011). Then, maintenance of biodiversity and finally ecosystem functioning could be at risk in areas composed of forest remnants embedded in a matrix without sufficiently dark corridors. Possibly, such a scenario may be realized in many tropical countries, as both deforestation and light pollution proceed at high rates across the tropical climate domain (Hölker *et al.* 2010; FAO & JRC 2012).

On a global scale, bats are known to disperse seeds not only of *Piper* but also seeds of hundreds of other tropical tree and shrub species that support biodiversity (Thomas 1991). In addition, many agriculturally produced fruits such as mango and shea as well as many economically relevant timber species are pollinated or dispersed by bats (Ghanem & Voigt 2012). The production of shea trees (a bat-dispersed species) was estimated to exceed 2.5 million metric tons each year (Lovett 2005), highlighting the relevance of bats as seed dispersers for species used by humans. Artificial light at night may severely affect these economies when pollinating and seed-dispersing services of bats are reduced.

Problems associated with artificial light may become even more aggravated on a larger geographical scale, considering that light pollution is increasing rapidly at an annual rate of about 6% world-wide (Hölker *et al.* 2010). Since the degree of light pollution parallels population growth and economic development (e.g. Elvidge *et al.* 2001), it can further be expected that artificial light at night increases at exceptionally high rates in many tropical countries. For example, the outdoor lighting market in Latin America is estimated to nearly double between 2010 and 2020 (Baumgartner *et al.* 2011). Due to the exponential growth rate of human populations in many tropical countries (UNPF state of world population 2011), people will encroach further into formerly pristine habitats than ever before. Since this encroachment is probably accompanied by an intensified use of artificial light, it might have deleterious consequences for nocturnal seed dispersal and habitat connectivity.

CONCLUSIONS & RECOMMENDATIONS

We conclude that the detrimental effects of light pollution are likely to increase and may have a great impact on biodiversity, particularly in the tropics where artificial light follows human encroachment in natural habitats at unprecedented rates.

Policy-makers should pay attention to the ecological impacts of artificial light, and policy should ensure artificial light is not excessively used. To mitigate the negative effects, artificial light should be restricted to (i) where it is needed, (ii) when it is needed and to (iii) an illumination level that achieves its purpose but does not exceed it. Particularly in the tropics, where nocturnal seed dispersers are crucial for ecosystem functioning, maintaining unlit

habitats large enough to guarantee viable populations of light-sensitive species should be of high priority, since even very low light intensities were sufficient to reduce the foraging activity of fruit-eating bats. To achieve this, it is essential to raise awareness of the ecological impacts of artificial light by informing people and policy about the deleterious effects light pollution can have on a wide range of taxa (reviewed in Rich & Longcore 2006).

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CHAPTER 3

Transition from conventional to light-emitting diode street lighting changes activity of urban bats

Transition from conventional to light-emitting diode street lighting changes activity of urban bats

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Summary

1. Light pollution is rapidly increasing and can have deleterious effects on biodiversity, yet light types differ in their effect on wildlife. Among the light types used for street lamps, light-emitting diodes (LEDs) are expected to become globally predominant within the next few years.

2. In a large-scale field experiment, we recorded bat activity at 46 street lights for 12 nights each and investigated how the widespread replacement of conventional illuminants by LEDs affects urban bats: we compared bat activity at municipal mercury vapour (MV) street lamps that were replaced by LEDs with control sites that were not changed.

3. *Pipistrellus pipistrellus* was the most frequently recorded species; it was 45% less active at LEDs than at MV street lamps, but the activity did not depend on illuminance level. Light type did not affect the activity of *Pipistrellus nathusii*, *Pipistrellus pygmaeus* or bats in the *Nyctalus/Eptesicus/Vespertilio* (NEV) group, yet the activity of *P. nathusii* increased with illuminance level. Bats of the genus *Myotis* increased activity 4–5-fold at LEDs compared with MV lights, but illuminance level had no effect.

4. Decreased activity of *P. pipistrellus*, which are considered light tolerant, probably paralleled insect densities around lights. Further, our results suggest that LEDs may be less repelling for light-averse *Myotis* spp. than MV lights. Accordingly, the transition from conventional lighting techniques to LEDs may greatly alter the anthropogenic impact of artificial light on urban bats and might eventually affect the resilience of urban bat populations.

5. *Synthesis and applications.* At light-emitting diodes (LEDs), the competitive advantage – the exclusive ability to forage on insect aggregations at lights – is reduced for light-tolerant bats. Thus, the global spread of LED street lamps might lead to a more natural level of competition between light-tolerant and light-averse bats. This effect could be reinforced if the potential advantages of LEDs over conventional illuminants are applied in practice: choice of spectra with relatively little energy in the short wavelength range; reduced spillover by precisely directing light; dimming during low human activity times; and control by motion sensors. Yet, the potential benefits of LEDs could be negated if low costs foster an overall increase in artificial lighting.

Key-words: artificial light at night, bats, Chiroptera, light pollution, light-emitting diode, phototaxis, pipistrellus, synanthropic, urban

Introduction

Global artificial lighting has increased by about 6% per year (0–20%, depending on geographic region) over the past decades and is expected to continue to increase in the foreseeable future (IEA 2006; Hölker *et al.* 2010a). This

excessive or inappropriate use of artificial light, which is termed ‘light pollution’, is a key threat to biodiversity (Hölker *et al.* 2010b). Nocturnal taxa such as bats are especially likely to suffer from light pollution since they are adapted to forage in a dark environment (Voigt & Lewanzik 2011). Bat orientation can be impaired by high illuminance levels (Bradbury & Nottebohm 1969). Accordingly, slow-flying, gleaning bat species such as

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Myotis nattereri usually emerge only after dusk in complete darkness from their day roost and also avoid street lights (Jones & Rydell 1994; Rowse *et al.* 2016). Additionally, light-averse species use rather faint echolocation calls that might be incompatible with hunting insects in a relatively open urban environment (Neuweiler 1984). Thus, light-sensitive species may disappear from urban and adjacent areas where about one-third of overall light emissions originate from streets (Kuechly *et al.* 2012).

Also, those nocturnal species that forage in illuminated areas might be adversely affected by light pollution when diurnal or crepuscular animals extend their activity into the night in lit habitats. Both diurnal and nocturnal species then make use of the 'night-light niche' simultaneously and accordingly may face increased interspecific competition. The scissor-tailed flycatcher *Tyrannus forficatus*, for example, preys upon insects at street lights for at least three hours after sunset, which may increase both exploitation and interference competition with insectivorous bats (Frey 1993).

In spite of the disadvantages in artificially illuminated areas, some bat species can be found foraging in city centres where they have to deal with intense levels of light pollution. Presumably, increased food availability and predictability at street lights compensate for the drawbacks associated with urban habitats. Reviews of existing literature generally suggest that relatively fast-flying, aerial-hawking species such as bats of the genera *Eptesicus*, *Nyctalus*, *Pipistrellus* and *Vespertilio* are rather tolerant of light and also forage around street lights (Mathews *et al.* 2015; Stone, Harris & Jones 2015; Rowse *et al.* 2016). The activity of crepuscular insects drops drastically after sunset, and thus, most of the bat species that feed on these insects emerge relatively early from their day roost (Jones & Rydell 1994). For them, light level is apparently only a minor constraint compared with prey availability. In urban habitats, primarily *Pipistrellus pipistrellus* intensively forage on insect aggregations at street lights (Gaisler *et al.* 1998).

The impact of street lamps on bats is presumably dependent on spectral characteristics of the light. High-pressure mercury vapour (MV) lamps, for instance, generally attract more insects than all other commonly used street light types since they emit relatively more energy in the ultraviolet (UV) range (Rydell 1992; Eisenbeis & Eick 2011; Fig. S1, Supporting Information). Also, several bat species have UV-sensitive photoreceptors and might therefore be more strongly affected by lights that also emit in the UV range (Gorresen *et al.* 2015).

In 2010, high-intensity discharge lamps such as MV lamps still accounted for more than 80% of the global outdoor lighting market (Baumgartner *et al.* 2011). Yet, since April 2015, MV lamps are virtually no longer available in Europe since they do not meet the minimum performance and efficiency standards set by the EU Commission Regulation (EU 2009). Many communities install light-emitting diode (LED) lamps as a substitute

mainly because they consume relatively little energy. Accordingly, the LED market share in outdoor lighting applications is expected to increase from 5% to about 70% between 2010 and 2020 (Baumgartner *et al.* 2011). Yet, hardly anything is known about the ecological impacts of LED light on nocturnal animals. To date, several studies focused on the effects of artificial light on bats mostly in rural habitats (as reviewed in Rowse *et al.* 2016), but not a single study has investigated the effects of a replacement of MV lights by LEDs on bats in urban environments where the majority of MV street lights are installed.

We hypothesized that a change from MV to LED street lights would alter the activity of bats in the vicinity of the lights. We predicted that aerial-hawking, light-tolerant bats that commonly forage on insect aggregations around urban street lights, particularly *P. pipistrellus*, would be less active at LEDs than at MV lights because LEDs induce less phototaxis of flying insects compared to MV lamps (Huemer, Kührtreiber & Tarmann 2010; Eisenbeis & Eick 2011). By contrast, we predicted that the activity of light-averse bat species would not be dependent on light type, since they do not make use of higher insect densities at MV lights. For light-averse species that can perceive UV, such as some species of the genus *Myotis*, we predicted the activity to increase at LEDs, since LEDs emit less UV than MV lights.

Materials and methods

BATCORDER RECORDINGS

From June until September 2011, we recorded bat echolocation calls using BATCORDERS (v.2.0, ecoObs GmbH, Nürnberg, Germany) at 46 MV street lights distributed across six urban regions in Germany (Fig. S2), each for six nights. Batcorders were fixed at lamp posts about 3 m above the ground; settings were 'quality' = 20, 'threshold' = -27 dB, post-trigger = 800 ms and 'critical frequency' = 14 kHz. We then repeated the recordings in 2012 (Freiburg/Ebringen: 2013) when 25 lamps were replaced by LED light (experimental lamps), while 21 remained MV (control) lamps. Within each urban region, recordings were made simultaneously at both control and experimental lamps. With the exception of Freiburg/Ebringen and a single lamp in Coburg, experimental and control lamps were at a distance of at least 800 m from each other, while the distance between experimental lamps or between control lamps was only about 100 m in some instances.

We recorded from sunset until 3.5 hours after sunset which includes the main peak in activity for most insectivorous bats of the temperate zone (Erkert 1982; Fig. S3). We excluded one occasion (recordings of one evening at one site), for which the batcorder failed to record until 210 min after sunset, from our analyses. We included only nights without precipitation (as verified by precipitation radar) and with at most low wind speeds and temperatures at sunset above 10 °C (own measurements).

All lamp posts monitored were situated in residential areas with different levels of housing density, but some vegetation was present in close proximity to all monitoring sites. The selected

street lamps represented a subset of various types which can be typically found in urban environments of Germany. To control for the differences between lamps and years, we measured illuminance levels at each lamp at 1.9 m above the ground in both years using a luxmeter (LX-1108, 0-400000 lux; Voltcraft, Hirschau, Germany) to the nearest 0.1 lux; the levels ranged between 0.5 and 239.4 lux (mean \pm SD = 41.8 \pm 50.5 lux).

SOUND ANALYSIS

First, we conducted an automatic call analysis using the software 'BC ADMIN' for the identification of bat calls within the recordings and 'batIdent' for species analysis (both: ecoObs GmbH, Nürnberg, Germany). To estimate the ratio of misidentifications, we randomly selected 2.5% of all recordings and analysed them manually. Additionally, we checked all recordings identified as calls from *Barbastella barbastellus*, *Plecotus* spp. and additional ones identified as *Myotis* spp. and *Pipistrellus pygmaeus* to get a reliable estimate of identification quality also for those species with relatively few recordings. Manual analyses revealed that 100% of *B. barbastellus*, 48% of *Pipistrellus nathusii*, 99.9% of *Pipistrellus pipistrellus*, 100% of *P. pygmaeus*, 97% of *Myotis* spp., 97% of NEV (*Nyctalus* spp. + *Eptesicus* spp. + *Vespertilio murinus*.) and 100% of *Plecotus* spp. identifications were assigned correctly. Due to a very limited number of recordings, *B. barbastellus* and *Plecotus* spp. were excluded from further analyses.

STATISTICAL ANALYSES

To model bat activity, we used a logistic regression framework in R (v. 3.1.0, R Core Team 2014). As a relatively unbiased measure of bat activity, we used the activity index, which is the ratio between the number of minutes in which a bat was recorded and the number of total recorded minutes (Miller 2001). We used the activity index instead of the raw number of bat passes because a single bat can trigger multiple recordings after another when circling in the vicinity of the same lamp. The activity index eliminates much of the inherent bias associated with counting bat passes and allows comparisons between sites, times and species (Miller 2001).

For each species (group), we modelled bat activity as a function of the fixed effects 'study period' (binary; first period before replacement/second period post-replacement), 'treatment' (binary; light type kept the same/changed) and 'standardized illuminance level' (numeric) and the interaction between 'treatment' and 'study period'. For species in which the interaction term was not significant, we present the main effects of the additive models (without the interaction). In all models, we additionally modelled 'lamp ID' as random effect (factor with 46 levels) nested in 'urban region' (factor with six levels) to account for the potential lack of independence of bat activity recorded at lamps within the same urban region over six nights. Also, we included an observation-level random effect to account for overdispersion in all models. As such, the models correspond to generalized linear mixed-effects models (GLMMs) fitted using the function 'glmer' from the package LME4 v. 1.1-6 (Bates *et al.* 2015).

We used the 'sim' function (package 'ARM') to simulate the posterior distribution of the model parameters. Values for fitted means and credible intervals are based on 1000 simulations. Fitted mean activity was calculated for the levels of one fixed effect while keeping the other fixed effects constant; when calculating fitted mean activity for pre- and post-replacement, we set

standardized illuminance level to zero and did separate calculations for experimental and control sites.

Results

Pipistrellus pipistrellus was by far the most frequently recorded bat species at all study sites (Fig. 1). This species was present in 14.3% and 11.3% of the recording minutes at MV and at LED lights, respectively. Bats belonging to the NEV group were found in 3.4% and 1.9% and *P. nathusii* in 1.2% and 0.7% of all minutes recorded at MV and LED lights, respectively. *Myotis* spp. were detected in less than 0.1% and 0.1% of recorded minutes at MV and LED lights, respectively, while *P. pygmaeus* occurred in less than 0.1% of recorded minutes at either light type. In total, we recorded *B. barbastellus* only twice at LEDs and *Plecotus* spp. twice at MV and once at LED lamps.

PIPISTRELLUS PIPISTRELLUS

The interaction between season and treatment proved highly significant for *P. pipistrellus* ($\chi^2 = 11.91$, d.f. = 1, $P < 0.001$), indicating that the seasonal change in activity differed between the treatments: activity was predicted to increase by 13% at control lamps and to decrease by 37% at experimental lamps (Fig. 2a). Consequently, activity was 45% lower at LED lights during the second season than what could be expected from the proportional activity difference between control and experimental sites during the first (control) season (51% activity at experimental lamps as compared to control lamps). This indicates that the replacement of MV lights by LEDs reduces *P. pipistrellus* activity by 45%. Illuminance level did not affect the activity of *P. pipistrellus* ($\chi^2 = 1.34$, d.f. = 1, $P = 0.247$; Table 1).

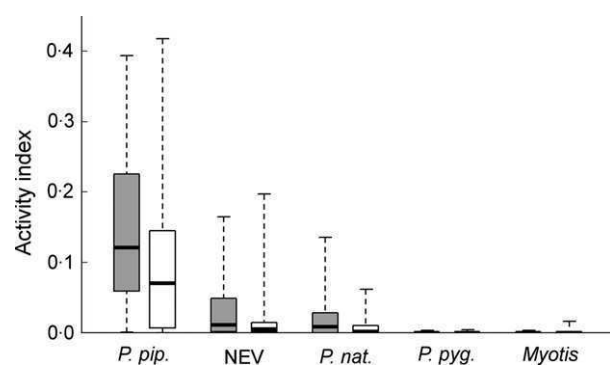


Fig. 1. Bat activity index (AI, the number of minutes with activity divided by 210 min recorded) as calculated from recordings made at 21 mercury vapour (MV) and 25 light-emitting diodes street lamps (grey and white, respectively) during the second sampling season. AI is based on recordings made until 3.5 h after sunset. Black lines indicate medians; lower and upper box margins represent 25% and 75% quartiles, respectively; and whiskers illustrate smallest and largest values, respectively. *P. pip.*: *Pipistrellus pipistrellus*; NEV: a species group consisting of the genera *Nyctalus*, *Eptesicus*, and *Vespertilio*; *P. nat.*: *Pipistrellus nathusii*; *P. pyg.*: *Pipistrellus pygmaeus*; *Myotis*: *Myotis* spp.

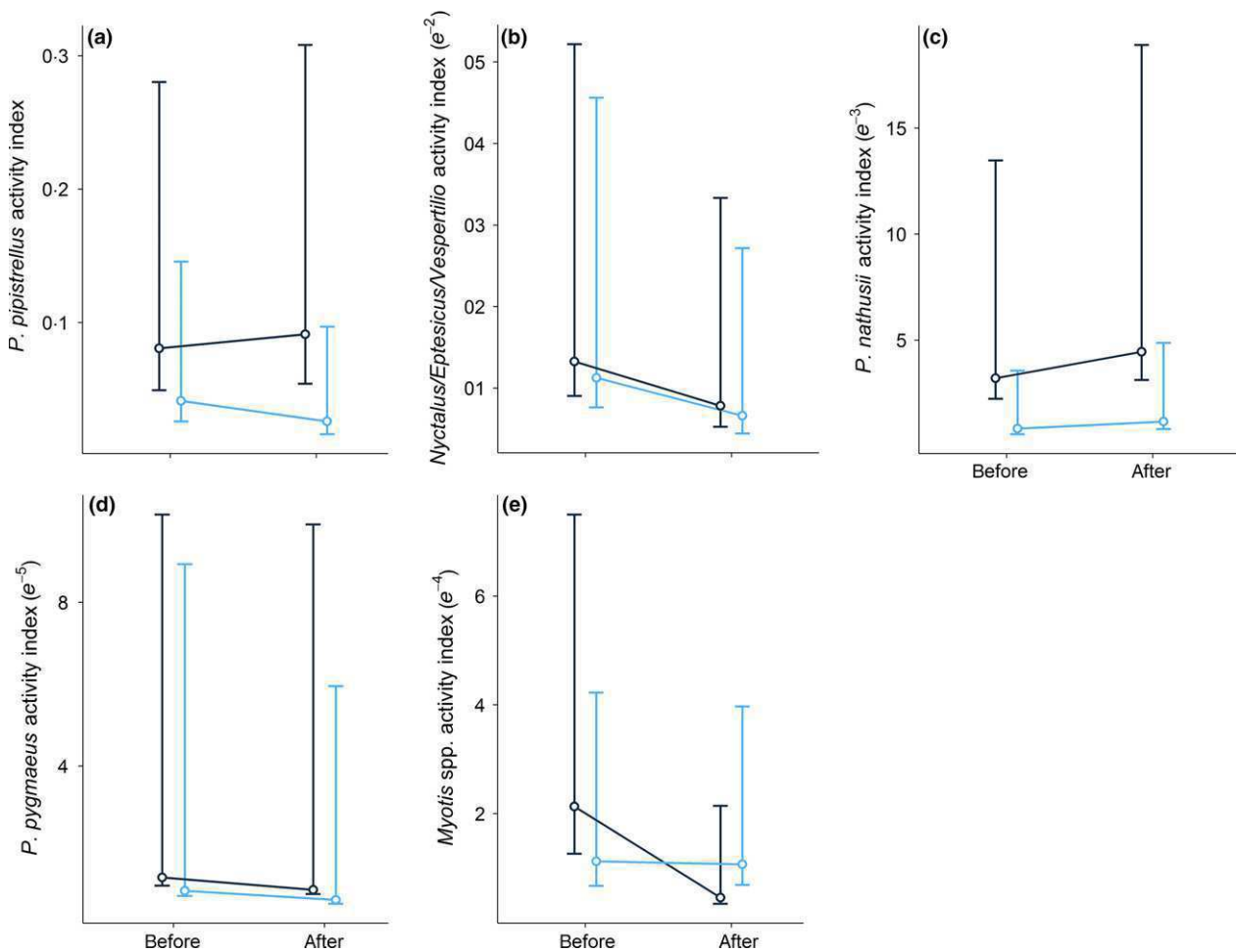


Fig. 2. Activity indices of five bat species (groups) that were recorded at urban street lights both before and after high-pressure mercury vapour (MV) illuminants of experimental lights (light blue) were replaced by light-emitting diodes, while control lamps (black) remained MV lamps throughout the entire study. Depicted are model predictions (dots) and 95% credible intervals (error bars). [Colour figure can be viewed at wileyonlinelibrary.com]

THE NEV GROUP (GENERA *NYCTALUS*, *EPTESICUS*, *VESPERTILIO*)

The interaction between season and treatment was not significant ($\chi^2 = 3.57$, d.f. = 1, $P = 0.059$). Overall, the activity dropped significantly between the first and second sampling season ($\chi^2 = 30.55$, d.f. = 1, $P < 0.001$), but bats of the NEV group were similarly active at control and experimental lamps ($\chi^2 = 0.21$, d.f. = 1, $P = 0.645$; Table 1). Illuminance level tended to affect the activity of bats in the NEV group positively, yet not significantly ($\chi^2 = 3.51$, d.f. = 1, $P = 0.061$; Table 1, Fig. 3). For instance, the activity was predicted to be 3% higher at 10 lux than at 1 lux and 41% higher at 100 lux compared with 10 lux (means over predictions made for different treatments and seasons).

PIPISTRELLUS NATHUSII

The interaction between season and treatment did not prove significant for *P. nathusii* ($\chi^2 = 1.42$, d.f. = 1, $P = 0.234$). Accordingly, the change of light type at experimental lamps did not affect *P. nathusii*'s activity. Yet, the

activity of *P. nathusii* increased between the two sampling periods ($\chi^2 = 5.32$, d.f. = 1, $P = 0.021$) and was generally higher at control than at experimental lamps ($\chi^2 = 9.25$, d.f. = 1, $P = 0.002$; Table 1, Fig. 2c). Also, the activity increased with higher illuminance levels ($\chi^2 = 4.77$, d.f. = 1, $P = 0.029$; Table 1, Fig. 3). For instance, the activity was predicted to be 6% higher at 10 lux than at 1 lux and 76% higher at 100 lux compared with 10 lux (means over predictions made for different treatments and seasons).

PIPISTRELLUS PYGMAEUS

The activity of *P. pygmaeus* was not affected by the change of light type (season \times treatment interaction: $\chi^2 = 0.27$, d.f. = 1, $P = 0.606$), sampling season ($\chi^2 = 0.20$, d.f. = 1, $P = 0.654$), treatment ($\chi^2 = 0.23$, d.f. = 1, $P = 0.630$; Fig. 2d), nor illuminance level ($\chi^2 = 0.19$, d.f. = 1, $P = 0.662$; Table 1).

MYOTIS spp.

The season \times treatment interaction was significant for *Myotis* spp. ($\chi^2 = 4.50$, d.f. = 1, $P = 0.034$), while the

Table 1. Model estimates (est.) and standard errors (SE) for the fixed effects 'season', 'treatment' (control/experimental lamps) and 'illuminance level' as well as for the interaction between 'season' and 'treatment' on bat activity. Models also included the random effect 'site' (nested in 'town') and an observation-level random effect. Control lamps remained equipped with high-pressure mercury vapour illuminants (MV) throughout the study, while the MV of experimental lamps was replaced by light-emitting diodes between the two study periods

	Est.	SE	P-value
<i>Pipistrellus pipistrellus</i>			
Intercept	-2.43	0.53	<0.001***
Season (post-replacement)	0.13	0.12	0.284
Treatment (change)	-0.71	0.47	0.129
Standardized illuminance	0.18	0.16	0.247
Season × treatment	-0.62	0.18	<0.001***
NEV			
Intercept	-4.31	0.60	<0.001
Season (post-replacement)	-0.53	0.10	<0.001***
Treatment (change)	-0.17	0.36	0.645
Standardized illuminance	0.28	0.15	0.061
<i>Pipistrellus nathusii</i>			
Intercept	-5.74	0.62	<0.001
Season (post-replacement)	0.33	0.14	0.021*
Treatment (change)	-1.36	0.45	0.002**
Standardized illuminance	0.46	0.21	0.029*
<i>Pipistrellus pygmaeus</i>			
Intercept	-11.27	0.91	<0.001***
Season (post-replacement)	-0.27	0.60	0.654
Treatment (change)	-0.29	0.61	0.630
Standardized illuminance	-0.17	0.39	0.662
<i>Myotis spp.</i>			
Intercept	-8.45	0.54	<0.001***
Season (post-replacement)	-1.55	0.57	0.006**
Treatment (change)	-0.64	0.63	0.311
Standardized illuminance	0.28	0.27	0.297
Season × treatment	1.50	0.71	0.034*

Significant effects (except intercept) are highlighted in boldface. NEV: a species group consisting of the genera *Nyctalus*, *Eptesicus* and *Vespertilio*. Significance levels: *0.05, **0.01, ***0.001

activity of *Myotis* spp. decreased at control lamps by 79%, it remained almost equal at experimental lamps (5% decrease) between the two sampling seasons (Fig. 2e). Accordingly, post-replacement activity at experimental sites was 4.5 times higher than what could be expected from the activity decrease as modelled for control lamps. This indicates that the replacement of MV lights by LEDs leads to a 4.5-fold increase in *Myotis* spp. activity. Yet, illuminance level did not affect the activity of *Myotis* spp. ($\chi^2 = 1.09$, d.f. = 1, $P = 0.297$; Table 1).

Discussion

This is the first study to show that replacing conventional MV street lights with LEDs has an impact on urban bats. Specifically, the most numerous bat species in urban habitats, *P. pipistrellus*, strongly reduced the activity at LEDs, while light-averse *Myotis* spp. increased the activity at the same sites. Given that species responded differently, the replacement of MV lamps by LEDs may cause alterations

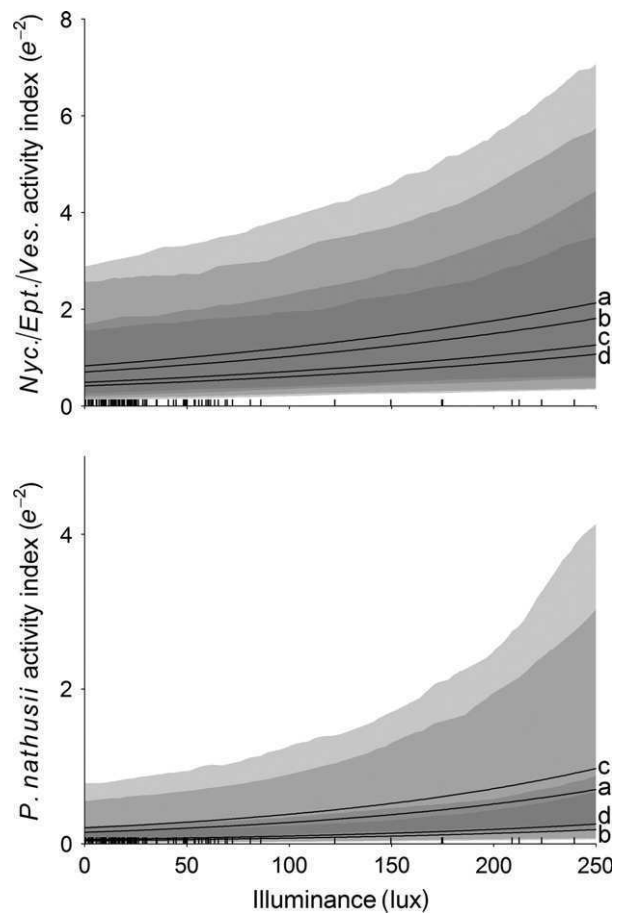


Fig. 3. Effects of illuminance on activity indices (AI) of the *Nyctalus/Eptesicus/Vespertilio* group and of *Pipistrellus nathusii*. Depicted are model predictions (solid lines) with 95% credible intervals (grey areas). Predictions are shown for the first year at control lamps (a, MV), for the first year at experimental lamps (b, MV), for the second year at control lamps (c, MV) and for the second year at experimental lamps (d, LED). Small vertical bars on x-axis indicate illuminance measurements. MV: high-pressure mercury vapour street light, LED: street light equipped with LED illuminant.

of entire urban bat ensembles. These findings are highly relevant for city planning and conservation management of urban bat ensembles not only in Germany but worldwide since LEDs are thought to become the prevailing illuminant globally by 2020 (Baumgartner *et al.* 2011).

LIGHT-TOLERANT BATS

Recent reviews suggest that bats of the genera *Pipistrellus*, *Nyctalus*, *Eptesicus* and *Vespertilio* are generally light tolerant and forage at street lights, where the activity levels depend on the lights' spectral signature (Mathews *et al.* 2015; Stone, Harris & Jones 2015; Rowse, Harris & Jones 2016; Rowse *et al.* 2016). However, at our urban recoding sites, the activity of *P. nathusii*, *P. pygmaeus* and bats of the NEV group was not affected by light type. Both *P. nathusii* and *P. pygmaeus* prefer to forage at forest edges and riparian woodland habitat (Vaughan, Jones &

Harris 1997; Ciechanowski 2015). Accordingly, we assume that the encounters of these species at our urban recording sites were mainly random passes or commuting flights and therefore not affected by light type. However, the activity of *P. nathusii* increased with illuminance level. *Pipistrellus nathusii* feeds mainly on small aquatic insects, which can be attracted several kilometres inland by artificial lights (Kovats, Ciborowski & Corkum 1996; Dietz, von Helversen & Nill 2007; Krüger *et al.* 2014). Only very bright lights are likely to attract aquatic insects from far in sufficiently high numbers, such that *P. nathusii* refrains from commuting to its normal, riparian or woodland foraging habitat to exploit those aggregations at bright lights instead. Yet, the results for *P. nathusii* should be interpreted with caution, since the automated species determination was correct in only 48% of files that were assigned *P. nathusii*.

Species of the NEV group generally fly fast and often in straight lines above the street lamps, only diving into the light cone to catch an insect (Rydell 1991; Jones & Rydell 1994). *Nyctalus noctula*, which presumably accounts for a large proportion of the recordings assigned to the NEV group, does not usually use defined foraging areas (Dietz, von Helversen & Nill 2007). Thus, bats of the NEV group have a higher potential to forage at the light types that they encounter 'by chance' than to use known local patches of high prey density in a predictable manner.

In contrast, *P. pipistrellus* often forages on small spatial scale around street lights and patrols along fixed routes (Dietz, von Helversen & Nill 2007). Thus, *P. pipistrellus* can benefit from establishing routes along MV lamps where prey is predictably available in high numbers. Accordingly, the activity of *P. pipistrellus* declined by 45% at LEDs compared with MV lamps. These results are in line with previous studies showing that the activity of light-tolerant bats at street lights strongly depends on the spectral signature, particularly the UV proportion of the emitted light. For instance, bat activity increased after a switch over from low-pressure sodium ('LPS'; no UV emission) to metal halide lamps which also emit in the UV range (Stone *et al.* 2015). Accordingly, no change in activity occurred when LPS lamps were replaced by LEDs, since none of those illuminants emit energy in the UV range (Rowse, Harris & Jones 2016). The proximate reason for the observed correlation between any light's UV emission and the activity of light-tolerant bats is most probably the availability of insects: illuminants that emit no or little energy in the short wavelength range attract fewer insects than UV-emitting illuminants such as MV lights (Huemer, Kühtreiber & Tarmann 2010; Eisenbeis & Eick 2011; Fig. S1). Accordingly, the potential benefits generally associated with MV light are reduced at LEDs and bats may shift their foraging to other sites. In a broader spatial context, light-tolerant bats may have to spend more time foraging and to invest more energy when hunting in an environment that is lit by LEDs (Geggie & Fenton 1985; Rydell 1992).

In conclusion, the expected global increase in LED street lights might prove disadvantageous for those light-tolerant bats that formerly exploited insect clusters at MV lights and might eventually even cause urban bat populations to decrease. In the long term, however, the reduced attraction of insects towards LEDs could benefit all insectivorous species if LEDs mitigate the observed declines of insect populations and, eventually, insect populations increase again in urban areas (Conrad *et al.* 2006).

LIGHT-AVERSE BATS

Myotis spp. are generally considered light averse, though we advise caution when generalizing over an entire genus (Stone, Harris & Jones 2015). Light-averse bats are typically forest-dwelling species whose short and broad wings facilitate the high manoeuvrability needed for flying in a cluttered environment but which only allow slow flight (Norberg & Rayner 1987). Possibly, their slow flight speed renders them vulnerable to visually orienting predators in the sphere of light (Stone, Harris & Jones 2015). Empirical evidence for increased predation pressure at lights is still missing and a strong influence of predators on bat behaviour is questionable, particularly for bats of the temperate zone (Lima & O'Keefe 2013). However, an echolocation system that is of limited use in open urban habitats might explain the very low number of *Myotis* spp. recordings: *Myotis* spp. use strongly frequency modulated but rather faint echolocation calls, which allow a high spatial resolution but only short-range detection of objects. Additionally, in urban habitats, bats are confronted with many other anthropogenic stressors that forest-dwelling species might find difficult to deal with, such as a lack of appropriate tree roosts, sufficient vegetation cover along commuting routes or preferred prey species.

We assume that the activity of *Myotis* spp. was not affected by illuminance levels because they primarily passed by street lights randomly or while commuting and, thus, did not make use of larger insect aggregations at brighter street lights. However, in contrast to all other species, the backfitting of MV street lights towards LEDs caused an increase in activity of *Myotis* spp. at those street lights. This finding indicates that the light emitted by LEDs is less repulsive to *Myotis* spp. than MV lights that emit more UV. For some species of the genus *Myotis*, evidence for UV sensitivity has been presented (Gorresen *et al.* 2015). Accordingly, *Myotis* spp. may perceive MV lights as brighter and, thus, as more disturbing than LEDs of the same illuminance level.

Our results suggest that light-averse bats can benefit from the global spread of LEDs: first, LEDs create less resistance than illuminants with a higher UV proportion, thus potentially allowing light-averse species to encroach further into towns and expand their habitat. Also, connectivity within the urban matrix can increase and new commuting routes and foraging habitats might become available (Hale *et al.* 2015). Secondly, a widespread

replacement of lamps with high UV light levels by LEDs might diminish the competitive advantage – the exclusive ability to forage on high-density insect aggregations at lights – for light-tolerant species. Together with improved commuting possibilities, the reduced competitive disadvantage could eventually increase the resilience of light-averse bats in urban habitats. Thirdly, the ‘vacuum cleaner’ effect, that is phototaxis of insects from far towards light, may contribute to population declines of light-averse bats (Arlettaz, Godat & Meyer 2000). Yet, LEDs induce less flight-to-light behaviour of insects than MV lights (Huemer, Kührtreiber & Tarmann 2010; Eisenbeis & Eick 2011). Accordingly, the replacement of MV lights by LEDs may increase insect availability and thus decrease competition for food among light-averse bats in remaining dark habitats, potentially fostering bat population growth. In conclusion, LEDs might help to head towards a more natural level of competition.

EFFECTS ON THE ECOSYSTEM LEVEL

Not all insects are attracted to artificial light in the same way (Acharya 1995; Altermatt, Baumeyer & Ebert 2009; van Langevelde *et al.* 2011). Hunting pressure might be particularly high for those insects gathering around artificial lights while insect species that do not behave phototactically are predated less (Svensson & Rydell 1998; Wakefield *et al.* 2015). We argue that a widespread replacement of high-UV-emitting lights by LEDs would probably not only reduce the anthropogenic impact on bats but might ultimately have far-reaching consequences for biodiversity and ecosystem functioning through cascading effects via the food web (Hölker *et al.* 2010b).

SYNTHESIS AND APPLICATIONS

Since lighting consumes about 20% of the entire global electricity, programmes to reduce energy consumption and CO₂ emissions of artificial lighting are implemented in the European Union, USA and Australia, for example (IEA; OECD/IEA 2006; EU 2009; Kyba, Hänel & Hölker 2014); many more countries are likely to follow this trend. These goals will be achieved mainly via the replacement of traditional street lamp illuminants by LEDs (Baumgartner *et al.* 2011). Our results suggest that this development might also mitigate the anthropogenic impact of artificial lighting on bats and their insect prey, specifically in areas in which LEDs replace conventional mercury vapour lamps. However, all potential benefits of LEDs could be negated if artificial lighting increases because low electricity consumption reduces running costs (Jenkins, Nordhaus & Shellenberger 2011).

Also, when compared to darkness, even LED light can affect bats and other taxa adversely (Stone, Jones & Harris 2012). Thus, as with artificial lighting in general, LED light should also be avoided if not necessary. Most of outdoor lighting runs all night long at full intensity. In contrast to

conventional illuminants, intensity of LEDs can be adjusted offering more flexibility concerning their usage; LEDs do not need a ‘warm-up’ time, but instantaneously operate at full efficiency (Gaston *et al.* 2012; Kyba, Hänel & Hölker 2014). Together with motion sensors, it is possible to run LEDs at minimal level and only increase intensity when actually needed. In that way, light pollution could be reduced tremendously, particularly in suburban and rural areas where human activity is low at night.

When artificial light needs to be used, its intensity should be limited to a level that does not exceed its purpose. Maximum levels for activities such as walking or driving a car urgently need to be defined. Kyba, Hänel & Hölker (2014) even argue that street lighting is no longer necessary on all urban roads, since modern automobile headlights suffice to warrant traffic safety. Further, Mathews *et al.* (2015) make the important point that ‘the UV component of artificial lighting is non-functional for humans and could be removed without loss while delivering potential benefits to a wide range of invertebrates and bats’.

Due to policy restrictions on the use of inefficient lighting techniques and their respective phase-out, a period of widespread change of installed street light types has just begun, in which tens of millions of street lamps will be installed and probably not replaced for decades (Kyba, Hänel & Hölker 2014). Thus, now more than ever we have the chance to reduce the ecological impact of street lighting.

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Data accessibility

Underlying data are available at Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.37rt1> (Lewanzik & Voigt 2016).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Overview of the urban areas sampled across Germany.

Fig. S2. Spectral composition of different illuminants commonly used for street lighting.

Fig. S3. Comparison of evening and entire night bat activity.

Supplementary Material

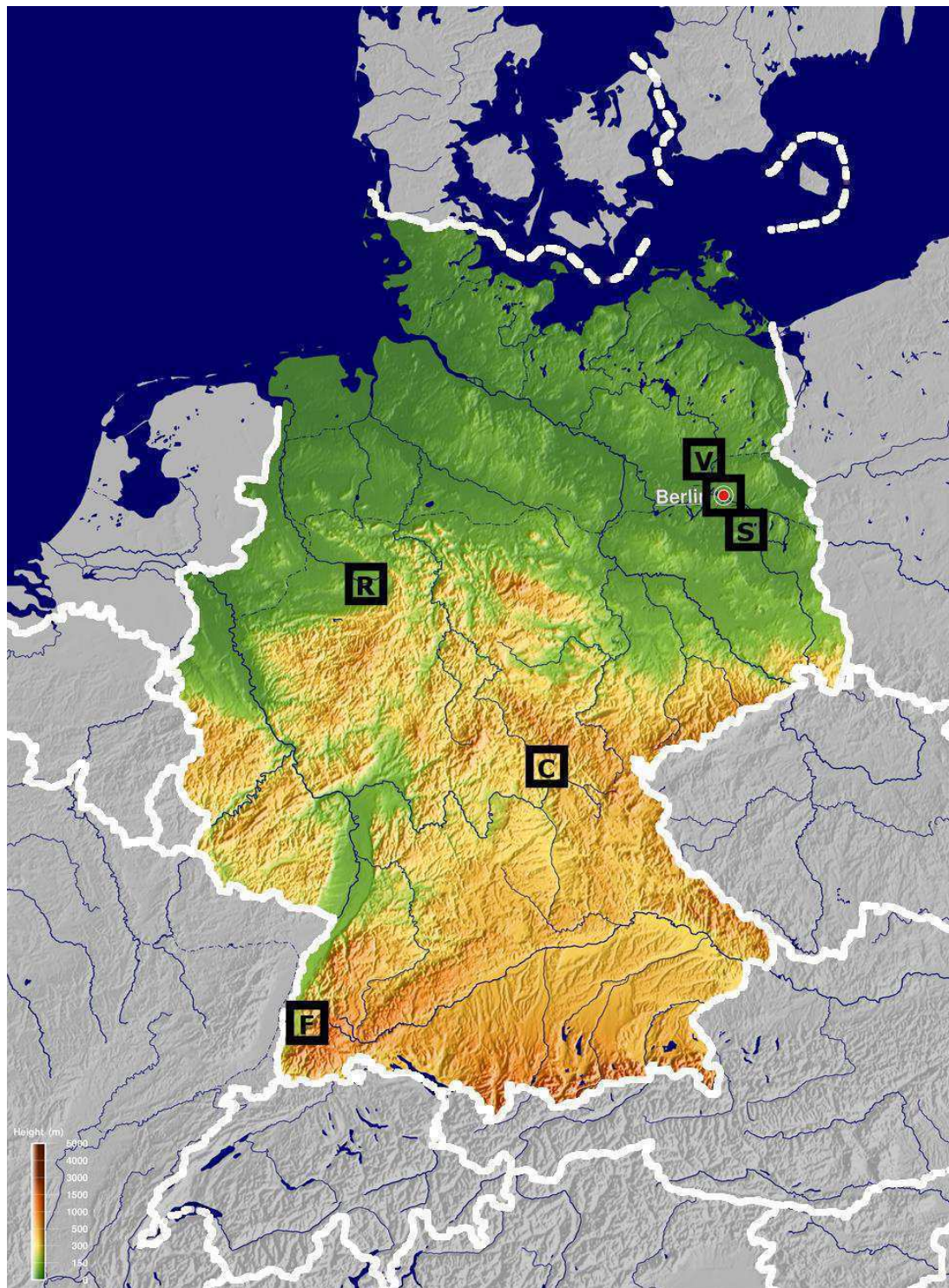


Fig. S1: Overview of the urban areas sampled across Germany. C: Coburg, F: Freiburg, R: Rietberg, S: Schulzendorf, red dot: Berlin. The underlying map was created by the GinkgoMaps project, is licensed under the CC-BY-3.0 and online available at <http://ginkgomaps.com>.

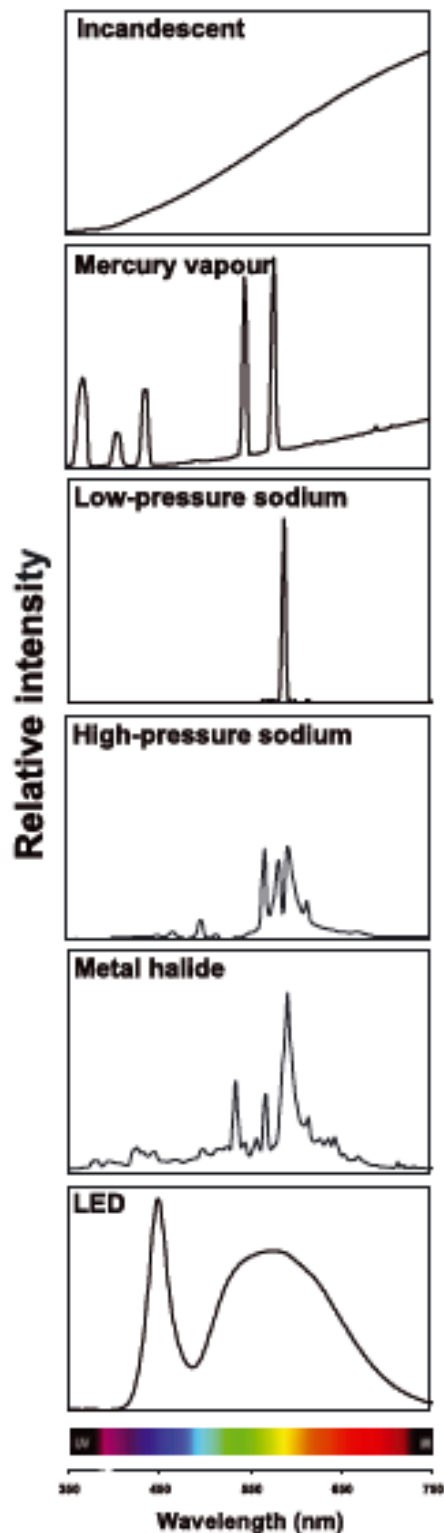


Fig. S2: Spectral composition of different illuminants commonly used for street lighting. UV light is at the short wavelength end of the spectrum and mainly present in mercury vapour light. From Gaston, K.J., Bennie, J., Davies, T.W. & Hopkins, J. (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological Reviews*, **88**, 912-927.

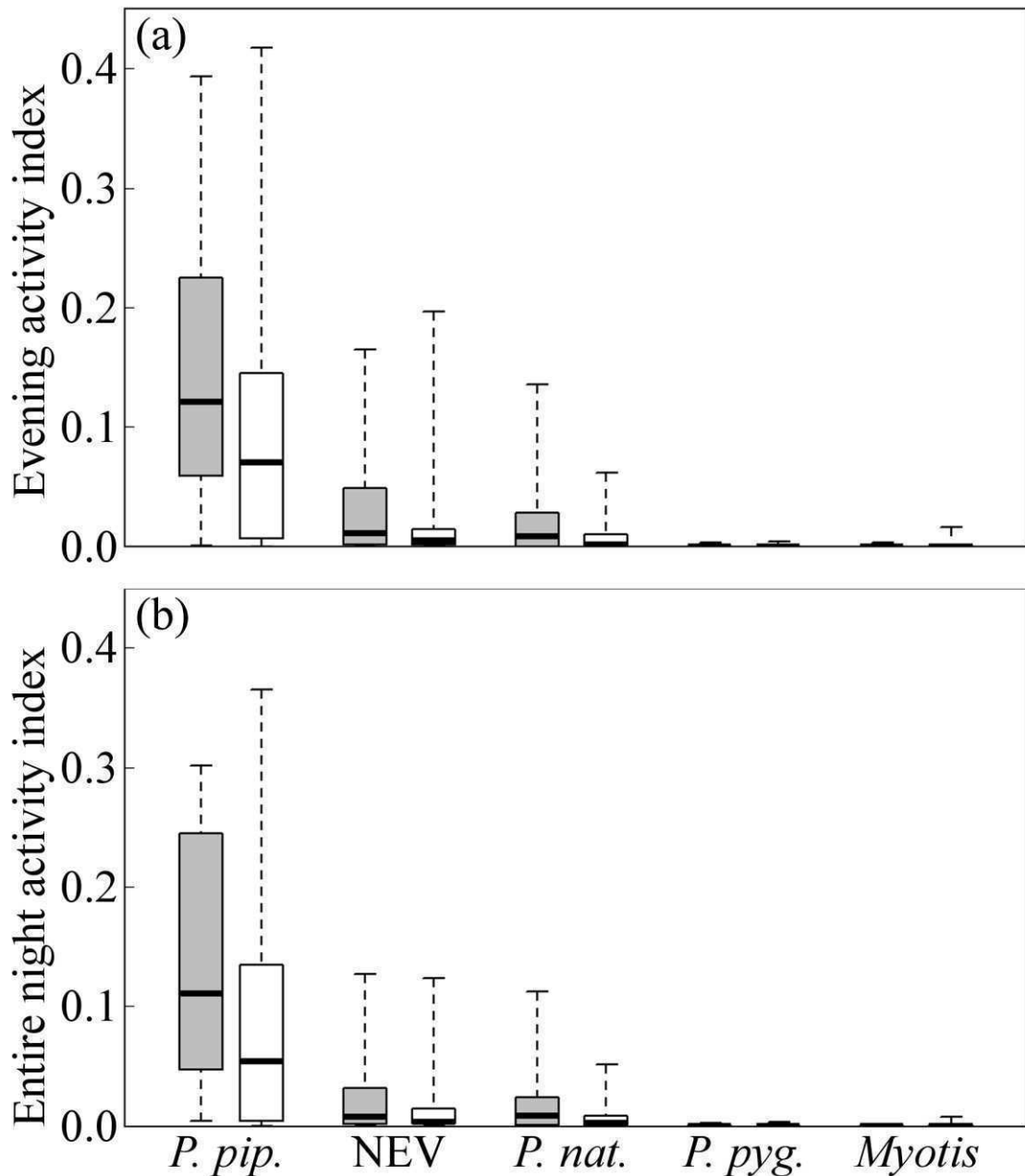


Fig. S3: Comparison of (a) evening bat activity (until 3.5 hours after sunset) and (b) entire night bat activity. Activity is presented as activity index (number of minutes with activity per number of recorded minutes), calculated from recordings made at 21 mercury vapour (MV) and 25 LED street lamps (grey resp. white) during the second sampling season. Black lines indicate medians, lower and upper box margins represent 25% resp. 75% quartiles and whiskers illustrate smallest resp. largest values. *P. pip.*: *Pipistrellus pipistrellus*; NEV: a species group consisting of the genera *Nyctalus*, *Eptesicus*, and *Vespertilio*; *P. nat.*: *Pipistrellus nathusii*; *P. pyg.*: *Pipistrellus pygmaeus*; *Myotis*: *Myotis spp.*

7. General Discussion

It is now widely recognized that anthropogenic environmental impacts are overriding natural processes that have dominated our planet for millions of years (Steffen et al. 2011). Particularly, artificial light – one of the most universal human-induced pollutants – affects bats species-specifically in space and time and, thus, causes an imbalance between light-averse species and those foraging at street lights (chapter 1 through 3).

In chapter 1, I showed that street lighting reduces the harvesting activity of frugivorous bats in the Neotropics and I elucidate the far-reaching consequences for tropical ecosystems. By demonstrating that LED street lights can reduce the anthropogenic impact on bats in urban environments I could significantly contribute to our understanding of how the expected alterations of the global ‘street light scape’ will affect urban bat communities (chapter 3).

In the following, I first discuss the causes of why bats are attracted to or repelled by artificial light, and use my own species-specific results of chapter 2 and chapter 3 and findings of other published studies to draw more general patterns. Then, I elaborate on the consequences that artificial light may have for bats’ spatiotemporal dynamics, bat conservation and eventually for ecosystems and human economies.

7.1. Causes of species-specific light avoidance and attraction

7.1.1. Light avoidance

Evidence mostly from Europe and North America suggest that particularly slow-flying gleaning bats, such as long-eared bats (*Plecotus* spp.) and most mouse-eared bats (*Myotis* spp.), as well as flutter-detecting horseshoe bats (*Rhinolophus* spp.) are light-averse; these species are rarely ever recorded in the vicinity of artificial light (Rydell 1992; Jones & Rydell 1994; Stone, Jones & Harris 2012; Mathews et al. 2015; Stone, Harris & Jones 2015; chapter 3). Yet, these forest-dwelling and gleaning species are probably underrepresented in acoustic studies due to their rather faint echolocation calls, especially when being compared with loud open-space foragers. However, evidence for light avoidance does not only come from studies acoustically comparing activity of light-averse and light-tolerant species at lights. Several studies measured bat activity before and after the installation of new lights (e.g. chapter 2), or before and after the changeover

from one light type to another (e.g. chapter 3). If no other factor than the light treatment is altered, the probability of recording a given species only depends on the treatment. *Rhinolophus hipposideros* and *Myotis* spp., for instance, cease foraging and commuting in areas that become illuminated, and *Myotis* spp. increase activity following the switch-over from MV to LED light even when the surroundings of the monitored street lights are otherwise not altered (Kuijper et al. 2008; Stone, Jones & Harris 2009 & 2012; chapter 3).

In chapter 2, I demonstrated for the first time that not only temperate insectivorous but also Neotropical frugivorous bats forage less in lit than in naturally dark environments. Hence, it seems to be a general principle across climatic zones and feeding guilds that slow-flying and forest-dwelling bat species behave in a light-averse manner. The ultimate and proximate causes behind light avoidance are still not entirely clear (Rydell 2006). Artificial light has a strong impact on both flying insects and ground-dwelling arthropods. Theoretically, a diminished abundance of prey species at artificial lights could explain the reduced activity of light-averse bats there. However, numbers of most insects and ground-dwelling arthropods are higher at lights; only very few taxa such as wolf spiders occur in smaller numbers at lights than elsewhere (Eisenbeis 2006; Frank 2006; Davies, Bennie and Gaston 2012). Moreover, bats usually forage opportunistically and feed on every non-poisonous arthropod they can detect and capture with the sensory system and morphology they are equipped with (Dietz, von Helversen & Nill 2007). Thus, in terms of prey availability, both aerial-hawking and gleaning insectivorous bats should generally benefit from foraging around artificial lights. Nevertheless, light-averse insectivorous bats cease foraging in response to the installation of lights although prey abundance often increases at the same time (Kuijper et al. 2008). Similarly, fruit-eating species do not harvest fruits in lighted surroundings even when available (chapter 2). These results indicate that factors other than food availability also play an important role in explaining the light avoidance behaviour of many bats. Potentially, bats avoid artificial light due to increased predation pressure and/or interference with their visual system.

7.1.1.1 Predation pressure

A major drawback of foraging around lights is the better visibility to predators. The slow flight of gleaning and flutter-detecting bats renders them vulnerable to predation in lighted surroundings (Speakman 1991; Rydell, Entwistle & Racey 1996; Stone, Jones & Harris 2009 & 2012; chapter 1). Presumably, the orientation and targeting capabilities of bat predators that rely on visual cues are better in lit surroundings. Empirical evidence for

increased predation pressure on bats at street lights is still lacking. However, an increased exposure to predators under naturally lit conditions is reflected by the fact that many tropical bat species exhibit strong lunar phobia. Those bats reduce foraging activity or fly closer to protective vegetation during nights with bright moonlight than during darker nights (Lima & O'Keefe 2013). Additionally, many diurnal species extend their activity into the night in artificially lit environments (Gaston et al. 2013). Thus, at lights both nocturnal and diurnal predators threaten bats simultaneously.

Even for bat predators that do not benefit from increased targeting capabilities in lit surroundings, hunting at artificial lights might still be advantageous if bats' orientation is impaired at lights (see 7.1.1.2) or if the presence of bats is more predictable and bat density higher than elsewhere (Rydell 2006). For instance, snakes have been observed hunting bats that reliably show up in large numbers at salt licks (pers. communication, S. J. Ghanem) and during the evening emergence at the exit of cave roosts (pers. observations). Given that the probability of encountering light-tolerant bats is also higher at artificial lights than elsewhere bat predators could specialise on hunting bats there.

In the temperate climate zone, bats are usually not lunar phobic, suggesting that they do not deal routinely with visually-oriented nocturnal predators (Lima & O'Keefe 2013). Yet, also in temperate latitudes, bats suffer predation by birds of prey when foraging already during twilight conditions (pers. observations). In fact, most observations of predation on bats were related to diurnal predators hunting in reasonable light conditions (Lima & O'Keefe 2013). Speakman (1991) estimated that in temperate climate regions the predation rate on bats is 100 – 1000 times higher during daylight than at night. Consequently, the emergence timing of insectivorous bats is shaped by a trade-off between food availability and predation risk. Insect abundance often peaks before sunset and declines substantially thereafter, but bats emerging early suffer the highest predation pressure (Rodríguez-Durán & Lewis 1987; Fenton et al. 1994; Jones & Rydell 1994; Speakman, Stone & Kerslake 1995; Rydell, Entwistle & Racey 1996; Duvergé et al. 2000). An increased predation risk when emerging already at relatively high natural light levels at dusk might have led to the evolution of an intrinsic light avoidance. This assumption is supported by the fact that species which do not depend on the activity peak of most insects at dusk emerge only late from their day roost; for instance, gleaning species like *Plecotus auritus* and moths specialists like *Barbastella barbastellus*.

The intrinsic 'fear of light' could cause the perceived predation risk to be higher at artificial lights at night than in dark habitats even if the actual predation risk is not.

Similarly, the perceived predation risk probably increases with light intensity. Since the suborder Yangochiroptera possess genes for UV-sensitive photo pigments, these bats possibly discriminate lights that do not emit UV as less bright and thus less ‘risky’ than UV-emitting lights (Zhao et al. 2009). This notion could explain why *Myotis* spp. increased activity more than four-fold after the replacement of mercury vapour street lights by LED lamps (chapter 3). If perceived as brighter than other lamps, UV-emitting mercury vapour lights could cause more blinding.

7.1.1.2 Blinding

Kim et al. (2008) postulated that the presence of cone photoreceptors in bat retinas might equip bats with the ability of vision at photopic light levels, i.e. at levels where mammalian cones usually operate. However, experimental studies show that cones in retinas of Microchiroptera become saturated at photopic levels and, at maximum, contribute to vision at mesopic light levels (Müller et al. 2009). The absolute light level at which the retina saturates correlates with the species’ average exposition to light in the roost and when foraging (Hope & Bhatnagar 1979). The retina of *Myotis myotis*, for example, saturates after test flashes of only 10 times electroretinogram threshold; photopic level flashes (10,000 times threshold) resulted in long-lasting total depression of retinal activity for several minutes. Similarly, after extended exposition to the light used while setting up the experiment, the *M. myotis* retina needed to be in darkness for hours before any electroretinogram response was measurable (Dieterich & Dodt 1970; but see Hope & Bhatnagar 1979).

The findings of those physiological studies are corroborated by behavioural experiments: the insectivorous bat *Eptesicus fuscus* discriminates between brightness cues best at around 10 lx, i.e. at levels which typically occur at dusk and dawn, and its performance remains good until as low as 0.001 lx (Ellins & Masterson 1974). Similarly, *Myotis lucifugus* crashes into obstacles more often under daylight than under dim light conditions (Bradbury & Nottebohm 1969). Great fruit-eating bats *Artibeus lituratus* are even better able to detect food items in scatter under low illumination resembling full moon levels than under twilight illumination (Gutierrez et al. 2014).

Taken together, those studies suggest that the comparably high light levels at street lights are likely to impair bats’ vision. Even though bats are able to fly in total darkness using exclusively their biosonar, they use vision as well when possible. Vision aids bats in long-distance navigation, predator surveillance, obstacle avoidance and, in

some species, prey detection (Davis & Barbour 1965; Eklöf 2003). Thus, in addition to increased (perceived) predation pressure at lights, light-averse bats probably avoid artificial light because it compromises their vision, too.

7.1.2. Attraction towards artificial light

Relatively fast-flying aerial-hawking bats with long-range biosonar are generally more tolerant towards artificial light. Many of those species even forage on insect aggregations at street lights (Rydell 1992; Mathews et al. 2015; Stone, Harris & Jones 2015; chapter 1 & 2). Those light-tolerant species usually emerge rather early from their day roost (Jones & Rydell 1994; Rydell, Entwistle & Racey 1996). They predominantly feed on small aerial prey, such as dipterans and other insect taxa whose activity drops markedly after dusk (Jones & Rydell 1994; Rydell, Entwistle & Racey 1996; Duvergé et al. 2000). For these light-tolerant species, the benefits of foraging early at considerable light levels must outweigh the cost of an increased risk of predation by diurnal raptors. Probably, the high flight speed of most aerial-hawking bats lowers their predation risk at dusk as well as in the sphere of artificial light (Jones & Rydell 1994; Mathews et al. 2015; Stone, Harris & Jones 2015; chapter 1).

In general, lights emitting UV attract significantly more insects than lights that do not contain UV (Eisenbeis 2006; Eisenbeis & Eick 2011; van Langevelde et al. 2011; Shimoda & Honda 2013; van Grunsven et al. 2014; Longcore et al. 2015; chapter 1). The observed activity pattern of light-tolerant bats at artificial lights usually matches well that pattern of insect density (Haffner & Stutz 1985). Light-tolerant bats are more active at UV-emitting lamps than at lights whose spectra do not contain UV (Rydell 1992; Blake et al. 1994; Rydell & Racey 1995; Stone et al. 2015; chapter 3). Further, their activity often does not differ between light types that have no or only negligible UV emission, such as LED and LPS (Rowse, Harris & Jones 2016). In conclusion, the activity level of light-tolerant bats at artificial lights is mainly determined by the wavelength-dependant phototaxis of their prey insects (Mathews et al. 2015; Stone, Harris & Jones 2015; chapter 1).

7.1.3 Light avoidance of ‘light-tolerant’ species

The term ‘light-tolerant’ might be misleading, since the tolerance is mostly limited to foraging on insect clusters at lights. *Pipistrellus pipistrellus*, for instance, is the most common species in many central European urban areas and forages preferentially at street lights (Rydell & Racey 1995; Hale et al. 2012 & 2015; Mathews et al. 2015; Stone et al.

2015; chapter 3). When commuting, however, *P. pipistrellus* behaves light-averse (Hale et al. 2015). Similarly, bats - also 'light-tolerant' species - are disturbed by artificial light at their roost, where it delays emergence (Downs et al. 2003; Boldogh, Dobrosi & Samu 2007). Except for foraging contexts, 'light-tolerant' species behave very much like light-averse ones. Their light avoidance is a function of their spectral sensitivity as well as the light's power spectrum and intensity. Shorter wavelengths (UV and 'blue') are more repelling than longer ('red') ones, but the effect of overall intensity is larger than the effect of light colour (Downs et al. 2003) This suggests that the magnitude of light aversion correlates with the perceived brightness of a light, which in turn depends on the power spectrum of the light.

Yet, the effect of artificial light on 'light-tolerant' bats is more complex than either attraction when foraging or aversion otherwise: activity of *P. pipistrellus*, *P. pygmaeus* and *Nyctalus/Eptesicus* spp. was not different between dark control nights and nights in which LED street lights were switched on in a rural habitat (Stone, Jones & Harris 2012). Similarly, bat activity is not higher at LPS lights than at dark control transects (Blake et al. 1994; Rydell & Racey 1995). Those studies further corroborate that bat activity at lights is the result of a trade-off between an intrinsic light-aversion and insect-related attraction. Given that LEDs do not attract insects in large numbers and LPS lights might not attract any insects (Rydell 1992; Eisenbeis & Eick 2011), low insect numbers do not seem to outweigh the light's repelling force. Similarly, *P. pygmaeus*, did not change its activity in response to the change-over from MV to LED street lighting in urban habitats (chapter 3). This species forages preferentially in riparian woodland habitats. Thus, I assume that at our urban recording sites *P. pygmaeus* were mainly commuting and therefore behaving light-averse (chapter 3); either they were not foraging at all and similarly repelled by both light types or a stronger aversion of UV-emitting MV lights was balanced by a higher insect availability there. As a result the overall activity did not differ between light types when commuting. This conclusion is supported by the finding that without tree cover, activity of 'light-tolerant' bats can be lower along lit than along unlit transects (Mathews et al. 2015). Here, the trade-off between benefits (higher insect availability) and disadvantages (blinding, predation risk) when foraging at lights seems to be dominated by the latter.

7.2. Consequences of artificial light for bats

7.2.1. Improved foraging opportunities

At artificial lights, particularly at UV-emitting light sources, opportunistically light-tolerant bats benefit not only from increased insect densities but also from high spatial prey predictability. Thus, insect clusters at lights are more profitable to exploit than dispersed insects (Stephens & Krebs 1986; chapter 1). Bats have to invest less time and, thus, energy for commuting and foraging when exploiting high-density insect aggregations at known street lights (Geggie & Fenton 1985; Salcedo et al. 1995; Hickey & Fenton 1996). As a consequence, the gross energy intake of *Eptesicus nilssonii*, for instance, is more than twice as high when foraging at street lamps instead of in woodlands (Rydell 1992). At the same time, bats that exploit insect aggregations at lights can spend significantly more time in their roost. Thereby, they reduce their risk of predation (“refuge effect”), since bats are rarely preyed on in the roost but mostly on the wing (Geggie & Fenton 1985; Lima & O’Keefe 2013). Moth-eating species can additionally take advantage of diminished moths’ escape responses at artificial lights and increase their capture success in that way (Svensson & Rydell 1998; Acharya & Fenton 1999; Wakefield et al. 2015). Even the small *P. pipistrellus*, which commonly forages mainly on small diptera (Dietz, von Helversen & Nill 2007), can include a large proportion of moths in its diet when accessible (Arlettaz, Godat & Meyer 2000). Recent evidence even suggests that the skull size of *Pipistrellus kuhlii* increased in response to the spread of artificial light and an associated shift in *P. kuhlii*’s diet from small-sized, soft-bodied dipterans to larger, harder-bodied moths (Tomassini et al. 2014). Thus, at street lights bats can potentially focus their foraging efforts on preferred and large prey and further increase their foraging efficiency. Presumably, a higher benefit-cost ratio when foraging on dense insect aggregations at artificial lights increases the fitness of opportunistically light-tolerant bats and could eventually foster population growth. Arlettaz et al. (1999; as cited in Arlettaz, Godat & Meyer 2000) speculated, for example, that the massive range expansion they documented for *P. pipistrellus* in Switzerland was related to its tendency to forage at street lights. On the other hand, artificial lighting might contribute to global insect population declines and could therefore be disadvantageous for opportunistically light-tolerant bats in the long-term (Frank 1988; Conrad et al. 2006; Fox 2013).

7.2.2 Detrimental effects on commuting, foraging, and roosting bats

Artificial light disturbs light-averse bats along commuting routes (Kuijper et al. 2008; Stone, Jones & Harris 2009 & 2012; chapter 1). For instance, when commuting routes of *Myotis dasycneme* became experimentally illuminated they hesitated and flew back and forth before passing the lights (Kuijper et al. 2008). Thereby, they increased commuting costs and potentially missed out on foraging opportunities. Similarly, activity of other *Myotis* spp. and of horseshoe bats decreased tremendously and commenced substantially later at lit compared with unlit commuting routes (Stone, Jones & Harris 2009 & 2012). When arrival time at foraging areas is delayed, bats have less time for foraging. Ultimately, delayed foraging could result in reduced energy intake. Also, if their commuting route becomes illuminated and no equally suitable routes are available, bats have to use suboptimal routes, thereby expending more energy or being more exposed to predators. Since low aspect ratio wings have lower flight efficiencies and higher flight costs when commuting than higher aspect ratio wings (Norberg & Rayner 1987), commuting costs increase particularly for light-averse species. In the worst case scenario, if no alternative commuting route is available, foraging habitats could effectively become inaccessible and bats would be restricted to lower quality foraging grounds. Importantly, not only light-averse species but probably most bats avoid artificial light along commuting routes (see 7.1.3).

Similarly, roads *per se* constitute a barrier for bats that are reluctant to traverse open space without vegetation cover (Altringham & Kerth 2016). Street lights probably pronounce that barrier effect and extend it to more species that might otherwise cross open gaps without artificial lighting. *Carollia sowelli*, for instance, commonly forages on fruits that grow in edge habitats, gaps and large open clearings but cease foraging there if those areas become lit (chapter 2). Thus, street lights likely contribute to habitat fragmentation and lower the sustainable population size (Altringham & Kerth 2016). Specifically, a lit road might reduce the gene flow between populations and eventually decrease their resilience. As a result of fragmentation, particularly less mobile bat species may suffer pronounced genetic erosion (Meyer, Kalko & Kerth 2009). Further, if lit roads limit the size of foraging areas, they might reduce the reproductive success of bats (Kerth & Melber 2009). Additionally, barriers like lit roads reduce the recruitment of individuals from neighbouring populations and thus slow down the recovery from local population declines, eventually increasing the local extinction risk (Altringham & Kerth 2016). Notably, those species that cope the worst with light pollution, i.e. species with short and

broad (and thus low aspect ratio) wings adapted to cluttered habitats, are also the ones that already face the highest extinction risk (Jones, Purvis & Gittleman 2003; Safi & Kerth 2004). *Plecotus auritus* and *Myotis emarginatus*, for example, forage within a radius of less than 2 km; such small foraging ranges likely reduce recolonization of empty patches and increase the probability of metapopulation extinctions (Jones, Duvergé & Ransome 1995; Jones, Purvis & Gittleman 2003). Yet, also on a global scale, species with low aspect ratio wings, such as megadermatids, hipposiderids, rhinolophids, and phyllostomids, generally have smaller foraging ranges, smaller colony sizes and low intercolony exchange rates, all of which contribute to an increased extinction risk (Jones, Purvis & Gittleman 2003).

Both fragmentation and habitat loss are among the greatest threats to global biodiversity and contributed significantly to the dramatic population declines observed for many bat species during the last century (Hilton-Taylor 2000; Hutson, Mickleburgh & Racey 2001; Jones et al. 2009). Besides fragmenting habitats and affecting accessibility to foraging areas, artificial light can also reduce the size of the actual foraging areas. For example, both temperate-zone insectivorous *Myotis dasycneme* (Vespertilionidae) and Neotropical frugivorous *Carollia sowelli* (Phyllostomidae) strongly reduce foraging in areas that become lit, even when the insect availability increases or ripe fruits are available, respectively (Kuijper et al. 2008; chapter 2). Thus, the effective foraging habitat size shrinks due to artificial lighting. That may have no fitness consequences, if, for example, bats can switch to equally suitable alternative habitats nearby (Rowse, Harris & Jones 2016). However, those alternative foraging habitats are probably already occupied by other bats and competition increases. Indeed, increased competition in adjacent dark areas is a likely explanation for why *C. sowelli* – a specialist of fruits of the genus *Piper* – eventually did harvest some fruits under street lights but about two hours later than in a naturally dark environment (chapter 2).

Importantly, habitats do not only become locally unsuitable as a consequence of direct illumination, but potentially also on a much larger spatial scale when sky glow increases light levels over large areas (Kyba et al. 2011). Even protected areas can experience light pollution as a consequence of sky glow from distant urbanisation (Gaston, Duffy & Bennie 2015). Notably, already very low light levels of on average 1.9 lx can affect bat community structure (Lacoeuilhe et al. 2014): *P. pipistrellus*, *P. pygmaeus*, *P. kuhlii*, *Eptesicus serotinus* and *Nyctalus noctula* were more active at sites

with relatively higher light intensity, while light intensity had a negative effect on activity of *N. leisleri*, *Myotis spp.* and *Plecotus spp.*

Sky glow can further mask natural rhythms of lunar sky brightness and, thus, disrupt for instance patterns of foraging and mating (Davies et al. 2013). Clouds can additionally amplify sky glow. At a rural location 32 km from the centre of Berlin (Germany), for example, the luminance increased more than 10-fold during overcast compared with clear nights and reached 1.4 mcd/m² (Kyba et al. 2011). This luminance level resembles sky luminance at the end of nautical twilight in unpolluted areas (Falchi et al. 2016). Thus, the ‘artificial twilight’ caused by sky glow masks the true night. Yet, very low light levels as experienced during full moon nights, i.e. around 0.1 lx, are already high enough to affect bat activity. First, many bats are lunar phobic, i.e. they strongly reduce their foraging activity or alter their movement patterns outside the roost during full-moon nights (Lima & O’Keefe 2013). Lunar phobia in bats is a direct effect of the elevated light intensity rather than the moon *per se* (Haeussler & Erkert 1978; but see Lang et al. 2006). Light levels from sky glow may therefore be high enough to considerably reduce activity of lunar phobic bats. Second, lunar cycles constitute an environmental *Zeitgeber* that plays an important role in circannual cycles, e.g. in timing of reproduction, and that is potentially involved in entraining the circadian rhythm (Beier 2006). An illuminance as low as 10⁻⁵ lx was sufficient for the entrainment of circadian rhythm of *Molossus molossus* in the lab; the lowest threshold value for photic entrainment in vertebrates (Erkert 2004). Given that an increasing part of the globe’s surface is exposed to light levels resembling twilight, it becomes obvious that artificial light affects bats on a very large spatial scale (Falchi et al. 2016).

When artificial light causes bats to use suboptimal commuting routes and foraging grounds or when increased artificial light levels reduce bats’ foraging efficiency due to ‘artificial lunar phobia’ or due to a circadian mismatch, the increase in energy expenditure and the reduced energy gain, respectively, are likely to translate into reduced resilience, decreased fitness and eventually population declines. Furthermore, the low reproductive rate of bats hinders quick recovery from population declines, making bats particularly susceptible to anthropogenic disturbance (Voigt & Kingston 2016).

7.3 Cascading effects at the ecosystem level

Bats interact with a large number of species from different taxa, primarily by acting as predators but also as prey. Given that the diet of the global bat fauna is extraordinarily diverse – ranging from insects, amphibians, birds and mammals to fruits, pollen and nectar – the biotic interactions are as manifold. Accordingly, when artificial light alters bat behaviour or community structure, it will eventually have cascading effects on the entire ecosystem. In the temperate climate zone, for instance, bats eliminate enormous numbers of herbivorous insects, many of which are considered pest species (Kunz et al. 2011; Ghanem & Voigt 2012). Boyles et al. (2011) estimated that the monetary value of bats to the agricultural industry of the continental United States equals \$3.7 – \$53 billion/year. Consequently, even a small negative effect of artificial light on the pest control ecosystem service that bats provide could eventually cause significant expenses in the agricultural sector. Presumably, the impact of artificial light on bat-mediated ecosystem services is even larger in tropical regions where numerous frugivorous and nectarivorous species function as pollinators and seed dispersers of a multitude of ecologically and economically important plants (Kunz et al. 2011; Ghanem & Voigt 2012). Further, they promote secondary succession and regeneration of disturbed areas by dispersing pioneer plants into open areas (Fleming 1988; Medellin & Gaona 1999). For these reasons, the order Chiroptera is considered a keystone taxon in the tropics (Willig et al. 2007). However, my findings of chapter 2 suggest that artificial light could reduce bat-mediated seed-dispersal when frugivorous species avoid lit areas and the plants within them. Eventually, diminished seed dispersal could slow-down reforestation of cleared tropical habitats, such as abandoned pastures, and result in pronounced land erosion.

Besides those direct effects on pest insect control, pollination, and seed-dispersal, artificial light can also indirectly reduce ecosystem services that are not mediated by bats. For example, moths often constitute the most numerous insect taxa at artificial lights. Yet, at lights eared moths do not show the evasive flight manoeuvres, which otherwise substantially increase their survival probability when being attacked by bats (Svensson & Rydell 1998; Acharya & Fenton 1999; Wakefield et al. 2015). Hence, at artificial lights bats prey more on moths than they do in a non-lit habitat (Belwood & Fullard 1984; Hickey & Fenton 1990; Acharya & Fenton 1999). This selective predation might eventually alter the local flora since moths constitute major nocturnal pollinators (Macgregor et al. 2015). It has already been demonstrated that pollination by moths is diminished in the vicinity of artificial lights due to reduced moth abundance at ground

level (Macgregor et al. 2016). Additionally, pollination by moths might be further lowered on a larger spatial scale if selective predation of bats on moths at artificial lights reduces moth population sizes. A reduced number of pollinators might cause changes in the plant community, which then probably would affect other species that depend on particular plant species. Thus, entire food web dynamics could be altered when light-tolerant bats selectively forage on those insect species that gather around artificial lights, but neglect others (Hölker et al. 2010).

7.4 Mitigation measures

Several simple measures have been proposed to minimise adverse effects of artificial light. In short, light should only be employed where and when it is truly necessary, intensity should be limited to the indispensable minimum, light trespass needs to be reduced by precisely directing light only to the intended target and, lastly, those light spectra with the least negative ecological consequences need to be used (for details see e.g. Gaston et al. 2012; Kyba, Hänel & Hölker 2014; chapter 1 through 3).

Yet, not every mitigation measure is as effective as intended. For instance, many municipalities have implemented part-night lighting schemes and switch off public lighting when human activity is low. Those regimes, however, seem only partially effective in reducing the adverse effects of public lights on bats. Many bats particularly forage during the first hours after sunset when part-night lighting schemes do not yet take effect (Jones & Rydell 1994; Azam et al. 2015; Day et al. 2015). While late-emerging species could potentially benefit from part-night lighting schemes, they do not necessarily do either. *Myotis* spp., for example, did not significantly increase activity during part-night lighting compared with full-night lighting schemes (Azam et al. 2015). Thus, the effect of part-night lighting schemes on bat activity might be species-specific and depends on latitude and season, as well as probably the local environment. This example emphasizes that the ecological effectiveness of any mitigation measure needs to be carefully monitored instead of only assumed.

Similarly, it is unlikely that only reducing light intensity would suffice to mitigate adverse effects of artificial light on bats. The lowest light level that still enables humans to orientate and that meets legislations for minimum illuminance is probably not sufficiently low for light-averse bats to not be repelled. Several bat species avoid even very low light levels, for instance 4.5 lx (chapter 2), 3.6 lx (Stone, Jones & Harris 2012),

3.2 lx (Kuijper et al. 2008) and 1.9 lx (Lacoeuilhe et al. 2014). For comparison, those levels are all lower than the average street level illuminance of residential side streets, which is about 5 lx (Gaston et al. 2013) and well below the average level measured at urban street lights in chapter 3, which was about 40 lx. Thus, it is crucial to retain existing dark corridors without any artificial lighting and – where lighting interrupts connectivity – to re-establish connectivity by creating new dark corridors. These dark corridors should be protected and established not only in rural habitats but particularly in otherwise heavily lit urban environments, since also urban-tolerant species like *P. pipistrellus* choose dark areas for commuting and avoid lit gaps (Gaston et al. 2012; Hale et al. 2015). First and foremost, since the knowledge of the effects of artificial light on wildlife is still very limited, the precautionary principle should be adopted and the use of artificial light limited as much as possible in space and time.

7.5 Conclusion

Artificial light affects bats in a species-specific manner. Species that are morphologically similar and use comparable foraging strategies and habitats can respond differently to anthropogenic disturbance in general and to artificial light in particular (Davidson-Watts, Walls & Jones 2006; Lintott et al. 2016; chapter 1 & 2). But why do some bats avoid light in all contexts while others forage at street lights? From the results of chapter 1 through 3, I infer that in principle all bats are intrinsically light-averse due to a combination of predator avoidance and blinding. For opportunistically light-tolerant species, however, the influence of predators is lowered as a result of their comparably fast flight. For them, the costs of foraging late in complete darkness and, similarly, to neglect dense insect clusters at artificial lights would presumably be higher than the costs of foraging in high light levels since prey availability decreases tremendously after sunset. For light-averse bats, in contrast, prey is available all night long, such that these slow flyers do not have to take higher predation risk early at night. Yet, their strict avoidance of higher light levels nowadays excludes these light-averse species from wide areas where humans artificially increase night light levels. Hence, the spread of artificial light introduces a competitive advantage for light-tolerant bats and selectively jeopardises populations of light-averse species and the ecosystem services they provide. Fortunately, the results of chapter 3 indicate that the imbalance that artificial light causes can be diminished by using illuminants that do not attract large numbers of insects.

It is very likely that the reported effects of artificial light on bats have fitness consequences and eventually influence population growth. Presumably, artificial light impacts fitness of opportunistically light-tolerant and of light-averse bats differentially. Currently, however, the field of light pollution is completely lacking studies demonstrating any fitness consequences of artificial light on bats, which would be of major interest for conservation. Understanding the fitness costs of artificial light on individual bats and at the population level is crucial to predict the long-term consequences of light pollution for bat populations and species persistence in an increasingly lit world, and to adapt lighting guidelines and legislation accordingly. Additionally, it needs to be considered that artificial light is intrinsically associated with human activity. Hence, where artificial light is used, an entire range of pollutants is usually released into the environment. For example, urban city centres, but also highways and industrial areas, are typically characterised by high levels of light pollution as well as chemical and acoustic emission. The co-occurrence of light, chemicals and sound may result in multimodal sensory pollution and the combination of different sensory pollutants could have additive or even synergistic effects (Halfwerk & Slabbekoorn 2015).

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9. CURRICULUM VITAE

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

For reasons of data protection, the curriculum vitae is not included in the online version.

Selbständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Doktorarbeit eigenständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen verwendet habe.

Starnberg, den 24.04.2017

Daniel Lewanzik