ANTECEDENTES ENTREGADOS POR ÁLVARO BOEHMWALD

1. ANTECEDENTES SOBRE BIODIVERSIDAD

- Ala-Laurila, P, (2016), Visual Neuroscience: How Do Moths See to Fly at Night?.
- Souza de Medeiros, B, Barghini, A, Vanin, S, (2016), Streetlights attract a broad array of beetle species.
- Conrad, K, Warren, M, Fox, R, (2005), Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis.
- Davies, T, Bennie, J, Inger R, (2012), Artificial light pollution: are shifting spectral signatures changing the balance of species interactions?.
- Van Langevelde, F, Ettema, J, Donners, M, (2011), Effect of spectral composition of artificial light on the attraction of moths.
- Brehm, G, (2017), A new LED lamp for the collection of nocturnal Lepidoptera and a spectral comparison of light-trapping lamps.
- Eisenbeis, G, Hänel, A, (2009), Chapter 15. Light pollution and the impact of artificial night lighting on insects.
- Gaston, K, Bennie, J, Davies, T, (2013), The ecological impacts of nighttime light pollution: a mechanistic appraisal.
- Castresana, J, Puhl, L, (2017), Estudio comparativo de diferentes trampas de luz (LEDs) con energía solar para la captura masiva de adultos polilla del tomate *Tuta absoluta* en invernaderos de tomate en la Provincia de Entre Ríos, Argentina.
- McGregor, C, Pocock, M, Fox, R, (2014), Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review.
- Votsi, N, Kallimanis, A, Pantis, I, (2016), An environmental index of noise and light pollution at EU by spatial correlation of quiet and unlit areas.
- Verovnik, R, Fiser, Z, Zaksek, V, (2015), How to reduce the impact of artificial lighting on moths: A case study on cultural heritage sites in Slovenia.
- Stavenga, D, Foletti, S, Palasantzas, G, (2006), Light on the moth-eye corneal nipple array of butterflies.

11. Whitney, H.M., Bennett, K.M.V., Dorling, M., Sandbach, L., Prince, D., Chittka, L., and Glover, B.J. (2011). Why do so many petals have conical epidermal cells? Ann. Bot. Lond. *10*, 609–616.

12. Whitney, H.M., Chittka, L., Bruce, T.J., and Glover, B.J. (2009). Conical epidermal cells allow bees to grip flowers and increase foraging efficiency. Curr. Biol. *19*, 948–953.

13. van der Kooi, C.J., Dyer, A.G., and Stavenga, D.G. (2015). Is floral iridescence a biologically relevant cue in plant-pollinator signaling? New Phytol. *205*, 18–20.

14. Thomas, M., Rudall, P., Ellis, A., Savolainen, V., and Glover, B.J. (2009). Development of a complex floral trait: the pollinator-attracting petal spots of the beetle daisy, *Gorteria diffusa* (Asteraceae). Am. J. Bot. *96*, 2184–2196.

15. van Kleunen, M., Nänni, I., Donaldson, J.S., and Manning, J.C. (2007). The role of beetle marks and flower colour on visitation by monkey beetles (Hopliini) in the greater cape floral region. South Africa. Ann. Bot. Lond. *100*, 1483–1489.

16. Dafni, A., Bernhardt, P., Shmida, A., Ivri, Y., Greenbaum, S., O'Toole, C., and Losito, L. (1990). Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. Israel J. Bot. *39*, 81–92.

17. Lunau, K., Piorek, V., Krohn, O., and Pacini, E. (2015). Just spines – mechanical defence of malvaceous pollen against collection by corbiculate bees. Apidologie *46*, 144–149.

Visual Neuroscience: How Do Moths See to Fly at Night?

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http://dx.doi.org/10.1016/j.cub.2016.01.020

A new study shows that moth vision trades speed and resolution for contrast sensitivity at night. These remarkable neural adaptations take place in the higher-order neurons of the hawkmoth motion vision pathway and allow the insects to see during night flights.

We spend most of our waking time in daylight or in the well-lit indoor spaces of modern life. Under these conditions vision provides us with a reliable representation of the world around us rich in colors and spatial details. But imagine being in the wilderness far from the city lights. Everything changes at sunset. The comfortable certainty of daytime vision is replaced by the uncertainty hidden in the deep shadows of twilight. As the sun's last rays create a faint golden rim on the horizon your visual experience becomes less dominant. The sounds of the night awaken your imagination and can cause even a slight sensation of fear of the invisible inhabitants of the wilderness hidden in the dark. Suddenly something passes you in the air flying — a hawkmoth! How on earth can a moth fly at these extremely low light levels? An answer to this question is provided in this issue of *Current Biology*: a new study by Stöckl *et al.* [1] shows that neural adaptations taking place in higher-order neurons of the moth motion vision pathway enable them to see 'on the wing' even in incredibly low light.

Seeing under very dim light poses a formidable challenge for the visual system. In these conditions, visual signals originating in a small number of photoreceptor cells have to be detected against neural noise originating in a much larger number of such cells, as well as in the neural circuitry processing these sparse signals. The randomness of rare photon arrivals makes it even harder to form reliable visual percepts in dim light. Yet many species show remarkable visual capabilities at extremely low light levels. The classic study by Selig Hecht and his colleagues [2] showed that dark-adapted humans can detect just a few light quanta absorbed on a small region of the peripheral retina. Dark-adapted toads can capture their prey easily in starlight [3]. Nocturnal Central American sweat bees can find their nest in the jungle at night [4]. Cockroaches show visually guided behaviour at light levels where only a few photons are captured among hundreds of photoreceptors [5]. Nocturnal African dung beetles can navigate with the aid of polarized moonlight [6]. In all of these cases, the striking behavioral performance of animals in dim light exceeds that of individual receptor cells at their visual inputs by orders of magnitude.

The basic trick for enhancing the quality of photos at night is well known to all photographers: pooling photons in space (increasing 'pixel size') and time (prolonging the exposure time) will boost the signals. There are mechanisms implementing similar pooling at multiple levels of the visual systems of both invertebrates and vertebrates. In our own retina, rod photoreceptors used mainly at low light levels have a longer integration time than cone photoreceptors that we use in daytime. This is one example of receptor-level temporal summation. Spatially, the visual circuits mediating rod signals in our own eyes pool signals from thousands of rods at the lowest light levels, whereas our highest resolution foveal cone vision relies on one-to-one connections between the cones and the midget ganglion cells at the retinal output. In many invertebrates, the migration of screening pigments allows dynamic control of the spatial summation at the receptor level [7]. It has also been proposed that the electrical coupling of rod photoreceptors in the vertebrate eye is more extensive at night time [8].

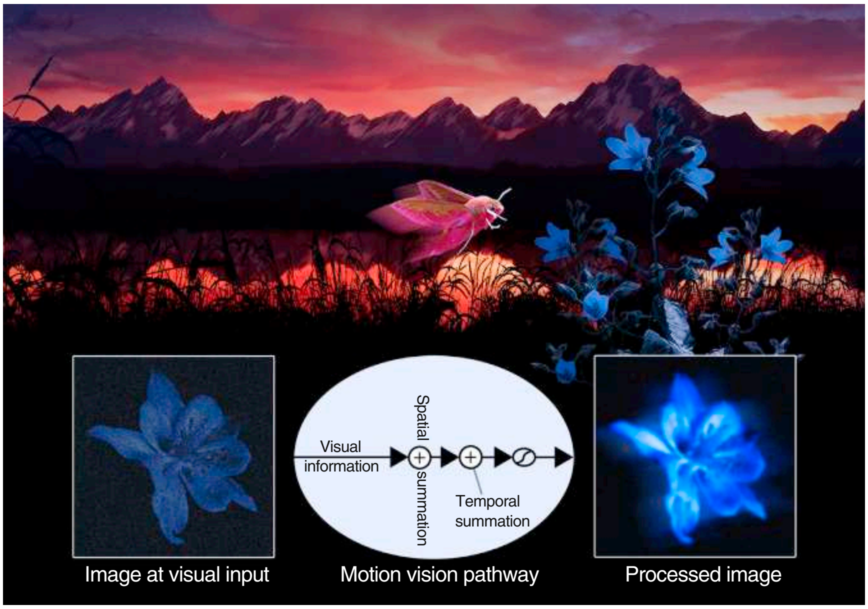

Figure 1. Visual processing in the motion vision pathway of a nocturnal hawkmoth.
The noisy image with low contrast present at the level of hawkmoth photoreceptors (inset, left) is enhanced in contrast (inset, right) by spatial and temporal summation taking place in the higher-order neurons. These neural computations are supralinear, producing higher contrast sensitivity than predicted by a simple linear model relying on spatial and temporal pooling only.

Unfortunately, there is no free lunch — especially not in biology. Pooling signals in space and time comes with fundamental limitations. First, although spatial pooling increases signals arising from photons, it also increases neural noise. Second, the more you pool in time and space the slower your vision is and the fewer fine spatial details you can see. These are especially hard problems for a flying insect. Their small body size will cause fast angular motions and thereby rapid changes in the visual scene during the flight. This would seem to require a fast visual system. Balancing sensitivity against acuity and speed is a trade-off problem where the optimal solution depends on light level and motion velocity.

So how can a moth then see at night? Stöckl *et al.* [1] took a novel and integrative approach to solve this fundamental problem by addressing it in a tractable model system in the motion vision pathway of the nocturnal elephant moth (*Deilephila elpenor*). They mastered demanding intracellular electrophysiological recordings both from photoreceptors at the visual input level and from the downstream neurons in the lobula plate of the motion vision pathway of the moth. The authors were able to quantify the spatial and temporal constraints set by the photoreceptors on contrast sensitivity and to compare these constraints to the contrast sensitivity measured at the level of the moth brain in the wide-field motion detecting neurons. This unique approach allowed them to quantify the amount of neural summation taking place in the visual pathway of the moth across a 10,000-fold range of light intensities comprising light levels from early sunset to dim moonlight.

Stöckl *et al.* [1] found that the postreceptoral neural circuits carry out extensive spatial and temporal summation at low light levels. Using a modeling approach the authors conclude that this summation enables hawkmoths to see at light levels 100 times dimmer than without such summation. Thus, the neural circuits of the moth motion vision pathway significantly trade speed and spatial resolution for contrast sensitivity, as illustrated in Figure 1.

But how far can the moth afford to sacrifice the speed of vision while flying at night? A recent behavioral study by another group of scientists brings an answer to this question. Sponberg *et al.* [9] showed that a closely-related hawkmoth species (*Manduca sexta*) slows down its behaviorally measured visual processing in perfect harmony to the speed of wind-blown flowers at night. Taking together the findings of these two beautiful studies, we now have a perfect answer. The Stöckel *et al.* [1] paper provides the neural account for this earlier behavioral result by directly showing that the moth brain slows down in the dark. These two studies [1,9] together suggest that the neural mechanisms of the moth visual system have been matched perfectly to the requirements of its environment.

What neural mechanisms underlie the spatial and temporal summation in the moth motion vision pathway? Stöckl *et al.* [1] do not give a direct answer to this question. However, their modeling predicts that the neural mechanism is supralinear, giving more advantage to contrast sensitivity than a simple linear summation of temporal and spatial effects would predict. This exciting prediction is in line with the idea that optimal performance at visual threshold relies on elegant nonlinear neural computations taking place in the visual circuits. Earlier literature in the vertebrate visual system showed that the detection of the weakest lights relies to a large extent on nonlinear noise filtering mechanisms at multiple levels of the neural circuit [10,11]. It remains to be seen in future studies how exactly the computations revealed by Stöckl *et al.* [1] are implemented and what noise sources truly limit detection under these conditions.

Similarly, it will be intriguing to understand the mechanisms that control the optimal tuning of spatial and temporal properties across multiple light levels in the moth. Recent studies [12,13] have unraveled neural circuit mechanisms underlying luminance-dependent changes in the spatial summation of the vertebrate retina. Further mechanistic understanding of evolution as an innovator at visual threshold might even help us to build more sensitive and efficient night vision devices in the future. Aside from these potential future innovations, this study reveals above all some of the key neural secrets underlying the night flight of a moth in the wilderness. This understanding as such is simply beautiful.

REFERENCES

1. Stöckl, A.L., O'Carroll, D.C., and Warrant, E.J. (2016). Neural summation in the hawkmoth visual system extends the limits of vision in dim light. Curr. Biol. *26*, 821–826.

2. Hecht, S., Shlaer, S., and Pirenne, M.H. (1942). Energy, quanta, and vision. J. Gen. Physiol. *25*, 819–840.

3. Aho, A.C., Donner, K., Hyden, C., Larsen, L.O., and Reuter, T. (1988). Low retinal noise in animals with low body temperature allows high visual sensitivity. Nature *334*, 348–350.

4. Warrant, E.J., Kelber, A., Gislen, A., Greiner, B., Ribi, W., and Wcislo, W.T. (2004). Nocturnal vision and landmark orientation in a tropical halictid bee. Curr. Biol. *14*, 1309–1318.

5. Honkanen, A., Takalo, J., Heimonen, K., Vahasoyrinki, M., and Weckstrom, M. (2014). Cockroach optomotor responses below single photon level. J. Exp. Biol. *217*, 4262–4268.

6. Dacke, M., Nilsson, D.E., Scholtz, C.H., Byrne, M., and Warrant, E.J. (2003). Animal behaviour: insect orientation to polarized moonlight. Nature *424*, 33.

7. Warrant, E.J., and McIntyre, P.D. (1993). Arthropod eye design and the physical limits to spatial resolving power. Prog. Neurobiol. *40*, 413–461.

8. Jin, N.G., Chuang, A.Z., Masson, P.J., and Ribelayga, C.P. (2015). Rod electrical coupling is controlled by a circadian clock and dopamine in mouse retina. J. Physiol. *593*, 2977–2978.

9. Sponberg, S., Dyhr, J.P., Hall, R.W., and Daniel, T.L. (2015). INSECT FLIGHT. Luminance-dependent visual processing enables moth flight in low light. Science *348*, 1245–1248.

10. Field, G.D., and Rieke, F. (2002). Nonlinear signal transfer from mouse rods to bipolar cells and implications for visual sensitivity. Neuron *34*, 773–785.

11. Ala-Laurila, P., and Rieke, F. (2014). Coincidence detection of single-photon responses in the inner retina at the sensitivity limit of vision. Curr. Biol. *24*, 2888–2898.

12. Grimes, W.N., Schwartz, G.W., and Rieke, F. (2014). The synaptic and circuit mechanisms underlying a change in spatial encoding in the retina. Neuron *82*, 460–473.

13. Farrow, K., Teixeira, M., Szikra, T., Viney, T.J., Balint, K., Yonehara, K., and Roska, B. (2013). Ambient illumination toggles a neuronal circuit switch in the retina and visual perception at cone threshold. Neuron *78*, 325–338.

Evolution: The End of an Ancient Asexual Scandal

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http://dx.doi.org/10.1016/j.cub.2016.01.034

Bdelloid rotifers were believed to have persisted and diversified in the absence of sex. Two papers now show they exchange genes with each other, via horizontal gene transfers as known in bacteria and/or via other forms of non-canonical sex.

Asexual organisms are believed to be evolutionarily short-lived. Most asexual lineages occur on the tips of the tree of life and few have succeeded like their sexual counterparts. Only a handful of asexual lineages have diversified into different types considered as ‘species’ — sets of morphologically and ecologically distinct forms classified into different genera, or even families, of exclusively asexual organisms. The most prominent examples of lineages that have persisted and diversified over millions of years in the absence of sex include oribatid mites [1], darwinulid ostracods [2] (a group of freshwater Crustaceans) and, up to now, bdelloid rotifers [3] (Figure 1). These lineages have been referred to as ‘ancient asexual scandals’ as they appear to challenge the view that sex is a prerequisite for the long-term evolutionary success of a lineage [2,4]. They have also been considered a ‘holy grail’ for developing insights into one of the most notorious unresolved questions in evolutionary biology: why is sexual reproduction so universally favored in natural populations? The idea is that if we can understand how ancient asexual scandals persisted and diversified in the absence of sex, we might develop insights into what the most fundamental benefits of sex are [5].

A new study in this issue of *Current Biology* by Debortoli *et al.* [6] shows that the answer to how bdelloid rotifers have persisted and diversified in the absence of sex might be that bdelloids engage in an unusual form of ‘parasex’ that allows for horizontal genetic exchange between individuals in the absence of regular meiosis and the production of gametes. The mechanisms mediating these horizontal gene transfers between individuals remain unknown. But the phenotype, horizontal gene transfer, brings an outstanding example of convergent evolution between bacteria and eukaryotes. Furthermore, elucidating the molecular details of horizontal gene transfer in bdelloids may open novel avenues to large-scale genome editing.

Bdelloid rotifers are abundant micro-invertebrates that occur in aqueous habitats throughout the world [7]. There are 461 described species, distinguished from each other mainly on the basis of morphology [8,9]. Many species are able to survive dry, harsh conditions by entering a desiccation-induced state of dormancy from which they can emerge upon re-hydration [7]. The first hint for horizontal gene transfers in bdelloid rotifers was published in 2008 when Gladyshev and colleagues showed that bdelloid genomes harbor unusually many genes of bacterial, fungal, and plant origin [10]. Later work in the species *Adineta ricciae* then demonstrated that many of these foreign genes are expressed, and that as many as 8–10 % of all transcripts are of foreign origin [11]. The publication of the genome of a related species, *Adineta vaga* [12], revealed a similar level of foreign gene content, with 8 % of predicted genes of non-metazoan origin. Finally, foreign gene uptake is ongoing in bdelloids and has contributed to functional differences among species [13] and therefore to adaptive evolution in bdelloids.

Given the evidence that bdelloid rotifers acquire and use genes from

Revista Brasileira de Entomologia 61 (2017) 74–79

SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
FUNDADA EM 1937

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Streetlights attract a broad array of beetle species

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ARTICLE INFO

Article history:
Received 8 August 2016
Accepted 30 November 2016
Available online 14 December 2016
Associate Editor: Rodrigo Kruger

Keywords:
Lighting
Coleoptera
Light pollution
Insects
Ultraviolet

ABSTRACT

Light pollution on ecosystems is a growing concern, and knowledge about the effects of outdoor lighting on organisms is crucial to understand and mitigate impacts. Here we build up on a previous study to characterize the diversity of all beetles attracted to different commonly used streetlight set ups. We find that lights attract beetles from a broad taxonomic and ecological spectrum. Lights that attract a large number of insect individuals draw an equally high number of insect species. While there is some evidence for heterogeneity in the preference of beetle species to different kinds of light, all species are more attracted to some light radiating ultraviolet. The functional basis of this heterogeneity, however, is not clear. Our results highlight that control of ultraviolet radiation in public lighting is important to reduce the number and diversity of insects attracted to lights.

Introduction

The effect of light pollution on ecosystems is a growing concern (Gaston et al., 2012; Longcore and Rich, 2004). Knowledge on how light affects the biota – and especially on organismal response to its various properties – can inform the development of environmentally friendly lighting (Gaston et al., 2012). Insects, in particular, are widely known to be attracted to lights, and knowledge on insect response to lights is generally used by collectors and in pest management (Shimoda and Honda, 2013), and it is also important in the control of vector-borne diseases (Barghini and de Medeiros, 2010). Except for a handful of species with economic or health importance, little is known about how different species respond to lights in natural ecosystems or even how this attraction affects populations (Eisenbeis, 2006; Fox, 2013). Insects are attracted to streetlights, sometimes in large numbers (Barghini and de Medeiros, 2012; Eisenbeis, 2006; Eisenbeis and Hassel, 2000), and their diversity is affected near lights even during the day (Davies et al., 2012). Street lights could have adverse effects on insect populations by a variety of mechanisms, including directly mortality caused by exhaustion or attraction of predators, or disruption of biological cycles. It is therefore important to understand what properties of street lighting cause insect attraction, and whether it affects only a few or a large array of species, in order to develop measures to minimize both the impact of lights on particular species and the number of species affected.

If compared to humans, insects have very different sensitivity spectra, usually with receptors maximally sensitive on the ultraviolet (UV), blue and green (Briscoe and Chittka, 2003). In spite of UV radiation being invisible to humans, many of the commonly used external light sources (such as high-pressure sodium vapor lamps and high-pressure mercury vapor lamps) radiate UV. These UV-radiating lamps are still widely used around the world, even though they are being steadily replaced by LED-based technologies. Several studies have shown that lamps emitting shorter wavelengths attract more insects (Barghini and de Medeiros, 2012; Eisenbeis, 2006; Eisenbeis and Hassel, 2000; Nowinszky, 2003; van Langevelde et al., 2011), and UV radiation is especially important in triggering the attraction behavior. For example, with the use of UV filters, the number of insects attracted of a blue (Hg vapor) and yellow (Na vapor) lamps are nearly indistinguishable (Barghini and de Medeiros, 2012). While it is not yet entirely clear why insects are especially attracted to UV-radiating lights, this is probably because terrestrial sources of UV interfere with insect navigation while flying (see a thorough discussion in Barghini and de Medeiros, 2010).

Most experiments on insect attraction to lights have been done in temperate environments and few have evaluated the different insect responses at the species level, without previously selecting target species to be studied, or the overall diversity of species attracted to lights. To date, this has been done mainly for moths. The abundance of moths attracted by a lamp correlates with the number of species attracted and larger moths exhibit a stronger preference for light sources radiating shorter wavelengths (Nowinszky

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http://dx.doi.org/10.1016/j.rbe.2016.11.004

et al., 2013; van Langevelde et al., 2011). In addition to size, there also seems to be differences in behavior according to taxonomy: Noctuidae moths are more attracted to shorter wavelengths, while Geometridae moths exhibit no preference (Somers-Yeates et al., 2013). Even though moths are conspicuous visitors to lights, they are not the most abundant group of insects attracted by them (Barghini and de Medeiros, 2012; Eisenbeis and Hassel, 2000; Poiani et al., 2014). It is unknown at this point if observations in moths can be generalized to other insect taxa, especially in more diverse tropical environments.

Here we study the diversity of Coleoptera, the most diverse insect order, attracted to different light sources. In a previous study, he have found that UV radiation, even in small amounts, is extremely important to trigger insect attraction to lights, but we have not studied the response of individual species (Barghini and de Medeiros, 2012). Coleoptera was one of the most abundant orders collected in our traps, and beetles represent the most species-rich order of insects, comprising over 380,000 described species (Slipiński et al., 2011), and encompassing also a wide ecological diversity (McKenna et al., 2015). To better understand the heterogeneity in insect attraction to lights in a natural setting and the diversity of insects attracted by each kind of lamp, in this study we have sorted and identified all species of Coleoptera attracted to lights in a subset of our previous sampling. We aim to understand whether commonly used street lamps that attract a larger number of individuals also attract more species in a natural setting, and also to characterize the heterogeneity in responses to lights among beetle species.

Material and methods

Collection

Here we used the material collected in the same set of experiments performed by Barghini and de Medeiros (2012), and details on the methods can be found on that paper. The test was conducted in a street surrounded by trees and isolated from urban lighting on the main campus of the University of São Paulo in the city of São Paulo. Static insect collecting traps similar to those used by Eisenbeis and Hassel (2000) were set up below lamps installed on seven-meter-tall lampposts, filled with 70% ethanol as killing agent. Each treatment utilized a full cut-off lighting fixture as follows: Hg: mercury vapor bulb protected with tempered glass; Na: high-pressure sodium vapor bulb with tempered glass; Na_F: sodium vapor bulb with tempered glass and a UV filter (Polycarbonate Lexan$^{\copyright}$ 2 mm); and Control: trap without lamp. Hg is a white lamp radiating UV and shorter wavelengths. Na is a yellow lamp that radiates longer wavelengths, but also some UV. Radiation spectra for the lamps used can be found in Barghini and de Medeiros (2012).

Collections were performed in two separate campaigns. The first comprised 24 collections between March and June 2005; the second an additional 13 collections between October and December 2005. On each collection date, traps were set up before twilight and taken down in the following morning. The Coleoptera were sorted into morpho-species and identified to the family or subfamily level using various sources (Arnett et al., 2002; Arnett and Thomas, 2000; Lawrence et al., 1999). After initial identification, the classification was updated to match that used in the most recent beetle phylogeny (McKenna et al., 2015). All the material was deposited in the Museu de Zoologia of the Universidade de São Paulo (MZSP).

Correlations between abundance and diversity

All statistical analyses were done in R Version 3.2.3 (R Core Team, 2015), and the data and scripts used to run the analyses and generate graphs and tables can be found in the first author's github repository (https://github.com/brunoasm/Medeiros_RBE_2016). To test whether the diversity of Coleoptera attracted to lamps is correlated with number of individuals, we used Spearman's rank correlation test considering each trap in each day as a data point. We used species richness and phylogenetic diversity (Faith, 1992) as diversity indexes, and we also tested the correlation between the two of them in the same way. To generate a phylogenetic tree to calculate phylogenetic diversity, we used the subfamily-level beetle tree from McKenna et al. (2015) as a backbone tree. Species found in this study were added by attaching a branch to a random position within the clade defined by the most recent common ancestor of the family or subfamily. Finally, species present in the backbone tree but not in this study were pruned. For the calculation of phylogenetic diversity, the age of the tree root was rescaled to 1, so that species richness and phylogenetic diversity are calculated in the same scale. We repeated the procedure to generate a total of 100 random trees to test sensitivity of the results. All manipulations used functions the R packages phytools v. 0.5-20 (Revell, 2012) and ape v. 3.4 (Paradis et al., 2004).

Effect of lamps on diversity and abundance of Coleoptera attracted

We used generalized linear mixed models to test for differences in the abundance, species richness and phylogenetic diversity of beetles collected in each treatment. In all models, the kind of lamp was considered a fixed effect and date of collection a random effect. We used a generalized linear model with Poisson error distribution and log link function for the count response variables (abundance and species richness) and a normal linear model for continuous response variables (phylogenetic diversity). In all cases, model fit was assessed graphically by generating quantile–quantile plots and predictor–residuals plots. The significance of trap as a predictor was tested with a Wald chi-square test. All calculations were done in R package lme4 v. 1.1-11 (Bates et al., 2015). To further test whether differences in diversity attracted to lights are simply a consequence of differences in abundance, we generated rarefaction curves for each lamp using functions in the R package picante v. 1.6-2 (Kembel et al., 2010).

Heterogeneity in Coleoptera preference to lights

To test for heterogeneity in the response of species to lights, we used two approaches. First, we tested whether some lamps consistently attract only a subset of beetle diversity. If that were the case, the diversity attracted to these lamps would result to be phylogenetically clustered with respect to our overall sampling. For each lamp, we calculated the mean pairwise phylogenetic distance (MPD) (Webb et al., 2002) of all species collected throughout the study, averaged over the 100 random trees. We calculated MPD both weighted and unweighted by abundance. To test whether the MPD in each lamp indicated phylogenetic clustering, we randomized the species × lamp matrix by using the trial-swap algorithm (Miklós and Podani, 2004), and drawing a new random phylogenetic tree (from the 100 trees we generated) in each replicate. We have done 10,000 replicates, with 100,000 iterations of the trial-swap algorithm per replicate. These analyses used functions in the R package picante v. 1.6-2 (Kembel et al., 2010).

We also modeled beetle behavior by using latent Dirichlet allocation (LDA) (Blei et al., 2012). The formal definitions of the model can be found in Blei et al. (2012), with a verbal explanation provided by Riddell (2014). This model is normally used in machine learning to study the distribution of topics in a collection of texts. In the traditional approach, each text document has words that are drawn from a number of topics. Each topic consists of a distribution of probabilities of usage of each word (for example, the word

'Coleoptera' has a high probability in a topic of biology and low in engineering). LDA takes as data the counts of each word in each document and, for a set number of topics, attempts to jointly infer: (1) the probability of usage of each word in each topic and (2) the probability that a randomly chosen word in a document is drawn from each topic. This model can be readily applied to our experimental set up if we consider that each species is composed of many individuals, each of which has a probability of exhibiting a given preference. Preferences are grouped into preference classes, which consist of the probabilities that an individual will be attracted to each lamp. LDA is more powerful than alternatives to characterize the preferences in our sampling because they are inferred from the whole data, including species that are common and those that are rare. The inference about each species, on the other hand, is conservative and a substantial number of specimens for a given species is needed to confidently assign it to a given preference class. In summary, we have used LDA to jointly cluster all species preferences in a minimal number of preference classes, and the probability that each species is assigned to each one of these classes. We did the inference in a Bayesian framework, using a Gibbs sampler as implemented by Griffiths and Steyvers (2004). The major adaptation needed from the document analysis context was the choice of a value for the alpha parameter. This parameter can be thought of as a control of how many specimens are needed to confidently assign a species to a behavior (or words needed to assign a document to a topic, in the original sense). Since the number of specimens per species here is much smaller than the typical number of words in a text, the traditionally used value for this parameter would be too conservative. Here we set alpha to $15/k$, where k is the number of behaviors in the model. To estimate the optimal number of preference classes for our data, we attempted to use model perplexity for a number of preference classes varying between 2 and 12. Parameters were estimated using a randomly chosen subset of 75% of the species and perplexity was calculated with the remaining 25%. After selecting the optimal number of k, we estimated model parameters using all species, running the Gibbs sampler for 1 million generations and discarding the first 100,000 generations as burn in. The chain was sampled every 100 generations and we used the sample with highest posterior probability to obtain estimates. We obtained the posterior probabilities for each lamp in the different behaviors found, as well as the taxonomy of the species that resulted to have >0.50 posterior probability of being associated with some behavior. All analyses were done using the R package topicmodels v. 0.2-3 (Grün and Hornik, 2011).

Results

We collected 1226 individuals of Coleoptera, comprising 266 species in 46 families and subfamilies (Table 1). The majority of the species resulted to be new to the collection of the MZSP. There was a large variation in the number of insects collected in different days, likely due to factors such as weather and lunar phase. Nonetheless, traps consistently collected beetles in the order Hg > Na > Na_F ≥ Control. The trend was the same for number of individuals, species richness and phylogenetic diversity (Fig. 1). Variation in the tree used to calculate phylogenetic diversity had little impact in these results. In all models, lamp type is a significant predictor, but the difference between Control and Na_F is small and not significant when taking standard errors into account (Table 2). The estimated effects were only 21% increase in abundance and 26% increase in species richness in Na_F if compared to control, but much higher for the other lights (Table 2). The use of different trees to calculate phylogenetic diversity had negligible impact on estimates and p-values, so here we present results for a randomly chosen tree. Quantile–quantile plots and analysis of residuals

Table 1
Beetles collected throughout the study. Numbers indicate number of species and (within parenthesis) number of individuals. Blank cells indicate that no individuals were collected.

	Lamps			
Family	Hg	Na	Na_F	Control
Aderidae	1 (1)	1 (1)	2 (2)	
Anthicidae	2 (2)	1 (1)		
Anthribidae				2 (2)
Archeocrypticidae	1 (1)		1 (3)	
Bostrichidae	2 (3)			2 (2)
Bothrideridae	2 (2)		1 (1)	1 (1)
Brentidae	1 (1)	1 (1)		
Cantharidae		1 (1)		
Carabidae	15 (25)	10 (19)		1 (1)
Cerambycidae	2 (2)	1 (1)	1 (1)	2 (5)
Cerylonidae			1 (1)	
Chrysomelidae	2 (2)	1 (1)	2 (2)	1 (1)
Ciidae	1 (1)			
Coccinellidae	1 (1)		1 (2)	1 (2)
Corylophidae		1 (1)	2 (2)	
Cryptophagidae	4 (43)	4 (28)	2 (24)	1 (16)
Curculionidae	2 (6)	1 (1)	3 (5)	
Curculionidae:Scolytinae	14 (41)	14 (59)	5 (11)	6 (31)
Dermestidae	1 (1)			
Dytiscidae	3 (4)			
Elateridae	1 (1)	2 (2)	2 (2)	
Endomychidae		1 (1)		
Erotylidae		2 (17)	1 (3)	
Histeridae		2 (2)		
Hybosoridae	1 (1)			
Hydrophilidae: Sphaeridiinae	5 (66)	5 (26)	2 (3)	
Laemophloeidae	5 (6)	2 (4)	1 (1)	2 (3)
Latridiidae	2 (4)	1 (18)	1 (3)	1 (5)
Leiodidae	1 (2)			
Monotomidae	3 (22)	2 (3)	1 (3)	2 (3)
Mordellidae		2 (2)		1 (1)
Mycetophagidae	1 (4)	1 (3)	1 (2)	
Nitidulidae	11 (17)	4 (8)	4 (5)	2 (2)
Phalacridae	1 (3)	2 (2)		
Ptiliidae	3 (35)	5 (29)	1 (2)	2 (2)
Ptilodactylidae	3 (3)	3 (4)	1 (3)	1 (1)
Ptinidae	3 (11)	1 (2)	1 (1)	
Ripiphoridae			1 (1)	
Scarabaeidae	7 (45)	5 (9)	1 (1)	
Scirtidae		1 (1)		
Silphidae	1 (1)			
Silvanidae	1 (5)	2 (23)	1 (4)	
Staphylinidae	62 (257)	37 (101)	14 (23)	10 (14)
Staphylinidae:Scydmaeninae	4 (6)	6 (9)	1 (1)	
Tenebrionidae	7 (8)	3 (6)		
Zopheridae	2 (2)	1 (1)		
Total	92 (38)	112 (55)	387 (126)	635 (178)

Table 2
Estimated parameters for inferred linear models, with standard errors. Significant parameters ($p < 0.05$) are highlighted in bold. Models for abundance and species richness have a log link function, so parameter estimates are multiplicative and reported in logarithmic scale. The exponential of the inferred parameters returns them to the original scale in these cases. In all models, the intercept represents counts in Control, so other parameters represent the increase in collections in relation to Control. For example, the Control treatment collected an average of exp(0.664) = 1.94 insect individuals per night, while Na_F collected exp(0.1967) = 1.21 times more than Control. For phylogenetic diversity, a normal linear model was used and effects are additive, not multiplicative. Wald chi-square tests compare a model with lamp type as a fixed effect with a model with only intercept, resulting in 3 degrees of freedom in all cases.

	Abundance	Species richness	Phylogenetic diversity
Intercept (control)	**0.664 ± 0.174**	**0.499 ± 0.166**	**1.54 ± 0.486**
Na_F	0.197 ± 0.149	0.231 ± 0.155	0.47 ± 0.497
Na	**1.437 ± 0.115**	**1.323 ± 0.131**	**3.51 ± 0.497**
Hg	**1.932 ± 0.111**	**1.819 ± 0.125**	**6.11 ± 0.497**
Wald chi-square	522.85 ($p < 0.001$)	352.92 ($p < 0.001$)	193.94 ($p < 0.001$)

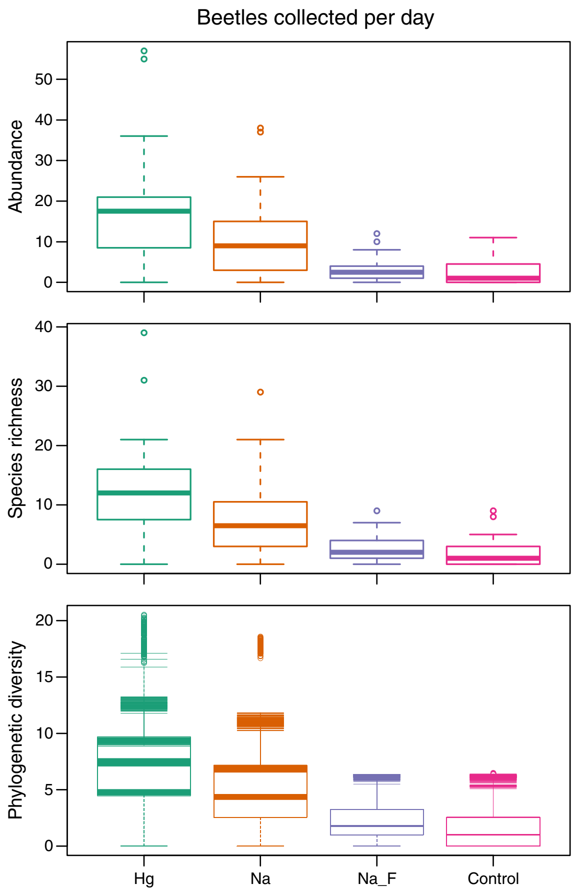

Fig. 1. Boxplots of beetle collections in each trap (each record here is a night of collection). These are standard boxplots, with whiskers representing the more extreme values within 1.5 inter-quartile range away from each quartile. For phylogenetic diversity, we superimpose 100 boxplots obtained from different random phylogenetic trees, to highlight the sensitivity of results to phylogenetic uncertainty. Phylogenetic uncertainty has little impact on the results.

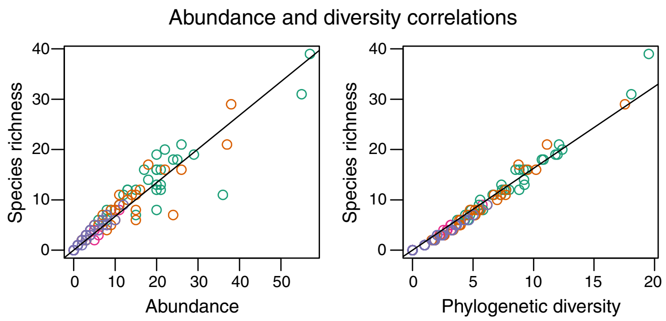

Fig. 2. Correlations between diversity and abundance across collections. Each record represents a night of collection in a given trap. Colors represent traps, with color code being the same as in Figs. 1, 3 and 4. Line represents the regression line between the two variables with intercept forced to 0.

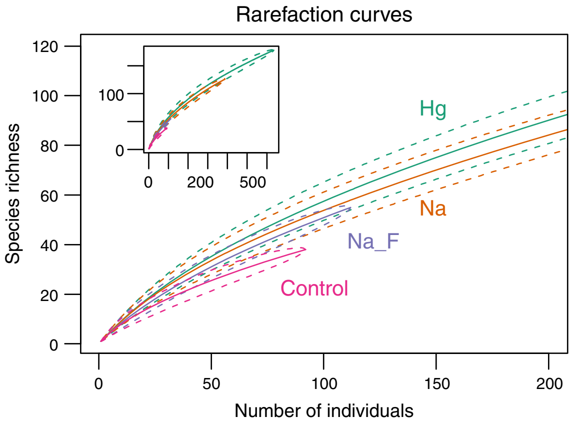

Fig. 3. Rarefaction curves. Solid lines indicate mean and dashed lines indicate 95% confidence intervals. Inset shows the full curves for Hg and Na.

Table 3
Standardized effect size of MPD for each lamp. We show observed and randomized MPD both weighted and unweighted by abundance. *p*-Values for the difference are shown within parentheses.

	Weighted by abundance		Unweighted	
	Observed MPD	Mean randomized MPD	Observed MPD	Mean randomized MPD
Control	323.4	355.6 (0.001)	382.7	392.0 (0.13)
Na_F	356.3	368.8 (0.03)	383.8	393.9 (0.06)
Na	382.1	380.3 (0.67)	399.6	397.8 (0.67)
Hg	381.4	382.1 (0.38)	401.8	400.3 (0.69)

MPD, mean pairwise phylogenetic distance.

indicate a good fit for models for abundance and species richness, but not so much for phylogenetic diversity. It is likely that the normal linear model in this case could not adequately account for the excess of zero counts. It seems, however, that species richness is a good proxy for diversity in this study. In fact, both species richness (correlation 0.98, $p < 0.001$) and phylogenetic diversity (correlation 0.97, $p < 0.001$) were highly correlated with the abundance of beetles caught in each trap, as well as to each other (correlation 0.995, $p < 0.001$) (Fig. 2). In fact, rarefaction curves indicate that, controlling for the number of specimens collected, there is no significant difference between lamps Hg, Na and Na_F in the number of species captured (Fig. 3). The only exception is the Control trap, which seems to have fewer species for a given number of individuals.

There is no evidence for phylogenetic clustering in beetles attracted to lamps Hg and Na, only weak evidence for Na_F, and strong evidence for the Control trap only when the MPD is weighted by number of individuals (Table 3). We could not use perplexity as a statistic to chose an optimal number of preference classes in LDA. Perplexity decreased as the number of preference classes increased for all numbers tested. However, a close inspection of the posterior estimates showed that, for models with four or more preference classes, some of the classes were replicated, indicating overfitting. For that reason, we chose the model with only three preference classes, which was the maximum number that yielded informative results. The classes found can be described as follows: (1) individuals that are only attracted to Hg, (2) individuals that are only attracted to Na and (3) individuals that are equally attracted to Hg, Na_F and Control. Only a few species had enough data to be assigned with >0.5 posterior probability to one of these preference classes, with the number of species and families being higher for behaviors 1 and 2 (Fig. 4).

Discussion

The first surprising finding of this study is the high diversity of beetles found in only 36 nights of collection in an urban setting. The area of study is a small fragment of secondary forest completely isolated from other fragments by the city of São Paulo. Yet, we could collect 267 species of beetles, with a little over half of them being singletons. There is no evidence for an asymptotic behavior in the rarefaction curves reported here, which suggests that the diversity of beetles potentially attracted to lights in the studied area is much higher than what we were able to sample. In spite of being attracted

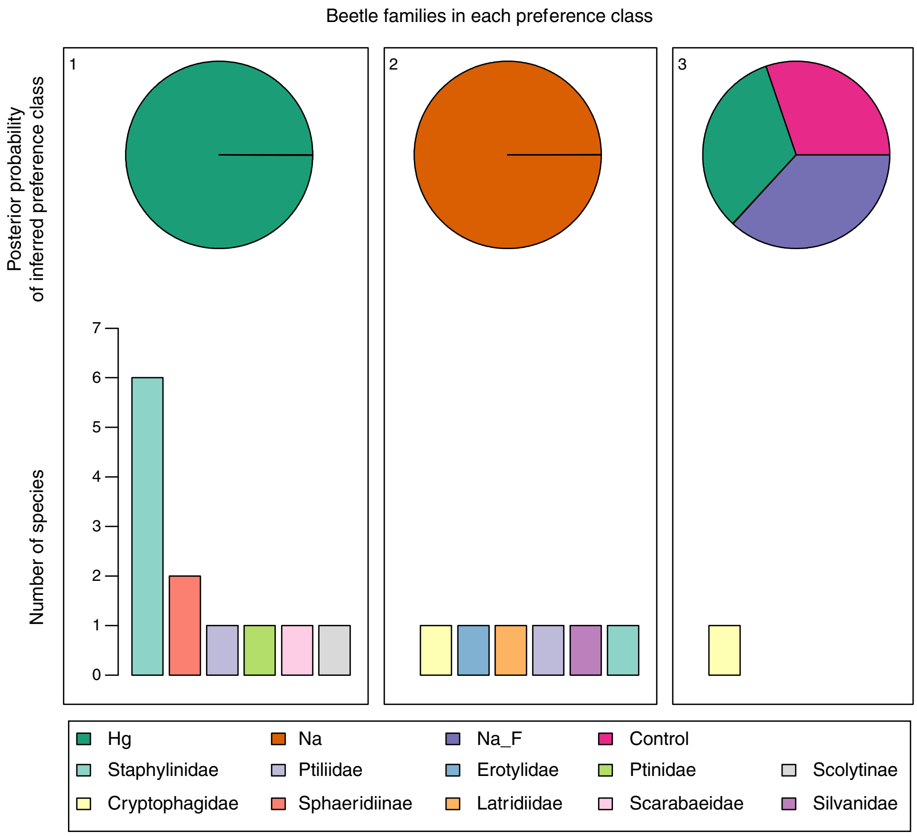

Fig. 4. Preferences estimated by LDA. Boxes enclose graphs associated with preference classes estimated by LDA, numbered as 1–3. Each pie chart indicates the posterior probability of preference for each trap for a given preference class (e.g. preference class 1 includes individuals exclusively attracted to Hg). Underneath each pie chart, bars indicate the number of species with >0.5 posterior probability of being associated with the corresponding preference class, binned by higher taxon.

by lights and being found in a major city, those beetles were underrepresented in the collections of MZSP, suggesting that there exists a large unexplored diversity of beetles even in areas within urban centers. Even though we did not measure specimens, it is clear that most of them represent very small beetles, ranging from 1 to 3 mm. It has been shown before that small species are less likely to be described than larger species (Stork et al., 2008), and the small size might also be the major reason why they were not collected and deposited in the MZSP before.

Beetles follow the same pattern as insects in general, in that UV-radiating lamps are more attractive and the use of a UV filter reduces collections to a level similar to the control with no light (Barghini and de Medeiros, 2012). The number of species attracted and their phylogenetic diversity also increases with number of individuals, and our results indicate that strongly attractive lamps are drawing insects from a broad taxonomic and ecological spectrum. This correlation between abundance and diversity attracted has also been found for moths (Somers-Yeates et al., 2013), indicating that it is a general pattern. It is noteworthy that the Na lamp emits only a very small fraction of its radiation in the UV range – only about 1.2% (Barghini and de Medeiros, 2012) – and yet it still attracts a significant amount of insects. The use of a UV filter in Na_F resulted in a 56% reduction in the number of species attracted and 71% in the number of individuals, highlighting the importance of controlling short-wavelength radiation in external lighting.

The use of ethanol as killing agent lured insects that are not necessarily attracted by lights. Inferred preference class 3, which consists of species attracted to almost all traps with equal probability, probably captured the dynamics of these species. In fact, the only species that was assigned to this behavior with high probability is a species of Cryptophagidae, and several less abundant species of Scolytinae also show a trend in this direction. Both taxa are known to be attracted to ethanol (Bouget et al., 2009; Flechtmann et al., 1999). These species are also probably responsible for the phylogenetic clustering in the Control trap when species abundances are considered. In this trap, over 51% of the individuals belong to Cryptophagidae and Scolytinae (against 31% in Na_F, 22% in Na and 13% in Hg).

Species that exhibited behavior 1 (attracted to Hg) or 2 (attracted to Na) belong to multiple families, with no obvious ecological trend, but staphylinids seem to be especially attracted to mercury vapor lamps. Since there is little to no biological information available for the species collected here, it is not possible to understand the functional significance of the difference in behavior between species highly attracted to Hg and those attracted to Na. It is clear, nonetheless, that there is heterogeneity in the behavior between insect species. Preference class 2 is composed of species attracted in higher numbers to Na if compared to Hg and the other lamps, even though the Na lamp is generally less visible to insects than Hg (Barghini and de Medeiros, 2012). In Na, very little of its irradiance spectrum lies in the UV and most of it is concentrated above 550 nm, while Hg has a broader spectrum with peaks from 370 to 700 nm (Barghini and de Medeiros, 2012). Our findings contrast with results found for moths, in which individual species were consistently more attracted to a short-wavelength light source, or equally attracted to both (Somers-Yeates et al., 2013). It is possible that UV radiation, whether radiated in small or large amounts, promotes long-distance attraction in both lamps, but that some beetles avoid the bright lights of Hg once in the vicinity of the lamp. We have proposed before that this might be a mechanism for attraction of insect vectors such as kissing bugs (Barghini and de Medeiros, 2010), and our findings here are compatible with this hypothesis.

While our experimental set-up allows us to observe the heterogeneity in behaviors across a large array of species in a natural setting, a better understanding of the behavioral and physiological correlates of high attraction to different lamps would require a laboratory study using multiple species with known biology and optical sensitivity.

It is also important to highlight that LDA was unable to estimate a preference class consistent with species being more attracted to Na_F than other lamps. While 100 species were exclusively found in Hg and 47 in Na, only 17 were exclusive to Na_F, with 16 of them being singletons. This indicates that, despite some heterogeneity in the behavior of beetles, UV radiation is still the single most important factor across species. Overall, it seems that highly attractive lamps attract beetles from a broad taxonomic and ecological spectrum, with the consequence that the attraction of more individuals also results in a larger impact on diversity.

Our study adds to the growing literature on the effects of streetlights on insect communities by recording the diversity of beetles attracted to lights in a tropical environment. The use of simple UV filters in the lighting fixture of commonly used streetlights, or of new technologies that do not radiate in the UV spectrum, may reduce both the abundance and diversity of insects collected. Our results indicate that lamps that collect more insect individuals also draw from a larger diversity, even if a few species exhibit preference for lamps that are less attractive for most species. LED lights, which are gradually replacing discharge lamps in public lighting, seem to be less attractive to insects (Poiani et al., 2014), but traditionally used insect response curves do not seem to be able to predict insect attraction to lights that do not radiate a significant amount of UV (van Grunsven et al., 2014). Nonetheless, their color spectrum is more easily customizable than that of discharge lamps, so it is possible to tune LED lamps to have an adequate color temperature for humans while being less attractive to insects (Longcore et al., 2015). A future avenue for research, therefore, includes investigations on the upper limit of wavelengths highly attractive to insects, and the variation between species. If insects interpret short-wavelength visible light (such as up to 480 nm) similarly to true UV, white LED lights not carefully tuned may still have a large impact on fauna.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

We thank Daniel Caetano da Silva for help with the collections and two anonymous reviewers whose comments greatly improved this manuscript. The first author received a Scientific Initiation Scholarship from CNPq.

References

Arnett Ross Jr., H., Thomas, M.C., Skelley, P.E., Frank, J.H., 2002. American Beetles, vol. II. CRC Press, Boca Raton, FL.

Arnett Jr., R.H., Thomas, M.C., 2000. American Beetles, vol. I. CRC Press, Boca Raton, FL.

Barghini, A., de Medeiros, B.A.S., 2012. UV radiation as an attractor for insects. Leukos 9, 47–56.

Barghini, A., de Medeiros, B.A.S., 2010. Artificial lighting as a vector attractant and cause of disease diffusion. Environ. Health Perspect. 118, 1503–1506.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67.

Blei, D.M., Ng, A.Y., Jordan, M.I., 2012. Latent Dirichlet allocation. J. Mach. Learn. Res. 3, 993–1022.

Bouget, C., Brustel, H., Brin, A., Valladares, L., 2009. Evaluation of window flight traps for effectiveness at monitoring dead wood-associated beetles: the effect of ethanol lure under contrasting environmental conditions. Agric. For. Entomol. 11, 143–152.

Briscoe, A.D., Chittka, L., 2003. The evolution of color vision in insects. Annu. Rev. Entomol., 471–510.

Davies, T.W., Bennie, J., Gaston, K.J., 2012. Street lighting changes the composition of invertebrate communities. Biol. Lett. 8, 764–767.

Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington, DC, pp. 281–304.

Eisenbeis, G., Hassel, F., 2000. Zur Anziehung nachaktiver Insekten durch Strassenlanternen – eine Studie kommunaler Beleuchtungseinrichtungen in der Agrarlandschaft Rheinhessens. Natur und Landschaft 75, 145–156.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10.

Flechtmann, C.A.H., Ottati, A.L.T., Berisford, C.W., 1999. Attraction of ambrosia beetles (Coleoptera: Scolytidae) to different tropical pine species in Brazil. Environ. Entomol. 28, 649–658.

Fox, R., 2013. The decline of moths in Great Britain: a review of possible causes. Insect Conserv. Divers. 6, 5–19.

Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. Reducing the ecological consequences of night-time light pollution: options and developments. J. Appl. Ecol. 49, 1256–1266.

Griffiths, T.L., Steyvers, M., 2004. Finding scientific topics. Proc. Natl. Acad. Sci. U. S. A. 101 (Suppl.), 5228–5235.

Grün, B., Hornik, K., 2011. topicmodels: an R package for fitting topic models. J. Stat. Softw. 40, 1–30.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464.

Lawrence, J.F., Hastings, A.P., Dallwitz, M.J., Paine, T.A., Zurcher, E.J., 1999. Beetles of the World: A Key and Information System for Families and Subfamilies.

Longcore, T., Aldern, H.L., Eggers, J.F., Flores, S., Franco, L., Hirshfield-yamanishi, E., Petrinec, L.N., Yan, W.A., Barroso, A.M., 2015. Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. Philos. Trans. R. Soc. Lond. B Biol. Sci. 370, 20140125.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198.

McKenna, D.D., Wild, A.L., Kanda, K., Bellamy, C.L., Beutel, R.G., Caterino, M.S., Farnum, C.W., Hawks, D.C., Ivie, M.A., Jameson, M.L., Leschen, R.A.B., Marvaldi, A.E., Mchigh, J.V., Newton, A.F., Robertson, J.A., Thayer, M.K., Whiting, M.F., Lawrence, J.F., Ślipiński, S.A., Maddison, D.R., Farrell, B.D., 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. Syst. Entomol. 40, 835–880.

Miklós, I., Podani, J., 2004. Randomization of presence-absence matrics: comments and new algorithms. Ecology 85, 86–92.

Nowinszky, L., 2003. The orientation of insects by light – major theories. In: The Handbook of Light Trapping. Savaria University Press, Szombathely, Hungary, pp. 15–18.

Nowinszky, L., Puskás, J., Tar, K., Hufnagel, L., Ladányi, M., 2013. The dependence of normal and black light type trapping results upon the wingspan of moth species. Appl. Ecol. Environ. Res. 11, 593–610.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290.

Poiani, S., Dietrich, C., Barroso, A., Costa-Leonardo, A.M., 2014. Effects of residential energy-saving lamps on the attraction of nocturnal insects. Light. Res. Technol. 47, 338–348.

R Core Team, 2015. R: A Language and Environment for Statistical Computing.

Revell, L.J., 2012. phytools: An R Package for Phylogenetic Comparative Biology (and Other Things).

Riddell, A.B., 2014. How to read 22,198 journal articles: studying the history of german studies with topic models. In: Erlin, M., Tatlock, L. (Eds.), Distant Readings: Topologies of German Culture in the Long Nineteenth Century. Camden House, Rochester, NY, pp. 91–114.

Shimoda, M., Honda, K.I., 2013. Insect reactions to light and its applications to pest management. Appl. Entomol. Zool. 48, 413–421.

Ślipiński, S.A., Leschen, R.A.B., Lawrence, J.F., 2011. Order Coleoptera Linnaeus, 1758. In: Zhang, Z.-Q. (Ed.), Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness. Zootaxa 1758. , pp. 203–208.

Somers-Yeates, R., Hodgson, D., McGregor, P.K., Spalding, A., Ffrench-Constant, R.H., 2013. Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. Biol. Lett. 9, 20130376.

Stork, N.E., Grimbacher, P.S., Storey, R., Oberprieler, R.G., Reid, C., Ślipiński, S.A., 2008. What determines whether a species of insect is described? Evidence from a study of tropical forest beetles. Insect Conserv. Divers. 1, 114–119.

van Grunsven, R.H.A., Donners, M., Boekee, K., Tichelaar, I., van Geffen, K.G., Groenendijk, D., Berendse, F., Veenendaal, E.M., 2014. Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. J. Insect Conserv. 18, 225–231.

van Langevelde, F., Ettema, J.A., Donners, M., WallisDeVries, M.F., Groenendijk, D., 2011. Effect of spectral composition of artificial light on the attraction of moths. Biol. Conserv. 144, 2274–2281.

Webb, C.O., Ackerly, D.D., McPeek, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. Annu. Rev. Ecol. Syst. 33, 475–505.

Folio N° 879

BIOLOGICAL CONSERVATION 132 (2006) 279–291

available at www.sciencedirect.com

journal homepage: www.elsevier.com/locate/biocon

Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis

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ARTICLE INFO

Article history:
Received 23 November 2005
Received in revised form
31 March 2006
Accepted 14 April 2006
Available online 30 June 2006

Keywords:
Biodiversity
Population trends
Population dynamics
Abundance
Occupancy
Lepidoptera

ABSTRACT

A fundamental problem in estimating biodiversity loss is that very little quantitative data are available for insects, which comprise more than two-thirds of terrestrial species. We present national population trends for a species-rich and ecologically diverse insect group: widespread and common macro-moths in Britain. Two-thirds of the 337 species studied have declined over the 35 yr study and 21% (71) of the species declined >30% 10 yr^{-1}. If IUCN (World Conservation Union) criteria are applied at the national scale, these 71 species would be regarded as threatened. The declines are at least as great as those recently reported for British butterflies and exceed those of British birds and vascular plants. These results have important and worrying implications for species such as insectivorous birds and bats, and suggests as-yet undetected declines may be widespread among temperate-zone insects.

1. Introduction

Insects are a vital component of terrestrial ecosystems and form a substantial proportion of terrestrial biodiversity. Despite this, knowledge of endangered insects lags behind that of vertebrates and vascular plants (New, 2004; Thomas et al., 2004). Whether recent extinction rates of insects are as great as for other groups has been debated keenly (Thomas and Morris, 1994; Lawton and May, 1995; McKinney, 1999). Most early estimates of insect extinction rates were much lower than those of birds, large mammals and plants, but attempts to quantify losses amongst insects were hampered by a lack of suitable data (Thomas and Morris, 1994; McKinney, 1999; New, 2004; Thomas et al., 2004).

Recently, Thomas et al. (2004) compared similarly measured changes in native butterfly, bird, and plant species and concluded that butterflies had declined more rapidly than these other groups in Britain; the first time such a comparison has been achieved for an insect taxon at the national scale. They proposed that if other insect groups are similarly sensitive to recent environmental change, then the unmeasured or under-recorded extinction rates of insects may rival or exceed those documented for vertebrates and plants (McKinney, 1999; Thomas et al., 2004). Furthermore, Thomas et al. (2004) argued that such high rates of extinction for insects would signal the 'sixth great extinction' (Wilson, 1992).

Here, we report severe national population declines among another intensively recorded insect group: the larger British moths, or 'macro-moths'. Thomas (2005) noted that long time series of species abundance should provide sensitive indicators of environmental change and cited the British marco-moths as one of three long-term datasets suitable for this purpose. In a previous paper (Conrad et al., 2004) we have described and validated our methodology for

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doi:10.1016/j.biocon.2006.04.020

estimating long-term population trends for British macro-moths and outlined some general patterns in the trends based on ecological characteristics of the moth species. In this paper we apply IUCN (IUCN World Conservation Union, 2001) criteria to identify nationally threatened species and compare macro-moth species declines to those reported for UK butterflies (Thomas and Clarke, 2004; Thomas, 2005). While the utility of butterflies as indicators of insect biodiversity has been questioned (Hambler and Speight, 2004; but see Thomas and Clarke, 2004; Thomas, 2005), moths form a much more ecologically diverse and species-rich group and are thus more likely to represent a greater range of terrestrial insects in Britain. We suggest, therefore, that declines in common and widespread moths provide further evidence of wider declines in British terrestrial insects.

2. Methods

2.1. Data source and selection criteria

Population data on British macro-moths were extracted from the Rothamsted Insect Survey (RIS, Woiwod and Harrington, 1994), one of the longest-running and spatially extensive datasets of a species-rich insect group anywhere in the world (Conrad et al., 2004). Established in the early 1960s to provide information on the spatial variation of insect abundance, the RIS has operated a national network of approximately 100 standard light-traps (Williams, 1948) annually since 1968. These traps provide standardized, nightly counts of individual moth species from a wide range of habitats (Woiwod and Harrington, 1994; Conrad et al., 2004). Catches are small, but consistent and representative, making the traps suitable for long-term monitoring of common and widespread species without affecting the moth populations being sampled (Williams, 1952; Taylor and French, 1974; Conrad et al., 2004). We analysed data for 337 species, each of which was represented by more than 500 individuals captured over the 35-yr sampling period (1968–2002), and derived annual national indices of abundance from the 199 sites that operated for a minimum of 48 weeks a year for 5 yr (Conrad et al., 2004).

2.2. Estimates of abundance and population change

We estimated indices of annual abundance, allowing for differences between sites, by fitting a generalised linear model with Poisson errors and logarithmic link, using version 3.2 of the TRIM (TRends and Indices for Monitoring data) software package (Pannekoek and Van Strien, 2001). By convention, the estimated abundance in the first year is set to one and each annual index, A_i, for year i, is calculated relative to the first, A_1. T, the 'TRIM trend index' is the overall slope of the regression of annual indices on a logarithmic scale (Pannekoek and Van Strien, 2001). T is a reliable and robust estimator of long-term trends that is suitable for comparisons across a range of species (Van Strien et al., 2001; Conrad et al., 2004). Annual rates of population change were calculated from T and 10-yr percentage declines were estimated from the annual rates of change (Van Strien et al., 2001).

We considered species population decline rates >30% 10 yr^{-1} to be of significant conservation concern. We further divided these rapidly declining species into two categories: vulnerable (30–50% 10 yr^{-1}) and endangered (>50% 10 yr^{-1}), according to the criteria and time period used to identify globally Vulnerable and Endangered species (IUCN World Conservation Union, 2001). Following the guidelines of Gardenfors et al. (2001), we applied the IUCN thresholds unaltered at the national level because the British populations can be regarded as effectively isolated, insular populations and their extinction risk is unlikely to be affected by populations in continental Europe (i.e., there is unlikely to be any significant 'rescue effect').

2.3. Regional variation

In order to assess geographical variation in population trends for common macro-moths we divided Great Britain into two regions along the 4500 N gridline of the British national grid system. The region to the north of 4500 N was called 'North' (N), and the region to the south of 4500 N was called 'South' (S). This division into regions was arbitrary but gave a reasonable number and distribution of sites for analysis in each region. More importantly, it provides the first steps in examining a number of species trends for the influences of climate change and changes in land-use already demonstrated to affect the decline of the once-common moth, *Arctia caja* (Conrad et al., 2002, 2003).

2.4. Comparison of short-term and long-term trap data

While the core number and geographical distribution of traps never changes significantly from year to year, there has been turnover of trapping sites during the 35 yr of our study (Conrad et al., 2004). In order to examine the effect of this turnover on our population trend estimates we calculated 10-yr percentage population changes using only traps that operated for 15 or more years and compared the results with those from our standard 'all sites' analysis, which used trapping sites that had operated for five or more years.

2.5. Light competition

'Astronomical light pollution' results from the cumulative effects of artificial lighting sources increasing the illumination of the night-time sky (Longcore and Rich, 2004) and may compete with light-traps and decrease their effectiveness. An increase in astronomical light pollution during our study period could thus decrease trap catches and lead to overestimates of downward population trends.

To examine the effects of 'light competition' on our trap catches, we obtained 'world change pair' images of the night-time sky from the Defense Meteorological Satellite Program Operational Linescan System (DMSP-OLS) dataset, provided by the US The National Oceanic and Atmospheric Administration's (NOAA) National Geophysical Data Centre (NGDC) (http://dmsp.ngdc.noaa.gov/html/download_world_change_pair.html). These images provide estimates of average annual night-time illumination of the earth's surface for the years 1992/93 and 2000. Illumination is recorded as pixels on a linear scale from 0 (dark) to 63 (instrument light saturation) (Elvidge et al., 2001). We selected the 116 RIS light-traps running between 1992 and 2000, and extracted the night-time illumination of the ~1 km^2 pixel containing each trap in 1992/93 and 2000. We divided the traps into two groups: 'dark', which included 35 trapping sites which scored 0 in 1992/93 and remained 0, or scored >0 in 1992/93 but were darker in 2000, and 'light' which comprised 81 sites that were >0 in 1992/93 and were lighter in 2000 (no sites initially >0 remained unchanged). We then estimated, for each of the two groups, the annual rate of change in total trap catch of the 337 moth species in this study for the period 1992–2000.

3. Results

3.1. *Rates of change of moth abundance and regional variation*

We found alarming declines in the overall abundance of widespread marco-moths. The annual total number of all macro-moths caught by the RIS light-trap network decreased by 31% over the 35-yr sampling period (Fig. 1). The majority of this decrease occurred in southern Britain, while the north showed no significant trend over time (Fig. 1). Year-to-year fluctuations in abundance are very similar in both the north and south despite the difference in overall trends (Fig. 1).

Two-thirds (0.66 ± 0.05, proportion ±95% CI) of the 337 individual moth species declined (Fig. 2). The median 10-yr population change was a decrease of 12% with a greater median decrease in the south (17%) than in the north (5%; Fig. 2). Of even greater concern, 21% ($N = 71$) of species displayed declines placing them in the vulnerable or endangered categories (Fig. 2). The total catch of each species and the trend index, T, were not correlated ($r = 0.020$, $N = 337$, $P = 0.714$; Fig. 3), so the total number of individuals captured did not affect whether a species was likely to increase or decline. Overall, 75% of species in the south declined compared to 55% in the north (Fig. 2).

3.2. *Land-use categories represented*

Although the light-trap network originated from an agricultural research station (Woiwod and Harrington, 1994), it was not intended to monitor agricultural pest species and a wide range of land-use categories have been sampled (Fig. 4). Because of trap turnover, the relative numbers of different types of biotope sampled each year varies over time (Fig. 4). The mean annual proportions of sites used corresponded with the following categories: coastal (8.9%); farmland (13.5%); mixed (15.3%); moorland (3.1%); parkland (22.8%); scrubland (2.6%); urban (15.9%) and woodland (17.8%). Only the proportion of scrubland changed significantly over time ($F_{1,33} = 30.34$, $P < 0.001$), and this is largely because no traps were sited in areas that were categorised as scrubland in the early years of the study. Annual variation in biotopes sampled was not systematically biased in any way.

3.3. *Comparison of short-term and long-term trap data*

Estimates for 222 decreasing species were obtained from sites that ran 15 or more years. These estimates were highly correlated with those from the 'all sites' analysis ($r = 0.95$, $N = 222$, $P = <0.001$), suggesting that light-trap turnover did not bias the results. Using only long-term trap sites to calculate trends had little impact on assigning species to the vulnerable and endangered categories (Fig. 5). A similar result was obtained when sites running 20 or more years were used (Conrad et al., 2004). Therefore, the all-sites analysis was used because it provides greater spatial coverage, larger sample sizes for individual species and enables estimates for a greater number of less common species.

3.4. *Light competition*

Contrary to expectation, the annual index of total trap catch (slope ± SE) at 'dark' sites (−0.044 ± 0.007) decreased marginally more than at 'light' sites (−0.035 ± 0.005) although the difference between these slopes was not significant ($t_{38} = 0.97$, $P = 0.34$). The decrease in total macro-moths captured was therefore as great or greater at sites that remained dark or became darker than at those where night-time illumination increased between 1992 and 2000. In addition, annual estimates

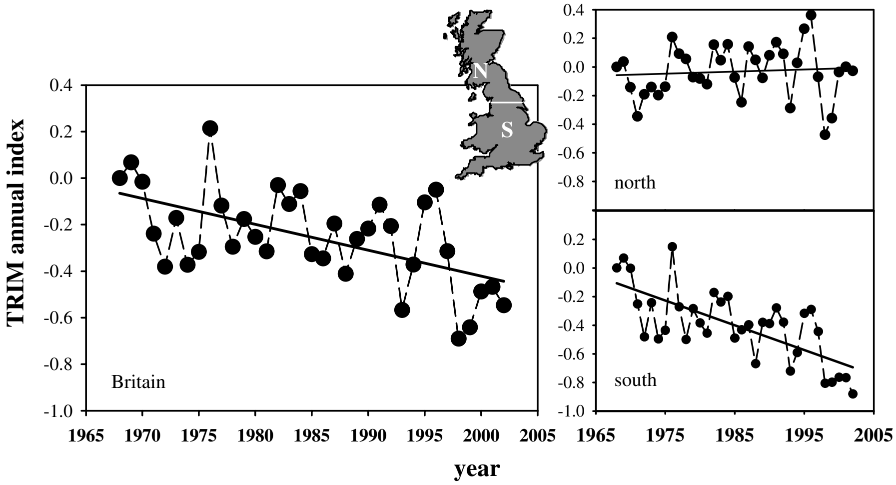

Fig. 1 – Decreases in total annual trap catches for all species. The decrease for Great Britain is significant ($t_{33} = 8.83$, $P < 0.001$), as is the decrease in the south ($t_{33} = 10.9$, $P < 0.001$), and represent 31% and 44% decreases in total macro-moths caught, respectively. Trap catches have increased by 5% in the north, but this trend is not significant ($t_{33} = 0.67$, $P = 0.51$).

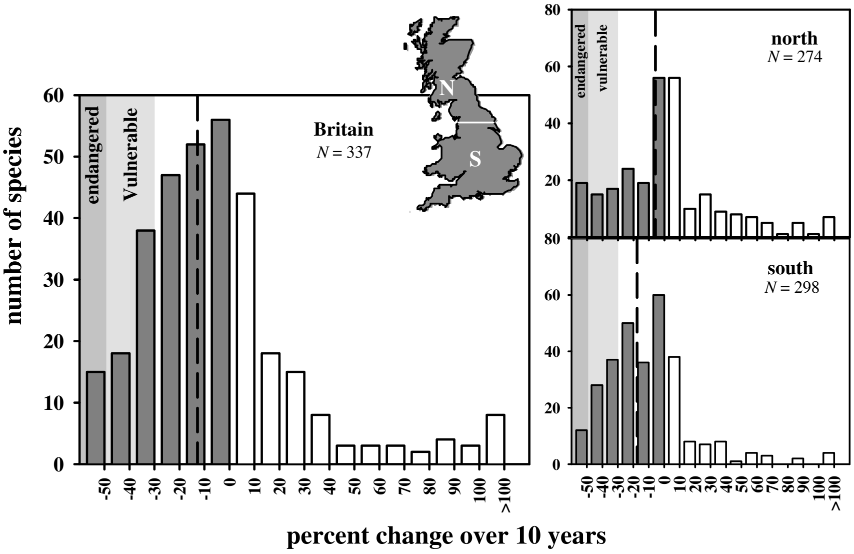

Fig. 2 – Frequency distributions of changes in abundance of British macro-moths. The figures plotted are the percentage changes over a 10-yr period, calculated from the annual rate of change estimated from long-term trends from 1968–2002. The vertical dashed line shows the median 10-yr change. *X*-axis labels are the upper limits of each class. Shaded areas correspond with the criteria thresholds for threatened species in the vulnerable and endangered categories.

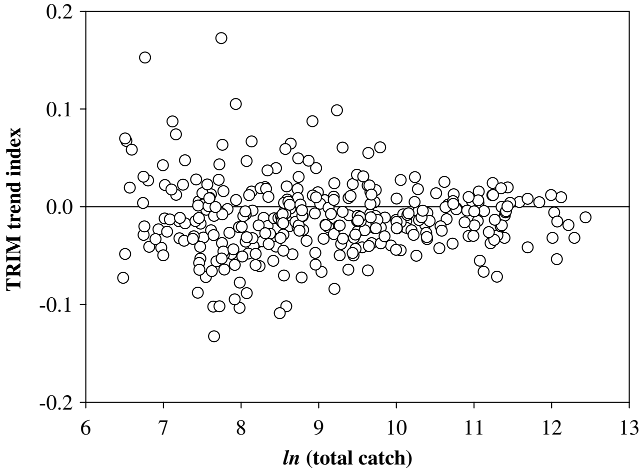

Fig. 3 – TRIM trend index versus the natural logarithm of total trap catch for each of the 337 species in the study. Frequently captured species are no more or less likely to decline or increase than less common species.

of abundance were very similar between groups. This indicates that the declines in moth abundance observed over the course of our study are not caused by decreased effectiveness of RIS light-traps due to increasing light competition, but does not preclude the possibility that light pollution has been a cause of moth population declines (Frank, 1988).

4. Discussion

This study has, for the first time, shown that the so-called "common and widespread" macro-moth species in Britain are undergoing severe population declines. These estimates of population change represent a wide variety of biotopes, are robust to trap turnover, are not affected by light competition and are independent of total catches for individual species.

The overall pattern of decline for so many species points to a widespread deterioration of suitable environmental conditions across the country. The deterioration has been most severe in the south of England where the rapid intensification of agriculture and forestry already has been implicated in the decline of butterflies, especially in the southeast (Warren et al., 2001). However, the fact that a large proportion of species are declining rapidly in both north and south Britain (Fig. 2) indicates that adverse environmental changes are impacting moth populations across the country.

The IUCN categories of threat are widely used to prepare 'Red lists' of threatened species and have become an important tool to identify ecological problems and guide conservation action (Mace and Lande, 1991; IUCN World Conservation Union, 2001; Dunn, 2002). While the quantitative data on population dynamics demanded by IUCN categories are lacking for almost all moths and other insects that are currently of conservation concern around the world (New, 2004), the extensive RIS dataset did allow us to determine, quantitatively, 10-yr rates of population change of a large group of British macro-moths. Following the criteria of the IUCN categories in our study provides a well-recognized scale of the severity of moth population declines.

In this study we found 71 common moth species that are declining at rates that should see them designated as endangered or vulnerable if the quantitative IUCN criteria are applied at the national scale (Gardenfors et al., 2001; Eaton et al., 2005). None of the threatened species is known for long-distance migrations and it is unlikely that the declining populations can be "rescued" by continental migrants.

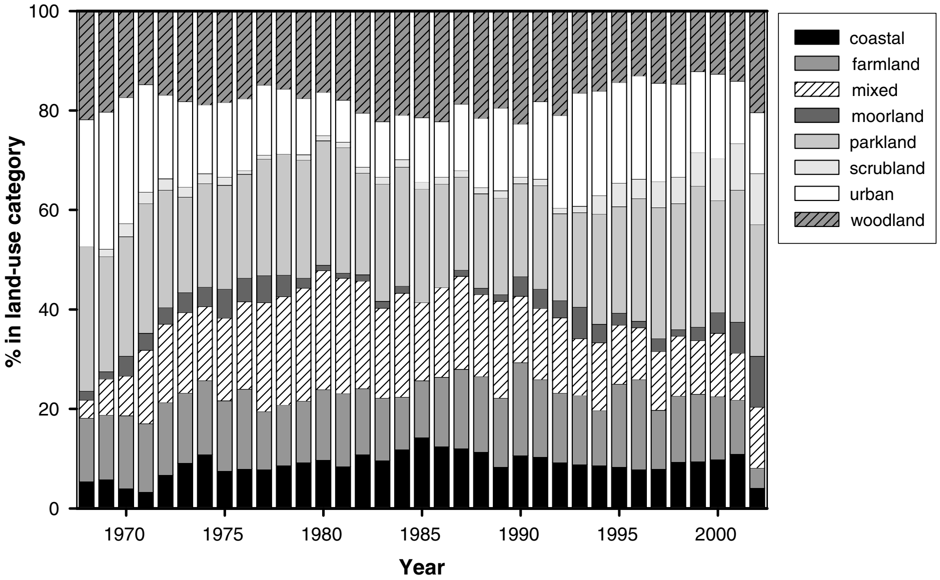

Fig. 4 – Annual proportions of land-use categories for light-traps used in the study.

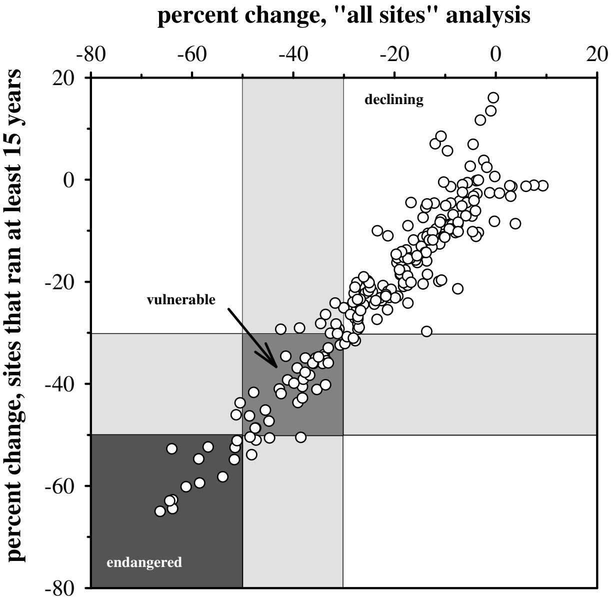

Fig. 5 – Comparison of 10-yr trends estimated by analysis of all light-trap sites and only using sites that operated for at least 15 yr. The four areas shaded pale grey delineate regions of assignment of rapid-decline categories between the two methods of estimating trends.

Even so, it is more important that the magnitude of the declines are sufficient that the species *could* be considered for threatened status. The number of potentially threatened species in this study is more than double the published British Red Data Book list of 33 species (Shirt, 1987), none of which was included in our analysis. This finding suggests we may be seriously underestimating the proportion of threatened British insects.

Designation of threatened status for common and widespread species on the basis of population decline rates alone has been criticized (Dunn, 2002) and the method of applying IUCN criteria at national rather than global scales is still being formalised, although their utility has been recognised (Gardenfors et al., 2001; Dunn, 2002; Eaton et al., 2005). Nevertheless, it is important that monitoring effort is directed toward understanding population changes among common species as well as rare ones (Conrad et al., 2002; Dunn, 2002). Common species may undergo dramatic population changes that go largely unnoticed by recorders and conservation managers, but which could provide valuable information for conservation and ecological studies (Thomas and Abery, 1995; Cowley et al., 1999; Leon-Cortes et al., 1999). Common species should represent a greater variety of habitats and species interactions and therefore play an important role in ecosystem functioning.

A brief examination of moth population trends in relation to ecological and life-history traits identified few significant associations and declines are taking place in a wide variety of biotopes (Conrad et al., 2004). While widely distributed species are more likely to be declining, increasing species are likely to be those that are expanding their range as well as increasing in abundance, and are often species apparently benefiting from human activity, such as those feeding on ornamental conifers (Conrad et al., 2004). The causes of long-term trends identified in this study are yet to be assessed in detail, and are likely to be a complex mixture of factors influencing the quantity, quality and spatial distribution of suitable habitat (e.g., land management, chemical and light pollution, climatic conditions). Causes of decline will also undoubtedly vary from species to species.

All of the moth species in our study are common and widespread. Truly specialised species, such as have been described for British butterflies (Warren et al., 2001) are too uncommon and too locally distributed (Quinn et al., 1997) to have been caught in sufficient numbers to be used in our analysis and are therefore under-represented. If, like specialist butterflies (Warren et al., 2001), these species are more likely to be declining, then we have underestimated the overall proportions of declining macro-moths.

Half of the species we studied experienced a 10-yr decline of at least 12%, and while the precise comparison of trends between different sampling methods is difficult and may give misleading results (Thomas, 1996) our results suggest that British macro-moths have undergone declines at least as severe as British butterflies (Thomas et al., 2004). Moreover, the percentage of moth species declining (66%) was similar to the proportion of butterflies declining (71%), and greater than the proportion of birds (54%) or plants declining (28%) (Thomas et al., 2004; Eaton et al., 2005). Thus, our findings support the view that insect biodiversity is declining very rapidly in Britain and probably at a greater rate than vertebrates and vascular plants (Thomas et al., 2004), with potentially serious consequences for ecosystem services.

Common macro-moths have undergone widespread and serious declines in Britain. Environmental changes that affect common and widespread herbivores, such as the macro-moths reported here, signal strong impacts on the wider ecosystem and at higher trophic levels such as predacious insects, insectivorous spiders, birds and bats (Pollard and Yates, 1993; Ormerod and Watkinson, 2000; Donald et al., 2001; Wickramasinghe et al., 2004). Compared to UK butterflies (Thomas et al., 2004), the macro-moths in this study include a greater number of species from a wider range of habitats and, therefore are more likely to be representative of terrestrial insect biodiversity. However, the observed declines of macro-moths, taken together with those of butterfly species, signal a biodiversity crisis for Britain and are a strong indicator that insects may be facing great losses in other temperate-zone industrialised countries. As yet, even correlative evidence of factors driving long-term moth population trends is lacking, but having identified so many decreasing trends, the next priority is to examine the relative roles of climate, chemical and light pollution, and changes in land-use in greater detail.

Acknowledgements

We wish to acknowledge the efforts of the numerous volunteers who help run and maintain the light-traps of the Rothamsted Insect Survey. Joe Perry, Suzanne Clark and Peter Rothery offered statistical advice and discussion. Arco van Strien provided excellent advice and support for TRIM. Marie Castellazzi extracted the UK light-change data from world maps kindly provided by Chris Elvidge from the US National Geophysical Data Centre. Georgina Mace and Erica Dunn advised on the use of IUCN criteria. This study was funded by the Esmée Fairbairn Foundation and the UK Biotechnology and Biological Sciences Research Council (BBSRC), from which Rothamsted Research receives grant-aided support.

Appendix A. List of species studied with rates of annual population change

Number = "Bradley number", from Checklist of Lepidoptera recorded from the British Isles (Bradley, 2000); annual change rate = annual rate of population change estimated from the 35-yr time series (see methods); 95% CI = 95% confidence interval for the annual change rate; change status: increasing = change rate >0, declining = change rate <0, vulnerable = greater than 30% · 10 yr^{-1} decline, endangered = greater than 50% 10 yr^{-1} decline.

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
14	Ghost Swift	*Hepialus humuli*	−0.036	−0.027, −0.046	Vulnerable
15	Orange Swift	*Hepialus sylvina*	0.023	0.031, 0.015	Increasing
17	Common Swift	*Hepialus lupulinus*	−0.005	0.003, −0.013	Declining
18	Map-Winged Swift	*Hepialus fusconebulosa*	−0.014	−0.007, −0.022	Declining
1631	December Moth	*Poecilocampa populi*	−0.030	−0.025, −0.034	Declining
1632	Pale Eggar	*Trichiura crataegi*	−0.054	−0.042, −0.065	Vulnerable
1634	The Lackey	*Malacosoma nuestria*	−0.063	−0.044, −0.082	Vulnerable
1640	The Drinker	*Euthrix potatoria*	−0.007	0.000, −0.015	Declining
1645	Scalloped Hook-Tip	*Falcaria lacertinaria*	−0.021	−0.013, −0.028	Declining
1646	Oak Hook-Tip	*Drepana binaria*	−0.047	−0.033, −0.061	Vulnerable
1648	Pebble Hook-Tip	*Drepana falcataria*	−0.020	−0.012, −0.027	Declining
1651	Chinese Character	*Cilix glaucata*	−0.018	−0.011, −0.024	Declining
1652	Peach Blossom	*Thyatira batis*	−0.028	−0.020, −0.036	Declining
1653	Buff Arches	*Habrosyne pyritoides*	−0.034	−0.026, −0.043	Declining
1657	Common Lutestring	*Ochropacha duplaris*	0.031	0.044, 0.018	Increasing
1658	Oak Lutestring	*Cymatophorima diluta*	−0.048	−0.023, −0.072	Vulnerable
1659	Yellow-Horned	*Achlya flavicornis*	0.015	0.022, 0.008	Increasing
1663	March Moth	*Alsophila aescularia*	−0.013	−0.008, −0.019	Declining
1665	Grass Emerald	*Pseudoterpna pruinata*	−0.030	−0.016, −0.044	Declining
1666	Large Emerald	*Geometra papilionaria*	0.009	0.016, 0.002	Increasing
1667	Blotched Emerald	*Comibaena bajularia*	−0.008	0.013, −0.029	Declining
1669	Common Emerald	*Hemithea aestivaria*	−0.008	−0.002, −0.014	Declining

Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
1673	Small Emerald	*Hemistola chrysoprasaria*	−0.049	−0.023, −0.074	Vulnerable
1674	Little Emerald	*Jodis lactearia*	−0.002	0.007, −0.010	Declining
1677	Birch Mocha	*Cyclophora albipunctata*	−0.020	−0.002, −0.038	Declining
1680	Maiden's Blush	*Cyclophora punctaria*	0.028	0.046, 0.011	Increasing
1682	Blood-Vein	*Timandra griseata*	−0.043	−0.037, −0.049	Vulnerable
1689	Mullein Wave	*Scopula marginepunctata*	−0.040	−0.021, −0.059	Vulnerable
1690	Small Blood-Vein	*Scopula imitaria*	−0.028	−0.021, −0.035	Declining
1692	Lesser Cream Wave	*Scopula immutata*	−0.003	0.023, −0.029	Declining
1693	Cream Wave	*Scopula floslactata*	−0.009	−0.003, −0.015	Declining
1694	Smoky Wave	*Scopula ternata*	−0.006	0.017, −0.030	Declining
1699	Least Carpet	*Idaea vulpinaria*	0.188	0.248, 0.128	Increasing
1702	Small Fan-Footed Wave	*Idaea biselata*	−0.006	−0.001, −0.011	Declining
1705	Dwarf Cream Wave	*Idaea fuscovenosa*	0.048	0.062, 0.034	Increasing
1707	Small Dusty Wave	*Idaea seriata*	0.013	0.022, 0.003	Increasing
1708	Single-Dotted Wave	*Idaea dimidiata*	0.013	0.019, 0.007	Increasing
1709	Satin Wave	*Idaea subsericeata*	−0.012	−0.001, −0.023	Declining
1711	Treble Brown-Spot	*Idaea trigeminata*	0.104	0.117, 0.090	Increasing
1712	Small Scallop	*Idaea emarginata*	−0.009	−0.001, −0.017	Declining
1713	Riband Wave	*Idaea aversata*	0.005	0.009, 0.001	Increasing
1715	Plain Wave	*Idaea straminata*	0.043	0.079, 0.008	Increasing
1716	The Vestal	*Rhodometra sacraria*	0.060	0.120, 0.000	Increasing
1719	Oblique Carpet	*Orthonama vittata*	−0.050	−0.034, −0.065	Vulnerable
1722	Flame Carpet	*Xanthorhoe designata*	0.018	0.026, 0.010	Increasing
1723	Red Carpet	*Xanthorhoe munitata*	−0.046	−0.035, −0.057	Vulnerable
1724	Red Twin-Spot Carpet	*Xanthorhoe spadicearia*	−0.016	−0.010, −0.022	Declining
1725	Dark-Barred Twin-Spot	*Xanthorhoe ferrugata*	−0.069	−0.062, −0.076	Endangered
1726	Large Twin-Spot Carpet	*Xanthorhoe quadrifasiata*	−0.010	0.001, −0.021	Declining
1727	Silver-Ground Carpet	*Xanthorhoe montanata*	−0.015	−0.010, −0.020	Declining
1728	Garden Carpet	*Xanthorhoe fluctuata*	−0.033	−0.028, −0.038	Declining
1732	Shaded Broad-Bar	*Scotopteryx chenopodiata*	−0.037	−0.029, −0.045	Vulnerable
1738	Common Carpet	*Epirrhoe alternata*	−0.004	0.002, −0.010	Declining
1739	Wood Carpet	*Epirrhoe rivata*	0.001	0.017, −0.014	Increasing
1740	Galium Carpet	*Epirrhoe galiata*	−0.040	−0.019, −0.062	Vulnerable
1742	Yellow Shell	*Camptogramma bilineata*	0.019	0.029, 0.009	Increasing
1744	Grey Mountain Carpet	*Entephria caesiata*	−0.044	−0.024, −0.064	Vulnerable
1745	The Mallow	*Larentia clavaria*	−0.009	0.001, −0.020	Declining
1746	Shoulder Stripe	*Anticlea badiata*	−0.032	−0.026, −0.038	Declining
1747	The Streamer	*Anticlea derivata*	−0.019	−0.012, −0.026	Declining
1748	Beautiful Carpet	*Mesoleuca albicillata*	0.004	0.024, −0.016	Increasing
1749	Dark Spinach	*Pelurga comitata*	−0.085	−0.061, −0.108	Endangered
1750	Water Carpet	*Lampropteryx suffumata*	0.005	0.012, −0.002	Increasing
1751	Devon Carpet	*Lampropteryx otregiata*	0.069	0.118, 0.020	Increasing
1752	Purple Bar	*Cosmorhoe ocellata*	−0.007	−0.001, −0.012	Declining
1753	Striped Twin-Spot Carpet	*Nebula salicata*	−0.010	0.010, −0.030	Declining
1754	The Phoenix	*Eulithis prunata*	0.012	0.026, −0.002	Increasing
1755	The Chevron	*Eulithis testata*	−0.015	−0.007, −0.022	Declining
1756	Northern Spinach	*Eulithis populata*	0.019	0.023, 0.015	Increasing
1757	The Spinach	*Eulithis mellinata*	−0.084	−0.060, −0.108	Endangered
1758	Barred Straw	*Eulithis pyraliata*	−0.020	−0.014, −0.026	Declining
1759	Small Phoenix	*Ecliptopera silaceata*	−0.042	−0.035, −0.049	Vulnerable
1760	Red–green Carpet	*Chloroclysta siterata*	0.057	0.067, 0.047	Increasing
1761	Autumn Green Carpet	*Chloroclysta miata*	−0.014	−0.005, −0.023	Declining
1762	Dark Marbled Carpet	*Chloroclysta citrata*	0.012	0.019, 0.005	Increasing
1764	Common Marbled Carpet	*Chloroclysta truncata*	−0.019	−0.014, −0.024	Declining
1765	Barred Yellow	*Cidaria fulvata*	−0.010	−0.003, −0.018	Declining

(*continued on next page*)

Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
1766	Blue-Bordered Carpet	*Plemyria rubiginata*	0.049	0.065, 0.032	Increasing
1767	Pine Carpet	*Thera firmata*	0.038	0.051, 0.025	Increasing
1768	Grey Pine Carpet	*Thera obeliscata*	0.005	0.011, –0.002	Increasing
1769	Spruce Carpet	*Thera britannica*	0.067	0.090, 0.044	Increasing
1771	Juniper Carpet	*Thera juniperata*	0.077	0.120, 0.034	Increasing
1773	Broken-Barred Carpet	*Electrophaes corylata*	–0.007	0.004, –0.018	Declining
1775	Mottled Grey	*Colostygia multistrigaria*	–0.026	–0.019, –0.034	Declining
1776	Green Carpet	*Colostygia pectinataria*	0.026	0.033, 0.018	Increasing
1777	July Highflyer	*Hydriomena furcata*	0.012	0.018, 0.006	Increasing
1778	May Highflyer	*Hydriomena impluviata*	–0.005	0.010, –0.020	Declining
1781	Small Waved Umber	*Horisme vitalbata*	0.014	0.033, –0.005	Increasing
1782	The Fern	*Horisme tersata*	–0.015	0.003, –0.032	Declining
1784	Pretty Chalk Carpet	*Melanthia procellata*	–0.056	–0.038, –0.074	Vulnerable
1789	Scallop Shell	*Rheumaptera undulata*	–0.017	–0.002, –0.031	Declining
1792	Dark Umber	*Philereme transversata*	–0.034	–0.021, –0.048	Declining
1794	Sharp-Angled Carpet	*Euphyia unangulata*	–0.031	–0.019, –0.042	Declining
1795	November Moth	*Epirrita dilutata*	–0.031	–0.027, –0.036	Declining
1797	Autumnal Moth	*Epirrita autumnata*	–0.011	–0.001, –0.020	Declining
1798	Small Autumnal Moth	*Epirrita filigrammaria*	–0.022	0.040, –0.084	Declining
1799	Winter Moth	*Operophtera brumata*	–0.004	0.003, –0.012	Declining
1800	Northern Winter Moth	*Operophtera fagata*	–0.011	–0.001, –0.020	Declining
1802	The Rivulet	*Perizoma affinitata*	–0.015	–0.006, –0.024	Declining
1803	Small Rivulet	*Perizoma alchemillata*	–0.003	0.009, –0.014	Declining
1807	Grass Rivulet	*Perizoma albulata*	–0.090	–0.067, –0.113	Endangered
1808	Sandy Carpet	*Perizoma flavofasciata*	–0.005	0.003, –0.013	Declining
1809	Twin-Spot Carpet	*Perizoma didymata*	0.028	0.036, 0.019	Increasing
1858	V-Pug	*Chloroclystis v-ata*	0.009	0.022, –0.004	Increasing
1864	The Streak	*Chesias legatella*	–0.042	–0.033, –0.051	Vulnerable
1865	Broom-Tip	*Chesias rufata*	–0.052	–0.022, –0.081	Vulnerable
1867	Treble-Bar	*Aplocera plagiata*	–0.032	–0.021, –0.044	Declining
1873	Welsh Wave	*Venusia cambrica*	0.005	0.021, –0.010	Increasing
1874	Dingy Shell	*Euchoeca nebulata*	0.020	0.065, –0.026	Increasing
1875	Small White Wave	*Asthena albulata*	0.001	0.030, –0.028	Increasing
1881	Early Tooth-Striped	*Trichopteryx carpinata*	0.032	0.041, 0.022	Increasing
1882	Small Seraphim	*Pterapherapteryx sexalata*	–0.033	–0.015, –0.051	Declining
1883	Yellow-Barred Brindle	*Acasis viretata*	0.023	0.036, 0.011	Increasing
1884	The Magpie	*Abraxas grossulariata*	–0.033	–0.025, –0.040	Declining
1887	Clouded Border	*Lomaspilis marginata*	–0.004	0.001, –0.010	Declining
1888	Scorched Carpet	*Ligdia adustata*	–0.020	–0.011, –0.029	Declining
1889	Peacock	*Semiothisa notata*	0.091	0.132, 0.050	Increasing
1890	Sharp-Angled Peacock	*Semiothisa alternaria*	–0.013	0.001, –0.027	Declining
1893	Tawny-Barred Angle	*Semiothisa liturata*	0.002	0.012, –0.008	Increasing
1894	Latticed Heath	*Semiothisa clathrata*	–0.058	–0.048, –0.067	Vulnerable
1897	The V-Moth	*Semiothisa wauaria*	–0.097	–0.072, –0.122	Endangered
1902	Brown Silver-Lines	*Petrophora chlorosata*	–0.005	0.000, –0.009	Declining
1903	Barred Umber	*Plagodis pulveraria*	0.021	0.031, 0.011	Increasing
1904	Scorched Wing	*Plagodis dolabraria*	0.002	0.010, –0.005	Increasing
1906	Brimstone Moth	*Opisthograptis luteolata*	–0.013	–0.009, –0.017	Declining
1907	Bordered Beauty	*Epione repandaria*	–0.008	0.000, –0.016	Declining
1910	Lilac Beauty	*Apeira syringaria*	–0.031	–0.023, –0.040	Declining
1912	August Thorn	*Ennomos quercinaria*	–0.047	–0.033, –0.061	Vulnerable
1913	Canary-Shouldered Thorn	*Ennomos alniaria*	–0.030	–0.024, –0.036	Declining
1914	Dusky Thorn	*Ennomos fuscantaria*	–0.103	–0.088, –0.119	Endangered
1915	September Thorn	*Ennomos erosaria*	–0.068	–0.056, –0.080	Endangered
1917	Early Thorn	*Selenia dentaria*	–0.026	–0.022, –0.030	Declining
1918	Lunar Thorn	*Selenia lunularia*	–0.015	–0.005, –0.026	Declining

Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
1919	Purple Thorn	*Selenia tetralunaria*	–0.032	–0.024, –0.041	Declining
1920	Scalloped Hazel	*Odontopera bidentata*	–0.004	0.001, –0.009	Declining
1921	Scalloped Oak	*Crocallis elinguaria*	–0.031	–0.026, –0.035	Declining
1922	Swallow-Tail Moth	*Ourapteryx sambucaria*	–0.024	–0.018, –0.031	Declining
1923	Feathered Thorn	*Colotois pennaria*	–0.024	–0.019, –0.029	Declining
1926	Pale Brindled Beauty	*Apocheima pilosaria*	–0.022	–0.012, –0.032	Declining
1927	Brindled Beauty	*Lycia hirtaria*	–0.046	–0.038, –0.055	Vulnerable
1930	Oak Beauty	*Biston strataria*	–0.003	0.004, –0.011	Declining
1931	Peppered Moth	*Biston betularia*	–0.027	–0.018, –0.035	Declining
1932	Spring Usher	*Agriopis leucophaearia*	0.010	0.034, –0.015	Increasing
1933	Scarce Umber	*Agriopis aurantiaria*	–0.028	–0.018, –0.039	Declining
1934	Dotted Border	*Agriopis marginaria*	–0.022	–0.017, –0.027	Declining
1935	Mottled Umber	*Erannis defoliaria*	0.000	0.012, –0.012	Increasing
1937	Willow Beauty	*Peribatodes rhomboidaria*	–0.015	–0.009, –0.022	Declining
1940	Satin Beauty	*Deileptenia ribeata*	0.111	0.153, 0.069	Increasing
1941	Mottled Beauty	*Alcis repandata*	0.010	0.015, 0.005	Increasing
1942	Dotted Carpet	*Alcis jubata*	0.062	0.077, 0.048	Increasing
1944	Pale Oak Beauty	*Serraca punctinalis*	0.007	0.022, –0.009	Increasing
1945	Brussels Lace	*Cleorodes lichenaria*	–0.011	0.011, –0.034	Declining
1947	The Engrailed	*Ectropis bistortata*	0.003	0.009, –0.003	Increasing
1950	Brindled White-Spot	*Paradarisa extersaria*	–0.008	0.014, –0.029	Declining
1951	Grey Birch	*Aethalura punctulata*	0.000	0.019, –0.020	Declining
1954	Bordered White	*Bupalus piniaria*	–0.011	0.004, –0.027	Declining
1955	Common White Wave	*Cabera pusaria*	0.016	0.021, 0.011	Increasing
1956	Common Wave	*Cabera exanthemata*	0.006	0.011, 0.000	Increasing
1957	White-Pinion Spotted	*Lomographa bimaculata*	0.010	0.031, –0.011	Increasing
1958	Clouded Silver	*Lomographa temerata*	–0.018	–0.012, –0.025	Declining
1961	Light Emerald	*Campaea margaritata*	0.007	0.011, 0.002	Increasing
1962	Barred Red	*Hylaea fasciaria*	0.003	0.010, –0.005	Increasing
1981	Poplar Hawk-Moth	*Laothoe populi*	–0.007	–0.001, –0.012	Declining
1994	Buff-Tip	*Phalera bucephala*	–0.022	–0.012, –0.031	Declining
2000	Iron Prominent	*Notodonta dromedarius*	–0.012	0.001, –0.025	Declining
2003	Pebble Prominent	*Eligmodonta ziczac*	–0.021	–0.011, –0.031	Declining
2005	Great Prominent	*Peridea anceps*	0.016	0.028, 0.003	Increasing
2006	Lesser Swallow Prominent	*Pheosia gnoma*	–0.019	–0.013, –0.026	Declining
2007	Swallow Prominent	*Pheosia tremula*	0.012	0.027, –0.003	Increasing
2008	Coxcomb Prominent	*Ptilodon capucina*	–0.025	–0.019, –0.030	Declining
2011	Pale Prominent	*Pterostoma palpina*	–0.009	–0.002, –0.017	Declining
2014	Marbled Brown	*Drymonia dodonaea*	–0.011	0.000, –0.023	Declining
2015	Lunar Marbled Brown	*Drymonia ruficornis*	0.022	0.039, 0.006	Increasing
2020	Figure of Eight	*Diloba caeruleocephala*	–0.081	–0.071, –0.090	Endangered
2028	Pale Tussock	*Calliteara pudibunda*	–0.015	–0.005, –0.024	Declining
2030	Yellow-Tail	*Euproctis similis*	–0.006	0.000, –0.013	Declining
2033	Black Arches	*Lymantria monacha*	0.020	0.036, 0.005	Increasing
2035	Round-Winged Muslin	*Thumatha senex*	0.013	0.039, –0.014	Increasing
2037	Rosy Footman	*Miltochrista miniata*	0.040	0.054, 0.026	Increasing
2038	Muslin Footman	*Nudaria mundana*	0.022	0.034, 0.010	Increasing
2040	Four-Dotted Footman	*Cybosia mesomella*	0.004	0.014, –0.005	Increasing
2044	Dingy Footman	*Eilema griseola*	0.063	0.076, 0.049	Increasing
2047	Scarce Footman	*Eilema complana*	0.091	0.112, 0.070	Increasing
2049	Buff Footman	*Eilema deplana*	0.065	0.104, 0.027	Increasing
2050	Common Footman	*Eilema lurideola*	0.010	0.016, 0.004	Increasing
2057	Garden Tiger	*Arctia caja*	–0.062	–0.054, –0.071	Vulnerable
2059	Clouded Buff	*Diacrisia sannio*	–0.028	–0.007, –0.050	Declining
2060	White Ermine	*Spilosoma lubricipeda*	–0.041	–0.035, –0.046	Vulnerable

(*continued on next page*)

Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
2061	Buff Ermine	*Spilosoma luteum*	−0.037	−0.031, −0.042	Vulnerable
2063	Muslin Moth	*Diaphora mendica*	0.007	0.015, −0.001	Increasing
2064	Ruby Tiger	*Phragmatobia fuliginosa*	0.007	0.015, −0.001	Increasing
2069	Cinnabar	*Tyria jacobaeae*	−0.049	−0.035, −0.063	Vulnerable
2077	Short-Cloaked Moth	*Nola cucullatella*	−0.021	−0.011, −0.030	Declining
2078	Least Black Arches	*Nola confusalis*	0.061	0.082, 0.040	Increasing
2081	White-Line Dart	*Euxoa tritici*	−0.069	−0.051, −0.088	Endangered
2082	Garden Dart	*Euxoa nigricans*	−0.097	−0.067, −0.126	Endangered
2085	Archer’s Dart	*Agrotis vestigialis*	−0.031	−0.016, −0.046	Declining
2087	Turnip Moth	*Agrotis segetum*	−0.032	−0.022, −0.042	Declining
2088	Heart & Club	*Agrotis clavis*	−0.002	0.012, −0.016	Declining
2089	Heart & Dart	*Agrotis exclamationis*	−0.031	−0.023, −0.040	Declining
2091	Dark Sword-Grass	*Agrotis ipsilon*	−0.025	−0.003, −0.047	Declining
2092	Shuttle-Shaped Dart	*Agrotis puta*	0.009	0.019, −0.001	Increasing
2098	The Flame	*Axylia putris*	−0.021	−0.014, −0.029	Declining
2102	Flame Shoulder	*Ochropleura plecta*	−0.001	0.005, −0.007	Declining
2107	Large Yellow Underwing	*Noctua pronuba*	0.025	0.030, 0.019	Increasing
2109	Lesser Yellow Underwing	*Noctua comes*	0.017	0.024, 0.011	Increasing
2110	Broad-Bordered Yellow Underwing	*Noctua fimbriata*	0.070	0.094, 0.046	Increasing
2111	Lesser Broad-Bordered Yellow Underwing	*Noctua janthe*	0.008	0.015, 0.002	Increasing
2114	Double Dart	*Graphiphora augur*	−0.097	−0.084, −0.110	Endangered
2117	Autumnal Rustic	*Paradiarsa glareosa*	−0.070	−0.060, −0.079	Endangered
2118	True Lover’s Knot	*Lycophotia porphyrea*	−0.029	−0.023, −0.036	Declining
2120	Ingrailed Clay	*Diarsia mendica*	−0.031	−0.026, −0.036	Declining
2121	Barred Chestnut	*Diarsia dahlii*	0.033	0.045, 0.021	Increasing
2122	Purple Clay	*Diarsia brunnea*	−0.018	−0.012, −0.025	Declining
2123	Small Square-Spot	*Diarsia rubi*	−0.052	−0.045, −0.060	Vulnerable
2126	Setaceous Hebrew Character	*Xestia c-nigrum*	0.004	0.010, −0.003	Increasing
2127	Triple-Spotted Clay	*Xestia ditrapezium*	−0.020	0.002, −0.041	Declining
2128	Double Square-Spot	*Xestia triangulum*	−0.014	−0.008, −0.019	Declining
2130	Dotted Clay	*Xestia baja*	−0.014	−0.007, −0.021	Declining
2132	Neglected or Grey Rustic	*Xestia castanea*	−0.047	−0.029, −0.065	Vulnerable
2133	Six-Striped Rustic	*Xestia sexstrigata*	−0.021	−0.012, −0.029	Declining
2134	Square-Spot Rustic	*Xestia xanthographa*	0.005	0.011, −0.001	Increasing
2135	Heath Rustic	*Xestia agathina*	−0.052	−0.029, −0.074	Vulnerable
2136	The Gothic	*Naenia typica*	−0.032	−0.012, −0.051	Declining
2138	Green Arches	*Anaplectoides prasina*	0.019	0.031, 0.007	Increasing
2139	Red Chestnut	*Cerastis rubricosa*	−0.021	−0.014, −0.029	Declining
2145	The Nutmeg	*Discestra trifolii*	−0.017	0.001, −0.035	Declining
2147	The Shears	*Hada plebeja*	0.010	0.020, 0.001	Increasing
2150	Grey Arches	*Polia nebulosa*	−0.015	−0.001, −0.029	Declining
2154	Cabbage Moth	*Mamestra brassicae*	−0.015	−0.006, −0.025	Declining
2155	Dot Moth	*Melanchra persicariae*	−0.059	−0.044, −0.073	Vulnerable
2158	Pale-Shouldered Brocade	*Lacanobia thalassina*	0.003	0.011, −0.005	Increasing
2160	Bright-Line Brown-Eye	*Lacanobia oleracea*	−0.011	−0.004, −0.018	Declining
2163	Broom Moth	*Ceramica pisi*	−0.041	−0.032, −0.049	Vulnerable
2173	The Lychnis	*Hadena bicruris*	−0.024	−0.010, −0.037	Declining
2176	Antler Moth	*Cerapteryx graminis*	−0.031	−0.024, −0.038	Declining
2177	Hedge Rustic	*Tholera cespitis*	−0.098	−0.087, −0.110	Endangered
2178	Feathered Gothic	*Tholera decimalis*	−0.065	−0.052, −0.077	Vulnerable
2179	Pine Beauty	*Panolis flammea*	0.044	0.057, 0.032	Increasing
2182	Small Quaker	*Orthosia cruda*	0.008	0.021, −0.004	Increasing
2186	Powdered Quaker	*Orthosia gracilis*	−0.040	−0.030, −0.050	Vulnerable
2187	Common Quaker	*Orthosia cerasi*	0.006	0.013, −0.002	Increasing
2188	Clouded Drab	*Orthosia incerta*	−0.008	−0.002, −0.014	Declining
2189	Twin-Spotted Quaker	*Orthosia munda*	−0.001	0.009, −0.011	Declining

Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
2190	Hebrew Character	*Orthosia gothica*	−0.011	−0.006, −0.015	Declining
2192	Brown-Line Bright-Eye	*Mythimna conigera*	−0.023	−0.012, −0.035	Declining
2193	The Clay	*Mythimna ferrago*	−0.009	−0.004, −0.015	Declining
2198	Smoky Wainscot	*Mythimna impura*	0.000	0.006, −0.006	Declining
2199	Common Wainscot	*Mythimna pallens*	−0.029	−0.021, −0.036	Declining
2205	Shoulder-Striped Wainscot	*Mythimna comma*	−0.036	−0.024, −0.048	Vulnerable
2225	Minor Shoulder-Knot	*Brachylomia viminalis*	−0.037	−0.025, −0.048	Vulnerable
2227	The Sprawler	*Brachionycha sphinx*	−0.049	−0.040, −0.057	Vulnerable
2229	Brindled Ochre	*Dasypolia templi*	−0.063	−0.040, −0.085	Vulnerable
2231	Deep-Brown Dart[a]	*Aporophyla lutulenta*	−0.064	−0.044, −0.084	Vulnerable
2232	Black Rustic	*Aporophyla nigra*	−0.032	−0.019, −0.044	Declining
2237	Grey Shoulder-Knot	*Lithophane ornitopus*	0.072	0.101, 0.044	Increasing
2240	Blair's Shoulder-Knot	*Lithophane leautieri*	0.165	0.243, 0.087	Increasing
2241	Red Sword-Grass	*Xylena vetusta*	−0.013	0.002, −0.028	Declining
2243	Early Grey	*Xylocampa areola*	0.004	0.013, −0.005	Increasing
2245	Green-Brindled Crescent	*Allophyes oxyacanthae*	−0.044	−0.038, −0.050	Vulnerable
2247	Merveille Du Jour	*Dichonia aprilina*	0.005	0.020, −0.009	Increasing
2248	Brindled Green	*Dryobotodes eremita*	0.040	0.058, 0.023	Increasing
2250	Dark Brocade	*Mniotype adusta*	−0.043	−0.027, −0.058	Vulnerable
2254	Grey Chi	*Antitype chi*	−0.023	−0.005, −0.041	Declining
2255	Feathered Ranunculus	*Eumichtis lichenea*	−0.007	0.003, −0.018	Declining
2256	The Satellite	*Eupsilia transversa*	0.024	0.035, 0.014	Increasing
2258	The Chestnut	*Conistra vaccinii*	0.012	0.017, 0.007	Increasing
2259	Dark Chestnut	*Conistra ligula*	−0.019	−0.009, −0.029	Declining
2262	The Brick	*Agrochola circellaris*	−0.028	−0.021, −0.035	Declining
2263	Red-Line Quaker	*Agrochola lota*	0.007	0.016, −0.001	Increasing
2264	Yellow-Line Quaker	*Agrochola macilenta*	0.014	0.020, 0.007	Increasing
2265	Flounced Chestnut	*Agrochola helvola*	−0.058	−0.043, −0.072	Vulnerable
2266	Brown-Spot Pinion	*Agrochola litura*	−0.039	−0.031, −0.048	Vulnerable
2267	Beaded Chestnut	*Agrochola lychnidis*	−0.064	−0.057, −0.072	Vulnerable
2269	Centre-Barred Sallow	*Atethmia centrago*	−0.038	−0.029, −0.046	Vulnerable
2270	Lunar Underwing	*Omphaloscelis lunosa*	0.020	0.027, 0.013	Increasing
2272	Barred Sallow	*Xanthia aurago*	−0.017	−0.005, −0.029	Declining
2273	Pink-Barred Sallow	*Xanthia togata*	−0.018	−0.012, −0.025	Declining
2274	The Sallow	*Xanthia icteritia*	−0.048	−0.040, −0.056	Vulnerable
2275	Dusky-Lemon Sallow	*Xanthia gilvago*	−0.070	−0.036, −0.104	Endangered
2284	Grey Dagger	*Acronicta psi*	−0.041	−0.028, −0.054	Vulnerable
2289	Knot Grass	*Acronicta rumicis*	−0.045	−0.035, −0.054	Vulnerable
2293	Marbled Beauty	*Cryphia domestica*	0.051	0.062, 0.039	Increasing
2299	Mouse Moth	*Amphipyra tragopogonis*	−0.037	−0.030, −0.044	Vulnerable
2302	Brown Rustic	*Rusina ferruginea*	−0.015	−0.010, −0.019	Declining
2303	Straw Underwing	*Thalpophila matura*	−0.031	−0.022, −0.040	Declining
2305	Small Angle Shades	*Euplexia lucipara*	−0.019	−0.011, −0.027	Declining
2306	Angle Shades	*Phlogophora meticulosa*	0.011	0.018, 0.004	Increasing
2312	The Olive	*Ipimorpha subtusa*	0.031	0.061, 0.001	Increasing
2318	The Dun-Bar	*Cosmia trapezina*	0.000	0.007, −0.008	Declining
2319	Lunar-Spotted Pinion	*Cosmia pyralina*	−0.026	−0.010, −0.042	Declining
2321	Dark Arches	*Apamea monoglypha*	−0.009	−0.004, −0.014	Declining
2322	Light Arches	*Apamea lithoxylaea*	−0.035	−0.026, −0.043	Declining
2326	Clouded-Bordered Brindle	*Apamea crenata*	−0.003	0.007, −0.014	Declining
2330	Dusky Brocade	*Apamea remissa*	−0.039	−0.028, −0.051	Vulnerable
2333	Large Nutmeg	*Apamea anceps*	−0.058	−0.034, −0.081	Vulnerable
2334	Rustic Shoulder-Knot	*Apamea sordens*	−0.027	−0.018, −0.036	Declining
2335	Slender Brindle	*Apamea solopacina*	0.016	0.038, −0.006	Increasing
2340	Middle-Barred Minor	*Oligia fasciuncula*	−0.013	−0.006, −0.019	Declining

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Appendix A – *continued*

Number	Vernacular name	Species	Annual change rate	95% CI	Change status
2341	Cloaked Minor	*Mesoligia furuncula*	0.022	0.032, 0.012	Increasing
2342	Rosy Minor	*Mesoligia literosa*	−0.047	−0.035, −0.058	Vulnerable
2343	Common Rustic	*Mesapamea secalis*	0.004	0.009, −0.002	Increasing
2345	Small Dotted Buff	*Photedes minima*	−0.020	−0.015, −0.025	Declining
2350	Small Wainscot	*Photedes pygmina*	−0.024	−0.016, −0.031	Declining
2352	Dusky Sallow	*Eremobia ochroleuca*	0.009	0.022, −0.004	Increasing
2353	Flounced Rustic	*Luperina testacea*	−0.019	−0.013, −0.024	Declining
2357	Large Ear	*Amphipoea lucens*	−0.019	0.006, −0.044	Declining
2360	Ear Moth	*Amphipoea oculea*	−0.035	−0.019, −0.051	Vulnerable
2361	Rosy Rustic	*Hydraecia micacea*	−0.054	−0.047, −0.060	Vulnerable
2364	Frosted Orange	*Gortyna flavago*	−0.012	−0.002, −0.022	Declining
2367	Haworth's Minor	*Celaena haworthii*	−0.062	−0.045, −0.079	Vulnerable
2368	The Crescent	*Celaena leucostigma*	−0.048	−0.030, −0.066	Vulnerable
2375	Large Wainscot	*Rhizedra lutosa*	−0.054	−0.042, −0.066	Vulnerable
2380	Treble Lines	*Charanyca trigrammica*	0.007	0.019, −0.004	Increasing
2381	The Uncertain	*Hoplodrina alsines*	0.002	0.009, −0.005	Increasing
2382	The Rustic	*Hoplodrina blanda*	−0.039	−0.030, −0.048	Vulnerable
2384	Vine's Rustic	*Hoplodrina ambigua*	0.048	0.077, 0.019	Increasing
2387	Mottled Rustic	*Caradrina morpheus*	−0.037	−0.030, −0.044	Vulnerable
2389	Pale Mottled Willow	*Caradrina clavipalpis*	0.023	0.038, 0.007	Increasing
2394	The Anomalous	*Stilbia anomala*	−0.075	−0.052, −0.097	Endangered
2410	Marbled White-Spot	*Protodeltote pygarga*	0.018	0.032, 0.005	Increasing
2422	Green Silver-Lines	*Pseudoips prasinana*	0.027	0.040, 0.015	Increasing
2425	Nut-Tree Tussock	*Colocasia coryli*	0.015	0.023, 0.007	Increasing
2434	Burnished Brass	*Diachrysia chrysitis*	−0.024	−0.018, −0.030	Declining
2439	Gold Spot	*Plusia festucae*	0.018	0.036, 0.000	Increasing
2441	Silver Y	*Autographa gamma*	−0.019	−0.014, −0.024	Declining
2442	Beautiful Golden Y	*Autographa pulchrina*	−0.009	−0.002, −0.015	Declining
2443	Plain Golden Y	*Autographa jota*	−0.004	0.009, −0.017	Declining
2444	Gold Spangle	*Autographa bractea*	0.002	0.016, −0.012	Increasing
2450	The Spectacle	*Abrostola tripartita*	0.012	0.019, 0.005	Increasing
2473	Beautiful Hook-Tip	*Laspeyria flexula*	−0.029	−0.016, −0.041	Declining
2474	Straw Dot	*Rivula sericealis*	0.031	0.046, 0.016	Increasing
2475	Waved Black	*Parascotia fuliginaria*	−0.004	0.009, −0.016	Declining
2477	The Snout	*Hypena proboscidalis*	−0.006	0.000, −0.012	Declining
2489	The Fan-Foot	*Herminia tarsipennalis*	−0.013	−0.006, −0.021	Declining
2492	Small Fan-Foot	*Herminia grisealis*	−0.016	−0.011, −0.021	Declining
–	Lead/July Belle Aggregate[b]	*Scotopteryx spp*	−0.035	−0.024, −0.045	Declining

a Deep-brown dart *Aporophyla lutulenta*, and Northern deep-brown dart *A. luenerbergensis* were not initially recorded as separate species and appear in the table as an aggregate of counts of both species.

b After compiling the data we determined that Lead Belle (*Scotopteryx mucronata*, 1733) and July Belle (*S. luridata*, 1734) could not be reliably distinguished on the basis of external appearance, gross morphology, phenology or distribution, so the catches of the two species were combined.

REFERENCES

Bradley, J.D., 2000. Checklist of Lepidoptera Recorded from the British Isles, second ed. Bradley & Bradley, Fordingbridge.

Conrad, K.F., Woiwod, I.P., Perry, J.N., 2002. Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. Biological Conservation 106, 329–337.

Conrad, K.F., Woiwod, I.P., Perry, J.N., 2003. East Atlantic teleconnection pattern and the decline of a common arctiid moth. Global Change Biology 9, 125–130.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R., Warren, M.S., 2004. Long-term population trends in widespread British moths. Journal of Insect Conservation 8, 119–136.

Cowley, M.J.R., Thomas, C.D., Thomas, J.A., Warren, M.S., 1999. Flight areas of British butterflies: assessing species status and decline. Proceedings of the Royal Society of London Series B-Biological Sciences 266, 1587–1592.

Donald, P.F., Green, R.E., Heath, M.M., 2001. Agricultural intensification and collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B-Biological Sciences 268, 25–29.

Dunn, E.H., 2002. Using decline in bird populations to identify needs for conservation action. Conservation Biology 16, 1632–1637.

Eaton, M.A., Gregory, R.D., Noble, D.G., Robinson, J.A., Hughes, J., Procter, D., Brown, A.F., Gibbons, D.W., 2005. Regional IUCN red listing: the process as applied to birds in the United Kingdom. Conservation Biology 19, 1557–1570.

Elvidge, C.D., Imhoff, M.L., Baugh, K.E., Hobson, V.R., Nelson, I., Safran, J., Dietz, J.B., Tuttle, B.T., 2001. Night-time lights of the world: 1994–1995. Isprs Journal of Photogrammetry and Remote Sensing 56, 81–99.

Frank, K.D., 1988. Impact of outdoor lighting on moths: an assessment. Journal of the Lepidopterists Society 42, 63–93.

Gardenfors, U., Hilton-Taylor, C., Mace, G.M., Rodriguez, J.P., 2001. The application of IUCN red list criteria at regional levels. Conservation Biology 15, 1206–1212.

Hambler, C., Speight, M.R., 2004. Extinction rates and butterflies. Science 305, 1563.

IUCN World Conservation Union. 2001. IUCN Red List categories and criteria: Version 3.1. IUCN Species Survival Commission, Gland, Switzerland and Cambridge, UK.

Lawton, J.H., May, R.M., 1995. Extinction Rates. Oxford University Press, oxford.

Leon-Cortes, J.L., Cowley, M.J.R., Thomas, C.D., 1999. Detecting decline in a formerly widespread species: how common is the common blue butterfly *Polyommatus icarus*? Ecography 22, 643–650.

Longcore, T., Rich, C., 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2, 191–198.

Mace, G.M., Lande, R., 1991. Assessing extinction threats: toward re-evaluation of IUCN threatened species categories. Conservation Biology 5, 148–157.

McKinney, M.L., 1999. High rates of extinction and threat in poorly studied taxa. Conservation Biology 13, 1273–1281.

New, T.R., 2004. Moths (Insecta: Lepidoptera) and conservation: background and perspective. Journal of Insect Conservation 8, 79–94.

Ormerod, S.J., Watkinson, A.R., 2000. Editor's introduction: birds and agriculture. Journal of Applied Ecology 37, 699.

Pannekoek, J., Van Strien, A.J. 2001. TRIM 3 Manual (TRends & Indices for Monitoring data) Statistics Netherlands, Voorburg.

Pollard, E., Yates, T., 1993. Monitoring Butterflies for Ecology and Conservation, first ed. Chapman and Hall, London.

Quinn, R.M., Gaston, K.J., Blackburn, T.M., Eversham, B.C., 1997. Abundance-range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. Ecological Entomology 22, 453–461.

Shirt, D.B., 1987British Red Data Books, vol. 2. Insects Nature Conservancy Council, Peterborough.

Taylor, L.R., French, R.A., 1974. Effects of light-trap design and illumination on samples of moths in an English woodland. Bulletin of Entomological Research 63, 583–594.

Thomas, L., 1996. Monitoring long-term population change: why are there so many analysis methods? Ecology 77, 49–58.

Thomas, J.A., 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B-Biological Sciences 360, 339–357.

Thomas, C.D., Abery, J.C.G., 1995. Estimating rates of butterfly decline from distribution maps – the effect of scale. Biological Conservation 73, 59–65.

Thomas, J.A., Clarke, R.T., 2004. Extinction rates and butterflies. Science 305, 1563–1564.

Thomas, J.A., Morris, M.G., 1994. Patterns, mechanisms and rates of extinction among invertebrates in the United Kingdom. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 344, 47–54.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T., Lawton, J.H., 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303, 1879–1881.

Van Strien, A.J., Pannekoek, J., Gibbons, D.W., 2001. Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. Bird Study 48, 200–213.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65–69.

Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan Jennings, N., 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. Conservation Biology 18, 1283–1292.

Williams, C.B., 1948. The Rothamsted light trap. Proceedings of the Royal Entomological Society of London A 23, 80–85.

Williams, C.B., 1952. Some notes on killing insects for collections and for scientific research. The Entomologist 85, 271–279.

Wilson, E.O., 1992. The Diversity of Life. Penguin Press, London.

Woiwod, I.P., Harrington, R., 1994. Flying in the face of change: The Rothamsted Insect Survey. In: Leigh, R., Johnston, A. (Eds.), Long-Term Experiments in Agricultural and Ecological Sciences. CAB International, Wallingford, pp. 321–342.

Global Change Biology

Global Change Biology (2013) **19**, 1417–1423, doi: 10.1111/gcb.12166

Artificial light pollution: are shifting spectral signatures changing the balance of species interactions?

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Abstract

Technological developments in municipal lighting are altering the spectral characteristics of artificially lit habitats. Little is yet known of the biological consequences of such changes, although a variety of animal behaviours are dependent on detecting the spectral signature of light reflected from objects. Using previously published wavelengths of peak visual pigment absorbance, we compared how four alternative street lamp technologies affect the visual abilities of 213 species of arachnid, insect, bird, reptile and mammal by producing different wavelength ranges of light to which they are visually sensitive. The proportion of the visually detectable region of the light spectrum emitted by each lamp was compared to provide an indication of how different technologies are likely to facilitate visually guided behaviours such as detecting objects in the environment. Compared to narrow spectrum lamps, broad spectrum technologies enable animals to detect objects that reflect light over more of the spectrum to which they are sensitive and, importantly, create greater disparities in this ability between major taxonomic groups. The introduction of broad spectrum street lamps could therefore alter the balance of species interactions in the artificially lit environment.

Keywords: animals, artificial light spectra, pollution, species interactions, street lighting, vision ecology

Received 13 November 2012; revised version received 1 February 2013 and accepted 2 February 2013

Introduction

Artificial lights have been used to illuminate the night-time environment for over a century, during which numerous alternative lighting technologies have arisen, each emitting light with unique spectral characteristics (Elvidge *et al.*, 2010). Now widely distributed, artificial lighting is spreading at a rate of 6% per year globally (Hölker *et al.*, 2010). Indeed, by 2001 it was estimated that the fraction of land under skies that were artificially brightened above natural background levels already exceeded 10% in 66 nations across the planet (Cinzano *et al.*, 2001). Organisms have evolved under the intensities, timings and spectral composition of light emitted from the sun and stars, and reflected from the moon. However, artificial lighting is changing all these aspects of natural light regimes (Gaston *et al.*, 2012) leading to a potentially diverse array of ecological impacts (Longcore & Rich, 2004; Perkin *et al.*, 2011; Gaston *et al.*, 2013). A recent surge in research activity has revealed that artificially lighting the nocturnal environment can have impacts ranging from changes in animal behaviour (Rydell, 1992; Bird *et al.*, 2004; Eisenbeis, 2006; Stone *et al.*, 2009; Titulaer *et al.*, 2012) to the composition of whole communities (Davies *et al.*, 2012). Yet, because artificial light pollution has only recently become widely recognized as an environmental issue, studies on its ecological effects remain relatively scarce.

Since the second half of the 20th century, narrow spectrum Low Pressure Sodium (LPS) lighting, with a characteristic orange hue, has been the most common form of street lighting in many regions. However, ongoing advances in street lighting technology have led to the increasing adoption of broader spectrum light sources such as High Pressure Sodium (HPS), Light Emitting Diode (LED) and Metal Halide (MH) lamps (Elvidge *et al.*, 2010), which provide improved colour rendering capabilities for humans. Shifting and broadening the spectra of street lamps may lead to unforeseen environmental impacts because the spectral signature reflected from objects is an important cue that guides a number of animal behaviours, including, for example, the detection of resources (Chittka *et al.*, 1994; Hempel de Ibarra & Vorobyev, 2009; Macedonia *et al.*, 2009; Chiao *et al.*, 2011; Zou *et al.*, 2011), mate selection (Andersson *et al.*, 1998; Hunt *et al.*, 2001; Robertson & Monteiro, 2005; Lim *et al.*, 2008) and navigation (Cheng *et al.*, 1986; Möller, 2002; Mappes & Homberg, 2004; Reppert *et al.*, 2004; Ugolini *et al.*, 2005). Here, we ask whether the use of broad spectrum street lighting technologies is likely to improve the ability of animals to perform tasks during the night which are guided by the detection of light reflected from objects, and whether this could alter the balance of species interactions.

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Materials and methods

Overview

We based our analysis on a novel collation of previously published wavelengths at which the visual pigments contained within the photoreceptors of 213 species of animal (comprising 7 arachnids, 112 insects, 16 birds, 32 reptiles and 46 mammals) maximally absorb light (λ_{max}) (see Table S1). Using a previously derived formula which describes the absorbance properties of visual pigments based on their λ_{max} (see Govardovskii *et al.*, 2000 for details), we then modelled the absorbance of the visual pigments in each species from 200 to 750 nm and estimated the maximum ($\max\lambda_{0.5}$) and minimum ($\min\lambda_{0.5}$) wavelengths of half maximum absorbance (Fig. 1) to determine the range of wavelengths detectable by each species ($\lambda_{0.5}$ range). By comparing the region of the light spectrum over which LPS, HPS, LED and MH lamps emit light (λ_{light} range) with the region of the light spectrum over which the visual pigments in animal eyes absorb more than half of the light passing through them ($\lambda_{0.5}$ range), we obtained a value of the proportion of the visually detectable wavelength range at greater than half maximum absorbance which is stimulated by each type of street lamp (% $\lambda_{0.5}$ range). By way of example, Fig. 1 illustrates how the % $\lambda_{0.5}$ range of the visual system in humans relates to the objects we can detect in the environment under each type of street lamp. LPS lamps emit light over a narrow region of the light spectrum to which human photoreceptors are sensitive, hence objects that reflect light mainly outside this region appear dim or are not seen at all. HPS, LED and MH lamps emit light over a greater proportion of the light spectrum to which humans are sensitive (Fig. 1), hence more objects are easily detected under these lighting technologies because they are better discriminated in colour and brightness. The % $\lambda_{0.5}$ range is a useful comparative index of the ability of animals to detect light reflected from ecologically relevant objects in their environment, because it represents the proportion of the visually detectable region of the light spectrum illuminated by a light source.

Values of % $\lambda_{0.5}$ range were compared both between lighting technologies within each animal class, and between animal classes within each lighting technology using Markov Chain Monte Carlo regression (see below). To aid the interpretation of any patterns observed in the data, we also estimated the average maximum and minimum wavelengths at which the visual pigments of each animal group absorb more than half of the light entering the photoreceptor (max $\lambda_{0.5}$ and min $\lambda_{0.5}$) (Fig. 2a).

Data collection (a) visual pigment λ_{max}

Values of photoreceptor visual pigment λ_{max} were collected for 248 species of animal through an extensive literature search (see Table S1), and used to model the α and the β absorbance curves of the corresponding visual pigments using a standard formula (Govardovskii *et al.*, 2000). Values of min $\lambda_{0.5}$, max $\lambda_{0.5}$ and $\lambda_{0.5}$ range were then calculated for each of the 213 species. The remaining 35 species were omitted from the analysis due to missing values of λ_{max} for the visual pigments of known photoreceptors. For example, while the majority of insects possess UV photoreceptor cells, they have not been characterized in every studied species due to technological limitations (Bernard & Stavenga, 1979; Peitsch *et al.*, 1992; Briscoe & Chittka, 2001). In species of insect for which the spectral sensitivity functions were available separately for females and males, either the sex for which fewer visual pigment λ_{max} wavelengths were quantified was omitted from the analysis, or if the number of visual pigments quantified was identical between sexes the male was omitted from the analysis. New World primates of the same species can be either dichromatic or trichromatic (Jacobs & Deegan, 2003). To prevent duplicating results for any one species, it was assumed that all individuals of each polymorphic species were trichromatic. The short, medium and long wave sensitive photoreceptors of birds and some diurnal reptiles are associated with oil droplets which alter the transmittance of light to the visual pigment and change the maximum wavelengths at which these pigments half maximally absorb light (UV sensitive photoreceptors and all photoreceptors in nocturnal reptiles possess clear oil droplets which do not affect the transmittance of light to the visual pigment; e.g., Hart & Vorobyev, 2005). For the birds and diurnal reptiles, changes in the absorbance curves of short, medium and long wavelength photoreceptors due to oil droplet transmittance were modelled prior to the estimation of min $\lambda_{0.5}$ and max $\lambda_{0.5}$ using the method outlined by Hart & Vorobyev (2005) and published values of oil droplet cut-off wavelengths (λ_{cut}) or wavelengths at half maximum absorbance (λ_{mid}) (see Table S1). In a few species, lens absorption produces a cut-off effect slightly limiting the visual range, but it has not been measured widely across species, therefore it was not included.

Data collection (b) light spectra

The spectral compositions of four glass housed street lamps, one representative of each of the LPS (35W Thorn Beta 5 installed 12/2009), HPS (250W ZX3, Urbis installed 07/2008), LED (120W Ledway, Ruud installed 11/2010) and MH (45W Evolo lantern, Urbis installed 12/2009) technologies, were collected from municipal lighting installations in Cornwall, UK. While some variation exists in the exact spectra emitted by different makes and models of each technology, our selection was representative of the common differences between these technologies (narrow vs. broad spectrum, and UV vs. non-UV emissive). Light spectra were quantified using a MAYA2000-Pro spectrometer collecting light from a CC-3-UV-S cosine corrector connected via a 1000 μm fibre optic cable (Ocean Optics). The cosine corrector was held at ground level during measurements to capture the light spectra that most animals are likely to be exposed to. The resulting light spectra were used to quantify the region over which each lamp technology emits light (λ_{light} range).

Data analysis

Photoreceptor signals are mainly determined by the maximum absorption of the photopigment at the wavelength λ_{max}, and a photoreceptor's sensitivity decreases steeply with increasing distance from this peak sensitivity wavelength (Fig. 1). Visual systems have mostly evolved sets of receptors where sensitivities are well separated to avoid overlapping within the receptor's most sensitive range, usually between the half maximally sensitive ($\lambda_{0.5}$) and $\lambda_{\max}$. Such spacing of photoreceptor sensitivities enables the effective coding of colours and increases an animal's ability to discriminate and recognize colours. Visual performance is influenced to a much lesser extent by the absorption of light in the low-sensitivity wavelength range. Therefore, the region of the light spectrum to which each species is more than half maximally sensitive ($\lambda_{0.5}$ range) was determined as the visual range. The percentage of $\lambda_{0.5}$ range stimulated by each street lamp technology (% $\lambda_{0.5}$ range) was then estimated as the fraction of the $\lambda_{0.5}$ range overlapped by the λ_{light} range (Fig. 1).

Means and 95% credibility interval values of min $\lambda_{0.5}$, max $\lambda_{0.5}$ and % $\lambda_{0.5}$ range were estimated for each animal class perceiving light emitted from each type of street lamp using zero intercept Markov Chain Monte Carlo regression (MCMCregress; CRAN: MCMCpack; Martin *et al*., 2010) (1001 : 11000 iterations). Means and 95% credibility intervals of the difference in % $\lambda_{0.5}$ range between street lamp types were estimated separately for each animal class, and separately for each street lamp type when comparing between animal classes, using MCMC regression with a fitted intercept (1001 : 11000 iterations). The resulting pairwise comparisons were interpreted in a manner analogous to parametric pairwise comparison tests. Where the credibility intervals of the difference between two street lamp types or animal classes did not bound 0, there is a 95% probability that they are different.

Results

The results indicate that the four street lighting technologies can be divided into three categories based on how likely they are to facilitate the detection of objects reflecting light in different regions of the spectrum (Table 1; Fig. 2b): narrow spectrum lamps which do not emit UV light (LPS), broad spectrum lamps which do not emit UV light (HPS and LED) and broad spectrum lamps which do emit UV light (MH). There was a greater than 95% probability that the narrow spectral range of light emitted by LPS lamps stimulated the

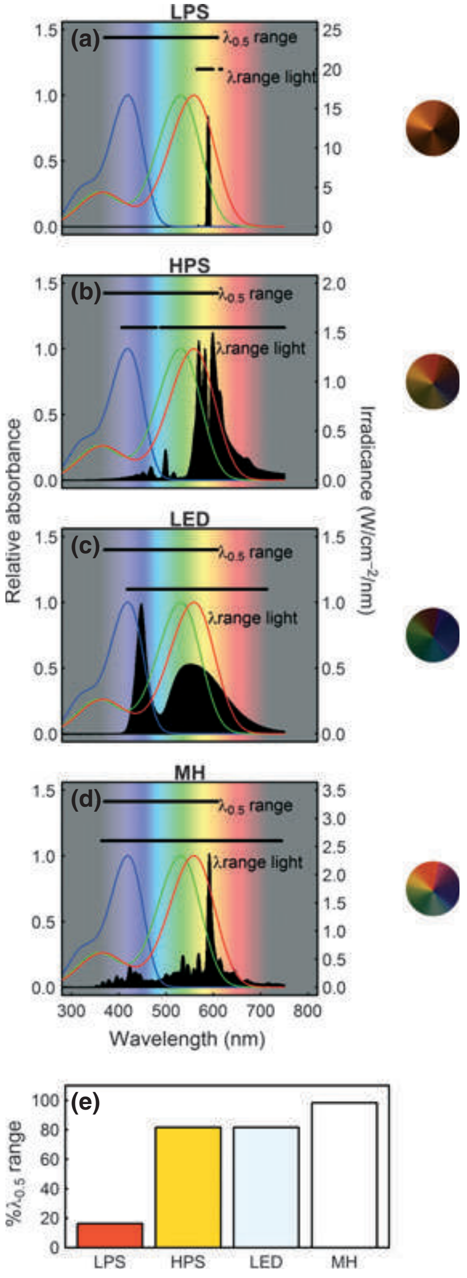

Fig. 1 The colour vision performance of human beings under light emitted from four contrasting street lighting technologies. (a). LPS lamps which emit light over a narrow region of the light spectrum (λ_{range} light) stimulate a smaller proportion of the region of the light spectrum to which human visual pigments are half maximally sensitive ($\lambda_{0.5}$ range) (dashed line), hence objects which reflect light outside of this range appear less bright (colour wheel insert). (b,c,d). Broad spectrum street lighting technologies (HPS, LED, MH) emit light across a broader region of the light spectrum to which humans are sensitive, allowing us to identify objects reflecting light across a broader range of wavelengths. (e). The visual performance of humans under each of the street lighting types can be compared using an index (% $\lambda_{0.5}$ range stimulated) calculated as the percentage of $\lambda_{0.5}$ range overlapped by λ_{range} light. A–D. Solid black lines represent the α and β band absorbance curves for the three visual pigments used to detect light in the human visual system. The emission spectrum of each street light is represented by the filled curve. The plot background approximates the colour of the light detected at each wavelength by the human visual system. UV light is emitted below 400 nm and infrared light above 700 nm. Colour wheel inserts are photographic images taken of the same colour wheel under each of the street lighting types using a standard digital SLR camera which detects red, green and blue light at approximately the same wavelengths as human visual pigments are maximally sensitive.

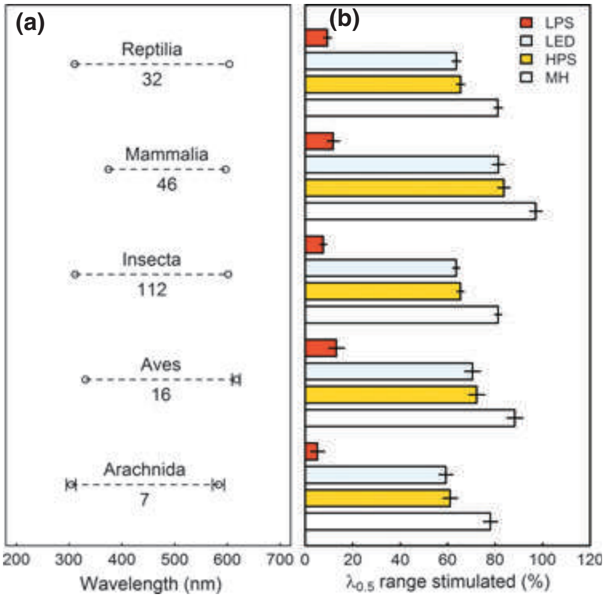

Fig. 2 The percentage of the visual range stimulated by four contrasting street lighting technologies in five classes of animal. (a) The $\lambda_{0.5}$ range of animals estimated for five classes. The average minimum and maximum wavelengths of half maximum visual pigment absorbance are denoted by points with error bars representing 95% credibility intervals estimated using MCMC regression. Values quoted under dashed lines represent the number of species on which derived values are based. (b) The percentage of the visual range at more than half maximum absorbance stimulated by each street light in each of five classes of animal. Means and 95% credibility intervals (error bars) were estimated using MCMC regression.

Table 1 The difference in the percentage of the visual range at greater than half maximum absorbance (% $\lambda_{0.5}$ range) stimulated by each of the four contrasting street lighting technologies compared within five classes of animal

		Street lamp type		
Class		LPS	HPS	LED
Arachnida	HPS	$\underline{55.9_{(51.7,60.1)}}$		
	LED	$\underline{54.1_{(50.0,58.3)}}$	$-1.8_{(-6.0,2.3)}$	
	MH	$\underline{72.9_{(68.6,77.0)}}$	$\underline{16.9_{(12.7,21.1)}}$	$\underline{18.8_{(14.5,22.9)}}$
Aves	HPS	$\underline{59.2_{(54.4,63.8)}}$		
	LED	$\underline{57.4_{(52.7,62.1)}}$	$-1.8_{(-6.5,2.9)}$	
	MH	$\underline{75.1_{(70.4,79.9)}}$	$\underline{16.0_{(11.2,20.6)}}$	$\underline{17.8_{(13.0,22.5)}}$
Insecta	HPS	$\underline{57.8_{(55.7,59.8)}}$		
	LED	$\underline{56.1_{(54.0,58.1)}}$	$-1.7_{(-3.8,0.3)}$	
	MH	$\underline{73.7_{(71.6,75.7)}}$	$\underline{15.9_{(13.8,18.0)}}$	$\underline{17.7_{(15.6,19.7)}}$
Mammalia	HPS	$\underline{71.9_{(68.2,75.5)}}$		
	LED	$\underline{69.7_{(66.0,73.3)}}$	$-2.3_{(-5.9,1.3)}$	
	MH	$\underline{85.4_{(81.7,89.0)}}$	$\underline{13.5_{(9.7,17.1)}}$	$\underline{15.7_{(12.0,19.4)}}$
Reptiles	HPS	$\underline{56.1_{(53.6,58.5)}}$		
	LED	$\underline{54.4_{(51.9,56.8)}}$	$-1.7_{(-4.2,0.7)}$	
	MH	$\underline{71.9_{(69.4,74.3)}}$	$\underline{15.8_{(13.3,18.2)}}$	$\underline{17.5_{(15.0,20.0)}}$

Values represent the mean difference and 95% credibility intervals of the difference (values in parentheses) in % $\lambda_{0.5}$ range stimulated by each lamp type. Values are derived from the pairwise comparison outputs from Markov Chain Monte Carlo simulations performed between factor levels going across the table subtracted from factor levels going down the table. Where values in parentheses do not bound zero there is a 95% probability that the two factor levels are different (underlined results).

smallest proportion of the light spectrum to which animals are sensitive (Table 1) spanning from 5 ± 3.66% $\lambda_{0.5}$ range in the arachnids to 13.1 ± 2.4% $\lambda_{0.5}$ range in the birds (Fig. 2b). Metal Halide (MH) lamps stimulated the largest proportion of the light spectrum to which animals are sensitive spanning from 77.9 ± 5.4% $\lambda_{0.5}$ range in the arachnids to 97.1 ± 2.1% $\lambda_{0.5}$ range in the mammals (Fig. 2b). There was a greater than 95% probability that MH lamps stimulated a larger percentage of the $\lambda_{0.5}$ range than each of the remaining lighting technologies (Table 1). HPS and LED lighting technologies stimulate similar percentages of the $\lambda_{0.5}$ range in all classes of animal studied (Table 1). The broad emission spectra of these technologies stimulate a higher percentage of the $\lambda_{0.5}$ range in comparison to LPS lamps with greater than 95% probability (Table 1) in all five animal classes, but to a lesser extent than MH lamps (Table 1; Fig. 2b).

In addition to changing the ability of animals to detect light reflected from objects in general, the contrasting lighting technologies also affected the comparative ability of different taxonomic groups to detect light reflected from objects. LPS lamps stimulate more of the $\lambda_{0.5}$ range of birds and mammals compared to arachnids, insects and reptiles with greater than 95% probability (Fig. 2b; Table 2). HPS, LED and MH lights, however, increase the number and magnitude of differences in % $\lambda_{0.5}$ range between animal classes with a greater than 95% probability (Table 2). These differences are greatest between the mammals and the remaining animal classes under LED and HPS lamp types (Table 2) because mammals detect light over a narrower region of the light spectrum (Fig. 2a). Similarly, the $\lambda_{0.5}$ range of birds extends less into the shorter wavelengths compared to insects, arachnids and reptiles (Fig. 2a), hence there was a greater than 95% probability that a higher percentage of the light spectrum detected by birds is stimulated under HPS, LED and MH lamps (Table 2).

Discussion

Our results suggest that the installation of broader spectrum lighting technologies in artificially lit habitats

Table 2 The difference in the percentage of the visual range at greater than half maximum absorbance (% $\lambda_{0.5}$ range) stimulated by each of four contrasting street lighting technologies compared between five classes of animal

Street lamp type		Class Arachnida	Aves	Insecta	Mammalia
LPS	Aves	$\underline{8.0_{(3.6,12.3)}}$			
	Insecta	$2.5_{(-1.3,6.2)}$	$\underline{-5.5_{(-8.1,-3.0)}}$		
	Mammalia	$\underline{6.7_{(2.8,10.6)}}$	$-1.3_{(-4.1,1.4)}$	$\underline{4.2_{(2.5,5.9)}}$	
	Reptilia	$\underline{4.3_{(0.3,8.3)}}$	$\underline{-3.8_{(-6.7,-0.8)}}$	$1.8_{(-0.2,3.7)}$	$\underline{-2.4_{(-4.6,-0.2)}}$
HPS	Aves	$\underline{11.3_{(3.4,18.9)}}$			
	Insecta	$4.4_{(-2.4,11.0)}$	$\underline{-6.9_{(-11.4,-2.3)}}$		
	Mammalia	$\underline{22.7_{(15.7,29.7)}}$	$\underline{11.4_{(6.4,16.4)}}$	$\underline{18.3_{(15.3,21.4)}}$	
	Reptilia	$4.4_{(-2.8,11.7)}$	$\underline{-6.8_{(-12.1,-1.6)}}$	$0.1_{(-3.4,3.6)}$	$\underline{-18.2_{(-22.2,-14.2)}}$
LED	Aves	$\underline{11.3_{(3.4,18.9)}}$			
	Insecta	$4.4_{(-2.3,11.1)}$	$\underline{-6.9_{(-11.4,-2.3)}}$		
	Mammalia	$\underline{22.2_{(15.2,29.2)}}$	$\underline{10.9_{(5.9,15.9)}}$	$\underline{17.8_{(14.8,20.8)}}$	
	Reptilia	$4.5_{(-2.7,11.8)}$	$\underline{-6.8_{(-12.1,-1.5)}}$	$0.1_{(-3.4,3.6)}$	$\underline{-17.7_{(-21.7,-13.7)}}$
MH	Aves	$\underline{10.3_{(3.8,16.6)}}$			
	Insecta	$3.4_{(-2.3,8.9)}$	$\underline{-6.9_{(-10.7,-3.2)}}$		
	Mammalia	$\underline{19.2_{(13.4,25.0)}}$	$\underline{8.9_{(4.8,13.0)}}$	$\underline{15.8_{(13.4,18.4)}}$	
	Reptilia	$3.3_{(-2.7,9.3)}$	$\underline{-7.0_{(-11.4,-2.6)}}$	$-0.1_{(-2.9,2.8)}$	$\underline{-15.9_{(-19.2,-12.6)}}$

Values represent the mean difference and 95% credibility intervals of the difference (values in parentheses) in % $\lambda_{0.5}$ range stimulated by each street lamp type. Values were derived from the pairwise comparison outputs from Markov Chain Monte Carlo simulations performed between factor levels going across the table subtracted from factor levels going down the table. Where values in parentheses do not bound zero there is a 95% probability that the two factor levels are different (underlined results).

is likely to improve the ability of animals to detect light reflected from objects in their environment at night, and has the potential to generate greater disparities in this ability between different classes of animal. These improvements in object detection under broad spectrum street lights are likely to affect the execution of visually guided behaviours in animals, altering their normal activity times and spatially extending or fragmenting habitats. All three broad spectrum lighting technologies provided significant improvements in the % $\lambda_{0.5}$ range in comparison to narrow spectrum LPS lamps. MH lamps provided the greatest improvements in all five taxonomic classes. Hence, where these are in use, a greater variety of objects reflecting light in different regions of the light spectrum will appear brighter and more colourful to animals compared with alternative street lamp technologies. While LPS lamps illuminate objects reflecting light across the smallest region of the light spectrum, our results suggest that in areas illuminated by LPS lamps, birds and mammals are better able to detect objects that reflect light in this region compared to arachnids, insects and reptiles. The introduction of broader spectrum technologies, however, increases the number, and the magnitude of the differences between animal classes, in the proportion of the visually detectable light spectrum illuminated, with mammals and birds displaying the largest improvements. Most mammals possess dichromatic vision spanning a less extended range of the light spectrum in comparison to birds, reptiles, arachnids and insects (Fig. 2a; see Table S1) that typically can detect light at wavelengths below 400 nm (UV) (Tovée, 1995; Briscoe & Chittka, 2001; Hart & Hunt, 2007; Osorio & Vorobyev, 2008). Birds do possess UV sensitive photoreceptors, but their sensitivity extends less into the shorter wavelengths compared to insects, arachnids and reptiles (Fig. 2a). Broad spectrum lamp types therefore stimulate a larger percentage of the $\lambda_{0.5}$ range in mammals and birds in general, compared with other classes of animal, improving their ability to perform visually guided behaviours with greater acuity and potentially upsetting the balance of interspecific interactions.

Our results provide an overview of how shifting artificial light spectra are likely to affect visually guided behaviours in broad taxonomic groups of animal. However, the $\lambda_{0.5}$ range of individual species can be variable within each taxonomic group, and therefore caution should be exercised when applying the results of a group in general to any one specific species within that group. For example, the number of photoreceptor types in insect eyes is variable between different orders (Table S1) giving rise to variation in the proportion of $\lambda_{0.5}$ range illuminated by each type of artificial light. In addition, the number of species for which λ_{max} values are available in the literature varies between taxonomic groups (Table S1), and while the main results of this study are unlikely to be affected, the $\lambda_{0.5}$ range will inevitably adjust as data become available for more species and additional photoreceptors in those groups which are not currently well investigated (for example the arachnids). These results are not therefore conclusive, rather they should be considered as a platform of predictions which incentivises further studies into the impact of broadening artificial light spectra on visually guided behaviours in animals.

The ecological impacts of artificially lighting the nocturnal environment are increasingly being recognized (Frank, 2006; Stone *et al.*, 2012; Titulaer *et al.*, 2012), with some studies drawing attention to the potential impact of shifting spectral signatures (Eisenbeis, 2006; Stone *et al.*, 2012). This study has highlighted that such changes may be affecting visually guided behaviours in species across the animal kingdom. The range of potential impacts are diverse and may include extending the times of foraging and sexual competition of diurnal and crepuscular animals into the night (Robertson & Monteiro, 2005; Somanathan *et al.*, 2009; Titulaer *et al.*, 2012), improving both prey detection and predator avoidance (Roth & Kelber, 2004), changing the ability of organisms to navigate around their environment (Warrant *et al.*, 2004, Somanathan *et al.*, 2008; Stone *et al.*, 2009; van Langevelde *et al.*, 2011) and affecting the ability of pollinating species to detect nectar resources (Kelber *et al.*, 2002; Hempel de Ibarra & Vorobyev, 2009). Whether broadening artificial light spectra will elicit positive or negative species responses is likely to depend on the species and the behaviour being considered. For example, the presence of LED lighting increases feeding rates in nesting Great Tits *Parus major* (Titulaer *et al.*, 2012), while the bat *Rhinolophus hipposideros* avoids areas lit by HPS and LED lighting (Stone *et al.*, 2009, 2012) potentially due to perceived predation risk (Rydell, 1992). Metal Halide (MH) lamps are likely to provide the largest improvements in animal vision because they emit light that is both broad and contains UV in its spectral composition. Many of the above tasks depend on the perception of UV light reflected from objects by animals that can detect light at these wavelengths. Hence, the introduction of broader spectrum lighting technologies containing UV may have more profound consequences for biological systems than non-UV broad spectrum lighting technologies. All three broad spectrum technologies, however, create larger disparities in % $\lambda_{0.5}$ between animal groups compared with narrow spectrum LPS lamps, and so have greater potential to alter the balance of interspecific interactions in the environment. Evaluating the direct environmental impacts of each of these different lamp types is clearly essential in a world where the artificially lit night-time environment is increasingly becoming ‘white’.

Acknowledgements

The research leading to this manuscript has received funding from the European Research Council under the European Union’s Seventh Framework Programme (FP7/2007–2013)/ERC grant agreement no. 268504 to K.J.G.

References

Andersson S, Ornborg J, Andersson M (1998) Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B*, **265**, 445–450.

Bernard GD, Stavenga DG (1979) Spectral sensitivities of retinular cells measured in intact, living flies by an optical method. *Journal of Comparative Physiology A*, **134**, 95–107.

Bird BL, Branch LC, Miller DL (2004) Effects of coastal lighting on foraging behavior of beach mice. *Conservation Biology*, **18**, 1435–1439.

Briscoe AD, Chittka L (2001) The evolution of color vision in insects. *Annual Review of Entomology*, **46**, 471–510.

Cheng K, Collett TS, Wehner R (1986) Honeybees learn the colours of landmarks. *Journal of Comparative Physiology A*, **159**, 69–73.

Chiao C-C, Wickiser JK, Allen JJ, Genter B, Hanlon RT (2011) Hyperspectral imaging of cuttlefish camouflage indicates good color match in the eyes of fish predators. *Proceedings of the National Academy of Sciences, U.S.A.*, **108**, 9148–9153.

Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Research*, **34**, 1489–1508.

Cinzano P, Falchi F, Elvidge CD (2001) The first world atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, **328**, 689–707.

Davies TW, Bennie J, Gaston KJ (2012) Street lighting changes the composition of invertebrate communities. *Biology Letters*, **8**, 764–767.

Eisenbeis G (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: *Ecological Consequences of Artificial Night Lighting* (eds Rich C, Longcore T), pp. 281–304. Island Press, Washington.

Elvidge CD, Keith DM, Tuttle BT, Baugh KE (2010) Spectral identification of lighting type and character. *Sensors*, **10**, 3961–3988.

Frank KD (2006) Effects of artificial night lighting on moths. In: *Ecological Consequences of Artificial Night Lighting* (eds Rich C, Longcore T), pp. 305–344. Island Press, Washington.

Gaston KJ, Davies TW, Bennie J, Hopkins J (2012) Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, **49**, 1256–1266.

Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of night-time light pollution: a mechanistic appraisal. *Biological Reviews*, (in press).

Govardovskii VI, Fyhrquist N, Reuter T, Kuzmin DG, Donner K (2000) In search of the visual pigment template. *Visual Neuroscience*, **17**, 509–528.

Hart NS, Hunt DM (2007) Avian visual pigments: characteristics, spectral tuning, and evolution. *The American Naturalist*, **169**, S7–S26.

Hart NS, Vorobyev M (2005) Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *Journal of Comparative Physiology A*, **191**, 381–392.

Hempel de Ibarra N, Vorobyev M (2009) Flower patterns are adapted for detection by bees. *Journal of Comparative Physiology A*, **195**, 319–323.

Hölker F, Moss T, Griefahn B *et al.* (2010) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, **15**, report number 13.

Hunt S, Cuthill IC, Bennett ATD, Church SC, Partridge JC (2001) Is the ultraviolet waveband a special communication channel in avian mate choice? *Journal of Experimental Biology*, **204**, 2499–2507.

Jacobs GH, Deegan JF (2003) Cone pigment variations in four genera of new world monkeys. *Vision Research*, **43**, 227–236.

Kelber A, Balkenius A, Warrant EJ (2002) Scotopic colour vision in nocturnal hawkmoths. *Nature*, **419**, 922–925.

van Langevelde F, Ettema JA, Donners M, WallisDeVries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, **144**, 2274–2281.

Lim MLM, Li J, Li D (2008) Effect of UV-reflecting markings on female mate-choice decisions in *Cosmophasis umbratica*, a jumping spider from Singapore. *Behavioral Ecology*, **19**, 61–66.

Longcore T, Rich C (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, **2**, 191–198.

Macedonia JM, Lappin AK, Loew ER *et al*. (2009) Conspicuousness of Dickerson's collared lizard (*Crotaphytus dickersonae*) through the eyes of conspecifics and predators. *Biological Journal of the Linnean Society*, **97**, 749–765.

Mappes M, Homberg U (2004) Behavioral analysis of polarization vision in tethered flying locusts. *Journal of Comparative Physiology A*, **190**, 61–68.

Martin AD, Quinn KM, Hee Park J (2010) MCMCpack: Markov chain Monte Carlo (MCMC) package. R package version 1.0-7.

Möller R (2002) Insects could exploit UV-green contrast for landmark navigation. *Journal of Theoretical Biology*, **214**, 619–631.

Osorio D, Vorobyev M (2008) A review of the evolution of animal colour vision and visual communication signals. *Vision Research*, **48**, 2042–2051.

Peitsch D, Fietz A, Hertel H, Souza J, Ventura DF, Menzel R (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. *Journal of Comparative Physiology A*, **170**, 23–40.

Perkin EK, Holker F, Richardson JS, Sadler JP, Wolter C, Tockner K (2011) The Influence of artificial light on stream and riparian ecosystems: questions, challenges and perspectives. *Ecosphere*, **2**, 1–16.

Reppert SM, Zhu H, White RH (2004) Polarized light helps monarch butterflies navigate. *Current Biology*, **14**, 155–158.

Robertson KA, Monteiro AN (2005) Female *Bicyclus anynana* butterflies choose males on the basis of their dorsal UV-reflective eyespot pupils. *Proceedings of the Royal Society B*, **272**, 1541–1546.

Roth LSV, Kelber A (2004) Nocturnal colour vision in geckos. *Proceedings of the Royal Society of London. Series B*, **271**, S485–S487.

Rydell J (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744–750.

Somanathan H, Borges RM, Warrant EJ, Kelber A (2008) Nocturnal bees learn landmark colours in starlight. *Current Biology*, **18**, R996–R997.

Somanathan H, Kelber A, Borges R, Wallén R, Warrant E (2009) Visual ecology of Indian carpenter bees II: adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. *Journal of Comparative Physiology A*, **195**, 571–583.

Stone EL, Jones G, Harris S (2009) Street lighting disturbs commuting bats. *Current Biology*, **19**, 1123–1127.

Stone EL, Jones G, Harris S (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology*, **18**, 2458–2465.

Titulaer M, Spoelstra K, Lange CYMJG, Visser ME (2012) Activity patterns during food provisioning are affected by artificial light in free living Great Tits (*Parus major*). *PLoS ONE*, **7**, e37377.

Tovée MJ (1995) Ultra-violet photoreceptors in the animal kingdom: their distribution and function. *Trends in Ecology & Evolution*, **10**, 455–460.

Ugolini A, Boddi V, Mercatelli L, Castellini C (2005) Moon orientation in adult and young sandhoppers under artificial light. *Proceedings of the Royal Society B*, **272**, 2189–2194.

Warrant EJ, Kelber A, Gislen A, Greiner B, Ribi W, Wcislo WT (2004) Nocturnal vision and landmark orientation in a tropical halictid bee. *Current Biology*, **14**, 1309–1318.

Zou Y, Araujo DP, Lim MLM, Li D (2011) Ultraviolet is a more important cue than reflection in other wavelengths for a jumping spider to locate its spider prey. *Animal Behaviour*, **82**, 1457–1463.

Supporting Information

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

Table S1. The wavelengths of maximum absorbance (λ_{max}) of the visual pigments contained within the photoreceptors of animal eyes.

Folio N° 899

Biological Conservation 144 (2011) 2274–2281

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Effect of spectral composition of artificial light on the attraction of moths

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ARTICLE INFO

Article history:
Received 17 February 2011
Received in revised form 31 May 2011
Accepted 4 June 2011
Available online 29 June 2011

Keywords:
Light pollution
Cascading effects
Body-size dependent effect
Ecology of the night
Lepidoptera

ABSTRACT

During the last decades, artificial night lighting has increased globally, which largely affected many plant and animal species. So far, current research highlights the importance of artificial light with smaller wavelengths in attracting moths, yet the effect of the spectral composition of artificial light on species richness and abundance of moths has not been studied systematically. Therefore, we tested the hypotheses that (1) higher species richness and higher abundances of moths are attracted to artificial light with smaller wavelengths than to light with larger wavelengths, and (2) this attraction is correlated with morphological characteristics of moths, especially their eye size. We indeed found higher species richness and abundances of moths in traps with lamps that emit light with smaller wavelengths. These lamps attracted moths with on average larger body mass, larger wing dimensions and larger eyes. Cascading effects on biodiversity and ecosystem functioning, e.g. pollination, can be expected when larger moth species are attracted to these lights. Predatory species with a diet of mainly larger moth species and plant species pollinated by larger moth species might then decline. Moreover, our results indicate a size-bias in trapping moths, resulting in an overrepresentation of larger moth species in lamps with small wavelengths. Our study indicates the potential use of lamps with larger wavelengths to effectively reduce the negative effect of light pollution on moth population dynamics and communities where moths play an important role.

1. Introduction

During the last decades, artificial night lighting has increased globally (Cinzano et al., 2001; Garstang, 2004). The use of street lighting, security lighting and other urban light sources negatively affected many animal and plant species (Rich and Longcore, 2006), and it is considered to be one of the major threats to moth populations (Frank, 2006; Conrad et al., 2006; Groenendijk and Ellis, 2011). Only recently, the effects of artificial night lighting on individuals (e.g. flight-to-light behavior, Frank, 1988), population dynamics (e.g. reduced reproduction, De Molenaar et al., 2000) and communities of nocturnal species (e.g. increased predation, Gotthard, 2000) are getting more attention (Longcore and Rich, 2004; Rich and Longcore, 2006; Settele, 2009).

Artificial night lighting attracts many moths, especially light with high ultraviolet (UV) emission (Frank, 1988, 2006; Nowinszky, 2003). A common, but still not fully convincing and complete explanation for their flight-to-light behavior is that moths mistake a strong light source for the moon and fly to it (Hsiao, 1973). This artificial lighting might have several effects on foraging and reproduction activities of moths and their interspecific interactions (Frank, 2006). For example, moths flying around streetlights at night may experience increased predation by bats and other nocturnal and diurnal predators which have learnt to take advantage of these artificial feeding stations (Rydell, 1992, 2006; but see Kuijper et al., 2008).

As different types of artificial lights are being used, knowledge about the effects of different types of lights on moths is important for their conservation. These light sources might largely differ in intensity and spectral composition, which determine their attraction to insects (Mikkola, 1972; Eguchi et al., 1982; Kelber et al., 2002). For example, it has been shown that high pressure sodium lights attract moths, because of the presence of ultraviolet wavelengths, while low pressure sodium lights of the same intensity, but not producing ultraviolet light, attract less (Rydell, 1992; Eisenbeis and Hassel, 2000; Eisenbeis, 2006). Moreover, artificial light with high ultraviolet emission could affect visual images perceived by moths, for example by accentuating ultraviolet markers which serve as "nectar guides" (Barth, 1985). It has been suggested for the protection of moths that these low pressure sodium vapor lamps should be used, while mercury vapor lamps and other lamp

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doi:10.1016/j.biocon.2011.06.004

types with high ultraviolet emissions should be avoided or equipped with filters to block ultraviolet light (Frank, 2006). However, the effect of the spectral composition of artificial lighting on moth species richness and moth abundance has not been studied systematically (Johnsen et al., 2006).

Several studies document differences in the species' tendency to fly to light (Kolligs, 2000; Nowinszky, 2003). Some moth species are highly attracted to artificial lights, whereas others almost never come to these light sources, even though they occur in the direct vicinity (Kolligs, 2000; Frank, 2006). To predict effects of artificial lighting on moth species richness and moth abundance by attracting individuals, it is important to know which species are attracted and might experience high mortality. This attraction is thought to be determined by their sensitivity to light, which might be related to body size as larger eyes have higher light sensitivity than smaller eyes (Moser et al., 2004; Yack et al., 2007). This is supported by the findings that larger insect species have more sensitive vision than smaller species (Zollikofer et al., 1995; Jander and Jander, 2002; Spaethe and Chittka, 2003), which is also found in butterflies (Rutowski et al., 2009). If some moth species are more attracted to light than others, the traits related to this attraction could help us to predict effects of artificial light on communities of nocturnal species (Frank, 2006).

In this study, we tested the hypotheses that (1) artificial light with smaller wavelengths attracts higher species richness and higher abundances of moths than light with larger wavelengths, and (2) this attraction is correlated with morphological characteristics of moths, especially their eye size.

2. Methods

2.1. Experimental field study

To test the hypotheses, we conducted a field experiment to attract moths with 18 Heath's collapsible portable traps with 6 Watt T5 fluorescent lamps. We used six lamp types that varied in spectral composition (Fig. 1, thus $n = 3$ per lamp type). Besides the standard warm white (Philips color \29, lamp *c* in Fig. 1) and Actinic (lamp *a*) lamps, four custom made lamp types were used. Lamp *b* contained only the green phosphor CBT ($(\mathrm{(Ce, Gd)MgB5O10{:}Tb})$),

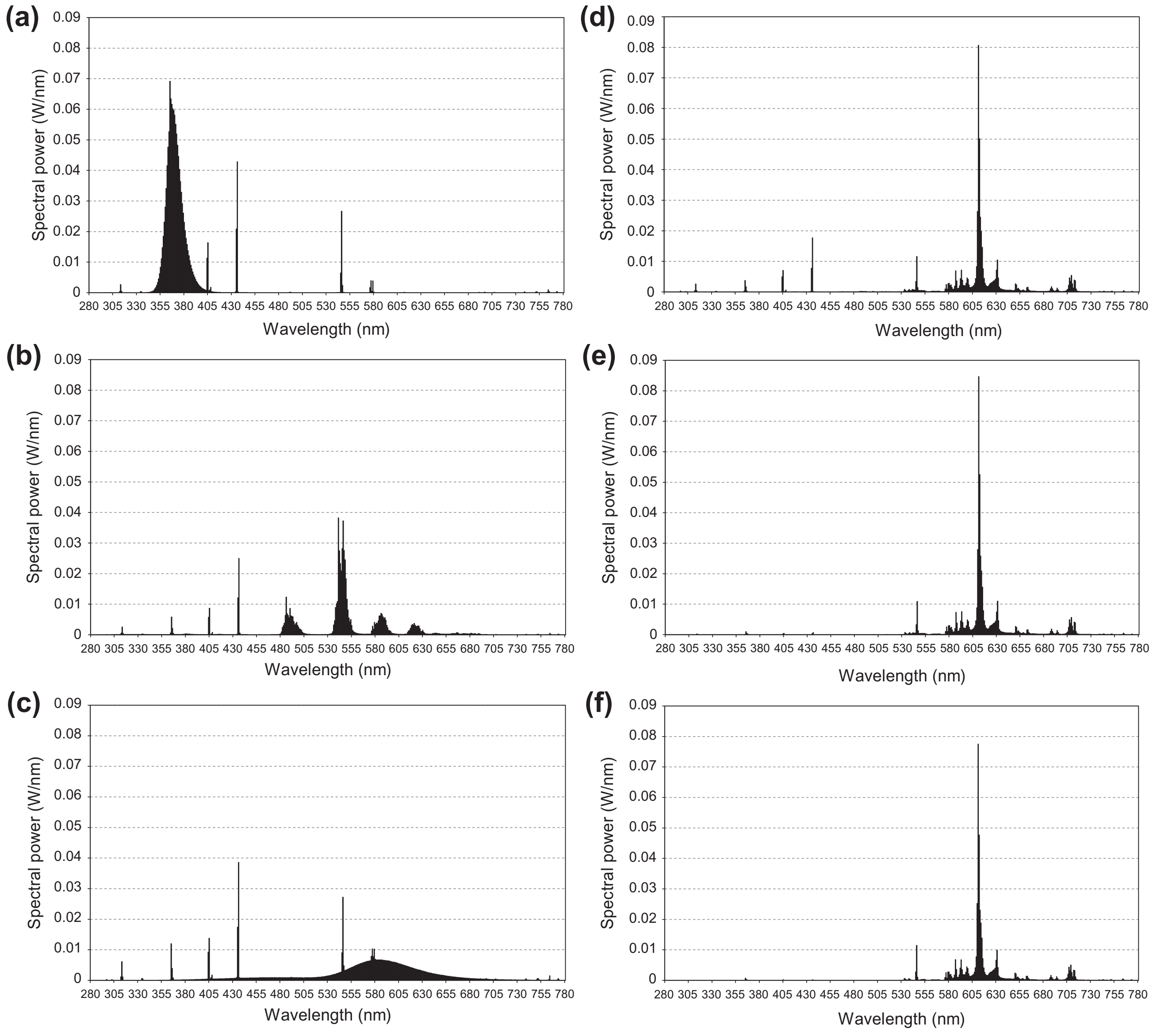

Fig. 1. Spectral power distribution (W/nm) of the six lamp types (with the weighted mean wavelength of the lamp types): *a* (381.8 nm), *b* (534.3 nm), *c* (554.0 nm), *d* (597.1 nm), *e* (616.6 nm) and *f* (617.6 nm).

with a peak wavelength at 542 nm. Lamp types *e* and *f* were all based on the red emitting phosphor YOX (Y_2O_3:Eu) with a peak wavelength of 612 nm. Lamp types *d* and *f* also contained small amounts of a white phosphor mix using BAM ($BaMgAl_{10}O_{17}$:Eu) and CAT ((Ce, Gd)$MgAl_{11}O_{19}$:Tb). The lamp types *d*–*f* were coated with a high-pass filter layer, effectively blocking all radiation below 520 nm. Apart from the actinic lamp, none of the lamps emitted significant amounts of UV (below 380 nm) (Table 1). The different lamp types can be described by the flux (in lumens), correcting for the human eye sensitivity resulting in a measure of brightness as perceived by humans; the number of photons emitted per second; and the spectral power, or radiant flux, which is the power of the radiation emitted by the lamp (in Watt). These properties are determined in the wavelength range from 380 to 780 nm. Ps, Pm and Pl denote the fraction of the spectral power emitted in the ranges 380–504 nm, 505–589 nm and 590–780 nm, respectively. As shown in Fig. 1, each lamp type contains peaks at different wavelengths. To characterize the spectral composition of the different lamp types with a single value, i.e. the dominant wavelength, we calculated the mean of the wavelengths weighted for the spectral power per wavelength (W/nm) (see Fig. 1 for values). As can be expected, the weighted mean wavelength is negatively correlated with Ps (Pearson correlation coefficient $r = -0.998$, $P < 0.001$, $n = 6$) and positively correlated with Pl (Pearson correlation coefficient $r = 0.869$, $P < 0.024$, $n = 6$), but not correlated with Pm (Pearson correlation coefficient $r = -0.089$, $p = 0.867$, $n = 6$).

The study was carried out in Kampina, a nature reserve situated in the province of Noord Brabant in The Netherlands (51°34′13.43″N, 5°16′08.59″E), from July 12 until August 25, 2009. This site is a homogeneous area to avoid differences in moth species richness and moth abundances between the individual lamps. During these six weeks, we trapped moths twice per week (thus 12 trapping moments). Each trapping night, the lamps were randomly distributed over 18 pre-selected locations. These trapping locations were all situated in the same wet meadow system of 2.3 ha surrounded by trees, and the distance to the surrounding trees was kept constant at 10 m for each location. According to Baker and Sadovy (1978), trapping with a 125 W mercury vapor lamp situated at 60 cm above ground level generates an effective response by moths at a distance of 3 m on a moonless night. Our traps were situated on the ground and located at least 50 m from a neighboring trap to prevent light interference. Traps were set at least 60 min before sunset and checked for moths at about one hour after sunrise. Each trap contained three glasses with 50 ml ethyl acetate which was used to prevent moths from escaping the trap once they entered. After each trapping night, the traps were removed from their location, the caught moth species identified to species level, and the number of individuals per species counted.

As moth activity might be influenced by environmental conditions (Frank, 2006; Reardon et al., 2006), we collected data on the mean daily wind speed, mean daily temperature at 10 cm above ground, mean cloud cover and mean daily relative humidity from a weather station of the Royal Netherlands Meteorological Institute (KMNI) at Eindhoven which is approximately at 15 km distance from the study site. Given the potential effect of moon phase on collecting moths, we tested for possible differences between the collection nights.

2.2. Allometric relationships of moth traits

We measured forewing length and width, dry body weight and eye diameter of the males of 40 moth species found in the traps. Pictures of moth eyes were taken using a CANON 350D with a Tamron 100 mm lens and a Tamron 1:1 macro converter at a minimum distance of 15 cm. Each moth's eye diameter was measured from these photographs using ImageJ. Forewing length and width were measured using a ruler up to 0.1 mm. For dry weight determination, each specimen was dried in an oven at 80 °C for 12 h and weighed using a 0.00001 g balance. Moth species characteristics represent means taken from at least three individuals.

2.3. Statistical analysis

A general linear model (GLM) was used to test for differences in overall moth species richness and moth abundance between the six light types, which was also separately done for the main moth families in our traps. In these analyses, we tested the effect of trap location (as random factor) and the average environmental conditions during the trapping moments to account for differences between these moments (as covariates). If needed, data were ln-transformed to satisfy the assumption of normality of the residuals. We used the Bonferroni test for multiple comparisons between the lamp types.

Using Reduced Major Axis regression (RMA regression, as our independent variable body mass is measured with an error, Sokal and Rohlf, 1995), we tested the allometric relationships for the measured morphological characteristics of the moth species. We calculated the abundance weighted mean for each of the morphological characteristics for the species that were caught in the traps for each lamp type and for which we measured the morphological characteristics. Again, we used RMA regression to test the relationship between the spectral composition of the lamps and these abundance weighted mean morphological characteristics.

3. Results

3.1. Moth species richness and moth abundance

A total number of 112 moth species were caught in 18 traps during 6 weeks. There was a strong correlation between overall moth species richness and moth abundance caught in each trap per trapping moment (Pearson correlation coefficient $r = 0.917$, $P < 0.001$, $n = 212$). For moth species richness, a significant differ-

Table 1

Photometrical properties of the six lamps used in the experiment: flux, photon flux and spectral power emitted by the lamps between 380 and 780 nm. Ps, Pm and Pl denote the fraction of the spectral power emitted in the ranges 380–504 nm, 505–589 nm and 590–780 nm, respectively. The weighted mean wavelength is calculated as the mean of the wavelengths weighted for the spectral power per wavelength. The spectral composition of the lamps is given in Fig. 1.

Lamp	*a*	*b*	*c*	*d*	*e*	*f*
Flux (lm)	22	293	297	162	153	143
Photons (mol/s)	3332	2953	3848	2818	2540	2366
Spectral power (W)	1.04	0.66	0.83	0.56	0.49	0.46
Ps	0.84	0.25	0.20	0.08	0.00	0.00
Pm	0.13	0.61	0.42	0.12	0.12	0.12
Pl	0.03	0.14	0.38	0.80	0.88	0.88
Weighted mean wavelength (nm)	381.8	534.3	554.0	597.1	616.6	617.6

ence was found between the six lamp types ($F_{5,121.2} = 10.264$, $P < 0.001$), whereas there was neither a significant difference between the trap locations ($F_{17,110.8} = 1.001$, $P = 0.463$) nor an interaction between lamp type and trap location ($F_{73,116} = 0.622$, $P = 0.985$). After removing trap location as random factor, our model contained lamp type ($F_{5,205} = 14.034$, $P < 0.001$) and relative humidity (more species with greater humidity) as covariate ($F_{1,205} = 5.077$, $P = 0.025$). The other environmental variables did not contribute significantly to this model. Lower species richness of moths was found in traps with lamps that emit light at larger wavelengths (Fig. 2). A similar pattern was found for the species richness of the Noctuidae, the Geometridae and the Arctiidae. Note that the latter family is now no longer considered a separate family but is included in the Noctuidae. For the Pyralidae, there were hardly any differences in species richness between the lamp types.

Similar results were found for differences in moth abundance between lamp types. A significant difference was found between the six lamp types ($F_{5,112.5} = 10.774$, $P < 0.001$). There was no significant difference in moth abundance between the trap locations ($F_{17,103.8} = 0.635$, $P = 0.857$), and also the interaction between lamp type and trap location was not significant ($F_{73,116} = 0.741$, $P = 0.768$). After removing trap location as random factor, the model contained lamp type ($F_{5,205} = 12.895$, $P < 0.001$) and relative humidity as covariate (with a positive sign, $F_{1,205} = 6.514$, $P = 0.011$). The highest abundances were found in the traps with the lamps that emit light with the shortest wavelengths, whereas

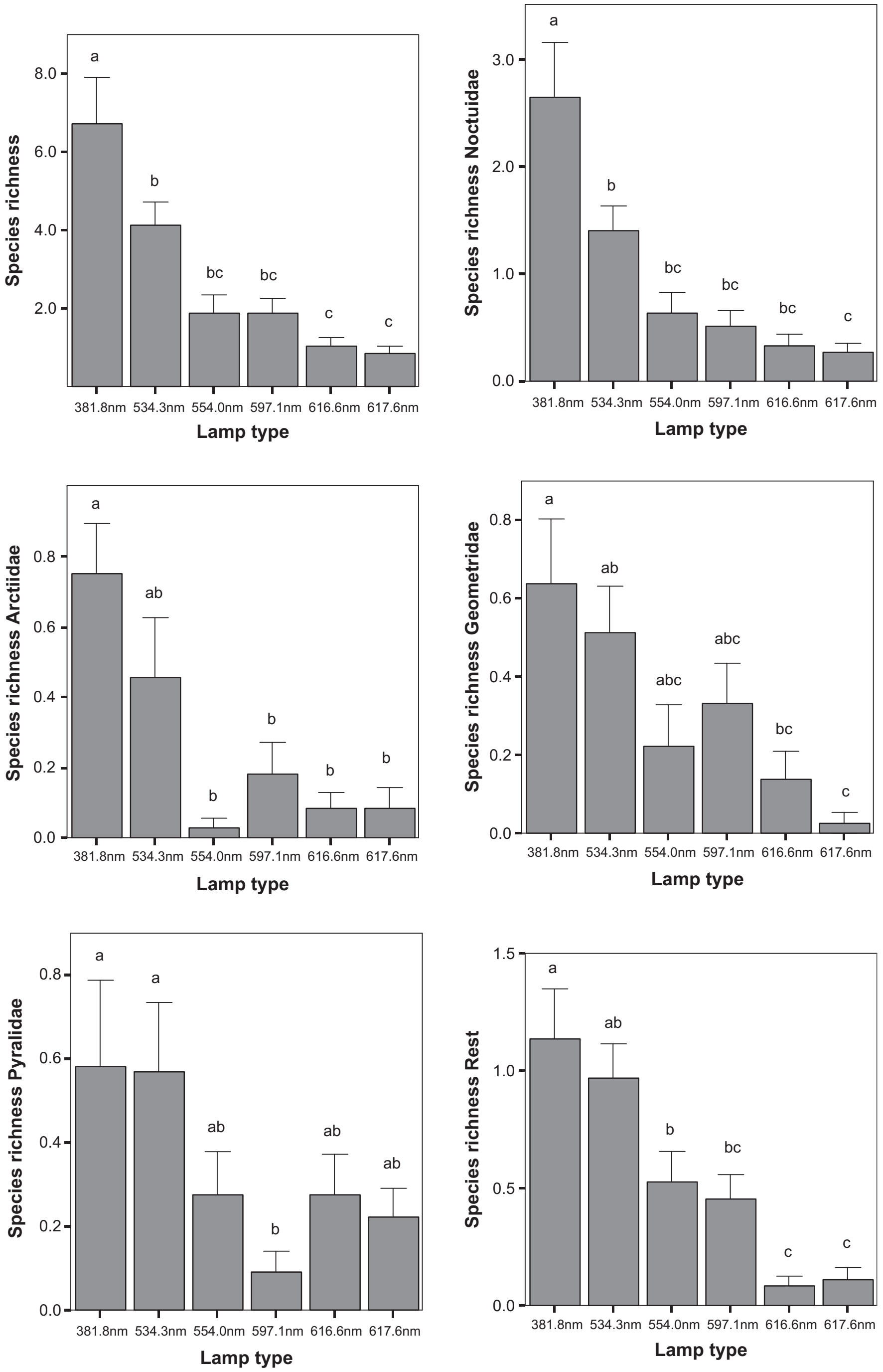

Fig. 2. Mean moth species richness (± s.e.) for the different lamp types, which can be characterized by the weighted mean wavelength (see Fig. 1). Letters indicate significant differences between the lamp types.

there were no differences between the other lamp types (Fig. 3). Again a similar pattern was found for the abundances of the Noctuidae, and the abundances of the Geometridae and Arctiidae decreased for lamp types with larger wavelengths. For the Pyralidae, no differences in abundances were found between the lamp types.

3.2. Relation between moth morphological characteristics and light attraction

The dry weight of the measured 40 moth species varied between 0.004 g (*Cabera exanthemata*; Geometridae) and 0.375 g (*Laothoe populi*; Sphingidae). We found allometric relationships for eye diameter (range 0.67–3.54 mm), forewing length (range 0.98–3.70 cm) and width (range 0.35–1.85 cm). For eye diameter, the intercept of the RMA regression was 6.118 (S.E. = 0.140, $P < 0.001$) and the slope was 0.347 (S.E. = 0.038, $P < 0.001$) with $R^2 = 0.54$, resulting in the allometric relationship $454 \times \mathrm{BM}^{0.347}$ (BM is body mass in g). The relationship between body mass and forewing length could be described by the equation $4.25 \times \mathrm{BM}^{0.262}$ (both coefficients $P < 0.001$, $R^2 = 0.45$), and forewing width by $2.77 \times \mathrm{BM}^{0.368}$ (constant $P = 0.122$, coefficient for forewing width $P = 0.004$, $R^2 = 0.20$). We found strong negative relationships between the weighted mean wavelength of the lamp

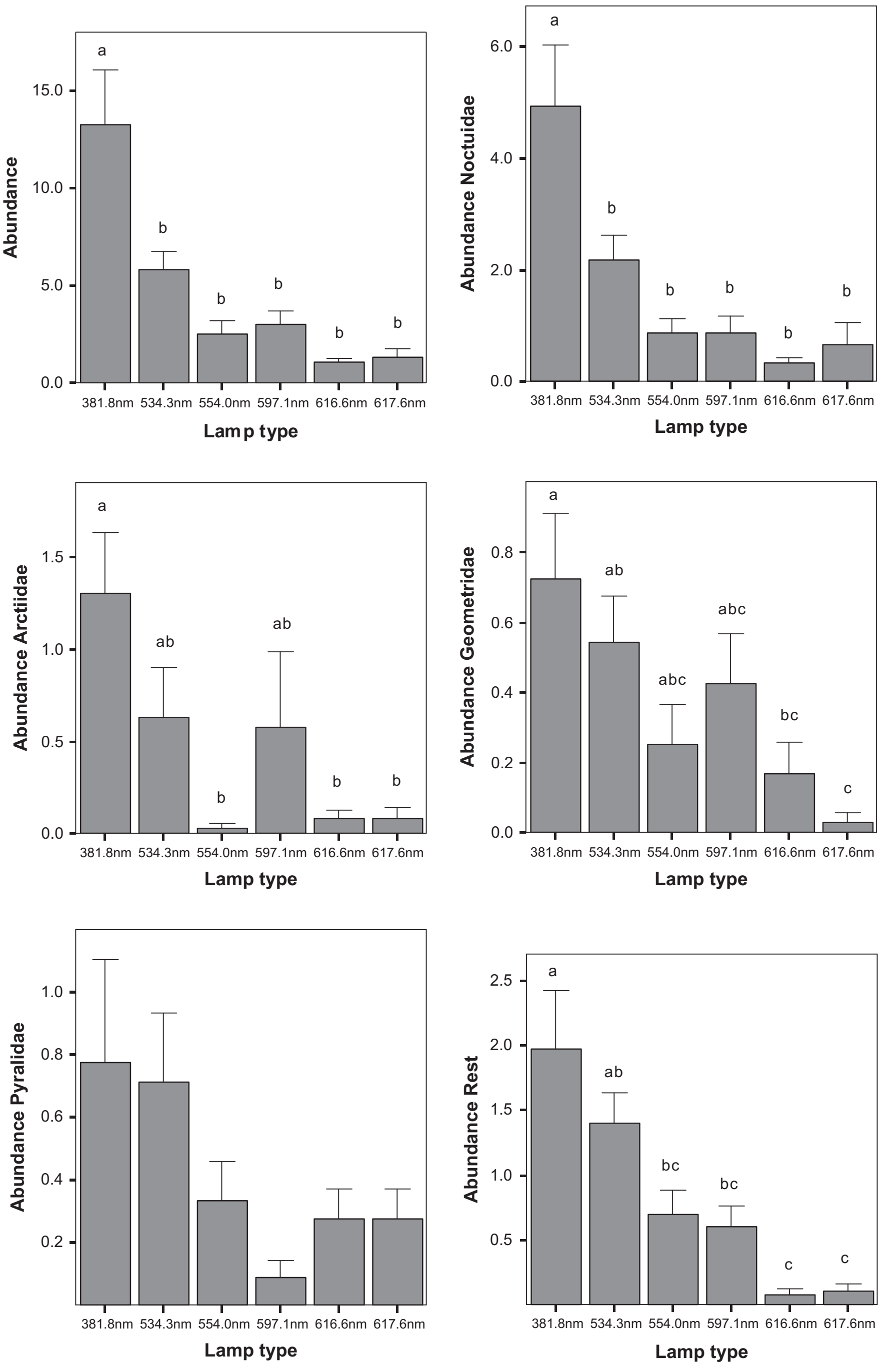

Fig. 3. Mean moth abundance (± s.e.) for the different lamp types. The weighted mean wavelength of the lamp types are given (see Fig. 1). Letters indicate significant differences between the lamp types.

Table 2
The effects of the dominant wavelength of the different lamp types on moth morphological characteristics ($n = 16$ lamps, as two lamps provided insufficient data for the analysis). The dominant wavelength is calculated as the weighted mean of the wavelengths for each lamp type, and the moth characteristics are calculated as the abundance-weighted mean for the species that were caught in the traps for each lamp type.

Moth characteristics	R^2	Slope (± s.e.)	P
Forewing length	0.70	−0.030 (± 0.005)	<0.001
Forewing width	0.66	−0.015 (± 0.003)	<0.001
Dry weight	0.42	−0.001 (± 0.0002)	0.007
Eye diameter (ln-transformed)	0.46	−0.002 (± 0.001)	0.005

types and the moth morphological characteristics (Table 2). Moths with larger body mass, larger wing dimensions and larger eyes were attracted to light dominated by smaller wavelengths.

4. Discussion

4.1. Effects of spectral composition

In this study, we manipulated the spectral composition of artificial light and recorded the number of moth species and moth abundances that were attracted to these lights. We found that the lamp types that are dominated by smaller wavelengths attracted higher species richness and abundances of moths. This agrees with studies on the effects of streetlight where more insects were found in traps with high pressure mercury vapor lamps, followed by high pressure sodium–xenon vapor lamps, and then by high pressure sodium vapor lamps (Eisenbeis and Hassel, 2000; Eisenbeis, 2006). Our results also agree with a study in the City of Düsseldorf where they found the least insects attracted by LEDs that did not emit any UV (Eisenbeis and Eick, 2010). In the traps with a mean weighted wavelength of around 382 nm (lamp type *a*), we caught the highest overall moth species richness and abundance. This lamp type, the Actinic lamp (type *a*), had a large UV-part, which may account for the strong attraction of moths. This agrees with the findings of Cowan and Gries (2009), who found in a laboratory experiment that light of 400–475 nm wavelength attracted more individuals of the Indian meal moth (*Plodia interpunctella*, Pyralidae) than other wavelengths (475–600 nm, 575–700 nm and 590–800 nm). Light of 405 nm wavelength attracted the most individuals compared to the 435, 450 or 470 nm light. Moreover, they found in electroretinogram recordings that light of 405 nm wavelength elicited significantly stronger receptor potentials from both female and male eyes than light of 350 nm. Although we did not find an effect of lamp type on the species richness and abundance of moths of the Pyralidae, the study of Cowan and Gries (2009) clearly shows that some species of the Pyralidae do respond to the spectral composition of light. Besides the finding that moths are attracted to light dominated by smaller wavelengths, our results also show that artificial lights with mean weighted wavelengths of around 617 nm (lamp types *e* and *f*) attract the lowest moth species richness and moth abundance.

We also found that artificial light dominated by smaller wavelengths attracted relatively larger moth species and a higher abundance of these larger species. The high correlation between species richness and abundance stresses the negative effects of the lamp types: not only more species with on average a larger body mass, but also more individuals of these species are attracted. This size-dependent attraction could be explained by findings that larger insect eyes, i.e. larger insects have generally larger eyes (Jander and Jander, 2002; Rutowski et al., 2009), are more sensitive to light (Moser et al., 2004; Yack et al., 2007). Because lamps with short wavelengths are still commonly used (Eisenbeis, 2006), their great attraction of larger moth species might have significant consequences for the ecology of the night.

4.2. Cascading effects of size-dependent mortality

Because moths attracted to artificial lights suffer an increased mortality (Frank, 1988, 2006; Warren, 1990; Nowinszky, 2003; Longcore and Rich, 2004), the trait(s) related to this attraction will be under selection. Our results suggest indeed a possible selection pressure from artificial light on body size of moth species, as it favors individuals of smaller moth species that are less inclined to fly to light than individuals of larger moth species. We therefore hypothesize that relatively smaller moth species are found with relatively higher abundances in areas with high light pollution compared to areas with low artificial light emission during the night. Moreover, we hypothesize that this size-dependent mortality has cascading effects for both trophic interactions and ecosystem services where moths are involved.

It has indeed been recognized that artificial light can have a large effect on interspecific interactions resulting in ecosystem effects (Longcore and Rich, 2004). A large part of the diet of many spider, bird and bat species may contain moths or their caterpillars (Sierro and Artellaz, 1997; Visser et al., 2006; Rydell, 2006; Whittaker and Karatas, 2009). Although hardly quantified, it is likely that a significant part of the diet of some of these predatory species contains larger moth species (Sierro and Artellaz, 1997). For example, the diet of the Brown long-eared bat (*Plecotus auritus*) includes almost exclusively larger moth species from the Noctuidae (83%). The dominant moth species in the diet was the relatively large *Anaplectoides prasina* (Rostovskaya et al., 2000). Another example is the migratory bird European nightjar (*Caprimulgus europaeus*), which mainly feeds on moths during its presence in northwestern Europe from late April to early September (Sierro et al., 2001). The adult birds feed their young mainly with individuals of larger moth species as the breeding season progresses in summer (Cramp, 1985). The widespread decline in larger moth species in The Netherlands and the United Kingdom is expected to have strong effects on this bird species (Groenendijk and Ellis, 2011), as many passerine birds feed their young with caterpillars (Visser et al., 2006). The decrease in larger moth species due to attraction to artificial light could cause a change in the size distribution of prey species, which might have large consequences for predatory species. We expect that declining abundances of larger moth species due to light pollution might result in food reductions for these predatory species, with subsequent decreases in their abundance.

Some moth species are important pollinators (Boggs, 1987; Pettersson, 1991), but effects of artificial light on pollination are hardly known. Besides the misleading effects on the visual images perceived by moths by high ultraviolet emission (Barth, 1985), size-dependent mortality of moths might reduce pollination by larger moth species. For example, the moth *Hadena bicruris* (relatively large moth species from the Noctuidae) is known to be the main pollinator of *Silene latiflora*, a short-lived perennial plant (Jürgens et al., 1996), and the orchid *Platanthera bifolia* is mainly pollinated by moths of the Sphingidae and Noctuidae, which contain mainly large species (Nilsson, 1983). Another example is *Silene sennenii*, only occurring in the north-eastern Iberian Peninsula, which also largely depends on larger moth species for its pollination (Martinell et al., 2010). A decline in such specialist pollinators due to light pollution might lead to a decline in the density of the plant species. Besides pollination, herbivory is another effect that moths can have on the vegetation (Bernays et al., 2004). As the larvae of the majority of larger moth species have a generalized spectrum of host plants (Groenendijk and Ellis, 2011), the decline in their abundance due to light pollution might translate in a general decline in herbivore pressure. Further experiments should reveal the effects of a reduction in larger moth species and their abundances on the vegetation.

4.3. Size-biased flight-to-light behavior of moths

Light traps have been used for years to study the biology and biogeography of moths (Nowinszky, 2003) and to monitor occurrence and abundance of pest species in order to reduce their populations (Weissling and Knight, 1994). Recently, it has been shown that there might be a male-biased flight-to-light behavior of moths (Altermatt et al., 2008), which affects the reliability of estimating abundances using light traps. Our study suggests that artificial lights might also cause a size-biased flight-to-light behavior, as relatively larger moth species and higher abundances of these moth species are caught in traps, especially using lamps dominated by small wavelengths. An alternative explanation for this pattern might be that we have drawn a random sample from the available species abundances, and that larger moth species occur in higher density than smaller moth species. This would contradict often found relationships between body mass and abundance that predict a decline in abundance with increasing body mass (Brown et al., 2004). Moreover, we located our traps in one site where all lamp types are exposed to the same pool of moth species. From this pool, we found that lamp types with smaller wavelengths attracted relatively more large moth species than lamp types with larger wavelengths, suggesting that there is indeed a size-bias resulting in an overrepresentation of larger moth species in lamps with smaller wavelengths. Further experimental testing of our findings is needed as this possible size-bias in flight-to-light behavior might have large implications for population and conservation biology of moths.

4.4. Synthesis

The increase in artificial night lighting (Cinzano et al., 2001) increases the urge to study effects of light pollution to support nature management options. The size-dependent attraction to artificial light we found in moths, could entail possible cascading effects for biodiversity and ecosystem services, e.g. pollination where moth species are involved, when larger moth species decline due to light pollution. To prevent these effects, this study provides evidence on spectral compositions of artificial light that have the least attraction for moths, which could be used in cities and along roads. Our results indicate the potential use of lamps with larger wavelengths to effectively reduce the negative effect of light pollution on moth population dynamics and communities that include these moths or their caterpillars.

Acknowledgements

We would like to thank Leo de Bruijn from Natuurmonumenten for giving us the opportunity to collect data, for providing free access and storing opportunities for traps at Kampina nature reserve. In addition, Jippe van der Meulen from Dutch Butterfly Conservation is kindly acknowledged for his time and efforts in the identification of the samples.

References

Altermatt, F., Baumeyer, A., Ebert, D., 2008. Experimental evidence for male biased flight-to-light behaviour in two moth species. Entomologia Experimentalis et Applicata 3, 259–265. doi:10.1111/j.1570-7458.2008.00817.x.

Baker, R.B., Sadovy, Y., 1978. The distance and nature of light-trap response of moth. Nature 276, 818–821.

Barth, F.G., 1985. Insects and Flowers: The Biology of a Partnership. Princeton University Press, Princeton, New Jersey.

Bernays, E.A., Singer, M.S., Rodrigues, D., 2004. Foraging in nature: foraging efficiency and attentiveness in caterpillars with different diet breaths. Ecological Entomology 29, 389–397.

Boggs, C.L., 1987. Ecology of nectar and pollen feeding in Lepidoptera. In: Slansky, F., Rodriguez, J.G. (Eds.), Nutritional Ecology of Insects, Mites, Spiders, Related Invertebrates. Wiley, New York, pp. 369–391.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789.

Cinzano, P., Falchi, F., Elvidge, C.D., 2001. The first world atlas of the artificial night sky brightness. Monthly Notices of the Royal Astronomical Society 328, 689–707.

Conrad, K.F., Warren, M., Fox, R., Parsons, M., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation 132, 279–291. doi:10.1016/j.biocon.2006.04.020.

Cowan, T., Gries, G., 2009. Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*. Entomologia Experimentalis et Applicata 131, 148–158. doi:10.1111/j.1570-7458.2009.00838.x.

Cramp, S. (Ed.), 1985. Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic, vol. IV. Terns to Woodpeckers. Oxford University Press, Oxford.

De Molenaar, J.G., Jonkers, D.A., Henkens, R.J.H.G., 2000. Wegverlichting en natuur. I. Een literatuurstudie naar de werking en effecten van licht en verlichting op de natuur. DWW Ontsnipperingsreeks deel 34, Delft.

Eguchi, E., Watanabe, K., Hariyama, T., Yamamoto, K., 1982. A comparison of electrophysiologically spectral responses in 35 species of Lepidoptera. Journal of Insect Physiology 28, 675–682.

Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 281–304.

Eisenbeis, G., Eick, K., 2010. Attraction of nocturnal insects to street lights with special regard to LEDs. Abstracts of the Society for Conservation Biology, 24th Annual Meeting: <http://www.conbio.org/activities/meetings/2010/images/abstracts.pdf> (checked 10.04.11).

Eisenbeis, G., Hassel, F., 2000. Zur Anziehung nachtaktiver Insekten durch Straßenlaternen: eine Studie kommunaler Beleuchtungseinrichtungen in der Agrarlandschaft Rheinhessens. Natur und Landschaft 75, 145–156.

Frank, K.D., 1988. Impact of outdoor lighting on moths: an assessment. Journal of the Lepidopterists' Society 42, 63–93.

Frank, K.D., 2006. Effects of artificial night lighting on moths. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 305–344.

Garstang, R.H., 2004. Mount Wilson observatory: the sad story of light pollution. Observatory 124, 14–21.

Gotthard, K., 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. Journal of Animal Ecology 69, 896–902.

Groenendijk, D., Ellis, W.N., 2011. The state of the Dutch larger moth fauna. Journal of Insect Conservation 15, 95–101. doi:10.1007/s10841-010-9326-y.

Hsiao, H.S., 1973. Flight paths of night-flying moths to light. Journal of Insect Physiology 19, 1971–1976.

Jander, U., Jander, R., 2002. Allometry and resolution of bee eyes (Apoidea). Arthropod Structure & Development 30, 179–193.

Johnsen, S., Kelber, A., Warrant, E., Sweeney, A.M., Widder, E.A., Lee Jr, R.L., Hernández-Andrés, J., 2006. Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. Journal of Experimental Biology 209, 789–800. doi:10.1242/jeb.02053.

Jürgens, A., Witt, T., Gottsberger, G., 1996. Reproduction and pollination in central European populations of Silene and Saponaria species. Botanica Acta 109, 316–324.

Kelber, A., Balkenius, A., Warrant, E.J., 2002. Scotopic colour vision in nocturnal hawk moths. Nature 419, 922–925.

Kolligs, D., 2000. Ökologische Auswirkungen künstlicher Lichtquellen auf nachtaktive Insekten, insbesondere Schmetterlinge (Lepidoptera). Faunistisch-Oekologische Mitteilungen Supplement 28, 1–136.

Kuijper, D., Schut, J., Van Dullemen, D., Toorman, H., Goossens, N., Ouwehand, J., Limpens, H.J.G.A., 2008. Experimental evidence of light disturbances along the commuting routes of pond bats (*Myotis dasycneme*). Lutra 51, 37–49.

Longcore, T., Rich, C., 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2, 191–198.

Martinell, M.C., Dötterl, S., Blanché, C., Rovira, A., Massó, S., Bosch, M., 2010. Nocturnal pollination of the endemic *Silene sennenii* (Caryophyllaceae): an endangered mutualism? Plant Ecology 211, 203–218.

Mikkola, K., 1972. Behavioral and electrophysiological responses of night-flying insects, especially Lepidoptera, to near-ultraviolet and visible light. Annales Zoologici Fennici 9, 225–254.

Moser, J.C., Reeve, J.D., Bento, J.M.S., Della Lucia, T.M.C., Cameron, R.S., Heck, N.M., 2004. Eye size and behaviour of day- and night-flying leafcutting ant alates. Journal of Zoology (London) 264, 69–75. doi:10.1017/S0952836904005527.

Nilsson, L.A., 1983. Process of isolation and introgressive interplay between *Platanthera bifolia* (L.) Rich. and *P. chlorantha* (Custer) Reichb. (Orchidaceae). Botanical Journal of the Linnean Society 87, 325–350.

Nowinszky, L. (Ed.), 2003. The Handbook of Light Trapping. Savaria University Press, Szombathely, Hungary.

Pettersson, M.W., 1991. Pollination by a guild of fluctuating moth populations: Option for unspecialization in *Silena vulgaris*. Journal of Ecology 79, 591–604.

Reardon, B.J., Sumerford, D.V., Sappington, T.W., 2006. Impact of trap design, windbreaks, and weather conditions on captures of European corn borer (Lepidoptera: Crambidae) in pheromone-baited traps. Journal of Economic Entomology 99, 2002–2009.

Rich, C., Longcore, T. (Eds.), 2006. Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC.

Rostovskaya, M.S., Zhukova, D.V., Illarionova, A.E., Ustyugova, S.V., Borissenko, A.V., Sviridov, A.V., 2000. Insect prey of the long-eared bat *Plecotus auritus* (L.) (Chiroptera: Vespertilionidae) in central Russia. Russian Entomological Journal 9, 185–189.

Rutowski, R.L., Gislén, L., Warrant, E.J., 2009. Visual acuity and sensitivity increase allometrically with body size in butterflies. Arthropod Structure & Development 38, 91–100. doi:10.1016/j.asd.2008.08.003.

Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology 6, 744–750.

Rydell, J., 2006. Bats and their insect prey at streetlights. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, pp. 43–60.

Settele, J., 2009. Ecologists should join astronomers to oppose light pollution. Nature 576, 379.

Sierro, A., Artellaz, R., 1997. Barbastelle bats (*Barbastella* spp.) specialize in the predation of moths: implications for foraging tactics and conservation. Acta Oecologica 18, 91–106.

Sierro, A., Arlettaz, R., Naef-Daenzer, B., Strebel, S., Zbinden, N., 2001. Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme. Biological Conservation 98, 325–3310, doi:10.1016/S0006-3207(00)00175-0.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: the principles and practice of statistics in biological research, third ed. Freeman and Co, New York.

Spaethe, J., Chittka, L., 2003. Interindividual variation of eye optics and single object resolution in bumblebees. Journal of Experimental Biology 206, 3447–3453.

Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. doi:10.1007/s00442-005-0299-6.

Warren, A.D., 1990. Predation of five species of Noctuidae at ultraviolet light be the Western Yellowjacket (Hymenoptera: Vespidae). Journal of the Lepidopterists' Society 44, 32.

Weissling, T.J., Knight, A.L., 1994. Passive trap for monitoring codling moths (Lepidoptera, Tortricidae) flight activity. Journal of Economic Entomology 87, 103–107.

Whittaker, J.O., Karatas, A., 2009. Food and feeding habits of some bats from Turkey. Acta Chiropterologica 11, 393–403. doi:10.3161/150811009X485611.

Yack, J.E., Johnson, S.E., Brown, S.G., Warrant, E.J., 2007. The eyes of Macrosoma sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. Arthropod Structure & Development 36, 11–22. doi:10.1016/j.asd.2006.07.001.

Zollikofer, C.P.E., Wehner, R., Fukushi, T., 1995. Optical scaling in conspecific Cataglyphis ants. Journal of Experimental Biology 198, 1637–1646.

Nota Lepi. **40**(1) 2017: 87–108 | DOI 10.3897/nl.40.11887

A new LED lamp for the collection of nocturnal Lepidoptera and a spectral comparison of light-trapping lamps

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http://zoobank.org/2DB5B76D-CC0A-4393-8830-017E2B0F9676

Received 20 January 2017; accepted 16 February 2017; published: 24 April 2017
Subject Editor: Jadranka Rota.

Abstract. Most nocturnal Lepidoptera can be attracted to artificial light sources, particularly to those that emit a high proportion of ultraviolet radiation. Here, I describe a newly developed LED lamp set for the use in the field that is lightweight, handy, robust, and energy efficient. The emitted electromagnetic spectrum corresponds to the peak sensitivity in most Lepidoptera eye receptors (ultraviolet, blue and green). Power LEDs with peaks at 368 nm (ultraviolet), 450 nm (blue), 530 nm (green), and 550 nm (cool white) are used. I compared the irradiance (E_e) of many commonly used light-trapping lamps at a distance of 50 cm. Between wavelengths of 300 and 1000 nm, irradiance from the new lamp was 1.43 W m^{-2}. The new lamp proved to be the most energy efficient, and it emitted more radiation in the range between 300 and 400 nm than any other lamp tested. Cold cathodes are the second most energy-efficient lamps. Irradiation from fluorescent actinic tubes is higher than from fluorescent blacklight-blue tubes. High-wattage incandescent lamps and self-ballasted mercury vapour lamps have highest irradiance, but they mainly emit in the long wave spectrum. The use of gauze and sheets decreases the proportion of UV radiation and increases the share of blue light, probably due to optical brighteners. Compared with sunlight, UV irradiance is low at a distance of 50 cm from the lamp, but (safety) glasses as well as keeping sufficient distance from the lamp are recommended. In field tests, the new LED lamp attracted large numbers of Lepidoptera in both the Italian Alps and in the Peruvian Andes.

Introduction

Light-trapping has long been known as an efficient method for collecting of nocturnal insects in general and Lepidoptera in particular (e.g. Taylor and French 1974; Holloway et al. 2001; Infusino et al. 2017). Early on, it was observed that moths can be attracted to the light of fire or candlelight and might even get burned – the family name Pyralidae probably relates to this observation (Emmet 1991). Light-trapping, either manual or with automatic traps, has become a standard and widespread method in ecology, taxonomy, and Lepidoptera monitoring schemes, and it is supposed to represent the only method allowing a large number of clades to be sampled quantitatively in large numbers (Holloway et al. 2001). Light sources with a high proportion of ultraviolet (UV) radiation tend to attract a greater number of individuals and more taxa (van Langevelde et al. 2011). A research focus in recent years has been to investigate the impact of modern street lighting on insects (“light pollution”: e.g. Huemer et al. 2011; van Langevelde et al. 2011; Somers-Yeates et al. 2013; Pawson and Bader 2014; van Grunsven et al. 2014; Macgregor et al. 2016), including implications of anthropogenically driven selection on flight behaviour in urban areas (Altermatt and Ebert 2016).

A wide range of lamp and trap types for light-trapping has been used in entomological research. Although standardisation is desirable, the availability of new designs and lamps has continually led to changes in the lamp set-ups used. Depending on the requirements of research, it is (a) either more important to stress continuity and use a standard method that has been used in previous studies, or it is (b) more important to apply the most efficient and best available technology. A good example of (a) are Rothamsted traps (Williams 1948) that are operated with strong incandescent lamps with a tungsten filament. The use of this 'old-fashioned' technology can be justified in long-term monitoring programmes that are intended to be continued without a substantial methodological change (Southwood et al. 2003). Established methods such as the use of incandescent or high-pressure mercury vapour (MV) self-ballasted lamps also offer the advantage of long-term experience and published comparative studies on their performance (e.g., Intachat and Woiwod 1999).

The use of established light trapping methods does, however, have some disadvantages. For example, incandescent lamps have largely been abandoned in Europe because they are primarily producing long-wave radiation including a large proportion of invisible infrared radiation (Fig. 5a) that contributes relatively little to attracting insects (e.g. Cowan and Gries 2009), while the lifespan of such lamps is rather limited (Infusino et al. 2017). MV lamps emit a more favourable spectrum of radiation (Fig. 5a), but the longevity of the commonly employed self-ballasted type is similarly limited as incandescent lamps (Infusino et al. 2017). Moreover, high pressure MV lamps are being phased out due to their content of toxic mercury, which is banned by new legislations in many countries. Both types of lamps require high voltage, which means that during field work heavy and bulky generators are required. Despite containing mercury, fluorescent tubes of all types are still widely used (e.g. 'energy-saving lamps'). For insect collectors, particularly popular types of fluorescent tubes emit large proportions of UV radiation, including actinic / blacklight (BL) tubes as well as blacklight-blue (BLB) tubes – the latter with a dark-blue filter coating that absorbs most light. More recently, cold cathodes have become available through their use as backlighting of monitors and as decorative illumination in computer cases. These vary in their wavelengths and one can therefore choose those that include the UV range. However, little seems to be known about their performance in light-trapping so far. The use of LEDs is now increasingly common in light-trapping (Green et al. 2012; Price and Baker 2016; Infusino et al. 2017). LEDs have also been employed in experimental studies because a wide range, with different radiation peaks, is available (e.g. Cowan and Gries 2009; Kadlec et al. 2016).

Although lamp emission data are sometimes provided by the manufacturers, standardized comparisons of the emission or irradiation of different lamps are rare in the entomological literature. A comparison of six light sources with an emphasis on street lighting was given by van Grunsven et al. (2016). Papers can also easily be overlooked if published in journals or in languages with limited readership, as exemplified by a paper by Steidel and Plontke (2008) that graphically shows the qualitative emission spectra of various lamps.

Here, I describe a new LED lamp design intended for use in light trapping under field conditions, including remote tropical locations. The lamp was developed with the aim to minimize weight and size and to maximize energy efficiency and longevity. The aim was to be able to power this lamp with cheap and widely available 5 V lithium batteries ('powerbanks'), as well as the option of using 12 V batteries. Overall emission was intended to be of comparable or higher quantity

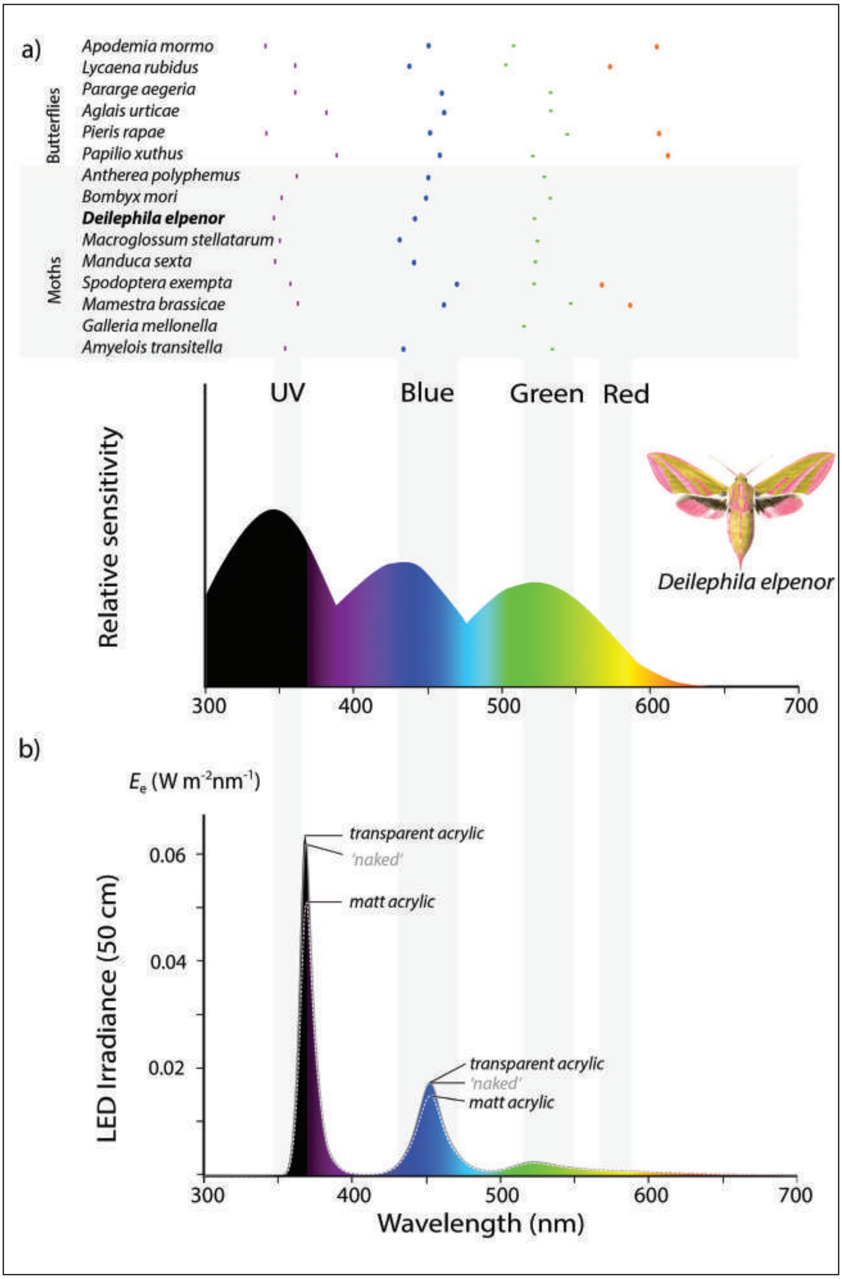

Figure 1. a. Values of maximum spectral sensitivity of Lepidoptera eyes, modified from Briscoe and Chittka (2001) and Johnsen et al. (2006), and sensitivities of the photoreceptors of the hawk moth *Deilephila elpenor* as an example, with peak absorption wavelengths of 350, 440, and 525 nm (Johnsen et al. 2006). **b.** The spectral composition of the new LED lamp (operated at 350 mA) is oriented towards the spectral sensitivity of moth eye receptors (background grey bars). A transparent acrylic cylinder has only a minimal influence on the irradiation from the lamp whereas a matt acrylic cylinder (dashed white line) slightly decreases the performance of the lamp, see also Table 1.

than fluorescent BL and BLB tubes used in many previous field studies (e.g. Brehm and Axmacher 2005), and to provide a higher output than in previously described LED-based designs (Green et al. 2012; Price and Baker 2016; White et al. 2016; Infusino et al. 2017).

The spectral composition of the lamp is orientated towards the peak sensitivity of lepidopteran eye receptors as suggested e.g. by Steidel and Plontke (2008), Mobbs (2016), and Price and Baker (2016). The available data on lepidopteran eye receptor sensitivity is still limited but includes a broad range of taxa (Briscoe and Chittka 2001, Fig 1a). These data suggest that three types of receptors are commonly found in moths, exemplified in the hawkmoth *Deilephila elpenor* (L.) (Johnsen et al. 2006): one in the ultraviolet, one in the blue, and one in the green range (Fig. 1a). *Synanthedon myopaeformis* (Borkhausen) (Sesiidae) is sensitive both in the ultraviolet and green range (Eby et al. 2013). Further receptors can be present and are possibly even widespread, such as red receptors known from the noctuids *Spodoptera exempta* (Walker) and *Mamestra brassicae* (L.) (Fig. 1a). As an extreme case, photoreceptors of 15 distinct spectral sensitivities were found in the butterfly species *Graphium sarpedon* (L.) (Papilionidae) (Chen et al. 2016). Given the large empirical success of lamps with a high proportion of UV radiation (including MV lamps, fluorescent tubes, cold cathodes, and UV LEDs), the emission of this short wave radiation was considered to be particularly important.

The emission of the new lamp is described in detail and quantitatively compared with a range of lamps commonly used by entomologists. Measurements include transparent clear and matt protective acrylic glasses, sheets, and gauze. Lamp emissions at different distances are compared with sunlight and the roles of spectacles and sun spectacles as eye protection are discussed briefly. Finally, the new LED lamp was tested under field conditions in more than 50 sampling events in the Italian Alps and Peruvian Andes, to confirm that nocturnal Lepidoptera were indeed attracted to the lamp and opening perspectives for further research.

Material and methods

Lamp design

The outer shape of a cylinder was considered as the best choice, not least because this allows the use of the lamp within existing trap designs. Power LEDs with a maximum power consumption of 3 W were chosen because they are generally more energy efficient than Power LEDs ≤ 1 W as found for example in LED stripes (White et al. 2016; Infusino et al. 2017). On the other hand, LEDs with higher wattage (e.g., 5 or 10 W) were not considered since this would have easily surpassed the desired maximum power consumption of ca. 15 W. Irradiance from a number of different LEDs was measured (see below, Appendix 1) and those with the best performance were chosen. LEDs with different wavelengths were used in order to reflect different sensitivity peaks in moth eye receptors (Fig. 1), with an emphasis on short wave radiation (UV and blue). For the final lamp design, eight Power LEDs on star circuit boards were arranged at two levels, each separated by 90° (Fig. 2). Four UV LEDs (SSC Viosys UV CUN66A1B), two Cree XP-E2 Royal Blue LEDs, one Cree XP-E2 Green LED, and one Cree XP-L V6 Cool White LED were finally selected. LEDs were glued with a thermal adhesive on a cooling aggregate (Fischer Elektronik LAM 31005) in order to avoid overheating and to maximize LED lifespans. A small axial fan (ca. 0.15 W) on top of the aggregate additionally removes heat from the inside. Airflow is directed from the bottom to the top of the lamp, supporting air convection. Metal gauze at the bottom and the top of the lamp

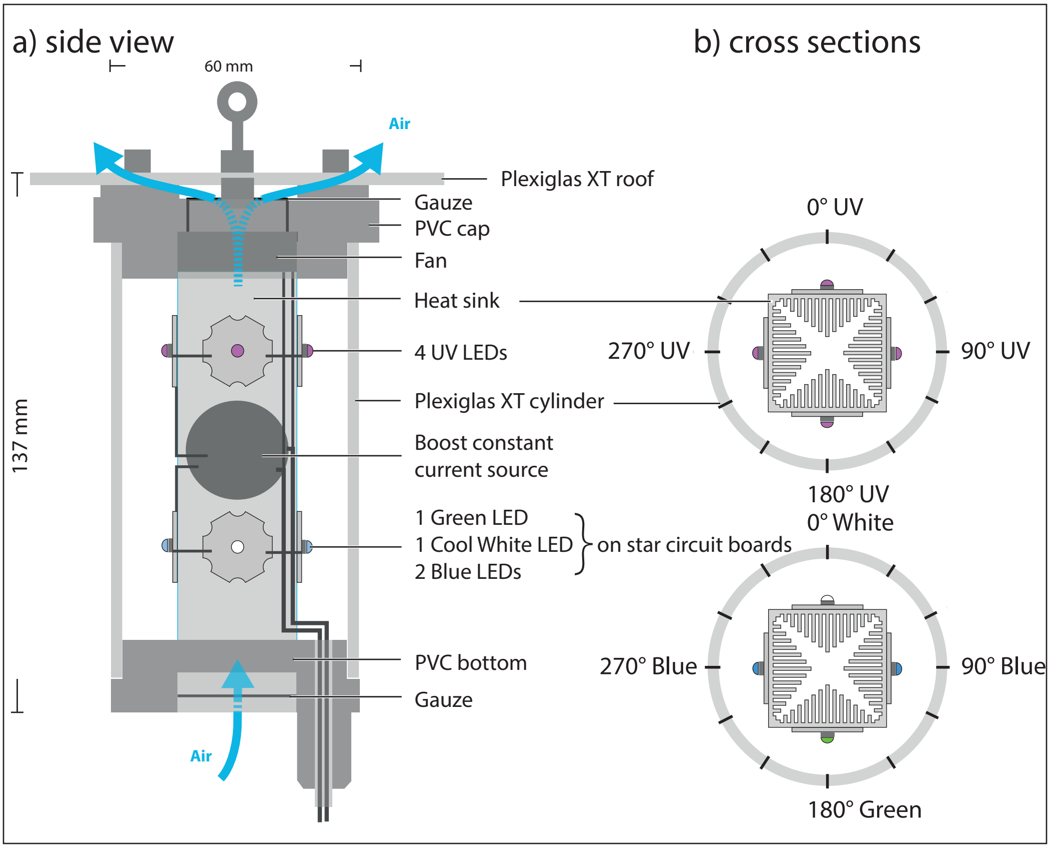

Figure 2. Design of the new LED lamp (scale 1:2). A total of 8 Power LEDs is arranged at two levels (4 UV, 2 blue, 1 green, 1 cool white).

prevents small insects and dirt from entering, and a transparent acrylic (Plexiglas® XT) roof protects the lamp from rain. The protective cylinder around the LEDs also consists of Plexiglas XT characterized by high transmission rates including for UV radiation (Fig. 1b). Alternatively, a matt Plexiglas cylinder can be used (Fig. 1b, Table 1). The bottom and top of the lamp are made of PVC. Inside is a cooling aggregate (heat sink) and outside a Plexiglas cylinder. In future models, PVC will be replaced by anodized aluminium. LEDs are connected in series to a Boost LED constant current source (pcb components Led Senser V2 Rev.2) that allows an input current in the given design of ca. 5–12 V DC. After performance tests with different currents, the output current was set to 350 mA.

Spectral measurements

The irradiance (E_e) of different lamps was measured in a dark room with a Specbos 1211 UV broadband spectro-radiometer aligned to the centre of the lamps at a distance of 50 cm (Fig. 3). Irradiance is defined as radiant flux (or intensity) received by a surface per unit area, here expressed as W $m^{-2}nm^{-1}$ and measured at wavelengths between 300 and 1000 nm. While irradiance refers to

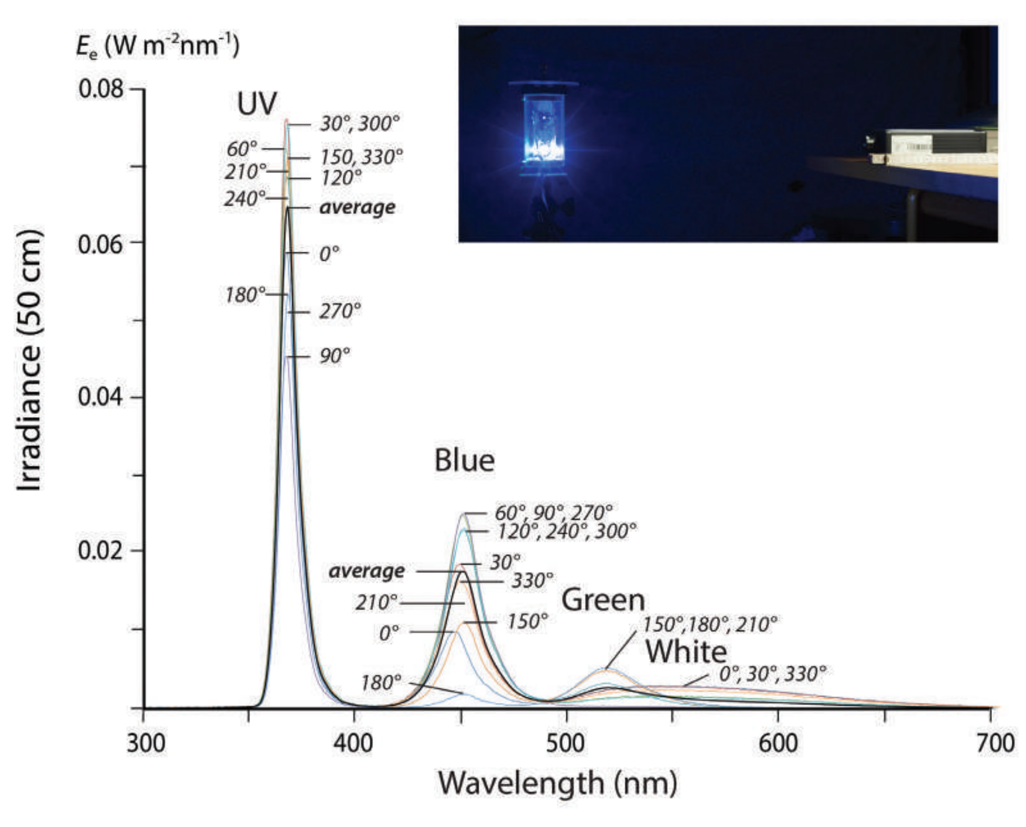

Figure 3. The irradiance of the new lamp was measured at a distance of 50 cm around its circumference at 12 points giving 30° between each. Average value: black line.

a receiving surface, the terms “radiance” and “emission” refer to the radiant source. Irradiance was calculated in total as well as separately for the spectral bands 300–400 nm, 401–650 nm, and 651–1000 nm. Because of the unequal emission patterns of the new LED lamp, irradiance was measured 12 times, at 30° angular intervals around the lamp, and the average was calculated for each wavelength (Fig. 3). Apart from the LED lamp, a number of lamps commonly used in light-trapping were also assessed (Table 1, Appendix 1). In cases where more than one lamp was measured, modest variation in the data was observed, as expected for standard industry products. For a comparison of UV irradiance of lamps and sunlight, irradiance from sunlight was measured on a sunny but hazy day on 17.iii.2016 at 10:50 in Jena, Germany (50.9° N). In addition, lamp and sunlight were filtered with regular clear glasses (Fielmann: Essilur, allyl diglycol carbonate (= CR 39) with additives, super-nonreflecting) and sun glasses (Fielmann: Rupp and Hubrach, allyl diglycol carbonate with additives, polarized, 85% grey).

The wattage of the lamps was measured with a Muker-J7 USB Multimeter QC2.0 QC3.0 and a REV Ritter ‘energy cost measuring device’ (Nr. 002580). The ratio between irradiance and watt-

Table 1. Irradiation of selected lamps and LEDs at wavelengths between 300 and 1000 nm, measured at a distance of 50 cm. A full list is provided in Appendix 1. *Italics*: Measurement of lamp within a gauze tower. Grey cells: wavelength band with highest irradiance. *Unlike other lamps in the test, the GemLight emits only into a single direction (max. 180°). ** Wattage and efficiency of the new LED lamp depend on the input voltage; Values are provided for 12 V and 5 V DC input, respectively.

Lamp	**300–400 nm**	**401–650 nm**	**651–1000 nm**	**300–1000 nm**	**Effective wattage (W)**	**Irradiation/ wattage (efficiency)**
Low pressure mercury vapour						
350 nm actinic tube in acrylic glass	0.44	0.04	0.01	**0.49**	8	0.06
in gauze tower	*0.25*	*0.10*	*0.01*	***0.36***	*8*	--
350 BLB in acrylic glass	0.14	0.01	0.01	**0.15**	8	0.02
in gauze tower	*0.08*	*0.02*	*0.01*	***0.11***	*8*	--
368 nm actinic tube in acrylic glass	0.45	0.04	0.01	**0.50**	8	0.06
in gauze tower	*0.26*	*0.12*	*0.01*	***0.39***	*8*	--
8 W BLB in acrylic glass	0.04	0.00	0.01	**0.05**	4	0.01
in gauze tower	*0.02*	*0.01*	*0.01*	***0.04***	*4*	--
Revoltec cold cathodes (twin sets)						
Cold cathode UV	0.32	0.01	0.00	**0.33**	3.9	0.09
Cold cathode blue	0.00	0.48	0.01	**0.49**	3.9	**0.13**
Cold cathode green	0.01	0.23	0.00	**0.24**	6.8	0.04
Tungsten filament lamps						
160 W mercury vapour	0.57	3.316	7.09	**10.98**	190	0.06
in gauze tower	*0.33*	*3.010*	*6.45*	***9.79***	*190*	--
200 W incandescent	0.04	1.54	8.36	**9.94**	180	0.06
LED lamps						
GemLight*	0.10	0.02	0.00	**0.13**	--	--
400 nm Infusino et al. (2017)	0.13	0.10	0.00	**0.23**	8	0.03
New LED lamp**						
(350 mA) in Plexiglas cylinder	0.77	0.64	0.01	**1.43**	10.4 / 13.4	**0.14 / 0.11**
without Plexiglas cylinder	*0.77*	*0.66*	*0.01*	***1.44***	10.4 / 13.4	**0.14 / 0.11**
with matt Plexiglas cylinder	*0.64*	*0.59*	*0.01*	***1.24***	10.4 / 13.4	**0.11** / 0.09
with sheet in background	*0.76*	*0.94*	*0.02*	***1.72***	10.4 / 13.4	--
in gauze tower	*0.34*	*0.71*	*0.01*	***1.06***	10.4 / 13.4	--

age at 50 cm between 300 and 1000 nm expresses the energy efficiency of the lamps. Temperature of LEDs was measured with an Omega hypodermic needle probe connected to an Omega HH21 thermometer.

Field work performance

A prototype, operated with an output current of 500 mA, was first tested in dry grassland near Leutra, Jena, Germany (29.vi.2016), and later in similar habitats in South Tyrol, Italy: Oberversant (2–13.vii.2016) and Innerunterstell (4.vii.2016). After the successful first field tests, a series of ten LED lamps, operated with an output current of 350 mA, became available in August 2016 and was used for a quantitative moth survey along a rain forest elevational gradient in the Cosñipata valley (Cusco province, Peru) for more than 50 sampling events (23.viii.–4.ix.2016, 12.8868° S, 71.4012° W–13.2003° S, 71.6172° W, 520–3500 m). Detailed analyses of this sampling campaign will be published in due course, but selected photographs illustrate the attraction of Lepidoptera to the lamp.

Results

Features of the new LED lamp

Pronounced irradiation peaks from the new LED lamp occur at 368 nm (UV), at 450 nm (blue), and at 520 nm (green) (Figs 1, 3–6). The mean irradiance of wavelengths between 300 and 1000 nm at a distance of 50 cm is 1.43 W m^{-2}. The irradiance without the protective Plexiglas cylinder is only minimally higher (1.44 W m^{-2}, Fig 1b), and the irradiance with a matt Plexiglas cylinder is ca. 13% lower (1.24 W m^{-2}, Fig. 1b). As expected, UV irradiation is relatively constant at all angles around the lamp, whereas more pronounced spatial peaks occurred with the blue, green, and white LEDs (Fig. 3). A white sheet in the background behind the lamp increases irradiance to 1.72 W m^{-2} (Fig. 4a). However, in this case irradiance is a theoretical value because a sheet can only be placed on one side of the lamp, and irradiance on the reverse of the sheet will be far lower. A gauze tower around the lamp led to a decrease of irradiance to 1.07 W m^{-2} (Fig. 4a), but in-depth comparisons are hindered by increased stray light–the whole gauze tower appears illuminated (Fig. 7). Remarkable in both cases is a partial shift from UV to blue irradiation. This can also be observed when measurements with and without a surrounding gauze tower are compared for a single UV LED (Fig. 4b).

When operated with a 12 V battery, the wattage of the lamp is ca. 10.4 W. When operated with a 5 V (powerbank) battery, the wattage is ca. 13.4 W. Without an axial fan, the LEDs reach (at room temperature) temperatures of between 43 and 53° C. With an operating fan, the temperature range is 30–33° C with a 12 V battery, and 33–39° C with a 5 V battery.

Comparison of lamps

Both the self-ballasted MV and the incandescent lamp assessed surpass by far the irradiance (full range 300–1000 nm) of the new LED lamp (Fig. 5a, Table 1). However, ca. two thirds of their respective irradiation is in the long wave spectrum (> 650 nm), much of it infrared. Remarkably, irradiation from the new LED lamp in the near-UV range between 300 and 400 nm is higher (Table 1)–despite having more than tenfold lower wattage. The MV lamp shows various narrow radiation peaks reflecting the characteristic spectral lines of mercury vapour and an increasing proportion of long wave radiation due to the tungsten filament. The incandescent lamp produces a continuously increasing long wave radiation spectrum but practically no UV radiation.

None of the other lamps that were compared surpass the irradiation from the new LED lamp, neither in total nor in a single wavelength band (Fig. 5b, Table 1, Appendix 1). All tested fluorescent low-pressure mercury tubes (BL / BLB) either show peaks around 350 or 368 nm (Fig. 5b). The highest total irradiation is from 368 nm and 350 nm actinic BL tubes (0.50 and 0.49 W $m^{-2}nm^{-1}$, respectively) whereas the 350 nm BLB tube shows a considerably lower irradiation (0.15 W $m^{-2}nm^{-1}$). All cold cathodes show clearly visible peaks in UV, blue, and green, with irradiance sums of 0.33, 0.49, and 0.24 W $m^{-2}nm^{-1}$, respectively.

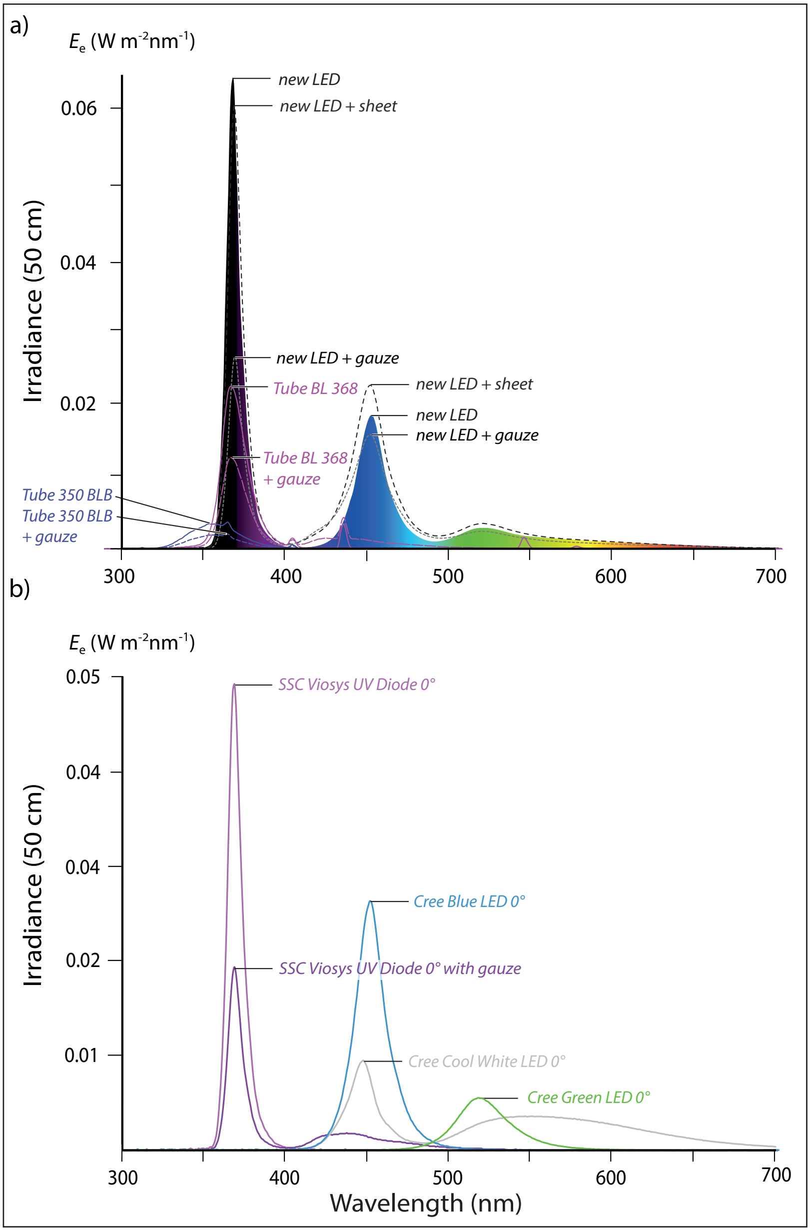

Figure 4. a. Irradiance from the four LED types used in the new LED lamp, measured at 50 cm distance and at 0° (see Fig. 3), and influence of Bioform 'light tower' gauze on the spectral composition of the UV LED. UV irradiance decreases significantly and a new blue peak appears at ca. 440 nm, probably due to optical brighteners applied to the textile. **b.** Influence of Bioform 'light tower' gauze and a white sheet on the irradiance of the new LED lamp, of a 368 nm fluorescent actinic BL tube and a 350 nm fluorescent BLB tube. In all cases, a part of the UV radiation is absorbed and re-emitted by the textile as blue light, caused by optical brighteners. Distance between measuring device and lamp: 50 cm. The tower gauze was placed between the measuring device and the lamp. The sheet was placed 15 cm behind the lamp (increased irradiation due to reflection).

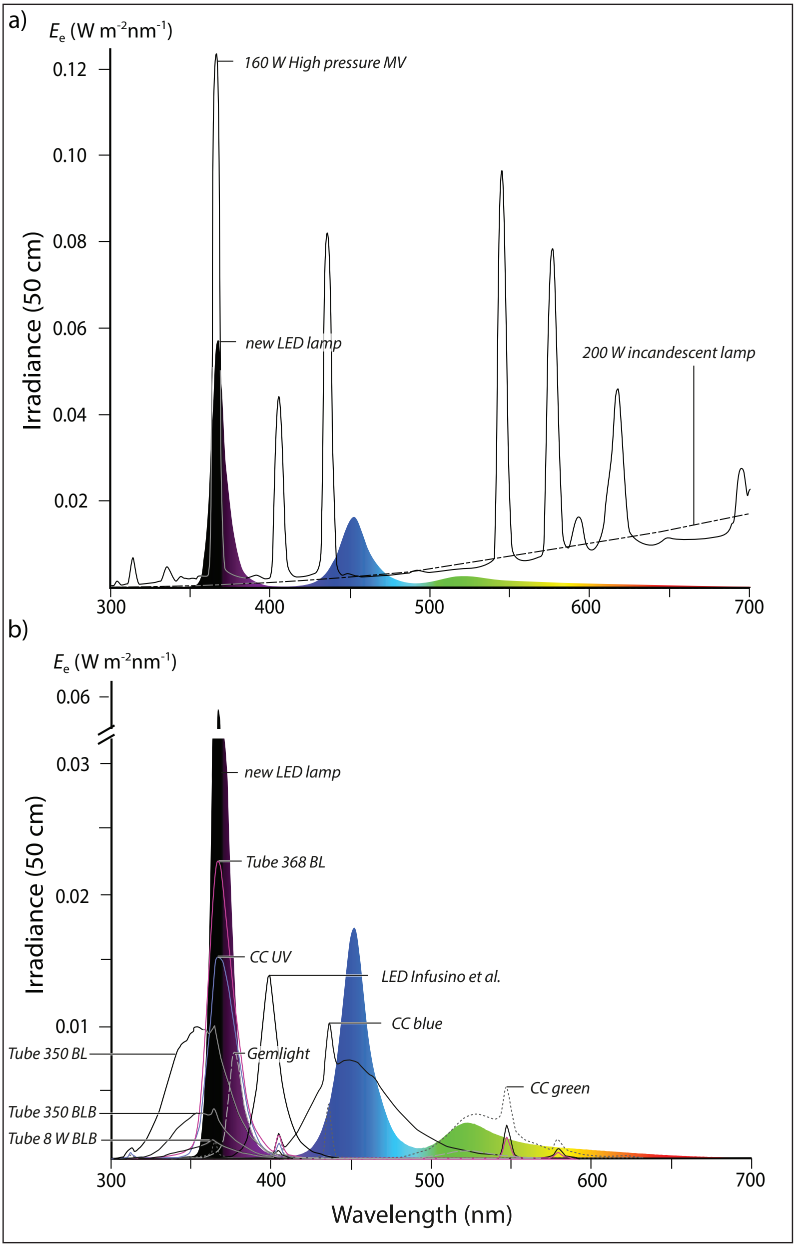

Figure 5. Irradiance from the new LED lamp (in colour), compared with other lamps. **a.** Compared with irradiation from a 190 W high-pressure mercury vapour (MV) bulb with tungsten filament (black line), and a 200 W incandescent lamp with tungsten filament (dashed black line). **b.** Irradiance from the new LED lamp (in colour), as compared to irradiance from various commonly used lamps used for insect collecting. CC blue: Blue cold cathode; CC green: Green cold cathode; CC UV: ultraviolet cold cathode; tube 350: low pressure actinic mercury vapour tube with 350 nm emission peak; tube 350 BL: low pressure mercury vapour blacklight tube with 350 nm emission peak; tube 368: low pressure mercury vapour tube with 368 nm emission peak. GemLight: GemLight UV LED at 0°. LED Infusino et al.: 400 nm LED stripe applied by Infusino et al. (2017).

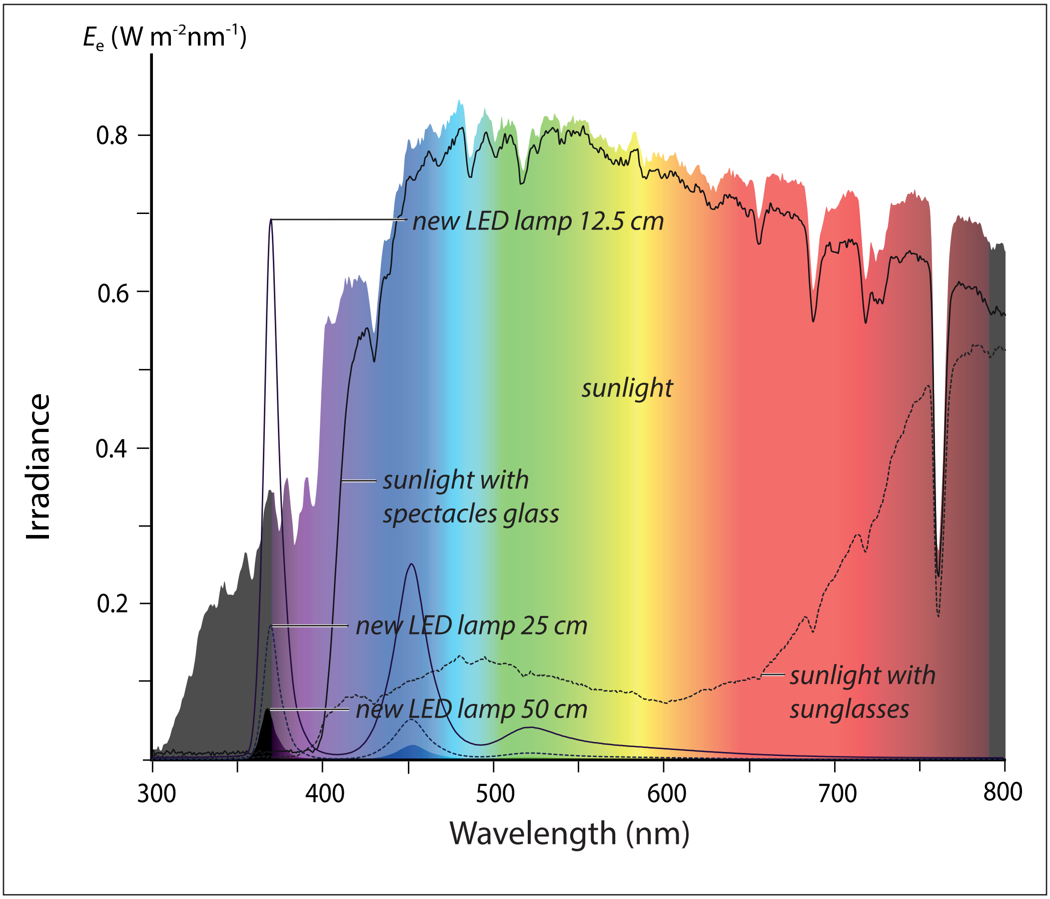

Figure 6. Irradiance from sunlight (in colour; 50.9° N, on a sunny, hazy day at 10:50h in March 2016), irradiance from sunlight with clear synthetic glasses (solid line), irradiance from sunlight with synthetic sunglasses (dashed line), and irradiance from the new LED lamp at distances of 50 cm (see all other Figs), 25 cm, and 12.5 cm. The two spectacle lens types almost completely absorb UV radiation.

Sunlight comparison and UV protection

Fig. 6 shows a comparison of the irradiance on a sunny March day in Jena with the irradiance of the new LED lamp at different distances from the measuring device. The UV irradiation from the new lamp at a distance of 50 cm (the same as in all standardized measurements) is small compared with the irradiance from the sun. However, irradiance from the LED lamp becomes higher at shorter distances. Normal spectacle glasses (allyl diglycol carbonate with additives) almost completely filter away UV radiation but allow almost full transmission of radiation > 400 nm. Sunglasses (allyl diglycol carbonate with additives) again filter UV radiation and also a large proportion of longer wavelengths.

First results from field work

Generally, the LED lamps attracted moths very well, including e.g. Geometridae, Noctuidae, Erebidae, Pyraloidea, Sphingidae, and many other taxa. Lamps were either mounted in front of a white

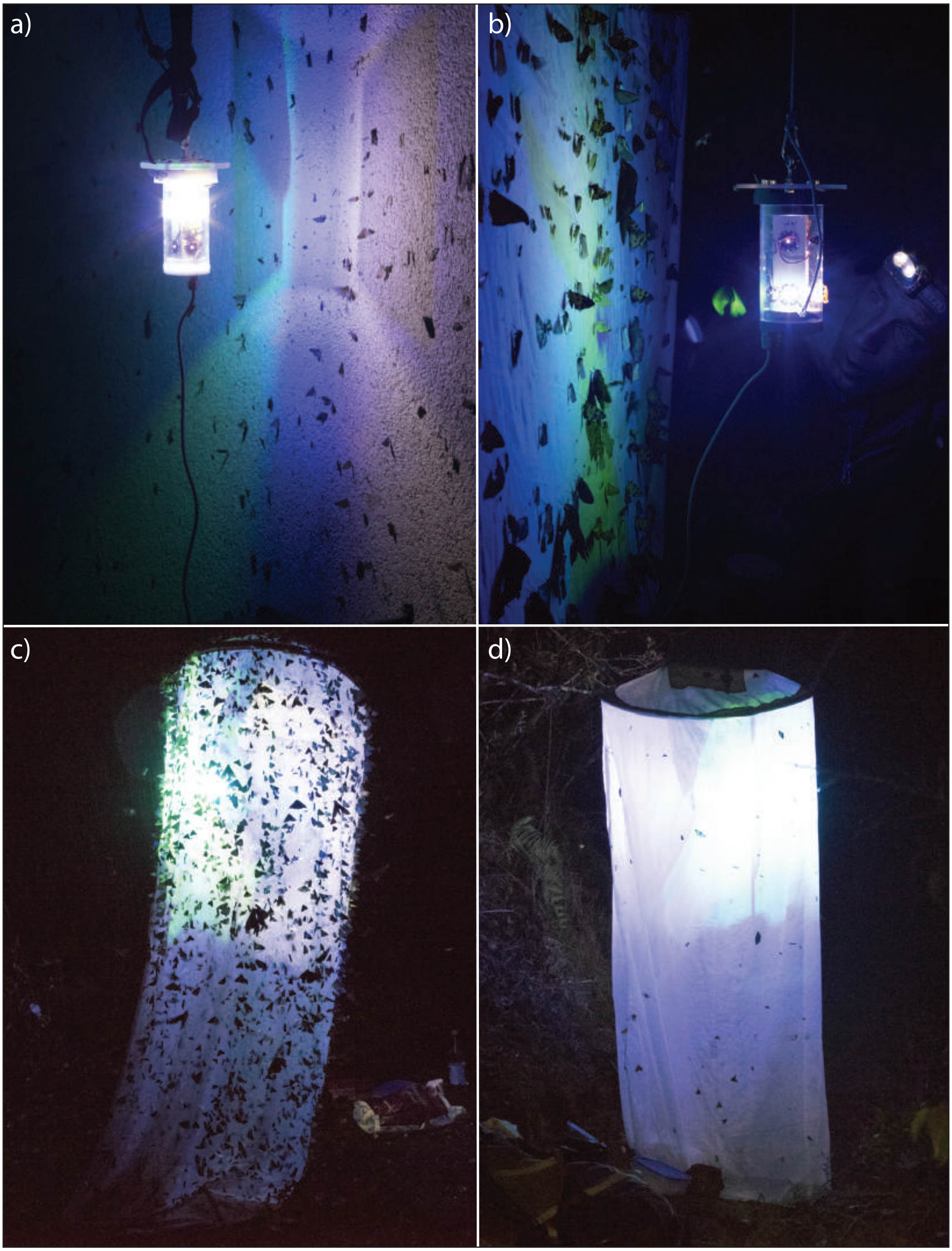

Figure 7. LED lamp used in field work. **a.** Lamp operating in front of a house wall, Oberversant, South Tyrol, Italy (8.vii.2016). **b.** Lamp operating in front of a white sheet, Paradise Lodge, Cosñipata valley, Cusco Province, Peru, 1360 m (30.viii.2016). **c.** Lamp operating in a gauze tower, Cosñipata valley, Peru, 1940 m (3.ix.2016). **d.** Lamp operating in a gauze tower, near Wayqecha station, Peru, 2890 m (4.ix.2016).

house wall in South Tyrol (Fig. 7a), in front of a white sheet in Peru (Fig. 7b) or in a gauze tower in Peru (Figs 7c,d). Most individual moths along the rain forest elevational gradient in Peru were collected at low and medium elevations. The “busiest” night in Peru occurred two days after new moon (3.ix.2016) at 1940 m (Figure 7c). Geometrid moths were the most abundant moth family at this elevation, and I estimate that at least 1000 individuals were attracted within less than three hours after dusk. Only one night later, far fewer specimens (ca. 100 individuals of Geometridae) were collected in a partly clear night at 2890 m (Fig. 7d).

Discussion

The new LED lamp was constructed with the aims of being lightweight, handy, robust, and energy efficient, and these aims were clearly fulfilled. First field tests have demonstrated that the lamp is very attractive to nocturnal Lepidoptera (Fig. 7), and a detailed analysis of the samples will be published in due course. The measurements carried out concentrate on irradiance rather than on total emission of the lamp, first because the required measuring device, a two-meter diameter Ulbricht sphere, was not available in Jena. Second, the chosen approach allowed comparison of irradiance from lamps in combination with gauze and sheets, as well as with incoming sunlight. Generally, comparisons between different lamps are never simple because lamps differ in their design, in their dimensions, and in the way radiation is emitted. All of these factors could possibly influence moth behaviour, and therefore measurement results should be regarded as an approximation of potential moth attractiveness, to be supplemented by field studies and physiological measurements.

The age and the cumulative operating hours of the lamps could have an impact on their performance, but it was beyond the scope of this paper to explore this effect in detail. For example, the emission of fluorescent tubes drops with age to ca. 80% in new-generation lamps (Sylvania BL 368 nm) and to ca. 50% in old-generation tubes (e.g. Sylvania BL 350 nm) (Havells-Sylvania 2012). Decreases are also expected to occur in LEDs, accelerated by high temperatures and high currents. For this reason, LEDs in the lamp are not being operated at the maximum possible current (700 mA) but only at 350 mA, aided by an efficient cooling system. Ageing of acrylic glass and other materials possibly also influences the radiation flux.

Clearly, a cross calibration study with other lamps is desirable. Such comparative studies have regularly shown that even lamps with fundamentally different light spectra attract similar moth assemblages. For example, Geometroidea samples attracted to an incandescent and a MV lamp were surprisingly similar (Intachat and Woiwod 1999; Infusino et al. 2017; Jonason et al. 2014). On the other hand, noctuid moths were more attracted to short wave radiation than geometrid moths (Somers-Yeates et al. 2014), so certain differences in samples obtained with different methods must be expected.

An unexpected result was the appearance of a blue peak at ca. 440 nm when ‘light tower’ gauze and a white sheet were used in combination with various lamps. In all cases, a part of the UV radiation is absorbed and re-emitted by the textile as blue light, caused by commonly used optical brighteners in textile production and in washing powders. This means that supposedly ‘pure’ UV sources such as BLB tubes and UV LEDs combined with a textile also emit a certain amount of blue light. This lowers energy efficiency to some extent, but the additional blue light possibly increases the attractiveness to insects.

The lamp itself has a weight of less than 500 g, and it can be operated for five to six hours with a standard powerbank, e.g. an Easy Acc battery (5 V, 26 Ah, 400 g). Since powerbank batteries are a mass product on the market used for mobile phones etc., their prices are reasonable, they can easily be transported in carry-on baggage and recharged with mobile solar panels in remote areas. The total equipment, including the lamp, powerbank and charging device (220 V AC to 5 V DC USB charger) weighs less than 1 kg. In comparison, any equipment operated with generators is far heavier because a generator alone weighs ca. 13 kg. Equipment operated with 12 V is usually connected to (heavy) lead batteries. For example, field work in Ecuador and Costa Rica (Brehm and Axmacher 2005; Brehm 2007) was undertaken with a 15 W actinic BL tube and a 15 W BLB tube, operated with a lead battery (12 V, 7 Ah, 2 kg). Together with the charging device, the equipment weighed ca. 4 kg. The size of the new LED lamp (6 x 14 cm) is also small, so that it easily fits into travel bags and backpacks. The lamp has furthermore proven to be robust in the field. In one case, the axial fan broke when a gauze tower was blown down in a thunderstorm. However, the lamp remained fully functional without the fan, but since a working fan reduces the temperature of the LEDs (by ca. 10° C), which leads to a longer lifetime of the diodes, it is recommended that a broken fan is replaced when it is practical to do so (it takes only a few minutes).

In terms of energy efficiency, the new LED lamp outperformed every other lamp that was tested (Table 1, Appendix 1), and total irradiance between 300 and 400 nm was greater than from any other tested lamp, even including strong, self-ballasted MV bulbs. If efficiency is to be maximized, the use of 12 V batteries is recommended but from a weight-optimising point of view, 5 V powerbank batteries are the better choice. The second most energy-efficient tested lamps are cold cathodes with an input voltage of 12 V (Table 1). Their use nonetheless requires heavier batteries or a step-up converter that lowers energy efficiency. Cold cathodes (especially blue ones) are very lightweight and appear to have the best price / performance ratio.

The new LED lamp emits the desired spectrum of different wavelengths (UV, blue, and green). Half of the LEDs are UV diodes because UV is particularly attractive to moths. However, the additional diodes are expected to contribute further to the attractiveness of the lamp, and to stimulate eye receptors sensitive to longer waves. When MV lamps are compared with BL and BLB tubes, MV lamps usually attract more moth species and individuals (e.g., Jonason et al. 2014; Tikoca et al. 2016). A possible reason is that MV lamps emit not only more UV radiation, but also a much broader spectrum, than fluorescent tubes. A major advantage of LEDs is that a light mix can experimentally be assembled from a wide range of available diodes (Cowan and Gries 2009; Kadlec et al. 2016). Future studies could assess whether a maximisation of UV radiation on the one hand versus a mixture of wavelengths on the other hand, results in a higher number of attracted moth species and individuals. The new LED lamp could easily be used for such experiments, and mixtures of different LEDs could be tested. In principle, the lamp could also be modified in such a way that more diodes, e.g. 12, 16, or 20, are mounted on an extended design.

Safety considerations

Ultraviolet radiation is well known for its harmful effects on skin and eyes, being linked to accelerated ageing, various forms of skin cancer, eye cataracts etc. (O'Sullivan and Tait 2014). Protection with appropriate glasses and sunscreen is therefore strongly recommended to all lepidopterists who often work in open sunlight. The potential hazard of light-trapping lamps used by entomologists has received little consideration to date. The data presented here suggest that UV irradiance at a distance

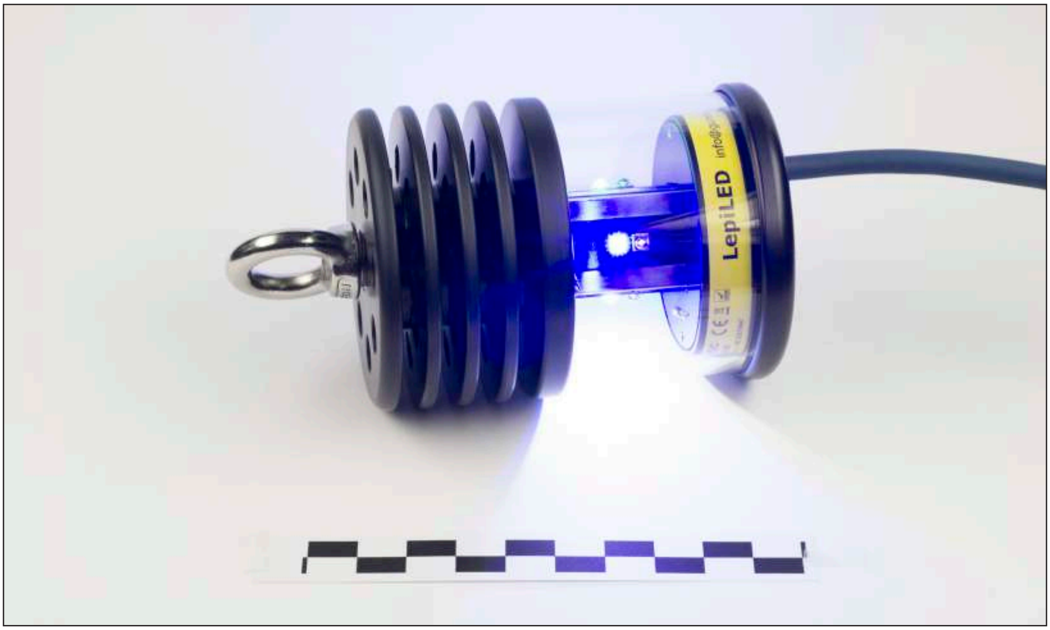

Figure 8. First exemplar of the commercially available lamp "LepiLED", height ca. 88 mm, diameter ca. 62 mm. Scale bar: 10 cm.

of 50 cm from the lamp is low compared with sunlight, which was relatively weak (51° N, low angle) compared to sunlight at lower latitudes, at higher angles, and at high elevations. This of course does not mean that UV lamps are generally harmless: irradiance strongly increases as distance decreases between lamp and exposed surface. As a general rule, it is certainly advisable to keep a reasonable distance from the lamp, depending on its type, and to avoid exposure of skin and eyes to the UV source at a short distance. High quality glasses (but not normal spectacle glasses) will often provide a sufficient protection, but UV transmission of glasses should individually be checked by an optician. In doubt, one can easily purchase safety-glasses which also protect from stray light. Good quality sun-glasses also protect from UV radiation, but only models with weak shading will be practicable for use at night.

Outlook

Further studies are required with regard to cross-calibration of the new LED lamp with existing lamps, including cold cathodes, which have been poorly studied so far. The lamp design is also open to experimental approaches in the field with different sets of LEDs. So far, only a small series of lamps has been available. However, a professionally manufactured model will be available for 395 € from the author (info@gunnarbrehm.de) in 2017. This model uses the same basic design as the lamp described in this paper. It weighs ca. 470 g, has a height of 88 mm and a diameter of 62 mm, the same input voltage (5–12 V) and a very similar set of LEDs (manufacturer: Nishia). Also, this model has almost identical emissions to the lamp described here. It is manufactured with anodized aluminium and borosilicate glass, and instead of a fan, it uses a passive cooling element and is totally waterproof. This model will hopefully make the LED technology available to a larger community of lepidopterists and other entomologists.

Acknowledgements

I am indebted to Jan Axmacher, Konrad Fiedler, Jeremy Holloway, Luisa Jaimes, Bernard Landry, Rolf Mörtter, and Eric Warrant for providing helpful comments, hints to literature, and linguistic assistance with the manuscript. Rainer Bark, Tobias Borchert, and Daniel Veit helped me to technically realize the project, B. Kühn checked the manuscript with regard to physics, and D. Veit kindly provided the photospectrometer for multiple measurements. Jan Axmacher, Konrad Fiedler, Egbert Friedrich, Kai Grajetzki, Marco Infusino, Rolf Mörtter, Rando Müller, Stefano Scalercio, and Axel Steidel kindly provided lamps and Jürgen Schmidl (Bioform) gauze for measurements. Field work in Peru was conducted together with Daniel Bolt, Juan Grados, Gerardo Lamas, and Matthias Nuß. Stella Beavan is thanked for the final language check of the manuscript.The Peru project was supported by the Deutsche Forschungsgemeinschaft (BR 2280/6-1).

References

Altermatt F, Ebert D (2016) Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. Biology Letters 12: 20160111. http://dx.doi.org/10.1098/rsbl.2016.0111

Brehm G (2007) Contrasting patterns of vertical stratification in two moth families in a Costa Rican lowland rain forest. Basic and Applied Ecology 8: 44–54. https://doi.org/10.1016/j.baae.2006.02.002

Brehm G, Axmacher JC (2005) A comparison of manual and automatic moth sampling methods (Lepidoptera: Arctiidae, Geometridae) in a rain forest in Costa Rica. Environmental Entomology 35: 754–764.

Briscoe DB, Chittka L (2001) The evolution of color vision in insects. Annual Review in Entomology 46: 471–510. https://doi.org/10.1146/annurev.ento.46.1.471

Chen P-J, Awata H, Matsushita A, Yang E-C, Arikawa K (2016) Extreme spectral richness in the eye of the Common Bluebottle Butterfly, *Graphium sarpedon*. Frontiers in Ecology and Evolution 4: 18. https://doi.org/10.3389/fevo.2016.00018

Cowan T, Gries G (2009) Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*. Entomologia Experimentalis et Applicata 131: 148–158. https://doi.org/10.1111/j.1570-7458.2009.00838.x

Eby C, Weis M, Gardiner MGT, Judd GJR, Gries G (2013) Spectral efficiency and microstructure of the compound eyes of *Synanthedon myopaeformis* (Lepidoptera: Sesiidae). Canadian Entomologist 145: 529–538. https://doi.org/10.4039/tce.2013.25

Emmet AM (1991) The scientific names of the British Lepidoptera. Their history and meaning. Harley Books, Colchester. 288 pp.

Green D, MacKay D, Whalen M (2012) Next generation insect light traps: The use of LED light technology in sampling emerging aquatic macroinvertebrates. Australian Entomologist 39: 189–194.

Havells-Sylvania (2012) Blacklight lamps. Havells-Sylvania, Tienen, 12pp. [Brochure]

Huemer P, Kühtreiber H, Tarmann GM (2011) Anlockwirkung moderner Leuchmittel auf nachtaktive Insekten–Ergebnisse einer Feldstudie in Tirol (Österreich). Wissenschaftliches Jahrbuch der Tiroler Landesmuseen 4: 110–135.

Holloway JD, Kibby G, Peggie D (2001) The families of Malesian moths and butterflies. Fauna Malesiana Handbook 3. Brill, Leiden, Boston, Köln.

Infusino M, Brehm G, Di Marco C, Scalercio S (2017) Assessing the efficiency of UV LEDs as light sources for macro-moth diversity sampling. European Journal of Entomology 114: 25–33. https://doi.org/10.14411/eje.2017.004

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Intachat J, Woiwod IP (1999) Trap design for monitoring moth biodiversity in tropical rainforests. Bulletin of Entomological Research 89: 153–163. https://doi.org/10.1017/S0007485399000243

Johnsen S, Kelber A, Warrant E, Sweeney AM, Widder EA, Lee Jr RL, Hernández-Andrés J (2006) Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. Journal of Experimental Biology 209: 789–800. doi:10.1242/jeb.02053

Jonason D, Franzén M, Ranius T (2014) Surveying moths using light traps: effects of weather and time of year. PLoS ONE 9: e92453. https://doi.org/10.1371/journal.pone.0092453

Kadlec T, Pikner M, Piknerova G (2016) Sex-biased response in activity to light sources with different spectral composition in geometrid moths with flightless females (Lepidoptera: Geometridae). Bulletin of Entomological Research 106: 581–590. https://doi.org/10.1017/S0007485316000298

Macgregor CJ, Evans DM, Fox R, Pocock MJ (2017) The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. Global Change Biology 23: 697–707. https://doi.org/10.1111/gcb.13371

Mobbs P (2016) A better moth trap using LEDs? https://petermobbs.wordpress.com/2015/05/09/a-better-moth-trap-using-leds [Accessed 22.xi.2016]

O'Sullivan N-A, Tait CP (2014) Tanning bed and nail lamp use and the risk of cutaneous malignancy: A review of the literature. Australasian Journal of Dermatology 55: 99–106. https://doi.org/10.1111/ajd.12145

Pawson SM, Bader MK-F (2014) LED lighting increases the ecological impact of light pollution irrespective of color temperature. Ecological Applications 24: 1561–1568. https://doi.org/10.1890/14-0468.1

Price B, Baker E (2016) NightLife: A cheap, robust, LED based light trap for collecting aquatic insects in remote areas. Biodiversity Data Journal 4: e7648. https://doi.org/10.3897/BDJ.4.e7648

Somers-Yeates R, Hodgson D, McGregor PK, Spalding A, Ffrench-Constant RH (2013) Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. Biology Letters 9: 20130376. http://dx.doi.org/10.1098/rsbl.2013.0376

Southwood TRE, Henderson PA, Woiwod IP (2003) Stability and change over 67 years-the community of Heteroptera as caught in a light-trap at Rothamsted, UK. European Journal of Entomology 100: 557–562. https://doi.org/10.14411/eje.2003.084

Steidel A, Plontke R (2008) Lichtfangtechnik auf Reisen. Mitteilungen des Thüringer Entomologenverbandes e.V. 15: 22–31.

Taylor LR, French RA (1974) Effects of light-trap design and illumination on samples of moths in an English woodland. Bulletin of Entomological Research 63: 583–594. https://doi.org/10.1017/S0007485300047829

Tikoca S, Hodge S, Tuiwawa M, Brodie G, Pene S, Clayton J (2016) An appraisal of sampling methods and effort for investigating moth assemblages in a Fijian forest. Austral Entomology 55: 455–462. https://doi.org/10.1111/aen.12209

van Grunsven RH, Donners M, Boekee K, Tichelaar I, Van Geffen KG, Groenendijk D, Berendse F, Veenendaal EM (2014) Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. Journal of Insect Conservation 18: 225–231. https://doi.org/10.1007/s10841-014-9633-9

van Langevelde F, Ettema JA, Donners M, Wallis DeVries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. Biological Conservation 144: 2274–2281. https://doi.org/10.1016/j.biocon.2011.06.004

White PJT, Glover K, Steward J, Rice A (2016) The technical and performance characteristics of a low-cost, simply constructed, black light moth trap. Journal of Insect Science 16: 25. https://doi.org/10.1093/jisesa/iew011

Williams CB (1948) The Rothamsted light trap. Proceedings of the Royal Entomologial Society, Series A 23: 80–85. https://doi.org/10.1111/j.1365-3032.1948.tb00623.x

Appendix 1

Table 2. Full list of tested lamps and LEDs with irradiance measured in different bands of wavelengths. Grey cells: LEDs used for the new LED lamp.

Type	Remarks / angle	Wattage effective (W)	Brand	Nr	300–400 nm	401–650 nm	651–1000 nm	300–1000 nm
Low pressure MV actinic tube (BL)	naked	8	Sylvania	Blacklight 368 F15W/T8/BL368	0.427	0.039	0.008	**0.474**
Low pressure MV actinic tube (BL)	naked in gauze tower	8	Sylvania	Blacklight 368 F15W/T8/BL368	0.256	0.090	0.007	**0.353**
Low pressure MV actinic tube (BL)	acrylic glass	8	Sylvania	Blacklight 368 F15W/T8/BL368	0.438	0.040	0.009	**0.487**
Low pressure MV actinic tube (BL)	acrylic glass in gauze tower	8	Sylvania	Blacklight 368 F15W/T8/BL368	0.251	0.098	0.008	**0.357**
Low pressure MV actinic tube (BL)	naked	8	Sylvania	Blacklight F15W/350 BL-T8	0.469	0.041	0.007	**0.517**
Low pressure MV actinic tube (BL)	naked in gauze tower	8	Sylvania	Blacklight F15W/350 BL-T8	0.264	0.126	0.008	**0.398**
Low pressure MV actinic tube (BL)	acrylic glass	8	Sylvania	Blacklight F15W/350 BL-T8	0.450	0.039	0.008	**0.497**
Low pressure MV actinic tube (BL)	acrylic glass in gauze tower	8	Sylvania	Blacklight F15W/350 BL-T8	0.256	0.124	0.008	**0.388**
Low pressure MV actinic tube (BL)	naked	9	Philips	PL-S 9W/12 Made in Poland	0.223	0.057	0.013	**0.293**
Low pressure MV actinic tube (BL)	naked in gauze tower	9	Philips	PL-S 9W/12 Made in Poland	0.109	0.063	0.012	**0.184**
Low pressure MV actinic tube (BL)	naked	13	Exo Terra	Repti Glo 5.0 UVB 13 W	0.053	0.492	0.054	**0.599**
Low pressure MV actinic tube (BL)	naked in gauze tower	13	Exo Terra	Repti Glo 5.0 UVB 13 W	0.029	0.482	0.053	**0.563**
Low pressure MV actinic tube (BL)	naked	12	Osram	Dulux S Blue UVA, 78 Color	0.441	0.075	0.022	**0.538**
Low pressure MV actinic tube (BL)	naked in gauze tower	12	Osram	Dulux S Blue UVA, 78 Color	0.247	0.137	0.016	**0.401**

Type	Remarks / angle	Wattage effective (W)	Brand	Nr	300–400 nm	401–650 nm	651–1000 nm	300–1000 nm
Low pressure MV actinic tube (BL)	naked	30	Kelly	Bug Killer 40W, ESL Lamp Nr. 71468	1.014	0.355	0.005	**1.374**
Low pressure MV actinic tube (BL)	naked in gauze tower	30	Kelly	Bug Killer 40W, ESL Lamp Nr. 71468	0.548	0.471	0.005	**1.024**
Low pressure MV blacklight-blue tube (BLB)	naked	8	No brand	F15 T8 BLB	0.144	0.005	0.013	**0.162**
Low pressure MV blacklight-blue tube (BLB)	naked in gauze tower	8	No brand	F15 T8 BLB	0.080	0.024	0.011	**0.115**
Low pressure MV blacklight-blue tube (BLB)	acrylic glass	8	No brand	F15 T8 BLB	0.135	0.005	0.010	**0.149**
Low pressure MV blacklight-blue tube (BLB)	acrylic glass in gauze tower	8	No brand	F15 T8 BLB	0.076	0.022	0.009	**0.106**
Low pressure MV blacklight-blue tube (BLB)	naked	8	No brand	F15 T8 BLB	0.141	0.004	0.007	**0.152**
Low pressure MV blacklight-blue tube (BLB)	naked in gauze tower	8	No brand	F15 T8 BLB	0.080	0.021	0.007	**0.108**
Low pressure MV blacklight-blue tube (BLB)	acrylic glass	8	No brand	F15 T8 BLB	0.129	0.003	0.006	**0.138**
Low pressure MV blacklight-blue tube (BLB)	acrylic glass in gauze tower	8	No brand	F15 T8 BLB	0.070	0.021	0.007	**0.098**
Low pressure MV blacklight-blue tube (BLB)	naked	19	Omnilux	Energy Saving Lamp 3U 20W E27	0.184	0.009	0.004	**0.197**
Low pressure MV blacklight-blue tube (BLB)	naked in gauze tower	19	Omnilux	Energy Saving Lamp 3U 20W E27	0.105	0.034	0.003	**0.142**
Low pressure MV blacklight-blue tube (BLB)	naked	4	no brand		0.041	0.002	0.008	**0.051**
Low pressure MV blacklight-blue tube (BLB)	naked in gauze tower	4	no brand		0.021	0.008	0.006	**0.035**
Cold cathode (twin set)	naked	3,9	Revoltec	UV RM130	0.324	0.009	0.001	**0.334**
Cold cathode (twin set)	naked	3,9	Revoltec	Blue RM128	0.004	0.483	0.005	**0.492**
Cold cathode (twin set)	naked	6,8	Revoltec	Green RM125	0.007	0.231	0.003	**0.241**

Type	Remarks / angle	Wattage effective (W)	Brand	Nr	300–400 nm	401–650 nm	651–1000 nm	300–1000 nm
High pressure MV lamp, self-ballasted	naked	190	Osram	HVL 160 W	0.567	3.316	7.093	**10.975**
High pressure MV lamp, self-ballasted	naked in gauze tower	190	Osram	HVL 160 W	0.331	3.010	6.454	**9.794**
High pressure MV lamp, self-ballasted	naked	190	Osram		0.694	3.132	6.330	**10.156**
High pressure MV lamp, self-ballasted	naked in gauze tower	190	Osram		0.348	2.443	4.879	**7.671**
High pressure MV BLB lamp, self-ballasted	naked	190	Omnilux	UV Lampe 160 W / E27	0.306	0.048	1.475	**1.829**
High pressure MV BLB lamp, self-ballasted	naked in gauze tower	190	Omnilux	UV Lampe 160 W / E27	0.211	0.113	1.466	**1.789**
Incandescent lamp	naked	180	no brand	200 W (E27)	0.035	1.541	8.364	**9.940**
LED UV + Green	naked	nA	Worldwide Butterflies	GemLight	0.104	0.024	0.000	**0.129**
LED UV + Green	naked in gauze tower	nA	Worldwide Butterflies	GemLight	0.055	0.035	0.000	**0.090**
LED UV	naked	8	no brand		0.129	0.104	0.000	**0.234**
LED UV	naked in gauze tower	8	no brand		0.069	0.108	0.000	**0.178**
LED UV	0°	at 350 mA	SSC Viosys	UV CUN66A1B	0.610	0.005	0.000	**0.615**
LED UV	0° gauze I	at 350 mA	SSC Viosys	UV CUN66A1B	0.274	0.099	0.000	**0.373**
LED UV	0° gauze II	at 350 mA	SSC Viosys	UV CUN66A1B	0.275	0.100	0.001	**0.375**
LED UV	30°	at 350 mA	SSC Viosys	UV CUN66A1B	0.526	0.011	0.002	**0.539**
LED UV	60°	at 350 mA	SSC Viosys	UV CUN66A1B	0.397	0.009	0.002	**0.408**
LED UV	0°	at 350 mA	Nishia	NCSU033B	0.446	0.004	0.000	**0.450**
LED UV	30°	at 350 mA	Nishia	NCSU033B	0.452	0.003	0.001	**0.456**
LED UV	60°	at 350 mA	Nishia	NCSU033B	0.218	0.002	0.000	**0.220**

Type	Remarks / angle	Wattage effective (W)	Brand	Nr	300–400 nm	401–650 nm	651–1000 nm	300–1000 nm
LED UV	90°	at 350 mA	Nishia	NCSU033B	0.000	0.000	0.000	**0.000**
LED UV	0° in gauze tower	at 350 mA	Nishia	NCSU033B	0.189	0.047	0.000	**0.236**
LED UV	0°	at 350 mA	Winger	WEPUV3-S2 Blacklight	0.137	0.252	0.001	**0.391**
LED UV	0° gauze I	at 350 mA	Winger	WEPUV3-S2 Blacklight	0.062	0.203	0.001	**0.266**
LED UV	0° gauze II	at 350 mA	Winger	WEPUV3-S2 Blacklight	0.064	0.213	0.001	**0.278**
LED UV	30°	at 350 mA	Winger	WEPUV3-S2 Blacklight	0.109	0.247	0.001	**0.357**
LED UV	60°	at 350 mA	Winger	WEPUV3-S2 Blacklight	0.096	0.225	0.001	**0.322**
LED UV	0°	at 350 mA	no brand		0.188	0.010	0.000	**0.199**
LED UV	30°	at 350 mA	no brand		0.160	0.009	0.000	**0.169**
LED UV	60°	at 350 mA	no brand		0.093	0.006	0.000	**0.100**
LED UV	90°	at 350 mA	no brand		0.002	0.000	0.000	**0.003**
LED Turquoise	0°	at 350 mA	Bridgelux	Turquoise	0.000	0.237	0.000	**0.238**
LED Turquoise	30°	at 350 mA	Bridgelux	Turquoise	0.001	0.214	0.000	**0.215**
LED Turquoise	60°	at 350 mA	Bridgelux	Turquoise	0.000	0.249	0.000	**0.250**
LED Turquoise	90°	at 350 mA	Bridgelux	Turquoise	0.000	0.029	0.000	**0.029**
LED Blue	0°	at 350 mA	Cree	XP-E2 Royal Blue	0.003	0.665	0.002	**0.670**
LED Blue	30°	at 350 mA	Cree	XP-E2 Royal Blue	0.002	0.555	0.003	**0.560**
LED Blue	60°	at 350 mA	Cree	XP-E2 Royal Blue	0.001	0.447	0.002	**0.451**
LED Blue	0°	at 350 mA	Bridgelux	Royal Blue	0.003	0.502	0.002	**0.507**
LED Blue	30°	at 350 mA	Bridgelux	Royal Blue	0.004	0.611	0.002	**0.617**
LED Blue	60°	at 350 mA	Bridgelux	Royal Blue	0.003	0.556	0.002	**0.560**
LED Blue	90°	at 350 mA	Bridgelux	Royal Blue	0.000	0.099	0.001	**0.101**
LED Blue	0° in gauze tower	at 350 mA	Bridgelux	Royal Blue	0.002	0.404	0.000	**0.407**
LED Blue	0°	at 350 mA	Winger	WEPRB3-S1 Royal Blue	0.002	0.483	0.002	**0.487**
LED Blue	0° gauze I	at 350 mA	Winger	WEPRB3-S1 Royal Blue	0.002	0.366	0.002	**0.371**
LED Blue	0° gauze II	at 350 mA	Winger	WEPRB3-S1 Royal Blue	0.001	0.364	0.003	**0.368**
LED Blue	30°	at 350 mA	Winger	WEPRB3-S1 Royal Blue	0.002	0.408	0.001	**0.411**

Type	Remarks / angle	Wattage effective (W)	Brand	Nr	300–400 nm	401–650 nm	651–1000 nm	300–1000 nm
LED Blue	60°	at 350 mA	Winger	WEPRB3-S1 Royal Blue	0.000	0.013	0.001	**0.014**
LED Green	0°	at 350 mA	Cree	XP-E2 Green	0.000	0.228	0.003	**0.231**
LED Green	30°	at 350 mA	Cree	XP-E2 Green	0.000	0.222	0.002	**0.225**
LED Green	60°	at 350 mA	Cree	XP-E2 Green	0.000	0.166	0.002	**0.169**
LED Green	0°	at 350 mA	Bridgelux	Emerald Green	0.000	0.213	0.001	**0.214**
LED Green	30°	at 350 mA	Bridgelux	Emerald Green	0.000	0.216	0.001	**0.217**
LED Green	60°	at 350 mA	Bridgelux	Emerald Green	0.000	0.202	0.000	**0.202**
LED Green	90°	at 350 mA	Bridgelux	Emerald Green	0.000	0.030	0.000	**0.031**
LED Green	0° in gauze tower	at 350 mA	Bridgelux	Emerald Green	0.000	0.230	0.001	**0.231**
LED Green	0°	at 350 mA	Winger	WEPGN3-S1 Green	0.000	0.236	0.001	**0.237**
LED Green	0° gauze I	at 350 mA	Winger	WEPGN3-S1 Green	0.000	0.167	0.001	**0.167**
LED Green	0° gauze II	at 350 mA	Winger	WEPGN3-S1 Green	0.000	0.168	0.001	**0.169**
LED Green	30°	at 350 mA	Winger	WEPGN3-S1 Green	0.000	0.236	0.000	**0.237**
LED Green	60°	at 350 mA	Winger	WEPGN3-S1 Green	0.000	0.213	0.000	**0.214**
LED Cool White	0°	at 350 mA	Cree	XP-L V6 Cool White	0.001	0.647	0.051	**0.699**
LED Cool White	0° gauze I	at 350 mA	Cree	XP-L V6 Cool White	0.001	0.417	0.036	**0.453**
LED Cool White	30°	at 350 mA	Cree	XP-L V6 Cool White	0.001	0.532	0.045	**0.578**
LED Cool White	60°	at 350 mA	Cree	XP-L V6 Cool White	0.001	0.359	0.034	**0.394**
LED Cool White	0°	at 350 mA	Bridgelux	Cool White	0.001	0.482	0.034	**0.518**
LED Cool White	30°	at 350 mA	Bridgelux	Cool White	0.001	0.399	0.030	**0.429**
LED Cool White	60°	at 350 mA	Bridgelux	Cool White	0.000	0.312	0.025	**0.338**
LED Cool White	90°	at 350 mA	Bridgelux	Cool White	0.000	0.014	0.001	**0.015**
LED Cool White	0° in gauze tower	at 350 mA	Bridgelux	Cool White	0.001	0.348	0.027	**0.375**
LED Cool White	0°	at 350 mA	Winger	WEPCW3-S1 Cool White	0.001	0.314	0.015	**0.331**
LED Cool White	0° gauze I	at 350 mA	Winger	WEPCW3-S1 Cool White	0.000	0.225	0.012	**0.237**
LED Cool White	0° gauze II	at 350 mA	Winger	WEPCW3-S1 Cool White	0.001	0.237	0.012	**0.250**
LED Cool White	30°	at 350 mA	Winger	WEPCW3-S1 Cool White	0.001	0.274	0.014	**0.289**
LED Cool White	60°	at 350 mA	Winger	WEPCW3-S1 Cool White	0.001	0.182	0.010	**0.193**

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and
Towns, Cambridge University Press, Cambridge 2009, p. 243-263

Chapter 15. Light pollution and the impact of artificial night lighting on insects

Gerhard Eisenbeis and Andreas Hänel

Introduction

The creation of urban environments has significant impacts on animals and insects throughout the world (Niemelä et al. Chapter 2; Caterall, Chapter 8; Nilon, Chapter 10; van der Ree, Chapter 11; Natuhara and Hashimoto, Chapter 12; Hochuli et al. Chapter; McIntyre and Rango Chapter 14). During the last decades both landscape and urban ecologists were confronted with a new phenomenon associated with cities and towns: 'light pollution'(Riegel 1973). Fast growing outdoor lighting as a threat to astronomy was first described by Riegel (1973). Astronomers need dark sky conditions to discriminate the faint light of astronomical sources from the sky background, which is due to a natural glow (airglow, scattered star light etc.) and artificial light scattered in earth's atmosphere. Since the invention of electric light and especially since World War II a steep increase of the outdoor lighting level has occurred and the natural darkness around human settlements has disappeared almost totally. Unwanted skylight produced by artificial night lighting is spreading from urban areas to less populated landscapes generating a modern sky glow.

The primary cause of this new phenomenal is the excessive growth of artificial lighting in the environment. It is related primarily to the general population growth, industrial development and increasing economic prosperity, but there has also occurred a significant technical improvement by applying lamps with higher and higher luminous efficiency. For example, the light output efficacy of an old-fashioned incandescent lamp is 10-20 lumens/watt and for a modern low pressure sodium vapor lamp it is nearly 200 lumens/watt. But, there is still another component that contributes significantly to light pollution which is the excessive and, at times, careless use of artificial outdoor lighting by humans, as well as the use of poorly design fixtures which allow a high proportion of upward flux of radiation. All these components contribute to an increased level of sky brightness often visible as 'sky glow' or as a far visible 'light dome' covering city centres.

This ubiquitous increase in night lighting in human settlements has resulted in a significant change in environmental conditions and should be regarded as a new challenge for ecologists involved in the conservation of biodiversity. Mizon (2002) and Cinzano (2002) have provided comprehensive reviews of the topic of light pollution. Several conference proceedings that are mainly focused on astronomical observations also discuss the negative influence of light pollution (Isobe and Hirayama, 1997, Cinzano, 2000, Cohen and Sullivan, 2001).

Although bright lights are associated with the world's thriving cities, there are some voices that are increasingly warning of the 'dark side of light' and its negative affects on plants, animals, and humans. The harmful impacts of night light on natural habitats and ecosystems have only recently been studied. In this context, an advisory report was published by the Health council of the Netherlands entitled 'Impact of outdoor lighting on man and nature' (Sixma 2000). There are many adverse effects of lighting known for animals, especially insects and birds (for a review see Schmiedel 2001, de Molenaar et al.

1997, 2000). The main effects on animals are the disturbance of biological rhythms, orientation and migration, and of basal activities like the search for nutrition, the mating behavior and the success of reproduction. Artificial night light can affect plants in many ways including altering their direction of growth, flowering times and the efficiency of photosynthetic processes.

The aim of this Chapter is to discuss the ecological impacts of light pollution in cities on insects. Insects are known for their great sensitivity to artificial light sources and in this context they can be regarded as a model group to demonstrate the negative effects of artificial lighting to nature. In addition, some thoughts of bad and good lighting design and placement are presented. Finally, our overall goal is to promote an environmentally friendly illumination system as an integral part of cities, town and villages and, finally the open landscape.

Light pollution from global to home level

The magnitude of artificial night lighting worldwide is best visualized by remote sensing techniques with the DMSP (Defence Meteorological Satellite Program) satellites applied by the Goddard Space Flight Centre of the NASA (data David Imhoff/Christopher Elvidge). The hot spots of night lighting in a continental view from the west coast of the USA to the east coast of Australia can be seen in Fig 15.1. It is evident that global city lights concentrate to the northern hemisphere of the earth. In the southern hemisphere only few big conurban areas (ie, aggregations of urban areas) are visible, e.g. Johannesburg conurban area, whereas most of the land mass belongs to the huge sparsely populated areas of South America, Africa and Australia. Further bright sources of artificial illumination can be found along many coasts of the Mediterranean, e.g. Cote d'Azur in France, Costa Brava in Spain and the coastal lines of Florida in USA. Another striking example are the big river valleys with a high population density, e.g. of the valley of the Nile which is visible as a winding light ribbon (Fig. 15.1). This kind of mapping gives a first impression of the distribution of artificial night lighting on earth.

Fig. 15.1 Global map of artificial night lighting based on remote sensing techniques with the Defence Meteorological Satellite Program - DMSP of the Goddard Space Flight Centre of the NASA (data according David Imhoff/Christopher Elvidge)

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

While these images show the direct light emitted from earth into space, Cinzano et al. (2000c) calculate the brightness of the sky background from calibrated satellite data. The upward emitted light is scattered in the atmosphere and using model calculation methods developed mainly by Garstang (1991), Cinzano et al. (2001) derived a world atlas of light pollution. They also compare the lighting level between years beginning with 1971. One of the best documented examples is that of Italy (Cinzano et al. 2000d). Cinzano and his group compared the increased level of artificial sky brightness with the level of natural sky brightness. They also compare the lighting levels in 1971 and 1998. Based on known growth rates for lighting between these periods they made a prediction for the year 2025 (Fig. 15.2). In 1971 the maximum sky brightness is about 1.1x the natural night brightness.

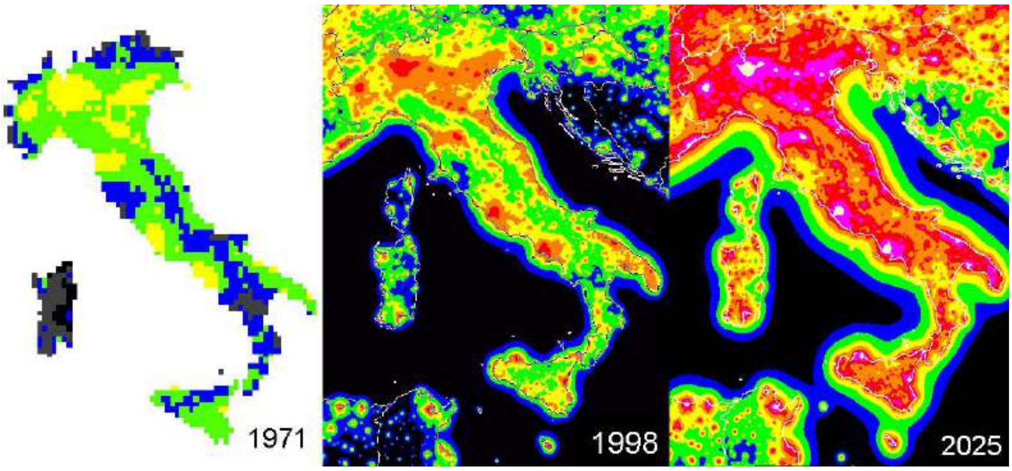

Fig. 15.2 Mapping of the artificial night lighting brightness of Italy for 1971 and 1998, and an estimated brightness for 2025 according to Cinzano et al. (2000b). The artificial sky brightness is given as increase above a reference natural sky brightness of 8.61 10^7 V phot cm^{-2} s^{-1} sr^{-1} (photons in the visual spectral range), corresponding approximately to 252 μcd/m^2 or 21.6 V mag $arcsec^{-2}$ (astronomical visual brightness (magnitude)). Key: green = 1X reference; red = 27X reference and white = >80X reference.

In 1998 the centres of conurbation of Milano and Roma are about 27 times brighter as the natural night brightness, and for the year 2025 they predict for these areas more than 100x. The same will occur in other parts of Europe, such as Belgium, the Netherlands, Great Britain and selected parts of Germany. Consequently it is possible that the natural darkness will disappear in extended areas of Europe, and also in other developed areas of the world.

An current example of a city with high levels of lighting is illustrated by a night photograph of Los Angeles from the nearby Mount Wilson Observatory (Fig. 15.3). On a smaller scale such over lighting is visible nearly in all modern cities but nowhere such an extended illuminated area can be found as in LA. City lighting planners distinguish different sorts of lighting: 1) primary lighting (public must lighting) which includes lighting for streets and public places, 2) secondary lighting (commercial must lighting) which involves lighting for each kind of advertising, public buildings and monuments, and tertiary lighting or non obligatory 'event lighting'. Flood lighting with cut-off floodlights, e.g. of sports grounds used for normal activities, should be classified as secondary lighting. But if a Mega soccer stadium is illuminated from the outside the whole night or if floodlights are visible from many kilometers we have clearly a case of tertiary lighting. Also citizens contribute to light pollution by illumination of gardens and houses for security or prestige reasons. White house fronts are true insect traps and gardens are losing their function as refugia for nature. If a residential building is illuminated by 20,000 Christmas lights it must be consequently regarded as very bad case of tertiary lighting. There is an urgent need to educate city planners, architects and the public to prevent the excessive use of bad lighting which can result in a variety of negative impacts on insects, animals and plants. It is apparent from the photograph of LA that all sorts of lighting sources contribute to the observed high overall lighting level. In a standard city it must be assumed, that the main sources of lighting are primary and secondary. Some cities though are introducing more tertiary lighting as a special local feature such as the city of Lyon (Cité lumière) in France and the city of Lüdenschein in Germany (Stadt des Lichtes). If such a tendency becomes more common practice then the projected light levels of Cinzano will become reality sooner than expected. Secondary and tertiary lighting are the main components of a new marketing strategy of cities which is called 'city marketing with light'. It is obvious, that light will be more and more used to promote the economic status of towns and cities. We regard this development for purely commercial and economic reasons as a great danger for the urban environment with potential unknown consequences. Some cities now plan to establish lighting master plans to improve their appearance and image. Principally we can support the idea of developing lighting master plans, but these plans need to include physical, social, economic and ecological considerations in order to develop truly sustainable cities.

Fig. 15.3 Artificial lighting panorama of Los Angeles February-19-2002 taken 9:00 p.m. from Mount Wilson with Nikon Coolpix 995, 100 ASA and 4 sec/F3

A strong growth of settlement areas, and consequently of artificial lighting, can be observed more and more in the rural landscapes throughout the world. Haas et al. (1997)

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

estimate that the increase of developed land in Germany is about 1 sq. km each day. The total yearly loss of the open, undeveloped landscape in Germany is about the size of Bremen County, one of the smaller Federal States in Germany. The typical European landscape shifts to a fine-meshed mosaic of settled areas, small isles of forests and open rural space. It is like an octopus that the illuminated areas penetrate deeply into formerly undeveloped and dark landscapes. A good indicator of the consequences of this development is the local sky domes and the bright horizons which are reducing the darkness and the exponential increase of streetlights. According to Kolligs (2000) the street light pool of the city of Kiel increased from 380 in 1949 to nearly 20,000 in 1998. Based on a population size of 240,000 in 1998 this equates to about 12 street lights per person. Similar trends have been reported for Great Britain (Campaign to Protect Rural England, 2003). Another example of the loss of darkness comes from the Eifel region of Germany. In the 1950’s the Hoher List Observatory at Bonn University was an excellent location for viewing the night sky, but today with the growth of nearby towns it is affected by light pollution).

Animal Behaviour Around Street Lamps and Other Light Sources

Many animals appear to be attracted by night lights. This applies primarily to flying insects, but also birds flying in swarms and those that migrate at night. Sometimes they are trapped by big light sources, particularly during periods of inclement weather. Approaching the lights of lighthouses, floodlit obstacles, ceilometers (light beams generally used at airports to determine the altitude of cloud cover), communication towers, or lighted tall buildings, they become vulnerable to collisions with the structures themselves. If collision is avoided, birds are still at risk of death or injury. Once inside a beam of light, birds are reluctant to fly out of the lighted area into the dark, and often continue to flap around in the beam of light until they drop to the ground with exhaustion. Then there is a secondary threat of predation resulting from their aggregation at lighted structures. In early August 2003, Eisenbeis (unpubl.) has observed a swarm of silver gulls orbiting permanently at the lighted top of Sydneys AMP Tower (305 m in height). It is possible that the gulls were searching for food but for whatever reason, they were attracted by the towers light space. From other observations it is known that if the light is turned off such a swarm is dispersed very fast (Cochran and Graber 1958).

Flight-to-light behavior of insects around artificial light sources disturbs the ecology of insects in many ways and can lead to high mortality (Bauer 1993, Eisenbeis 2001a). On the other hand there are many external factors, especially clear or cloudy conditions, that can also affect insect night behavior (Mikkola 1972, Blomberg et al. 1978, Kurtze 1974, Bowden 1982, Eisenbeis 2001a). Hsiao (1972) distinguished a 'near' from a 'far' phase for the approaching behavior of insects to lamps. Bowden (1982) emphasizes that most studies have focused on the 'near' phase within the zone of attraction, but 'far' effects derived from a changing background illumination, e.g. by moonlight, are very important determining how many insects are brought within the influence of a light source at all.

In this section we discuss observations of insect behavior near lamps which can be used to classify three different scenarios in which flight-to-light behavior manifests itself (Eisenbeis, 2006). In the first scenario, insects are disturbed from their normal activity by contact with an artificial illumination source such as a street lamp. For example, the scenario may begin with a moth searching for flowers. When it comes into the “zone of attraction" of a street lamp it can react in at least two different ways. The insect may fly directly onto the hot glass cover of the lamp and dies immediately. Far more frequently, the insect orbits the light endlessly until it is caught by predators or falls exhausted to the ground where it dies or is caught by other predators. Some insects are able to leave the nearest light space and to fly back seeking the shelter of the darker zone. There they rest on the ground or in the vegetation. It is assumed that the trigger for this behavior is a strong dazzling effect of the lamp. Some are able to recover and fly back to the lamp once more, and others proceed to be inactive, being exposed to an increased risk by predators. Many insects may fail to reach the light because they become dazzled and immobilized approaching the light. They may also rest on the ground or in the vegetation. Hartstack et al. (1968) have shown that more than 50% of moths approaching a light stopped their flight on the ground. We have termed all these variants of behavior the 'fixation' or 'captivity' effect, which means that insects are not able to escape from the near zone of lighting. Schacht and Witt (1986) neglect the fact that insects are actively attracted by lights themselves, for they argue that the flight to light behavior is only a blinding effect. The animals would try to flee, however, but they are no longer aware of the dark surroundings.

The second scenario describes the disturbance of long distance flights of insects by lights encountered in their flight path. The scenario begins with three insects flying through a valley along a small stream. They use natural landmarks such as trees, stars, the moon, or the profile of the horizon to have an orientation. The course of the flight is then intersected by both a street and a row of street lamps. The lights prevent the insects from following their original flyway. They fly directly to a lamp and are unable to leave the illuminated zone, suffering the same fate as described above for the first scenario. We have termed this the 'crash barrier' effect because of the interruption of insect's long distance fly way across the landscape.

The third scenario mentioned is called the 'vacuum cleaner' effect. During a summer season insects are attracted to the lights in large numbers. They are "sucked" out from their habitats as if by a vacuum, which may deplete local populations. Work by Kolligs (2001) and Scheibe (2003) suggest that outdoor lighting can significantly eliminate insects.

The magnitude of each of the effects on insect behavior depends on background illumination. Moonlight always competes with artificial light sources (Bowden, 1982, Danthanarayana 1986). Illumination from artificial lighting often creates higher illumination levels than natural night light sources such as the full moon. Kurtze (1974) measured near a parking lot at the city center of Kiel, Germany, an illumination level of 0.5 lux, about the double value of the full moon (0.3 lux), and the overall illumination by the urban sky glow of Vienna with a cloudy sky was measured at 0.178 lux (Posch, pers. comm., 2002). As yet no data are available about insect activity within settled areas which are constantly illuminated. More research is necessary to characterize such fundamental changes in the level of darkness.

Insects therefore perceive artificial lights at full moon only when they are in close proximity to the lights and consequently fewer insects are attracted to any given light. Under natural conditions, therefore, the zone of attraction changes during a lunar cycle. Additionally, changes may occur during a single night depending on weather by changing from clear to cloudy sky. Consequently the efficiency of catches around lamps depends on background illumination. On the other hand the low flight activity at artificial light sources during full moon doesn't necessarily mean that fewer insects fly on bright moon lit nights. For insects and many other animal groups it is known that the moonlight is steering their rhythmic activity (Bowden 1981, 1982). Numerous animals are active particularly at full moon or the days before or after, others behave opposite, they are active around the new moon (Endres and Schad 1997). To investigate insect's true nocturnal activity, other catch methods in addition to the light trapping have to be employed.

The Importance of Lamp Type

Several older studies reported that sodium street lamps are approached much less by insects than mercury lamps. The reason for is that the white shining mercury lamps do emit radiation both in the ultraviolet and blue green spectral range which is known to be very attractive to insects (Cleve 1967, Mikkola 1972). However, some of these examinations were not carried out under practical conditions and the data sets often were too small to statistically analyse. Therefore in 1997 a new project has been established by the nature conservation group BUND (German branch of Friends of the Earth) in cooperation with the University of Mainz and supervised by the local energy provider (Electric Power Plant of Rheinhessen – EWR) (see Eisenbeis and Hassel 2000). The aim of the project was to study insects flight to light activity around street lights during a full summer season in the rural landscape of the Rheinhessen district in southwest Germany.

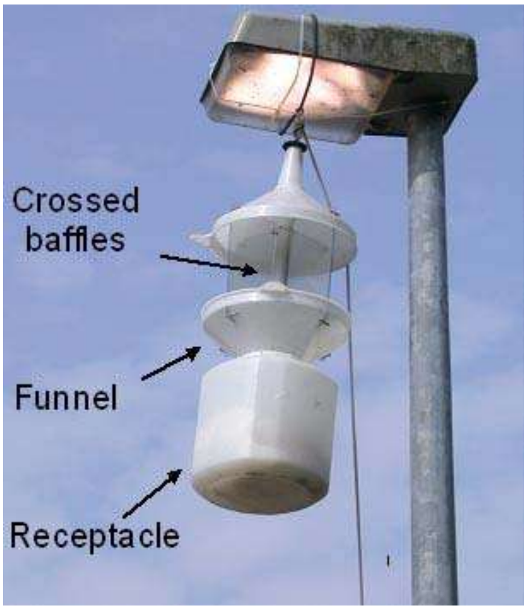

Fig. 15. 4 Insect trap exposed below a standard luminaire (street light).

The area is nearly treeless and characterized by viticulture and cultivation of cereals and sugar beet. Three sites were studied: 1) a housing area of Sulzheim village (with some garden ponds), 2) a farmhouse site (far from any water bodies), and 3) a road site near Sulzheim village. Nineteen light traps (Fig. 15.4) were mounted just below street lamp fixtures (luminaires) to capture insects. They were prepared each day before dusk, and remained exposed during the night until morning. We used two slightly modified trap models, but at any particular site, only one kind of trap was used. Insects were trapped in receptacles containing soft tissues and small vials filled with chloroform. The trapping period was June until the end of September 1997. The types of luminaires and lamps in the study were standard types commonly used for outdoor lighting in Germany. The lamps were high pressure mercury vapor (80 Watts) or high pressure sodium vapor (70 or 50 Watts).

Additionally, we tested high pressure sodium-xenon vapor lamps (80 Watts), and for special purposes some of the high pressure mercury vapor lamps were fitted with an ultraviolet absorbing filter membrane covering the glass cover of luminaires. From beginning of June to the end of September we collected 536 light trap samples containing a total of 44,210 insects, which were categorised into 12 orders. The main flight activity was in July with a maximum night catch of nearly 1700 insects in a single trap and some other catches were around 1000 insects trap^{-1} night^{-1}. Normal catch rates were less than 400 insects trap^{-1} night^{-1}. The main result is shown in Fig.15.5 giving the average catches for lamps and control in a single night. Most important are the data for high pressure mercury and high pressure sodium which are used to make the catch ratio. When we include all insects of the three study sites, we obtained a catch ratio of 0.45 which indicates that 55% less insects have been caught around high pressure sodium lamps. If we include only moths then the catch ratio is 0.25 which represents a 75% reduction in flight activity.

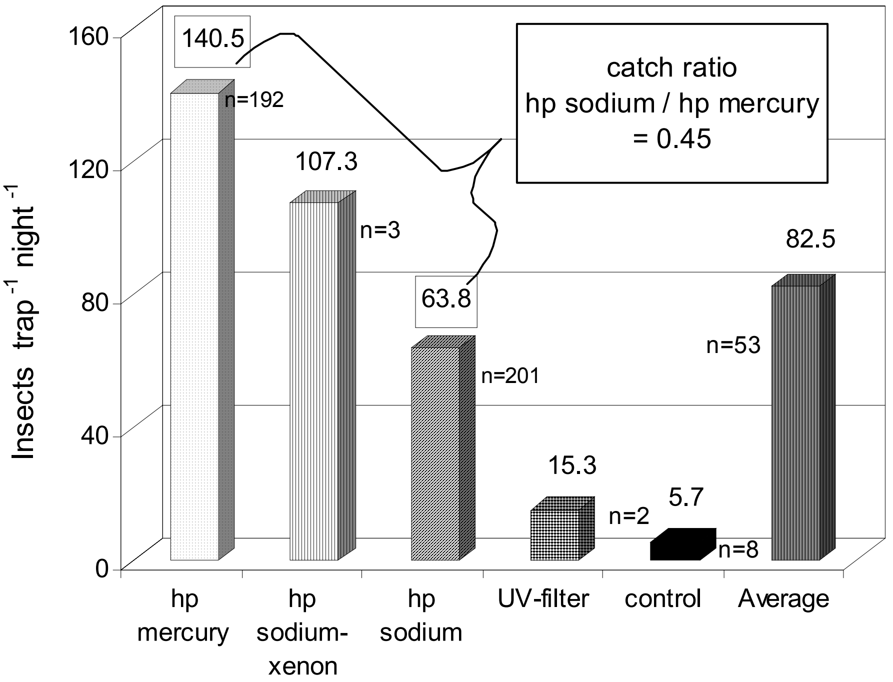

Fig. 15.5 Average insect catch rates for different lamp types in the rural landscape of Rheinhessen/Southwest Germany (according to Eisenbeis and Hassel 2000).

These data indicate that insects react differently depending on the light source. These data are only representative for the specific street light system used in our study. Besides the quality of lamps some other accessory parameters such as construction of luminaries,

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

permeability of glass covers, the height of light fixtures, and the composition of the insect fauna in the adjacent habitats determine the rates and the catch ratio. Therefore the catch ratios given above should be regarded as an estimation of the potential reduction for the flight activity of insects around street lights.

The pattern of twelve insect orders found at the three study sites is shown in Figure 15.6. The community at the road site near an open landscape with fields and vineyards was dominated by flies (Diptera, 67.6%), and the percentage of each of the other orders was lower than 10%. Insects caught at the housing area of Sulzheim village were dominated by beetles (Coleoptera, 30.7%) followed by moths (Lepidoptera, 15.9%), aphids (Aphidina 14.3%), flies (Diptera, 9.8%), caddisflies (Trichoptera, 8.1%), bugs (Heteroptera, 8.0%) and hymenopterans (Hymenoptera, 5.9%). The proportion of each of the remaining orders remained less than 5%. At the farm site three orders dominated the insect community: beetles (Coleoptera, 38.9%), moths (Lepidoptera, 19.4%) and bugs (Heteroptera, 12.8%). Each of the others contributed less than 10%. The aquatic caddisflies (Trichoptera) were found in high proportions (5.0, 8.1%) only at two sites, which were near small bodies of water such as ponds in gardens. The proportion of this order was small (0.7%) at the farmhouse site, where there were no aquatic habitats. These results indicates that each site has its specific insect community which reflects the type of vegetation and land use.

Further evaluation of the catches revealed that the ambient temperature and the moon phase are important key factors for insect’s flight to light activity (Eisenbeis 2001b). If the ambient temperature at 10 p.m. Central European daylight saving time was significantly lower than 17°C then the flight activity dropped down to zero. Reversed the normal and the peak activity occurred at temperatures significantly higher than 19°C at 10 p.m. Central European daylight saving time. Our data agree with previously published research in that the lowest flight activity around lamps occurred during the full moon, and the peak activity accumulated at and near the new moon. This can primarily be explained by the fact that there is a competition between moonlight (as a background light) and the artificial light source. Previous research also indicates that insects behave very differently depending on the moon phases, and both weather and cloudy conditions are important co-factors (Williams 1936, Kurtze 1974, Nowinszky et al. 1979, Bowden 1981, Danthanarayana 1986, Kolligs 2000).

One interesting observation often discussed in literature is that insects flight activity is different if street lamps such as high pressure mercury or high pressure sodium are used competitive (simultaneously) or non-competitive (only one type of lamp is visible for insects). According to Scheibe (1999) an increased flight activity to high pressure mercury would only occur under the condition of light competition, i.e. if high pressure mercury and high pressure sodium would be switched on together. Therefore Eisenbeis and Hassel (2000) made a separate study in which the types of lamps were changed from day to day over a period of weeks. The site for this experiment was at the farmhouse in a true dark area without any other light sources. The high pressure sodium lamps attracted

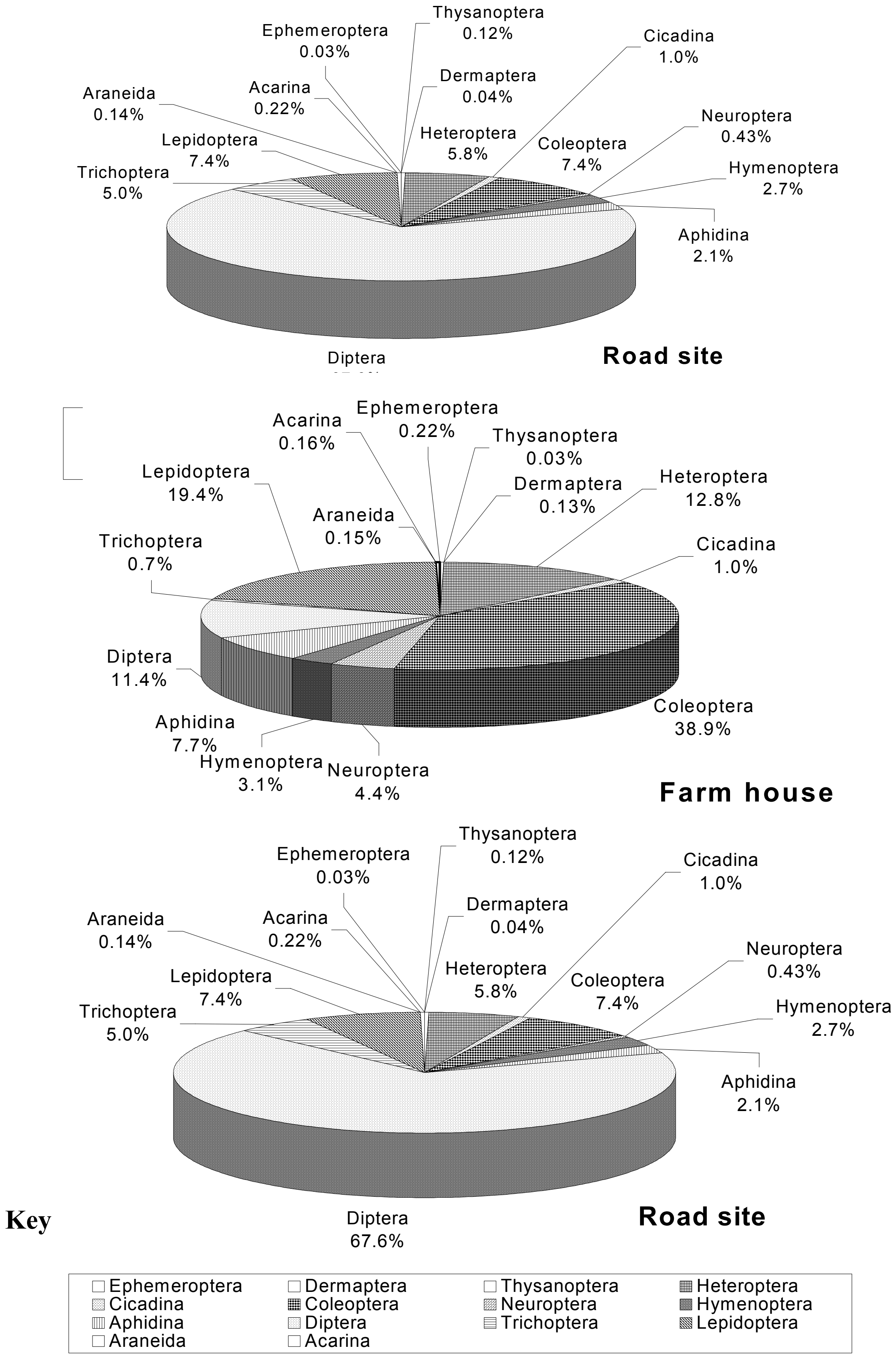

Fig. 15.6. Faunal diversity of insect groups at three sites in Germany according to Eisenbeis and Hassel 2000.

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published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

significantly less insects (1164 vs 2739; U-test, p=0.004) than high pressure mercury lamps with a catch ratio of 0.48. In addition, the average catch rate per night was higher in traps under mercury bulbs (average of 114 insects trap^{-1} night^{-1}) as opposed to those under sodium bulbs which had an average of 55 insects trap^{-1} night^{-1}. Bauer (1993) conducted a similar experiment and found that each type of lamp has its own power of attraction, although he noted that the data could not be confirmed statistically because only a few night catches were taken. To summarize, it is evident that the flight to light behavior of insects is influenced by the quality of light. High pressure mercury and high pressure sodium vapor lamps differ significantly. Comparing all known data about light trapping it is evident that insects are significantly less attracted by high pressure sodium lamps. Comparing the results of 6 German studies the insect attraction is reduced to about 57% (average catch ratio 0.43) (Fig. 15.7) for this lamp type.

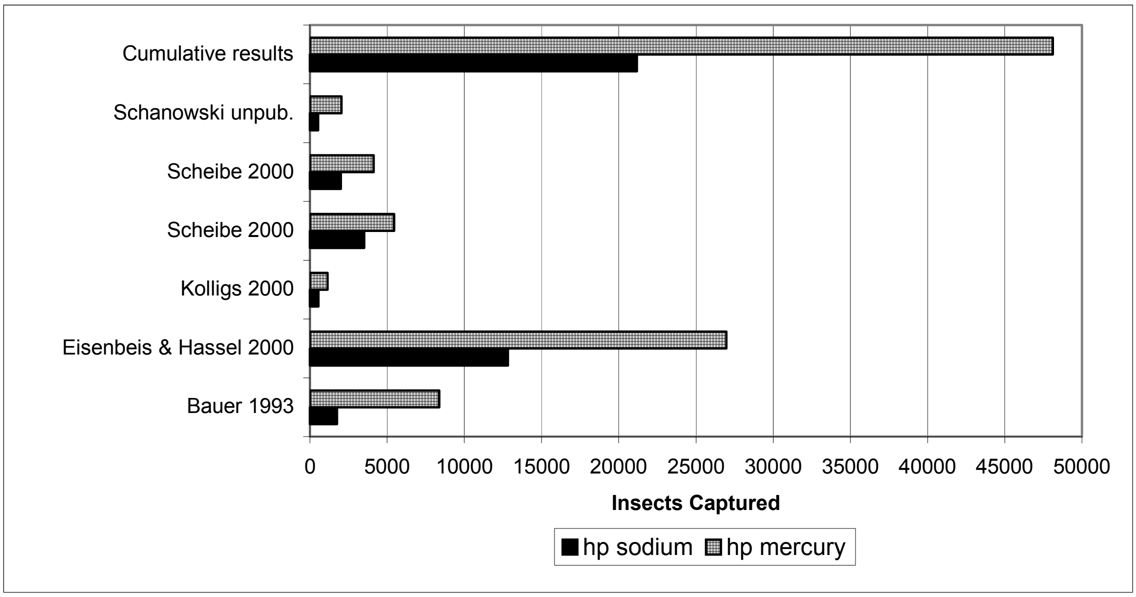

Fig. 15.7 Comparison of insect catch rates for hp sodium and hp mercury lamps based on 6 German studies.

On the other hand there are some 'losers' among insects which prefer to fly to high pressure sodium vapor lamps. In a recent study Schanowski, (unpubl.) reported 53 specimen of glow worms caught at high pressure sodium lamps and only 2 specimen were found around high pressure mercury vapor lamps. Other insect species show an indifferent behaviour, e.g. the bug *Pentatoma rufipes*, which was found in equal numbers around high pressure mercury and high pressure sodium lamps (Bauer 1993). There are also some groups of aquatic insects, especially the Chironomids, which seem to prefer the yellow light (Scheibe 2000, 2003). Therefore Scheibe (2003) recommended not to use yellow lighting near waters. In our opinion this recommendations is questionable for on the one hand the bulk of insects in Scheibe’s experimental series near a stream bank were attracted by a high pressure mercury lamp, on the other hand Scheibe never tested the yellow low pressure sodium lights. The relative high proportion of aquatic insects showing an increased preference for high pressure sodium lamps is reflected by the comparatively high catch rates found in Scheibe's investigation. Thirdly the spectrum of insects trapped in Scheibe's investigation is comparatively small, e.g. no nocturnal Lepidoptera (moths) and nearly no Coleoptera, Heteroptera (bugs), Hymenoptera and Neuroptera were found. Normally these groups are also found near waters and they should never be neglected in the context of the ecological consequences of artificial night lighting. In our opinion such an unfounded statement published by Scheibe (2003) contradicts all efforts to minimize the dying of insects around lamps used for outdoor lighting.

The Decline of Insects in Cities

In January 2003, the Wall Street Journal published an interview with Dr. Gerhard Tarmann, a Lepidopterologist from the Tyrolean State Museum Ferdinandeum at Innsbruck/Austria. The topic was the decline of butterflies in the Alps during the last decades. Dr. Tarmann is one of the founders of the Austrian Action against the ecological consequences of artificial night lighting which is called: 'Die helle Not' – freely translated 'The lighting disaster', and which has engaged the people to preserve the formerly very rich insect and butterfly fauna in Austria by the conversion of the public lamp systems to sodium lamps. In Tarmann's opinion the biggest impact on the butterfly fauna in Innsbruck were the Winter Olympics in 1964. The spectacular hyper lighting of bridges and walkways was succeeded by a strong devastation of city's butterflies. Within just three years the rich fauna disappeared to a minimum level. According to Tarmann the same sequence has been observed in remote valleys of the Alps. There the meadows contained a remarkable diverse fauna with hundreds of butterfly species, but after the opening of these valleys for tourists and the implementation of a far lighting infrastructure such as petrol stations, billboards, hotels and restaurants etc., the rich fauna significantly declined within few years of the installation of the lights.

Similar observations have been described in the older entomological literature. Malicky (1965) reported from his observations around newly built and strongly illuminated fuel stations that there was a high initial flight activity of insects during the first two years, which then quickly faded away. The same observation was made by Daniel (1950) around newly installed light points close to nature. In our opinion such personal observations must be considered as a serious indicator of a significant change of a local insect population caused by the 'vacuum cleaner' effect mentioned above.
Entomologists from the second half of the last century frequently reported extremely large light trap catches of many thousand insects in a night, but more recent catches have been much smaller. For example, Robinson and Robinson (1950) caught more than 50,000 moths in a single trap (equipped with a 125 Watts mercury lamp) in the night of August 20/21, 1949. Worth and Muller (1979) caught 50,000 moths with a single 15 W black light trap from May 2 to September 12, 1978 on an isolated farm site not close to competing lights. Eisenbeis and Hassel (2000) caught only 4,338 moths with 192 light trap samples at 80 Watts high pressure mercury lamps from May 29 to September 29, 1997, which corresponds to a rate of 22.6 moths trap^{-1} night^{-1}. Of course such simple enumeration (the sites, the lamps and the traps were different) does not allow for statistical evaluation, but these data strongly suggest a progressive decline in insect populations.

Eisenbeis (2001a) has calculated that about one third of insects approaching a street lamp are caught by a light trap. Based on Bauer's observations (Bauer 1993) he estimated a

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

death rate in the same order of magnitude. Thus, if about 450 insects approached a high pressure mercury street light during a night, we would expect about 150 would perish. As yet there are not quantitative data on the number of animals which become inactive in the nearer surroundings of a street light that are ultimately lost by secondary predation. There are estimated to be 8.2 million street lights in Germany and based on these early data on insect catches the loss of insects due to the lights throughout the Country could be in the order of 10^{11} during a summer season.

Heath (1974) describes in his report “A Century of Change in the Lepidoptera” some profound changes in Macrolepidoptera in Great Britain, which mainly can be attributed to changes in land use. Most changes involved extinction, declines, or restriction of species to few local spots, but there were some examples of colonization of new species and extension of existing ranges. Heath (1974) notes the main causes for the change of insect habitats are: 1) clear cutting of many acres of deciduous forests and their replacement with coniferous plantations, 2) conversion of heath lands and forests to agricultural use, 3) the agricultural revolution and changes in woodland management, 4) use of chemicals such as herbicides and insecticides in the environment, 5) urban sprawl, 6) construction of motorways, 7) human recreational pressure on the countryside, and 8) periods of climatic change. There was no discussion at that time the report was written of light pollution as a serious new hazard for insects.

Taylor et al. (1978) reported on the Rothamsted Agricultural Research Centre’s insect survey with relation to the urbanization of land in Great Britain, which was based on a light-trapping network. The industrial region of middle England and the London area were clearly identified on faunal maps as islands of low diversity and density. The authors used light trapping as their basic method, but they offered no comments about the possible role of increasing artificial lighting for the decline in diversity.

Bauer (1993) investigated the insect activity of three housing areas normally illuminated by street lamps and a semi-natural habitat that was not regularly illuminated before the study. He used light traps exposed in the light space of street lamps in the suburban area of Konstanz, a mid-sized town in Southern Germany. In the illuminated areas, the catch rates (5, 29, and 47 insects per trap per night in city centre and two housing areas) were about 2–5 times lower than in the semi-natural non-illuminated habitat (143 insects per trap per night), but altogether the results from the illuminated areas were heterogeneous. Moths were the dominant species and showed an average proportion of 14.9% for the illuminated sites and 34% at the non-illuminated site, but the differences among illuminated sites was high (2.7, 11.6 and 30.5%). For this reason, such data should only be regarded as a first quantitative monitoring of changes in the insect population.
Scheibe (1999) used suction trapping to study night flying insects along a wooded stream bank in a low mountain range of the Taunus area in Germany far from any artificial lighting. During eight nights he caught 2,600 insects per trap night with maximum catches of 11,600 and 5,100 insects. These data of flight activity outnumber all other data recently reported from illuminated areas in Germany. The results must be regarded as further evidence that the dark zones in the landscape have a much richer insect fauna than do lighted zones.

In his Ph.D. thesis, Scheibe (2000) tried to determine the capacity of such a trap to catch insects flying within the zone of attraction of a single street lamp. He measured the number of all aquatic insects (e.g. mayflies, caddis flies, dipterans, etc.) emerging from a

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small stream in the low mountain range of the Taunus area, standardized as “number of emerging insects” per 72 h per 1 m length of the stream bank. During the night following such a test of the emergence, he determined the number of aquatic insects flying to a street lamp positioned near the bank. He found that different taxa of aquatic insects reacted differently, but in many instances light catches significantly outnumbered the number of emerging insects. For example, the number of caddis flies caught in an August night by the lamp was approximately the same as the number of caddis flies emerging along 200 m of the bank. Therefore it can be concluded that the lamp has a long distance effect for light susceptible insect species and that by far more insects are attracted than would potentially be found in the are immediately surrounding a lamp. By extrapolation, if there were a row of street lamps along a stream, a species could become extinct locally in short time, which can be explained again by the "vacuum cleaner" effect of street lamps.

Another example of attraction of large numbers of insects around lamps is reported from mayflies along riversides and bridges. The swarming of the species *Ephoron virgo* (or other species) is described as summer snow drifting (Kureck 1996, Tobias 1996) because the insects are attracted in such masses that the ground near lights is covered by a centimeter thick layer of these insects. An estimated 1.5 million individuals have been recorded in one night on an illuminated road surface of a bridge. It is part of the fatal destiny of the animals that each female loses her egg cluster upon first contact with an object. Eggs that are not released into water must be regarded as a loss for the population, with potentially significant effects on the local population.

As discussed by Frank (1988), rare species are vulnerable to effects of artificial lighting. Kolligs (2000) reported capturing endangered “Red List” species as single individuals in a large study of assimilation lighting at a greenhouse. Such species can be regarded as endangered by artificial lighting. K-selected species with specialized habitat requirements and stable population sizes are most likely to be disrupted by artificial lighting (see also Eisenbeis 2001a,b). Reichholf (1989) research on moth populations revealed steep urban gradient between the outskirts with gardens close to nature (650 species), intermediate parks (small, 330 species), and city central (housing area, reduced density, 120 species).
This growing body of evidence strongly suggest that the diversity of insects has declined dramatically in Germany and England during the last decades. The implementation of insect friendly lighting systems may reduce the negative impacts on insects, but if the absolute lighting levels continue to increase then our cities will develop to nearly insect (and perhaps bird) free ghost towns far away from the formerly rich animal life.

Street lighting in Germany

Riegel (1973) and Sullivan (1984) estimated the growth of emitted light from electric power consumption for road lighting in the USA. While the power consumption increases linearly, the emission of light increased exponentially at an annual rate of 23 percent between 1967 and 1970. This is due to the use of more efficient lamps changing from incandescent to mercury high pressure and even sodium high pressure lamps. We have tried to estimate the light emission for Germany (Hänel, 2001). Therefore we compared the percentage increase of electric power consumption for the city of Osnabrück, for which we had detailed data about the road lighting, with Germany and the USA (Fig. 8).

published in : McDonnell, M. J.;, Hahs, A. H., Breuste, J. H.: Ecology of Cities and Towns, Cambridge University Press, Cambridge 2009, p. 243-263

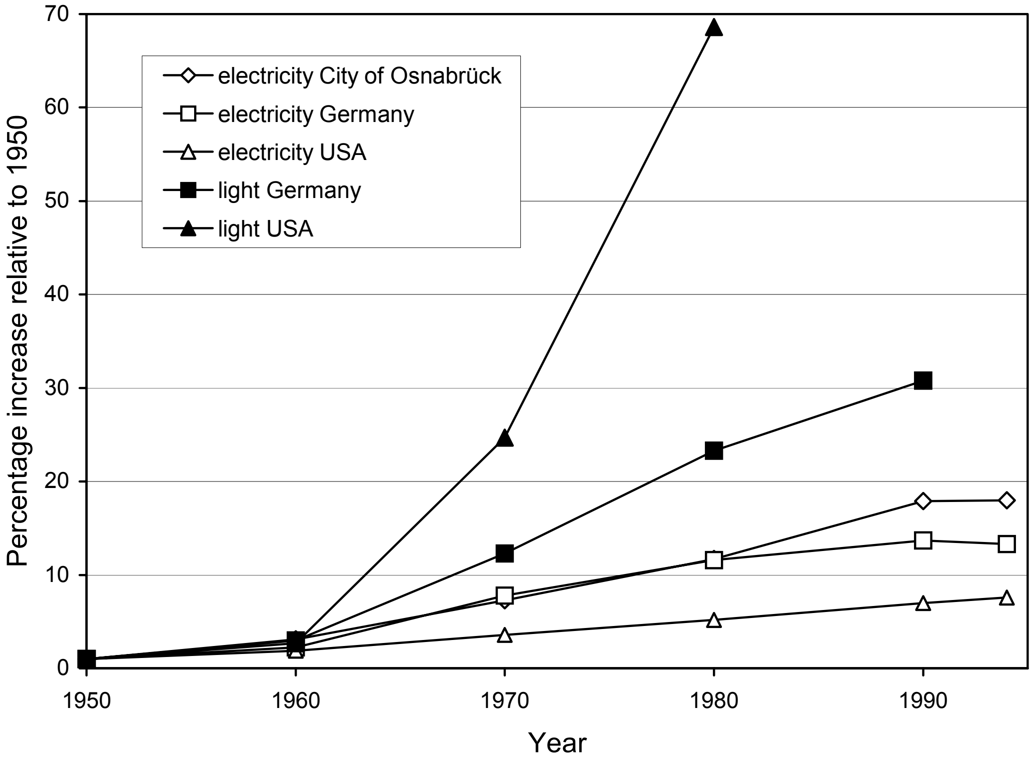

Fig. 8 The growth of electric power consumption and of light emission in the City of Osnabrück/Germany, Germany and the USA.

Assuming also a gradual change to sodium high pressure lamps we estimate a growth rate for the light emission of 7 percent annually between 1980 and 1990 and even less since then. These values provide an estimate of the increase of light. The amount of light emitted to the sky which ultimately increases the artificial sky brightness can not be estimated because we lack data on the numbers and manner of lamp housings. Nevertheless these indirectly derived values can be compared to the measurements of sky brightness in Italy which increased by about 10 percent annually between 1960 and 1995 (Cinzano 2000a). The growth of light pollution in Europe is less than in the USA most likely due to a variety of reasons. In addition, in Europe road lighting is regulated by norms, which require only minimal luminance values at the road surface. Germany also has a regulation that delimitates light emissions at 1-2 Lux.

Good Lighting and steps for the protection of the dark sky

In Europe, light pollution regulations have been issued in the provinces of Catalunya and Tenerife in Spain, Lombardia and others in Italy and in the Czech Republic for the first time on a nationwide level. These regulations mainly forbid any use of upward light and demand a cautious use of light. In addition, some cities in the USA have developed regulations for the use of artificial light during the night. Table 15.1 provides a list~~s~~ of suggested measures that could reduce the harmful impacts of night lighting on insects.

Table 15.1. Suggested methods to reduce the harmful impacts of night lighting on insects.

1. Use light only when it is necessary and use only as dim a light as possible.
2. Direct illumination of the sky should only be allowed if absolutely necessary, searchlights for commercial purposes must be forbidden.
3. Only full cut-off luminaries help to reduce the light glow domes over cities. The light emitted in horizontal planes contributes even more to these light domes than the direct upward light (Cinzano 2000b). Even luminaries installed with small inclinations to illuminate the opposite road side should be avoided and when possible they should be installed horizontally.
4. There is some research (Schanowski and Späth 1994) that indicates sodium low pressure lamps attract fewer insects. Therefore these lamps should be used when colour vision is not important and on streets in or close to rural landscapes. Colour perception with these lights is reduced due to the monochromatic sodium light (589 nm wavelength). But already small amounts of broad-spectrum lights from house lighting or automobile headlights can render essentially normal colour perception (Luginbuhl, 2001).
5. Elsewhere sodium high pressure lamps should be used while mercury pressure should not be used.
6. Road lighting should be dimmed or even switched off, when road use is negligible (eg.11pm. – 5 am.).

There are typically economic reasons proposed as to why measures to reduce light pollution are not feasible. But, there are examples such as the western Canary Islands (Tenerife and La Palma) where strict regulations allow only full cut-off luminaries (lights) in order to maintain a dark sky for their world famous astronomical observatories. Despite these regulations, tourists continue to visit the islands and the economy flourishes (Benn and Ellison, 1998).

In addition to regulations, it is important to develop programs that inform the public about the problem of light pollution. Some positive examples are brochures like “Die helle Not” in Austria (Tiroler Landesumweltanwalt, 2003) or activities like “Wieviele Sterne sehen wir noch?” in Austia (Posch et al., 2002) or “Night blight!” in England, (Campaign to Protect Rural England, 2003). Due to the growing worldwide concern about light pollution, in 1988 the International Dark Sky Association was founded to educate people about the problem and to develop methodologies to mitigate the effects of high levels of night lighting.

As a result of the UN Conference on Environment and Development - Rio de Janeiro, 1992 - a global programme for sustainable development was brought into being, the Agenda 21. In section II the main topics are the management of earth's resources, the protection of major biomes and conservation of biodiversity. It is recommended that all energy sources will need to be used in ways that respect the atmosphere, human health and the environment as a whole. As a consequence of Rio a 'Local Agenda 21' was established in Germany. It is used as a guideline for cities and regions to realise the ideas and recommendations of the global Agenda 21 on a local level. But unfortunately there is no mention of any link to the fact that light is wasted in huge dimensions dissipating energy and changing the night environment. In our opinion over lighting is recognised as modern component of atmospheric pollution. Therefore we recommend that the environmentally friendly use of artificial lighting should be a fixed part of strategies to promote sustainable development at all municipal levels. It contributes both to saving energy and conserves the diversity of organisms, especially of animals.

Summary

Artificial night lighting is increasingly affecting nature and ecosystems. Many groups of animals are affected directly or indirectly, especially birds and nocturnal insects. Our study in a rural landscape in Germany clearly demonstrates the importance of light quality for street lighting. The insect flight activity around high pressure sodium lights was reduced more than half in contrast to high pressure mercury lights. In the spirit of the comparative ecology theme of this book, there are numerous opportunities in the future for comparative studies of the affects of light pollution in cities on insects and other organisms because they all have very similar lighting fixtures, design and placement.

Literature

Bauer, R. (1993). Untersuchung zur Anlockung von nachtaktiven Insekten durch Beleuchtungseinrichtungen. Diploma thesis, Department of Biology, University of Konstanz, Germany.

Benn, C. R., Ellison, S. L. (1998). La Palma night-sky brightness, Isaac Newton Group (ING) La Palma Technical Note 115, La Palma. (http://www.ing.iac.es/Astronomy/observing/manuals/ps/tech_notes/tn115.ps.gz)

Blomberg, O., Itamies, J. and Kuusela, K. (1978). The influence of weather factors on insect catches in traps equipped with different lamps in northern Finland. *Annales Entomologici Fennici*, **44**, 56–62.

Bowden, J. 1981. The relationship between light- and suction-trap catches of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), and the adjustment of light-trap catches to allow for variation in moonlight. Bulletin of Entomological Research. 71: 621–629.

Bowden, J. (1982). An analysis of factors affecting catches of insects in light-traps. *Bulletin of Entomological Research*, **72**, 535–556.

Campaign to Protect Rural England, (2003). Night blight!, pp.1-32, London (http://www.cpre.org.uk/campaigns/light-pollution/index.htm)

Cinzano, P. (ed.). (2000). *Measuring and Modelling Light Pollution*. Memorie della Societa Astronomica Italiana Vol. 71, pp. 279, Italy.

Cinzano, P. (2000a). The Growth of Light Pollution in North-eastern Italy from 1960-1995. In *Measuring and Modelling Light Pollution*, ed. P. Cinzano, Memorie della Societa Astronomica Italiana,**71**, 159-165.

Cinzano, P. (2000b). The Propagation of Light Pollution in diffusely urbanised Areas. In *Measuring and Modelling Light Pollution*, ed. P. Cinzano, pp. 113-130. Memorie della Societa Astronomica Italiana, **71**, 93-112.

Cinzano, P., Falchi, F., Elvidge, C. D. and Baugh, K.E. (2000c). The artifical night sky brightness from DMSP satellite Operational Linescan System measurments. *Monthly Notices of the Royal Astronomical Society*, **318**, 641-657.

Cinzano, P. (ed.). (2002). *Light Pollution and the Protection of the Night Environment*. Proceedings of the Conference Light pollution and the Protection of the Night

Environment Venice 2002, Light Pollution and Science Technology Institute, pp. 356, Thiene, Italy.

Cinzano, P., Falchi, F., Elvidge, C. D., Baugh, K.E. (2000d): Mapping the Artificial Sky Brightness in Europe from DMSP Satellite Measurements: the Situation of the Night Sky in Italy in the Last Quarter of Century. Memorie della Societa Astronomica Italiana. **71**, p. 1194-1157.

Cinzano, P., Falchi, P. and C.D. Elvidge. (2001). The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, **328**, 689–707.

Cleve, K. (1967). Das spektrale Wahrnehmungsvermögen nachts fliegender Schmetterlinge. Nachrichtenblatt der Bayerischen Entomologen 16. Jg., 33-53.

Cochran, W. W. and Graber, R. R. (1958). Attraction of nocturnal migrants by lights on a television tower. *Wilson Bulletin*, **70**, 378-380.

Cohen, R.J. and Sullivan, W. T. (eds.) (2001). *Preserving the astronomical sky.* Proceedings of the 196th Symposium of the International Astronomical Union in conjunction with UNISPACE III at Vienna, Austria, July 12-16, 1999. ASP Conference Series, San Francisco.

Danthanarayana, W. (1986). Lunar periodicty of insect flight and migration. In: Danthanarayana, W. (ed.): Insect Flight: Dispersal and Migration pp. 88–119, Springer, Berlin, Heidelberg.

Eisenbeis, G., (in press). Artificial night lighting and insects: Insects at street lamps in a rural setting in Germany. In *Ecological consequences of artificial night lighting*, Rich, C. and Longcore, T. (eds.), Island Press, Covelo, California.

Eisenbeis, G. and Hassel, F. (2000). Zur Anziehung nachtaktiver Insekten durch Straßenlaternen – eine Studie kommunaler Beleuchtungseinrichtungen in der Agrarlandschaft Rheinhessens. *Natur und Landschaft 75. Jg.*, **4/2000**, 145–156.

Eisenbeis, G. (2001a). Künstliches Licht und Lichtverschmutzung – Eine Gefahr für die Diversität der Insekten? *Verhandlungen Westdeutscher Entomologen Tag 2000, Löbbecke-Museum*, pp. 31–50, Düsseldorf.

Eisenbeis, G. (2001b). Künstliches Licht und Insekten: eine vergleichende Studie in Rheinhessen. *Schriftenreihe für Landschaftspflege und Naturschutz*, **67**, 75–100.

Endres, K.-P. and Schad, W. (1997). *Biologie des Mondes – Mondperiodik und Lebensrhythmen*. pp. 308, S. Hirzel, Stuttgart, Leipzig.

Frank, K.D. (1988). Impact of outdoor lighting on moths: an assessment. *Journal of the Lepidopterists' Society*, **42**, 63–93.

Garstang, R.H. (1991). Dust and light pollution, *Publ. Astron. Soc. Pacific*, **103**, 1109-1116.

Haas, R., Kraeling, W. and Boulois, R. (1997). Lichtkontamination. – *UWSF – Zeitschrift für Umweltchemie Ökotoxikologie*, **9**, 24.

Hänel, A. (2001). The situation of light pollution in Germany. In: *Preserving the Astronomical Sky*. Cohen, R. J. and W.T. Sullivan (eds.). Proceedings of the 196th Symposium of the International Astronomical Union in conjunction with UNISPACE III at Vienna, Austria, July 12-16, 1999., pp. 142–146, ASP Conference Series, San Francisco.

Hartstack, A.W., Hollingsworth, J.P. and D.A. Lindquist. 1968. A technique for measuring trapping efficiency of electric insect traps. Journal of Economic Entomology 61, 546–552.

Heath, J. (1974). A century of change in the Lepidoptera. In *The Changing Flora and Fauna of Britain*, Hawksworth D.L. (ed.), *Systematics Association Special Volume*, **6**, 275-292.

Hsiao, H.S. (1972). *Attraction of moths to light and to infrared radiation*. pp. 89, San Francisco Press, San Francisco.

Isobe, S. and Hirayama, T. (eds.), (1998). Preserving the Astronomical Windows, ASP Conference Series, Vol. 139, San Francisco

Klyuchko, Z.F. (1957). On the flight of noctuids (Lepidoptera, Noctuidae) towards different light sources. *Doklady Biological Sciences : Proceedings of the Academy of Sciences of the USSR, Biological Sciences Sections*, **117**, 951–954.

Kolligs, D. (2000). Ökologische Auswirkungen künstlicher Lichtquellen auf nachtaktive Insekten, insbesondere Schmetterlinge (Lepidoptera). *Faunistisch-Ökologische Mitteilungen, Suppl.*, **28**, 1–136.

Kureck, A. (1996). Das Massenschwärmen der Eintagsfliegen am Rhein. Zur Rückkehr von *Ephoron virgo* (Olivier 1791). *Natur und Landschaft 67. Jg.*, **9/1992**, 407–409.

Kurtze, W. (1974). Synökologische und experimentelle Untersuchungen zur Nachtaktivität von Insekten. *Zoologische Jahrbücher Systematik*, **101**, 297–344.

Luginbuhl, C. B. 2001. Why Astronomy needs Low-Pressure Sodium Lamps in: Cohen, R.J. and Sullivan, W. T. 2001., p. 81-86

Malicky, H. (1965). Freilandversuche an Lepidopterenpopulationen mit Hilfe der Jermyschen Lichtfalle, mit Diskussion biozönologischer Gesichtspunkte. *Zeitschrift für Angewandte Entomologie*, **56**, 358–377.

Mikkola, K. (1972). Behavioural and electrophysiological responses of night-flying insects, especially Lepidoptera, to near-ultraviolet and visble light. *Annales Zoologici Fennici*, **9**, 225-254.

Mizon, B. (2002). *Light pollution - Responses and Remedies*. Patrick Moore's Practical Astronomy Series, pp. 216, Springer, London.

Molenaar, J.G. de, Jonkers, D.A. and R.J.H.G. Henkens. 1997. Wegverlichting en Natuur. *DWW series Ontsnipperingsreeks deel Ministerie van Verkeer en Waterstaat* (ed.), **34**, pp. 292, Delft, Netherlands.

Molenaar, J.G. de, Jonkers, D.A., and M.E. Sanders. (2000). Road illumination and nature III Local influence of road lights on a black-tailed gowit (*Limosa l. limosa*) population. *DWW series Ontsnipperingsreeks deel Ministerie van Verkeer en Waterstaat* (ed.), **38A***,* 85 pp., Delft, Netherlands.

Nowinszky, L., Szabó, S., Tóth, G., Ekk, I. and Kiss, M. (1979). The effect of the moon phases and of the intensity of polarized moonlight on the light-trap catches. *Zeitschrift für Angewandte Entomologie*, **88**, 337–353.

Posch, T., Hron, J. and Wuchterl, G. (2002). Wieviele Sterne sehen wir noch? *Sterne und Weltraum*, **41**, 62-63 (www.astro.uni.vie.ac.at/~scw)

Reichholf, J. (1989). *Siedlungsraum – Zur Ökologie von Dorf, Stadt und Straße*. Steinbachs Biotopführer, 222 pp., Mosaik, München.

Riegel, K.W. (1973). Light Pollution – Outdoor lighting is a growing threat to astronomy. *Science*, **179**, 1285–1291.

Robinson, H.S. and Robinson, P.J.M. (1950). Some notes on the observed behaviour of Lepidoptera in flight in the vicinity of light-sources together with a description of a light-trap designed to take entomological samples. *Entomologist's Gazette*, **1**, 3–20.

Schacht, W. and Witt, T. (1986). Warum nachtaktive Insekten künstliche Lichtquellen anfliegen (Insecta). *Zeitschrift für Entomologie*, 7, 121-128.

Schanowski, A. and Späth, V. (1994). *Überbelichtet – Vorschläge für eine umweltfreundliche Außenbeleuchtung*. Naturschutzbund Deutschland Kornwestheim (ed.), Kornwestheim.

Scheibe, M.A. (1999). Über die Attraktivität von Straßenbeleuchtungen auf Insekten aus nahegelegenen Gewässern unter Berücksichtigung unterschiedlicher UV-Emission der Lampen. *Natur und Landschaft 74. Jg.*, **4**, 144–146.

Scheibe, M.A. (2000). *Quantitative Aspekte der Anziehungskraft von Straßenbeleuchtungen auf die Emergenz aus nahegelegenen Gewässern (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae, Chironomidae, Empididae) unter Berücksichtigung der spektralen Emission verschiedener Lichtquellen*. Dissertation (PhD thesis), Fachbereich Biologie, Institut für Zoologie, Universität Mainz.

Scheibe, M. (2003). Über den Einfluss von Straßenbeleuchtung auf aquatische Insekten (Ephemeroptera, Plecoptera, Trichoptera, Diptera: Simuliidae, Chironomidae, Empididae). *Natur und Landschaft 78. Jg.*, **6**, 264-267.

Schmiedel, J. (2001). Auswirkungen von künstlichen Lichtquellen auf die Tierwelt – ein Überblick. *Schriftenreihe Landschaftspflege und Naturschutz*, **67**, 19-51.

Sixma, J.J. (2000). *Impact of outdoor lighting on man and nature*. Advisory Report of the Dutch Health Council, 46 pp., The Hague, Netherlands.

Steck, B. (1997). *Zur Einwirkung von Außenbeleuchtungsanlagen auf nachtaktive Inse*kten. In Deutsche Lichttechnische Gesellschaft (ed.), *LiTG-Publikationen*, **15**, 1–24, Berlin.

Sullivan, W. (1984). Our Endangered Night Sky. *Sky and Telescope*, **67**, 412

Taylor, L.R., French, R.A. and Woiwod, I.P. (1978). The Rothamsted insect survey and the urbanization of land in Great Britain. In *Perspectives in Urban Entomology*, Frankie, G.W. and Koehler, C.S. (eds.), pp. 31–65, Academic Press, London.

Tobias, W. (1996). Sommernächtliches 'Schneetreiben' am Main. Zum Phänomen des Massenfluges von Eintagsfliegen. *Natur und Museum (Frankfurt/M.)*, **2/1996**, 37–54.

Williams, C.B. 1936. The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap. *Philosophical Transactions of the Royal Society of London, Series B*, **226**, 357–389.

Worth, C.B. and Muller, J. (1979). Captures of large moths by an ultraviolet light trap. *Journal of the Lepidopterists' Society*, **33**, 261–264.

BIOLOGICAL
REVIEWS

Cambridge
Philosophical Society

Folio N° 949

Biol. Rev. (2013), **88**, pp. 912–927.
doi: 10.1111/brv.12036

The ecological impacts of nighttime light pollution: a mechanistic appraisal

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ABSTRACT

The ecological impacts of nighttime light pollution have been a longstanding source of concern, accentuated by realized and projected growth in electrical lighting. As human communities and lighting technologies develop, artificial light increasingly modifies natural light regimes by encroaching on dark refuges in space, in time, and across wavelengths. A wide variety of ecological implications of artificial light have been identified. However, the primary research to date is largely focused on the disruptive influence of nighttime light on higher vertebrates, and while comprehensive reviews have been compiled along taxonomic lines and within specific research domains, the subject is in need of synthesis within a common mechanistic framework. Here we propose such a framework that focuses on the cross-factoring of the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the ways in which light influences biological systems, particularly the distinction between light as a resource and light as an information source. We review the evidence for each of the combinations of this cross-factoring. As artificial lighting alters natural patterns of light in space, time and across wavelengths, natural patterns of resource use and information flows may be disrupted, with downstream effects to the structure and function of ecosystems. This review highlights: (*i*) the potential influence of nighttime lighting at all levels of biological organisation (from cell to ecosystem); (*ii*) the significant impact that even low levels of nighttime light pollution can have; and (*iii*) the existence of major research gaps, particularly in terms of the impacts of light at population and ecosystem levels, identification of intensity thresholds, and the spatial extent of impacts in the vicinity of artificial lights.

Key words: dark, information, light, moonlight, night, pollution, resources, rhythms, time.

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I. INTRODUCTION

It has been argued that the biological world is organized largely by light (Ragni & D'Alcalà, 2004; Foster & Roenneberg, 2008; Bradshaw & Holzapfel, 2010). The rotation of the Earth partitions time into a regular cycle of day and night (giving variation in light intensity of approximately 10 orders of magnitude; Table 1), while its orbital motion and the tilt of its axis cause seasonal variation in the length of time that is spent under conditions of light and darkness in each cycle. These major changes are overlain by more local variation caused by weather conditions, and the effect of the monthly lunar cycle on nighttime light. However, for any given latitude the light regime has been consistent for extremely long periods of geological time, providing a rather invariant context, and a very reliable set of potential environmental cues, against which ecological and evolutionary processes have played out.

Artificial lighting is a common characteristic of human settlement and transport networks (Boyce, 2003; Schreuder, 2010). The spread of electric lighting in particular has provided a major perturbation to natural light regimes, and in consequence arguably a rather novel environmental pressure, disrupting natural cycles of light and darkness (Verheijen, 1958, 1985; Outen, 1998; Health Council of the Netherlands, 2000; Longcore & Rich, 2004; Rich & Longcore, 2006*a*; Navara & Nelson, 2007; Hölker *et al.*, 2010*a*,*b*; Bruce-White & Shardlow, 2011; Perkin *et al.*, 2011). Changes in light regime can be characterized as changes in the spatial distribution, the timing and the spectral composition of artificial light sources. As human communities and lighting technologies develop, artificial light increasingly encroaches on dark refuges in space, in time, and across wavelengths.

(1) Space

Urbanisation, population growth and economic development have led to rapid, and ongoing, increases in the density and distribution of artificial lighting over recent decades (Fig. 1A; Riegel, 1973; Holden, 1992; Cinzano, Falchi & Elvidge, 2001; Cinzano, 2003; Hölker *et al.*, 2010*a*). A wide variety of lighting devices contribute, including public street lighting, advertising lighting, architectural lighting, domestic lighting and vehicle lighting. The highest intensities of artificial light are experienced in the close vicinity (within metres to tens of metres) of light sources. Within illuminated urban and suburban areas, direct light from street lighting, domestic and commercial sources, and light reflected from the surrounding surfaces, can create a highly patchy light environment. Over much larger areas surrounding towns and cities, a somewhat lower intensity of diffuse background light derives from 'sky glow', artificial light scattered in the lower atmosphere. Under cloudy conditions in urban areas, the sky glow effect has been shown to be of an equivalent or greater magnitude than high-elevation summer moonlight (Kyba *et al.*, 2011*a*); it has been estimated that around 23% of the United States, 37% of the European Union, 54% of Japan and 5% of the land surface area of the world regularly exceeds a similar threshold (Cinzano *et al.*, 2001).

Table 1. Variation in levels of illuminance. Although widely used, note that lux measurement places emphasis on brightness as perceived by human vision

	Lux
Full sunlight	103000
Partly sunny	50000
Cloudy day	1000–10000
Full moon under clear conditions	0.1–0.3
Quarter moon	0.01–0.03
Clear starry night	0.001
Overcast night sky	0.00003–0.0001
Operating table	18000
Bright office	400–600
Most homes	100–300
Main road street lighting (average street level illuminance)	15
Lighted parking lot	10
Residential side street (average street level illuminance)	5
Urban skyglow	0.15

From data in British Standards Institute (2003), Rich & Longcore (2006*b*), and Dick (2011).

(2) Time

Early municipal lighting systems often functioned only on moonless nights or prior to midnight (Jakle, 2001). Throughout the 20th century, the manufacture of cheaper lighting technologies led to more persistent street lighting in developed cities, typically from dusk until dawn, 365 days a year. Lights in commercial, industrial and residential premises may be kept permanently on or switched on intermittently during the hours of darkness for reasons of security or convenience, and amenity lighting, for example floodlighting of sports pitches, is often concentrated in the hours following sunset, leading to a varying light environment throughout the night (Fig. 1B). Economic pressures, limited energy supply and/or efforts to minimize energy consumption and carbon emissions have resulted in constraints on the timing of nighttime lighting in many regions of the world, and, led by developments in technology allowing automated timing and control, dimming or switching off of municipal lighting for periods during the night is being adopted in some developed countries (e.g. Lockwood, 2011).

(3) Spectral composition

Different forms of artificial lighting have unique spectral signatures, each emitting light at varying intensities over a distinctive range of wavelengths (Fig. 1C; Thorington, 1985; Boyce, 2003; Elvidge *et al.*, 2010; van Langevelde *et al.*, 2011). These spectral signatures differ from those of natural

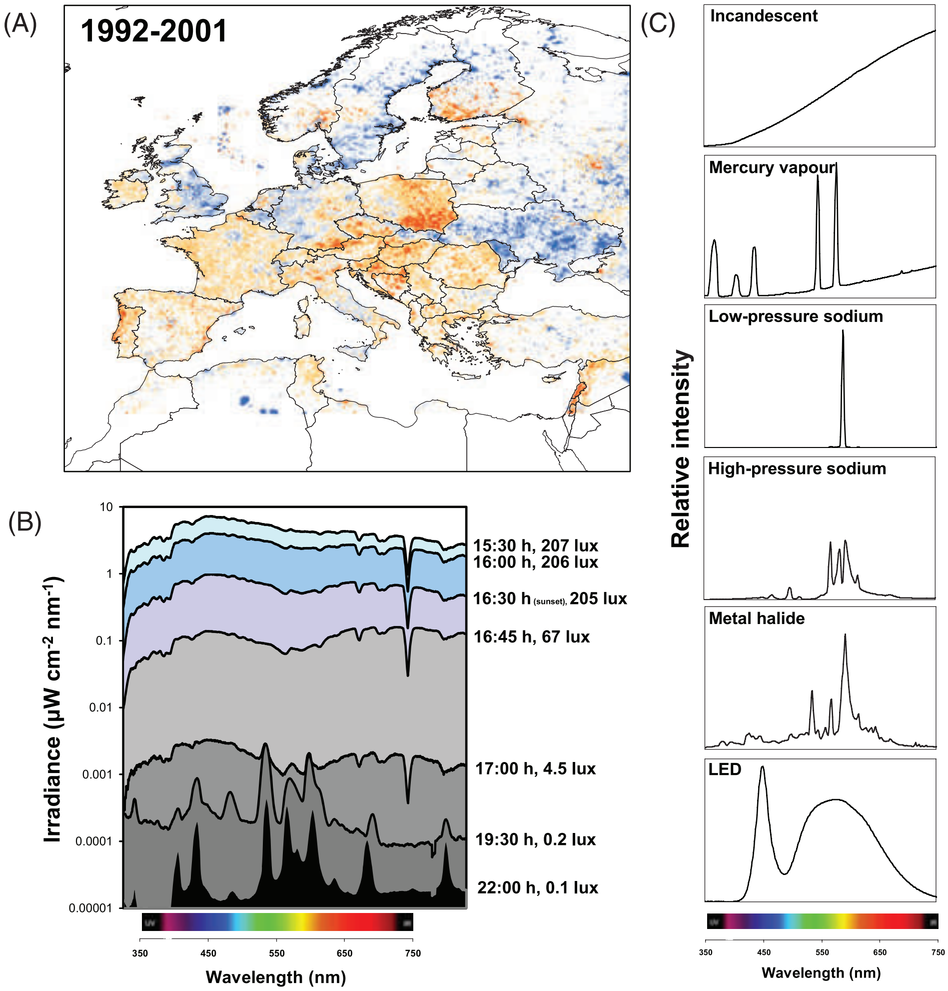

Fig. 1. Artificial nighttime light varies in space, time and along electromagnetic spectrum. (A) Spatial variation in relative brightness trends of nighttime lights in Europe, using annual DMSP satellite data from 1992 to 2001 inclusive from NOAA National Geophysical Data Center http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html. As there is no onboard cross-calibration for this dataset between years and satellites, values are calibrated for sensor drift relative to a control area [the island of Sicily, following Elvidge *et al.* (2009); red – rate of change in light significantly greater than the control region; blue – rate of change significantly lower than the control region]. Economic, technological and policy factors cause clear contrasts among countries and regions. (B) Temporal change in spectral irradiance of ambient light in grassland at Tremough, UK from day (blue) to night (black), 22.11.11; peaks at 19:30 h from indoor fluorescent lighting from nearby offices, and at 22:00 h from footpath lighting. (C) Spectral composition of main electric lighting types used since 1950, from data at http://www.ngdc.noaa.gov/dmsp/spectra.html. In (A) all illustrated changes are relative to the net change in the control region, calculated from cross-calibrated annual images using sixth-order regression with Sicily's nighttime lights. While Sicily was selected as the most suitable calibration region among several candidates by Elvidge *et al.* (2009), changes in lighting have undoubtedly occurred during this period on the island, and hence blue regions do not necessarily indicate decreasing absolute brightness during this period. Only pixels with statistically significant relative change over time at $P < 0.05$ are shown, calculated from Spearman's rank correlation on annual values from 1992 to 2001 inclusive. No trends are detected for highly urban areas where satellite sensor values are saturated.

direct and diffuse sunlight, twilight and moonlight, with certain types of lighting restricted to very narrow bandwidths, while others emit over a wide range of wavelengths. Early electric street lighting relied on incandescent bulbs (Jakle, 2001), emitting primarily in yellow wavelengths, while low-pressure sodium lighting, widely adopted in the 1960s and 1970s, emits a single narrow peak in the visible spectrum at 589.3 nm, giving objects a distinctive monochromatic orange hue. More recent light technologies emit over a broad range of wavelengths (high-pressure sodium lighting emits a yellow light allowing some colour discrimination; high-intensity discharge lamps emit a whiter light, with significant peaks in blue and ultra-violet wavelengths, and LED-based white street lighting typically emits at all wavelengths between around 400 and 700 nm, with peaks in the blue and green; Elvidge *et al.*, 2010). Over recent decades the spectral diversity of light sources has grown (Frank, 1988), and the trend towards adopting lighting technologies with a broader

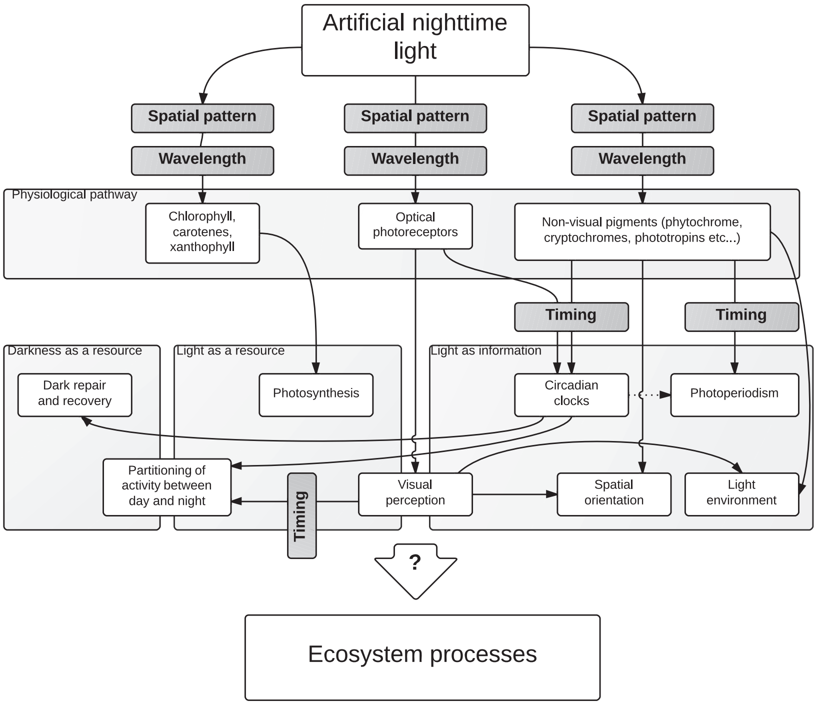

Fig. 2. Potential pathways for ecosystem effects of light pollution. Light affects organisms *via* the visual system in animals, the photosynthetic system in plants, and through various non-visual pigments in both plants and animals. The effects of artificial light are mediated by the spatial pattern, wavelengths and/or timing of the light sources (here shaded bands represent filters through which effects are dependent on space, wavelength and/or timing). Ecological effects can be characterised as disruption of information flows and/or changes in resource use and availability. The extent to which these effects influence ecosystem processes is currently largely unknown.

spectrum of 'white' light is likely to increase the potential for ecological impacts (including through changes in the colour of sky glow; Kyba *et al.*, 2012).

In combination, the increasing spatial, temporal and spectral distribution of nighttime light pollution provides the potential for major influences on ecological and evolutionary processes (Fig. 2; Navara & Nelson, 2007; van Langevelde *et al.*, 2011). Substantial attention has been paid to catastrophic events, such as the mortality that can follow from the disorientation of hatchling turtles and of birds by nighttime lighting (e.g. Howell, Laskey & Tanner, 1954; Verheijen, 1958, 1985; McFarlane, 1963; Reed, Sincock & Hailman, 1985; Witherington & Bjorndal, 1991; Peters & Verhoeven, 1994; Salmon *et al.*, 1995; Le Corre *et al.*, 2002; Jones & Francis, 2003; Black, 2005; Tuxbury & Salmon, 2005; Gauthreaux & Belser, 2006; Montevecchi, 2006; Evans *et al.*, 2007b; Lorne & Salmon, 2007; Gehring, Kerlinger & Manville, 2009; Tin *et al.*, 2009; Rodríguez, Rodríguez & Lucas, 2012). However, a much broader set of implications has been identified (Longcore & Rich, 2004; Hölker *et al.*, 2010*a*; Perkin *et al.*, 2011). In consequence, and echoing earlier statements (e.g. Verheijen, 1985), there have been several recent calls for a much improved understanding of these implications (e.g. Health Council of the Netherlands, 2000; Sutherland *et al.*, 2006; The Royal Commission on Environmental Pollution, 2009; Hölker *et al.*, 2010*a*,*b*; Perkin *et al.*, 2011; Fox, 2013).

Part of the challenge in providing this improved understanding lies in organizing the knowledge that already exists and in identifying the principal gaps. The literature that has developed to date is scattered, and largely lacks synthesis within a common mechanistic framework. Previous attempts to review this material have done so by taxonomic group (Rich & Longcore, 2006*b* – with sections on mammals, birds, reptiles and amphibians, fishes, invertebrates, plants), by different processes and/or levels of biological organization (Longcore & Rich, 2004 – with sections on behavioural and population ecology, community ecology, ecosystem effects; Longcore & Rich, 2006 – with sections on physiological ecology, behavioural and population ecology, community ecology, ecosystem ecology), and by research domain (Perkin *et al.*, 2011 – with sections on dispersal, evolution, ecosystem functioning, interactions with other stressors).

Here we propose a framework that focuses foremost on the cross-factoring (Table 2) of the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the ways in which light influences biological systems, particularly the distinction between light as a resource and light as an information source (Fig. 3). Reviews of the literature to date have highlighted examples of each of the different combinations of such a cross-factoring. However, many studies do not report, for example, the spectral properties, intensity, duration and/or spatial extent of the light regime, making it hard to draw

Table 2. Cross-factoring of the effects of nighttime lighting on the spatial, temporal and spectral components of light regimes, and of the organismal effects of light as a resource and as an information source

		Space	Time	Spectra
Light as a resource	Photosynthesis	Very localized, close to lights, probably only ecologically significant in naturally dark habitats (e.g. caves).	Most effective when light is continuous throughout naturally dark period – effects will be reduced with duration of lighting.	Effective at broad range of wavelengths between 400 and 700 nm, overlapping lighting systems for human vision; peak sensitivities in red and blue.
	Partitioning of activity between day and night	Impacts could be widespread, as sky glow effects allow increased nocturnal activity, or highly localized, as direct light in the vicinity of lamps allows diurnal/crepuscular species to extend their period of activity into hours of natural darkness. Spatial heterogeneity in light and dark patches may lead to spatial partitioning of the light resource.	Probably most critical around dusk and dawn, but continuous lighting may extend effects throughout the night.	Effective wavelengths likely to vary among taxa.
	Dark repair and recovery	Could be widespread – few data available on physiological mechanisms and required light intensities across species.	Could be effective throughout night; short pulses of light may be sufficient to disrupt melatonin production.	Emission in blue and UV-A may promote DNA repair through photoreactivation; blue light may disrupt melatonin production in higher vertebrates.
Light as an information source	Circadian clocks and photoperiodism	Effects could be widespread, but recorded instances usually in close proximity to light sources (e.g. retention of leaves in deciduous plants around street lighting).	Continuous and intermittent low lighting both shown to have effects; short pulses of light during night are sufficient to disrupt both circadian clocks and photoperiodism in some species.	Effects likely to vary among taxa; plants may be sensitive to the ratio of red to far-red light *via* the phytochrome pathway, rather than absolute intensity at a given wavelength. Plants and animals may also respond through to blue light through the cryptochrome pathway.
	Visual perception	Could be widespread over large areas; sky glow effects may be equal to or exceeding moonlight intensities.	Probably most effective around dawn and dusk, extending effective period of activity of normally diurnal and crepuscular species, but may also allow activity throughout night (e.g. wading birds).	Effective wavelengths will vary among species. Broader spectrum light sources will tend to give better colour definition and aid identification of objects from their background in most species.
	Spatial orientation and light environment	Species are often highly sensitive to directional light even at low intensity, so isolated light sources can have a major disruptive effect on navigation across spatial scales. Diffuse sources, such as atmospheric sky glow, may mask natural light signals used for navigation, including moon position and polarized atmospheric light.	Intermittent light may have reduced impact – lighting during key periods of movement (e.g. during migration events) may be most significant.	Lights with high UV (e.g. mercury vapour lamps) shown to be disruptive in many insects; red light in some bird species.

general conclusions applicable outside their geographical and taxonomic limits. For this reason perhaps, despite the global nature of increases in artificial light, the ecological impacts of light pollution are often considered to be localised and restricted to a few vulnerable species or taxonomic groups. Considering these individual studies within our proposed framework: (*i*) helps to unify understanding of particular effects of light pollution across taxa, and to draw conclusions relevant to whole ecosystems; (*ii*) highlights the mechanisms behind the observed ecological effects of light pollution, and

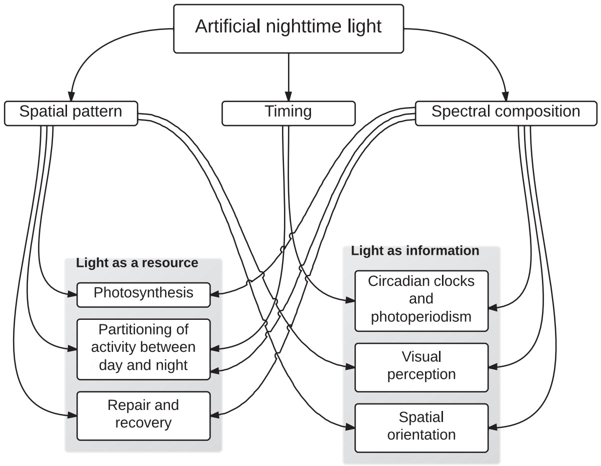

Fig. 3. Cross-factoring of the effects of nighttime lighting on the spatial, temporal and spectral components of light regimes, and of the organismal effects of light as a resource and as an information source.

defines clear criteria for future ecological studies; and (*iii*) provides guidance in detecting, predicting and mitigating against current and future adverse effects of light pollution.

In the sections below we review the evidence for each of the combinations of the cross-factoring. To avoid undue redundancy, and a bias towards certain well-studied systems, we have not attempted to provide an exhaustive list of studies on the ecological effects of light pollution, but rather in each section we aim to illustrate the key issues and identify progress and opportunities for further work.

II. LIGHT AS A RESOURCE

Both light and darkness can act as a resource for organisms (Kronfeld-Schor & Dayan, 2003; Gerrish *et al.*, 2009). Through photosynthesis, energy is captured by autotrophs in the form of light and cycled through ecosystems; furthermore, many physiological processes and behavioural activities require either light or dark conditions to operate. The balance between hours of light and of darkness constrains the time available for these processes and so changes in the availability of both light and darkness as a resource can have positive or negative effects on an organism, dependent on whether it is the presence or absence of light that poses the greater constraint.

(1) Photosynthesis

In green plants, light is absorbed for photosynthesis by chlorophylls and carotenoids at wavelengths between 400 and 700 nm. While this range encompasses much of the visible emissions by artificial lights, in most cases the levels of photosynthetically active radiation (PAR) associated with nighttime light pollution are extremely low relative to sunlit conditions (typically less than 0.5 μmol m^{-2} s^{-1} compared with between 100 and 2000 μmol m^{-2} s^{-1} for sunlit conditions) and the effect of light pollution on net carbon fixation is likely to be negligible in most cases. Although Raven & Cockell (2006) calculate that the combined PAR flux from sky glow in an urban area and moonlight from a full moon could theoretically exceed the lower limit for photosynthesis, in most cases only direct illumination in the close vicinity of light sources, for example the leaves of trees within a few centimeters of street lights, is likely to be sufficient to maintain net carbon fixation during nighttime and at lower light levels offset nocturnal respiratory losses. The consequences of this highly localized effect on individual plants and on ecosystems are largely unexplored.

One environment in which light pollution is known to have marked effects on ecosystems through photosynthesis is in artificially lit cave systems. The introduction of lighting into caves used as visitor attractions promotes highly localized growth of 'lampenflora' communities completely dependent on artificial light as a source of energy. These communities may include autotrophs such as photosynthetic algae, mosses and ferns growing in the vicinity of light fixtures, as well as fungi and other heterotrophs utilizing the input of organic matter (Johnson, 1979). These communities may displace or disrupt the trophic ecology of energy-limited cave ecosystems. Algal growth on the walls can also seriously damage and obscure geological and archaeological interest within caves (Lefèvre, 1974), and is an issue of some concern.

(2) Partitioning of activity between day and night

Partitioning of time has been thought to be a major way in which the ecological separation of species is promoted (Kronfeld-Schor & Dayan, 2003). Temporal niche partitioning between diurnal, crepuscular and nocturnal species occurs as they avoid competition by specializing in a particular section along the light gradient (Gutman & Dayan, 2005). Indeed, whilst ecological and evolutionary studies have focused foremost on diurnal species, a substantial proportion of species is adapted to be active during low-light conditions (Lewis & Taylor, 1964; Hölker *et al.*, 2010*b*). Natural variation in nighttime lighting, particularly in moonlight due to the phase of the moon and cloud-cover conditions, has been shown to affect the timing of activity in a range of species (e.g. Imber, 1975; Morrison, 1978; Gliwicz, 1986; Kolb, 1992; Tarling, Buchholz & Matthews, 1999; Baker & Dekker, 2000; Fernandez-Duque, 2003; Kappeler & Erkert, 2003; Beier, 2006; Woods & Brigham, 2008; Gerrish *et al.*, 2009; Penteriani *et al.*, 2010, 2011; Smit *et al.*, 2011). Spatial gradients in the amount and seasonal distribution of biologically useful semi-darkness (including moonlight and twilight) have been proposed as drivers of patterns of behaviour (Mills, 2008). Visually orienting predators have a reduced ability to detect prey in dark conditions, and may increase their activity or achieve higher rates of predation success under lighter conditions; prey species may reduce activity in lighter conditions in response to a perceived increased risk of predation. Some shorebird species use visual foraging by day but tactile foraging during hours of darkness – nighttime light may allow them to use visual foraging throughout the night (Rojas *et al.*, 1999). Moonlight-driven cycles in predator–prey activity have been observed in such taxonomically diverse species as zooplankton and fish (Gliwicz, 1986), predaceous arthropods (Tigar & Osborne, 1999), blue petrels *Halobaena caerulea* and brown skuas *Catharacta skua* (Mougeot & Bretagnolle, 2000), owls and rodents (Clarke, 1983), and lions *Panthera leo* and humans (Packer *et al.*, 2011). Prey species may respond to the increased risk of predation at night by decreasing their activity (e.g. Kotler, 1984; Daly *et al.*, 1992; Vásquez, 1994; Skutelsky, 1996; Kramer & Birney, 2001) or changing their microhabitat to utilize dark spaces such as the shelter of bushes (e.g. Price, Waser & Bass, 1984; Kolb, 1992; Topping, Millar & Goddard, 1999), and may compensate by greater activity at dawn and/or dusk; Daly *et al.* (1992) have shown how such 'crepuscular compensation' in response to high nocturnal predation rates can lead to increasing rates of predation by diurnal predators as prey activity encroaches into daylight hours. Diurnal and crepuscular predators may become facultative nocturnal predators under suitable light conditions (e.g. Milson, 1984; Combreau & Launay, 1996; Perry & Fisher, 2006). Conversely, nocturnal predators that rely on non-visual clues to hunt, such as snakes, may decrease activity during lighter nights in order to avoid detection by prey and their own predators (Bouskila, 1995; Clarke, Chopko & Mackessy, 1996). Behavioural changes are likely to induce changes in energetic costs; Smit *et al.* (2011) have shown that freckled nightjars *Caprimulgus tristigma* respond to dark nights by entering torpor, while moonlit nights allow foraging as food availability is sufficient to overcome the energetic costs of thermoregulation.

Despite the large number of studies that demonstrate the effect of moonlight in altering the behaviour of species, there have been relatively few that have formally examined the effect of artificial light in altering behaviour or restructuring temporal niche partitioning. Reports have long existed that some diurnal species exploit the 'night-light niche' and become facultatively nocturnal in urban environments, for example jumping spiders (Wolff, 1982; Frank, 2009), reptiles (Garber, 1978; Perry & Fisher, 2006), and birds (Martin, 1990; Negro *et al.*, 2000; Santos *et al.*, 2010). In rodents, Bird, Branch & Miller (2004) have shown that foraging behaviour in beach mice *Peromyscus polionotus* is restricted by artificial lighting, while Rotics, Dayan & Kronfeld-Schor (2011) have shown that while the nocturnal spiny mouse species *Acomys cahirinus* restricted activity under artificial light, its diurnal congener *Acomys cahirinus* did not expand its activity to compete during the hours of artificial illumination.

There are few known examples of artificial light as a resource directly mediating behaviour; although some species have been found to increase foraging activities and antipredator vigilance under such conditions (e.g. Biebouw & Blumstein, 2003), the vision of some nocturnal predators has been shown to be impaired by artificial lighting and their foraging success reduced (e.g. Buchanan, 1993). Reports of the effects of light in providing resources by attracting concentrations of prey are more frequent (e.g. Heiling, 1999; Buchanan, 2006). Increased foraging around street lights has been widely reported for some species of bats (e.g. Rydell, 1991, 1992, 2006; Blake *et al.*, 1994; Polak *et al.*, 2011), particularly around lamps which emit at low wavelengths, attract large numbers of insects, and which may interfere with prey defences (Svensson & Rydell, 1998); Rydell (2006) regards the habit of feeding around lights by bats as having become the norm for many species. Other bat species avoid lights (Kuijper *et al.*, 2008; Stone, Jones & Harris, 2009), possibly to minimise the risk of avian predation (Speakman, 1991; Rydell, Entwistle & Racey, 1996). Similarly, nocturnal orb-web spiders *Larinioides sclopetarius* preferentially build webs in areas which are well lit at night, where higher densities of insect prey are available; a behaviour that appears to be genetically predetermined rather than learnt (Heiling, 1999). This suggests the possibility of evolutionary responses to utilise novel niches created by artificial lighting.

The relative lengths of night and day can influence foraging opportunities, predation and/or competition costs and the trade-offs amongst these (e.g. Clarke, 1983; Falkenberg & Clarke, 1998; Berger & Gotthard, 2008). In turn this can influence the abundances of organisms (e.g. Carrascal, Santos & Tellería, 2012). Presumably nighttime lighting that served effectively to change perceived night and day lengths could amplify these effects.

(3) Dark repair and recovery

It has been suggested that continuous periods of darkness are critical for certain processes controlling repair and recovery of physiological function in many species, and hence that darkness can be seen as a resource for physiological activity. Seeking an explanation for an observed increase in ozone injury in plants at high latitudes, Vollsnes *et al.* (2009) have shown that dim nocturnal light, simulating the northern Arctic summer, inhibits recovery from leaf damage caused by atmospheric ozone in subterranean clover *Trifolium subterraneum*. Futsaether *et al.* (2009) found a similar result in red clover *Trifolium pretense* but not in white clover *Trifolium repens*. In *Arabidopsis thaliana*, Queval *et al.* (2007) have shown links between day length and the rate of oxidative cell death. Since the patterns of anthropogenic light pollution and ozone pollution are spatially correlated on a global scale (see e.g. Cinzano *et al.*, 2001; Ashmore, 2005), the extent to which low-intensity nighttime light could affect repair and recovery from ozone damage requires further investigation.

Gerrish *et al.* (2009) argued that hours of darkness provide organisms with time for repair to DNA damage to cells caused by solar UV-B radiation (285–315 nm). However, light in the blue to UV-A portion of the spectrum is necessary for DNA repair through photoreactivation *via* the photolyase enzyme (with maximum absorption at 380 and 440 nm), while 'dark repair' through the excision repair pathways is independent of light (Sutherland, 1981; Britt, 1996; Sinha & Häder, 2002). The role of darkness here is presumably limited to the lack of damage due to solar UV-B radiation during the night. Since artificial lighting typically emits negligible amounts of UV-B radiation it is unlikely that light pollution either increases DNA damage or inhibits the processes of repair in this instance; indeed, light sources emitting in the blue and UV-A may have an effect in promoting DNA repair through photoreactivation.

III. LIGHT AS AN INFORMATION SOURCE

The direction, duration and spectral characteristics of natural light are widely used by organisms as sources of information about their location, the time of day and year, and the characteristics of their natural environment (Neff, Fankhauser & Chory, 2000; Ragni & D'Alcalà, 2004). Indeed, considerable energetic costs are often borne in order to maintain the necessary sensory systems (Niven & Laughlin, 2008). Artificial lighting can disrupt this flow of information and provide misleading cues. The wavelengths of light are critical to its efficacy as an information source due to the varying spectral sensitivity of organisms' receptors. In vascular plants, for example, the most well-studied photoreceptors are phytochromes, which exist in two photo-interconvertible forms – a biologically inactive red-light-absorbing form (Pr) which upon absorption of red light is converted to a biologically active form (Pfr). Pfr is converted back to Pr on absorbing far-red photons, so under steady light of a given red/far-red ratio the active form of phytochrome reaches equilibrium (Lin, 2000; Neff *et al.*, 2000; Smith, 2000). The phytochrome system plays a key role in detecting shade and measuring day length, and has been shown to influence vegetative growth and architecture, the timing of germination, flowering, bud burst and dormancy and senescence, and the allocation of resources to roots, stems and leaves (Smith, 2000). In addition, blue and ultra-violet light receptors called cryptochromes influence light responses in many species of algae, higher plants, and animals (Cashmore *et al.*, 1999), and have been shown to play a role in regulating circadian clocks in mammals (Thresher *et al.*, 1998). In animals with vision, complex information on the spectral composition of light may be derived from several photoreceptors with varying spectral sensitivities (Kelber, Vorobyev & Osario, 2003), and in mammals retinal ganglion cells that are independent of the visual system may be involved in entraining circadian clocks (Berson, Dunn & Takao, 2002). In many cases organisms have been shown to be sensitive to extremely low levels of light at night, well within levels of anthropogenic light pollution (Kelber & Roth, 2006; Bachleitner *et al.*, 2007; Evans *et al.*, 2007a; Frank, Evans & Gorman, 2010).

(1) Circadian clocks and photoperiodism

Three natural periodic cycles in the light regime are detected by organisms – the daily cycle of day and night, seasonal changes in day length, and the monthly lunar cycle. The daily and seasonal cycles in particular provide cues that can be used to anticipate regular changes in the environment such as temperature or humidity that also follow a daily or annual cycle. The lunar cycle has importance for activity and reproduction in some species, which may be responding directly to the availability of light as a resource (see section II) alternatively they may utilise the lunar light cycle to anticipate environmental changes connected with nighttime light or tidal conditions (Taylor *et al.*, 1979), or purely as a regular cue to synchronise reproductive activity (e.g. Tanner, 1996; Baker & Dekker, 2000; Takemura *et al.*, 2006).

Light may influence circadian patterns of behaviour in two ways, entrainment and masking, which may be difficult to distinguish in natural systems. Virtually all plants and animals possess a circadian clock, an endogenous system that regulates aspects of their activity and physiology on a cycle that approximates 24 h, but which in the absence of external cues may drift out of phase with day and night (Sweeney, 1963). In order for the clock accurately to track the diurnal cycle, it is regulated by 'zeitgebers', environmental cues that entrain or reset the clock. The light environment is critical in providing such cues in many species. Entrainment occurs when regular patterns of light and darkness regulate the phase and frequency of the endogenous clock (Menaker, 1968). Artificial light after dusk or prior to dawn can cause phase shifts in the circadian rhythm, delaying or advancing the cycle. Low levels of light at night may disrupt melatonin production in fish, birds and mammals, with a wide range of downstream physiological consequences (Navara & Nelson, 2007; for examples see Cos *et al.*, 2006; Evans *et al.*, 2007a; Reiter *et al.*, 2007; Bedrosian *et al.*, 2011*a*,*b*). Since light pollution typically occurs both before dawn and after dusk, it is difficult to predict the effect of any shift in the circadian clock. In laboratory experiments, entrainment has been shown to occur at both persistent levels of low light and with short pulses of relatively bright light (Table 3; Brainard *et al.*, 1983; Haim *et al.*, 2005; Zubidat, Ben-Shlomo & Haim, 2007; Shuboni & Yan, 2010). The duration and intensity of light required to disrupt circadian rhythms under field conditions is unknown, but these studies suggest potential for impacts on species affected by widespread low-level light such as urban sky glow or less often considered transient lighting sources such as vehicle lights (Lyytimäki, Tapio & Assmuth, 2012).

Exposure to light at night has been shown to disrupt the circadian cycle of hormone production in humans, particularly melatonin, which has been linked to an increase in cancer risk in shift-workers (Stevens, 1987, 2009; Megdal *et al.*, 2005; Reiter *et al.*, 2011). Melatonin production is regulated by the circadian clock, which in mammals is entrained by retinal ganglion cells with a peak sensitivity in blue light at around 484 nm (Berson *et al.*, 2002). Melatonin production is similarly reduced in rats under nighttime light levels of 0.2 lux (Dauchy *et al.*, 1997), and in hamsters at levels above 1 lux (Brainard *et al.*, 1982), and has been shown to suppress immune responses and increase the rate of tumour growth (Dauchy *et al.*, 1997; Bedrosian *et al.*, 2011*b*). Similar

Table 3. Examples of the levels at which nighttime lighting has been observed to have biological effects

Species	Setting	Effect	Nighttime lighting	Source
Barred owl *Strix varia*	Lab	Location of prey	1.6×10^{-6} lux*	Dice (1945)
Long eared owl *Asia wilsonianus*	…	…	2.7×10^{-6} lux*	…
Barn owl *Tyto alba*	…	…	5.7×10^{-6} lux*	…
Burrowing owl *Speotyto cunicaria*	…	…	2.8×10^{-4} lux*	…
Common toad *Bufo bufo*	Lab	Increased prey detection	2.8×10^{-4} lux (constant)	Larsen & Pedersen (1982)
Syrian hamster *Mesocricetus auratus*	Lab	Altered circadian rhythm	0.01 lux (constant)	Evans *et al.* (2007a)
Salmon *Salmo salar*	Lab	Increased prey detection	0.01–5 lux (constant)	Metcalfe *et al.* (1997)
Fruitfly *Drosophila melanogaster*	Lab	Increased activity levels and shifted typical morning and evening activity peaks into night	0.03 lux (constant)	Bachleitner *et al.* (2007)
Brown rat *Rattus norvegicus*	Lab	Increased rates of tumor growth and metabolism	0.2 lux (constant)	Dauchy *et al.* (1997)
Brown rat *Rattus norvegicus*	Lab	Increased rate of tumor growth	0.21 lux (constant)	Cos *et al.* (2006)
Ringed plover *Charadrius hiaticula*	Field experiment	Higher prey intake	0.74 lux (constant)	Santos *et al.* (2010)
Kentish plover *Charadrius alexandrinus*		…		
Grey plover *Pluvialis squatarola*		…		
Dunlin *Calidris alpina*		…		
Redshank *Tringa totanus*		…		
Deer mouse *Peromyscus maniculatus*	Lab	Reduced nocturnal activity	0.93 lux (constant)	Falkenberg & Clarke (1998)
Prairie Rattlesnake *Crotalus viridis*	Lab	Reduced activity	1 lux	Clarke *et al.* (1996)
American robin *Turdus migratorius*	Field observations	Earlier initiation of singing	Mean 1.26 lux (range 0.05–3.06 lux; constant)	Miller (2006)
Leaf-eared mouse *Phyllotis xanthopygus*	Lab	Reduced nocturnal activity	1.5 lux (constant)	Kramer & Birney (2001)
Leaf-eared mouse *Phyllotis darwini*	Lab	Predator avoidance and reduced food consumption	< 2.0 lux (constant)	Vasquez (1994)
Siberian hamster *Phodopus sungorus*	Lab	Suppressed immune response	5 lux (constant)	Bedrosian *et al.* (2011*b*)
Green and blue-green algae	Field observations	Minimum artificial light required for continued photosynthetic growth in caves	10–50 lux	Johnson (1979)
Mosses	…		50–180 lux	…
Ferns	…		250 lux	…
Atlantic salmon *Salmo salar*	Field experiment	Altered timing of nocturnal migration	14 lux (constant; measured at stream surface)	Riley *et al.* (2012)
Pond bats *Myotis dasycneme*	Field observations	Reduced feeding rate, disturbed flight pattern	< 30 lux (constant)	Kuijper *et al.* (2008)
Lesser horseshoe bats *Rhinolophus hipposideros*	Field experiment	Reduced activity, onset of commuting delayed	51.67 lux (average; constant)	Stone *et al.* (2009)
Social vole *Microtus socialis*	Lab	Disruption of seasonal acclimatization of thermoregulation	450 lux (15 min pulse)	Zubidat *et al.* (2007)
Field mouse *Mus booduga*	Lab	Disruption of circadian rhythm	1000 lux (15 min pulse)	Sharma *et al.* (1997)

*Converted from reported values in foot candles.

Note that: (*i*) in many cases these represent levels of experimental treatments, and precisely where thresholds might lie remains unknown; and (*ii*) although widely used, lux measurement places emphasis on brightness at wavelengths perceived by human vision. Studies are ordered in increasing intensity of light.

melatonin-mediated effects of nighttime light on immune function are seen in laboratory studies of birds (Moore & Siopes, 2000). The requirement for continuous periods of darkness to entrain the circadian clock and regulate hormone activity may be widespread amongst animals, yet the ecological effects of potential disruption of the circadian clock are unknown.

By contrast, masking occurs when a light stimulus overrides the endogenous clock; for example artificial light at night may increase activity in diurnal or crepuscular species (positive masking) or suppress it in others (negative masking; see e.g. Santos *et al.*, 2010; Rotics *et al.*, 2011). The ecological effects of direct entrainment of circadian clocks by artificial light may be difficult to distinguish from opportunistic changes in light-resource use or direct effects of light on behaviour through masking. For example, light pollution has been shown to advance the initiation of dawn singing considerably in some temperate bird species in urban areas (Miller, 2006), with implications for breeding success (Kempenaers *et al.*, 2010). The extent to which this effect of light on behaviour is mediated by circadian rhythms, or whether light triggers this behaviour independently of an endogenous clock through masking is unknown.

In temperate and polar ecosystems, organisms frequently use day length as a cue to initiate such seasonal phenological events as germination, bud formation and burst, reproduction, senescence, eclosion, diapause, moult, embryonic development, and migration (e.g. Gwinner, 1977; Densmore, 1997; Dawson *et al.*, 2001; Niva & Takeda, 2003; Heide, 2006; Cooper *et al.*, 2011). By contrast, species whose ranges are restricted to lower latitudes are likely to be less dependent on day length to regulate annual cycles of activity (although in dry seasonal climates near the equator even very small differences in seasonal day length can be utilised by plants to trigger phenological events; see Rivera *et al.*, 2002). Over evolutionary time species have adapted to wide variation in the range of day length that they encounter – in the Permian period deciduous forests existed in Antarctica at latitudes of 80–85°S, experiencing total darkness for months in the winter and 24 h daylight during summer, a light environment without analogue in modern forests and unlikely to be within the survivable range of extant tree phenotypes (Taylor, Taylor & Cúneo, 1992). Photoperiod, and therefore presumably changes in what is perceived as photoperiod as a result of artificial lighting, has consequences for a variety of physiological traits. It has long been observed that certain species of deciduous tree maintain their leaves for longer in autumn in the vicinity of street lights (Matzke, 1936), potentially leaving them exposed to higher rates of frost damage in late autumn and winter. Experiments in horticultural systems have shown a wide range of responses to artificial nighttime lighting, depending both on the species and the spectral composition of the light source, including delay and promotion of flowering, and enhanced vegetative growth (Cathey & Campbell, 1975; Kristiansen, 1988). Animal species, including lizards (*Sceloporus occidentalis*; Lashbrook & Livezey, 1970) and rodents (*Microtus socialis*; Zubidat *et al.*, 2007) control their thermoregulatory activity in response to seasonal changes in photoperiod. Plant physiologists draw a distinction between 'long-day' responses, in which a long dark period suppresses an effect, and 'short day' responses, in which a long dark period promotes an effect. In animals, both day length and the relative change in day length may act as proximal triggers (Vepsäläinen, 1974). Species with a wide latitudinal range show local adaptation in their photoperiodic response (Bradshaw, 1976), and photoperiodic control allows species to coordinate key events in their life cycle with suitable weather conditions. Photoperiodic response has been shown to evolve rapidly in an invasive species expanding into different latitudes, reflecting changing relationships between the seasonal climate and the information given by day-length cues (Urbanski *et al.*, 2012). Disruption of this control may lead to organisms becoming out of step with their climate, with the timing of other organisms (such as pollinators or food sources), or unable to adapt to climatic change (Bradshaw, Zani & Holzapfel, 2004; Bradshaw & Holzapfel, 2010).

The biological rhythms of organisms are known to be linked across different levels of food webs, with, for example, plant-herbivore-parasitoid rhythms being synchronized both as a consequence of bottom-up and top-down processes (Zhang *et al.*, 2010). This raises the likelihood that disruptions to the rhythms of individual species by nighttime lighting can ramify widely.

(2) Visual perception

A wide range of adaptations exist throughout the animal kingdom to make use of reflected light at different levels and wavelengths, allowing the recognition of important features of the environment (Land & Nilsson, 2002; Warrant, 2004; Warrant & Dacke, 2011); discoveries about the breadth of the abilities of organisms in this regard continue to be made (e.g. Kelber, Balkenius & Warrant, 2002; Grémillet *et al.*, 2005; Allen *et al.*, 2010; Baird *et al.*, 2011; Hogg *et al.*, 2011). A substantial proportion of animal species are adapted to see at light levels well below those at which human vision is effective, in which they can often see colour and navigate well (Table 3; Warrant, 2004; Warrant & Dacke, 2010, 2011). The interaction between the intensity and spectral composition of artificial light and the adaptation of an organism's eyes will affect whether visual perception is enhanced, disrupted or unaffected by light pollution, and hence the potential downstream behavioural and ecological effects.

The intensity of light at which animals are able to identify objects varies considerably among species (Table 3). Many are able successfully to navigate visually and locate resources at light levels at which human vision is impossible (e.g. Dice, 1945; Larsen & Pedersen, 1982). A considerable proportion of nocturnal activity occurs during periods of 'biologically useful semi-darkness' (Mills, 2008), making use of the relatively low light intensities during twilight and moonlight; however, nocturnal species may also modify or reduce activity during such periods to avoid competition or predation (Clarke *et al.*, 1996). Light intensities recorded from artificial sources, from both direct illumination a considerable distance from a source and diffuse sky glow, are well within the range shown to be effective in enhancing animal vision and triggering behavioural changes (Tables 1 and 3). Less well known is the extent to which artificial nighttime light may disrupt vision systems adapted to dark conditions.

The light-sensitive photoreceptor pigments of animal eyes vary in the wavelengths of light to which they are most absorbant. Colour is perceived as a representation in a limited number of dimensions of the multi-dimensional spectral reflectance of an illuminated surface, and the information content of colour perception varies as a function of the number and spectral sensitivity of different types of photoreceptor pigments. The human eye contains three photoreceptors (trichromatic) that are used in photopic (daytime) vision and maximally absorb light at wavelengths of 558 (red), 531 (green) or 419 nm (blue) (Dartnall, Bowmaker & Mollon, 1983). Reptiles and birds commonly possess four photoreceptor pigment types, increasing the information content of colour perception across much of the spectrum [including ultraviolet (UV) light] compared to the majority of mammals which possess two photoreceptor pigment types (Osorio & Vorobyev, 2008). The mantis shrimp *Odonatodactlyus* represents an extreme case of colour sensitivity, with 12 photoreceptor pigment types (Marshall & Oberwinkler, 1999). Large numbers of types potentially allow organisms better to discriminate between objects of contrasting spectral reflectance in their environment, and the relative distribution of photoreceptor sensitivities determines the portions of the electromagnetic spectrum in which colour vision is most sensitive.

Changing the spectral properties of artificial lights is therefore likely to alter the environment which individual organisms are able to see in different ways. Broader spectrum light sources such as light-emitting diodes (LEDs) are often likely to provide improved colour discrimination. This may allow animals better to navigate, forage for resources, locate and catch their prey, and identify or display for mating (such as in the plumage feathers of birds; Hart & Hunt, 2007). The trichromatic and tetrachromatic visual systems of many hymenopteran and lepidopteran insects allow them to recognize and compare between the nectar sources provided by flowering plants (Chittka & Menzel, 1992). The colour of a flowering plant as perceived by an insect, and the ease with which the insect can recognize different flowers, are likely to be improved under broad-spectrum compared to narrow-spectrum lighting conditions. Changing the spectral composition of artificial light could therefore affect the competitive fitness of animals in a variety of ways. Given the current shift in lighting technology towards broader spectrum light sources, future research into the impact of different artificial light sources on the recognition of important environmental signals by animal groups is clearly necessary.

(3) Spatial orientation and light environment

Many organisms use lightscapes as cues for directional movement (Tuxbury & Salmon, 2005; Ugolini *et al.*, 2005; Warrant & Dacke, 2011). The restructuring of these lightscapes by light pollution can thus result in these movements being disrupted. Examples of such disruption have been documented for moths and other insects (e.g. Frank, 1988), frogs (Baker & Richardson, 2006), reptiles (e.g. Salmon *et al.*, 1995), birds (e.g. Gauthreaux & Belser, 2006; Rodríguez *et al.*, 2012), and mammals (Beier, 1995; Rydell, 2006).

The widespread attraction of moth species to nighttime lights has long been exploited in the design of traps for their capture. The reasons for such disruption of their natural movement patterns remain to be fully determined, although interference with the use of moonlight for navigation is likely important (Warrant & Dacke, 2011). Many insects, including members of the Hymenoptera, Lepidoptera and Coleoptera, can navigate using the pattern of polarized celestial light in the sky (e.g. Dacke *et al.*, 2003). The use of UV light as opposed to other wavelengths to detect polarized light patterns has been postulated to be advantageous because the degree of polarized light scattered downwards from clouds and forest canopies is higher in the UV (Barta & Horváth, 2004). The natural signal is diminished by urban sky glow (Kyba *et al.*, 2011*b*), and through this effect variation in sky glow may potentially explain geographic differences in the response of moth-trap catches to phases of the moon (Nowinsky & Puskás, 2010). Whether flight-to-light behaviour is driven by the disruption of natural polarized light patterns alone seems unlikely as this behaviour occurs even with artificial lights which emit no UV component (van Langevelde *et al.*, 2011). However, the use of polarized UV light detection for navigation by insects may explain why flight-to-light behaviour is disproportionately associated with emissions at shorter wavelengths (van Langevelde *et al.*, 2011). Polarized light patterns reflected back from the ground can also be used to locate water bodies due to the polarizing nature of their surfaces. Indeed, a number of cases exist where insects have been attracted to sources of polarized light reflected back from anthropogenic structures such as wet asphalt roads, leading to increasing concern over the deleterious effects of these and other light polarizing anthropogenic structures (Horváth *et al.*, 2009). It seems likely that such effects may be exacerbated by the introduction of artificial lighting, although ecological case studies have not to our knowledge been documented.

Beetles of the family Lampyridae are notable for their use of bioluminescence in mate location. It is possible that artificial light is playing a significant role in the decline of these taxa, due to disruption of mate location (Lloyd, 2006).

Migrating birds utilize at least two mechanisms for navigation that may be disrupted by artificial lighting. Magnetoreception is considered to be the principal mode of orientation. The detection systems for magnetoreception include the magnetic-field-dependent orientation of paired radical molecules in the photopigment that forms during photon absorption, and the presence of magnetite within the beak (Wiltschko *et al.*, 2010). Migration direction has been demonstrated to be determined using the blue and green photoreceptors in European robins *Erithacus rubecula*

(Wiltschko *et al.*, 2007), while red light disrupts migration direction in silvereyes *Zosterops l. lateralis* (Wiltschko *et al.*, 1993). This has led to calls for the spectral composition of artificial lighting to be managed to mitigate against disorientation of birds (Poot *et al.*, 2008), however the level of disorientation caused by particular wavelengths of light appears to vary according to intensity, and is not restricted to red lights alone (Wiltschko *et al.*, 2010).

In addition to possessing a magnetic compass for orientation, birds are also thought to calibrate this compass using celestial light during twilight or at night (Cochran, Mouritsen & Wikelski, 2004). In some species the mechanism of calibration has been demonstrated to be the detection of polarized light patterns during sunrise and sunset (e.g. Muheim, Phillips & Akesson, 2006). However, as is the case with insects, whether artificial lighting can affect these patterns, and the consequences this may have for navigation, are currently unknown.

In addition to the above examples of movement towards light, many motile organisms exhibit light-avoidance behaviours (e.g. Moore *et al.*, 2000; Buchanan, 2006; Boscarino *et al.*, 2009). It seems extremely likely that for many such taxa the avoidance of artificial illumination will result in reduction in the space and other resources available to them (e.g. Kuijper *et al.*, 2008). One of the ecologically most significant consequences of negative phototropic behaviour is the widespread diel migration of zooplankton in aquatic systems (e.g. Moore *et al.*, 2000) which would appear to be sensitive to levels of light oscillation well below those produced by artificial illumination (Berge *et al.*, 2009).

IV. CONCLUSIONS

(1) As human communities and lighting technologies develop, artificial light increasingly encroaches on dark refuges in space, in time, and across wavelengths. At a given latitude, natural light regimes have been relatively consistent through recent evolutionary time, and the global rapid growth in artificial light represents a potentially significant perturbation to the natural cycles of light and darkness. Natural light is utilized by organisms both as a resource and a source of information about their environment, and artificial light has the potential to disrupt the utilization of resources and flow of information in ecosystems.

(2) A broad set of case studies of ecological implications of light pollution have been documented. Across a wide range of species, there is evidence that artificial light affects processes including primary productivity, partitioning of the temporal niche, repair and recovery of physiological function, measurement of time through interference with the detection of circadian, lunar and seasonal cycles, detection of resources and natural enemies and navigation. However, the effects on population- or ecosystem-level processes, such as mortality, fecundity, community productivity, species composition and trophic interactions are poorly known. Furthermore, the studies identifying these processes to date are scattered within literature from a wide range of disciplines, are strongly weighted towards higher vertebrates and ecosystems and largely lack synthesis within a common mechanistic framework.

(3) We propose a framework that focuses foremost on the interactions between the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the mechanisms by which light influences biological systems, particularly the distinction between light as a resource and light as an information source. Such a framework focusses attention on the need to identify general principles that apply across species and ecosystems, and integrates understanding of physiological mechanisms with their ecological consequences.

(4) Reviewing the evidence for each of the combinations of this cross-factoring particularly highlights: (*i*) the potential influence of nighttime lighting at all levels of biological organisation (from cell to ecosystem); (*ii*) the significant impact that even low levels of nighttime light pollution can have; and (*iii*) the existence of major research gaps in understanding of the ecological impacts of light pollution.

(5) Future research on the ecological impacts of light pollution needs to address several key issues: (*i*) to what extent does the disruption of natural light regimes by artificial light influence population and ecosystem processes, such as mortality and fecundity rates, species composition and trophic structure; (*ii*) what are the thresholds of light intensity and duration at different wavelengths above which artificial lighting has significant ecological impacts; and (*iii*) how large do 'dark refuges', where the intensity and/or duration of artificial light falls below such thresholds, need to be to maintain natural ecosystem processes?

V. ACKNOWLEDGEMENTS

The research leading to this paper received funding from the European Research Council under the European Union's Seventh Framework Programme (*FP7/2007-2013*)/ERC grant agreement no. 268504 to K.J.G.

VI. REFERENCES

Allen, J. J., Mathger, L. M., Buresch, K. C., Fetchko, T., Gardner, M. & Hanlon, R. T. (2010). Night vision by cuttlefish enables changeable camouflage. *Journal of Experimental Biology* **213**, 3953–3960.

Ashmore, M. R. (2005). Assessing the future global impacts of ozone on vegetation. *Plant, Cell and Environment* **28**, 949–964.

Bachleitner, W., Kempinger, L., Wülbeck, C., Rieger, D. & Helfrich-Förster, C. (2007). Moonlight shifts the endogenous clock of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 3538–3543.

Baird, E., Kreiss, E., Wcislo, W., Warrant, E. & Dacke, M. (2011). Nocturnal insects use optic flow for flight control. *Biology Letters* **7**, 499–501.

Baker, G. C. & Dekker, R. W. R. J. (2000). Lunar synchrony in the reproduction of the Moluccan megapode *Megapodius wallacei*. *Ibis* **142**, 382–388.

Baker, B. J. & Richardson, J. M. L. (2006). The effect of artificial light on male breeding-season behaviour in green frogs, *Rana clamitans melanota*. *Canadian Journal of Zoology* **84**, 1528–1532.

Barta, A. & Horváth, G. (2004). Why is it advantageous for animals to detect celestial polarization in the ultraviolet? Skylight polarization under clouds and canopies is strongest in the UV. *Journal of Theoretical Biology* **226**, 429–437.

Bedrosian, T. A., Fonken, L. K., Walton, J. C., Haim, A. & Nelson, R. J. (2011*a*). Dim light at night provokes depression-like behaviors and reduces CA1 dendritic spine density in female hamsters. *Psychoneuroendocrinology* **36**, 1062–1069.

Bedrosian, T. A., Fonken, L. K., Walton, J. C. & Nelson, R. J. (2011b). Chronic exposure to dim light at night suppresses immune responses in Siberian hamsters. *Biology Letters* **7**, 468–471.

Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife Management* **59**(2), 228–237.

Beier, P. (2006). Effects of artificial night lighting on terrestrial mammals. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 19–42. Island Press, Washington.

Berge, J., Cottier, F., Last, K. S., Varpe, O., Søreide, E. L. J., Eiane, K., Falk-Petersen, S., Willis, K., Nygard, H., Vogedes, D., Griffiths, C., Johnsen, G., Lorentzen, D. & Brierley, A. S. (2009). Diel vertical migration of Arctic zooplankton during the polar night. *Biology Letters* **5**, 69–72.

Berger, D. & Gotthard, K. (2008). Time stress, predation risk and diurnal-nocturnal foraging trade-offs in larval prey. *Behavioral Ecology and Sociobiology* **62**, 1655–1663.

Berson, D. M., Dunn, F. A. & Takao, M. (2002). Phototransduction by retinal ganglion cells that set the circadian clock. *Science* **295**, 1070–1073.

Biebouw, K. & Blumstein, D. T. (2003). Tammar wallabies (*Macropus eugeni*) associate safety with higher levels of nocturnal illumination. *Ethology, Ecology and Evolution* **15**, 159–172.

Bird, B. L., Branch, L. C. & Miller, D. L. (2004). Effects of coastal lighting on foraging behaviour of beach mice. *Conservation Biology* **18**, 1435–1439.

Black, A. (2005). Light induced seabird mortality on vessels operating in the Southern Ocean: incidents and mitigation measures. *Antarctic Science* **17**, 67–68.

Blake, D., Racey, P. A., Rydell, J. & Speakman, J. R. (1994). Use of lamplit roads by foraging bats in southern England. *Journal of Zoology* **234**, 453–462.

Boscarino, B. T., Rudstam, L. G., Eillenberger, J. L. & O'Gorman, R. (2009). Importance of light, temperature, zooplankton and fish in predicting the nighttime vertical distribution of *Mysis diluviana*. *Aquatic Biology* **5**, 263–279.

Bouskila, A. (1995). Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* **76**, 165–178.

Boyce, P. R. (2003). Human Factors in Lighting. Second Edition (). Taylor & Francis, London.

Bradshaw, W. E. (1976). Geography of photoperiodic response in diapausing mosquito. *Nature* **262**, 384–386.

Bradshaw, W. E. & Holzapfel, C. M. (2010). Light, time, and the physiology of biotic response to rapid climate change in animals. *Annual Review of Physiology* **72**, 147–166.

Bradshaw, W. E., Zani, P. A. & Holzapfel, C. M. (2004). Adaptation to temperate climates. *Evolution* **58**, 1748–1762.

Brainard, G. C., Richardson, B. A., King, T. S., Matthews, S. A. & Reiter, R. J. (1983). The suppression of pineal activity by different light irradiances in the Syrian hamster: a dose–response relationship. *Endrocrinology* **113**, 293–296.

Brainard, G. C., Richardson, B. A., Petterborg, L. J. & Reiter, J. (1982). The effect of different light intensities on pineal melatonin content. *Brain Research* **233**, 75–81.

British Standards Institute (2003). *Road lighting part 2: performance requirements*. BS EN13201-2:2003, London.

Britt, A. B. (1996). DNA damage and repair in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **47**, 75–100.

Bruce-White, C. & Shardlow, M. (2011). *A Review of the Impact of Artificial Light on Invertebrates*. Buglife, Peterborough.

Buchanan, B. W. (1993). Effects of enhanced lighting on the behaviour of nocturnal frogs. *Animal Behaviour* **45**, 893–899.

Buchanan, B. W. (2006). Observed and potential effects of artificial night lighting on anuran amphibians. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 192–220. Island Press, Washington.

Carrascal, L. M., Santos, T. & Tellería, J. L. (2012). Does day length affect winter bird distribution? Testing the role of an elusive variable. *PLoS ONE* **7**, e32733.

Cashmore, A. R., Jarillo, J. A., Wu, Y.-J. & Liu, D. (1999). Cryptochromes: blue light receptors for plants and animals. *Science* **284**, 760–765.

Cathey, A. R. & Campbell, L. E. (1975). Effectiveness of five vision-lighting sources on photo-regulation of 22 species of ornamental plants. *Journal of the American Society for Horticultural Science* **100**, 65–71.

Chittka, L. & Menzel, R. (1992). The evolutionary adaptation of flower colours and the insect pollinators' colour vision. *Journal of Comparative Physiology A* **171**, 171–181.

Cinzano, P. (2003). The growth of the artificial night sky brightness over North Americaa in the period 1947–2000: a preliminary picture. In *Light Pollution: The Global View* (ed. H. E. Schwarz), pp. 39–47. Kluwer Academic, Dordrecht.

Cinzano, P., Falchi, F. & Elvidge, C. D. (2001). The first World atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society* **328**, 689–707.

Clarke, J. A. (1983). Moonlights influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behavioral Ecoology and Sociobiology* **13**, 205–209.

Clarke, J. A., Chopko, J. T. & Mackessy, S. P. (1996). The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). *Journal of Herpetology* **2**, 192–197.

Cochran, W. W., Mouritsen, H. & Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**, 405–408.

Combreau, O. & Launay, F. (1996). Activity rhythms of houbara bustards (*Chalmydotis undulate macqueenii*) in relation to some abiotic factors. *Journal of Arid Environments* **33**, 463–472.

Cooper, C. B., Voss, M. A., Ardia, D. R., Austin, S. H. & Robinson, W. D. (2011). Light increases the rate of embryonic development: implications for latitudinal trends in incubation period. *Functional Ecology* **25**, 769–776.

Cos, S., Mediavilla, D., Martínez-Campa, C., González, A., Alonso-González, C. & Sánchez-Barceló, E. J. (2006). Exposure to light-at-night increases the growth of DMBA-induced mammary adenocarcinomas in rats. *Cancer Letters* **235**, 266–271.

Dacke, M., Nilsson, D.-E., Scholtz, C. H., Byrne, M. & Warrant, E. J. (2003). Insect orientation to polarized moonlight. *Nature* **424**, 33.

Daly, M., Behrends, P. R., Wilson, M. I. & Jacobs, L. F. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent *Dipodomys merriami*. *Animal Behaviour* **44**, 1–9.

Dartnall, H. J. A., Bowmaker, J. K. & Mollon, J. D. (1983). Human visual pigments: microspectrophotometric results from the eyes of seven persons. *Proceedings of the Royal Society B* **220**, 115–130.

Dauchy, R. T., Sauer, L. A., Blask, D. E. & Vaughan, G. M. (1997). Light contamination during the dark phase in "photoperiodically controlled" animal rooms: effect on tumor growth and metabolism in rats. *Laboratory Animal Science* **47**, 511–518.

Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* **16**, 365–380.

Densmore, R. V. (1997). Effect of day length on germination of seeds collected in Alaska. *American Journal of Botany* **82**, 274–278.

Dice, L. D. (1945). Minimum intensities of illumination under which owls can find dead prey by sight. *American Naturalist* **79**(784), 385–416.

Dick, R. (2011). Royal astronomical society of Canada guidelines for outdoor lighting in urban star parks. Available at http://rasc.ca/lpa/guidelines Accessed 24.08.2012.

Elvidge, C. D., Keith, D. M., Tuttle, B. T. & Baugh, K. E. (2010). Spectral identification of lighting type and character. *Sensors* **10**, 3961–3988.

Elvidge, C. D., Ziskin, D., Baugh, K. E., Tuttle, B. T., Ghosh, T., Pack, D. W., Erwin, E. H. & Zizhin, M. (2009). A fifteen year record of global natural gas flaring derived from satellite data. *Energies* **2**, 595–622.

Evans, J. A., Elliott, J. A. & Gorman, M. R. (2007a). Circadian effects of light no brighter than moonlight. *Journal of Biological Rhythms* **22**, 356–367.

Evans, W. R., Akashi, Y., Altman, N. S. & Manville, A. M. II (2007b). Response of night-migrating songbirds in cloud to colored and flashing light. *North American Birds* **60**, 476–488.

Falkenberg, J. C. & Clarke, J. A. (1998). Microhabitat use of deer mice: effects of interspecific interaction risks. *Journal of Mammalogy* **79**(2), 558–565.

Fernandez-Duque, E. (2003). Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behavioral Ecology and Sociobiology* **54**, 431–440.

Foster, R. G. & Roenneberg, T. (2008). Human responses to the geophysical daily, annual and lunar cycles. *Current Biology* **18**, R784–R794.

Fox, R. (2013). The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity* **6**, 5–19.

Frank, K. D. (1988). Impact of outdoor lighting on moths: an assessment. *Journal of the Lepidopterists' Society* **42**, 63–93.

Frank, K. D. (2009). Exploitation of artificial light at night by a jumping spider. *Peckhamia* **78**, 1–3.

Frank, D. W., Evans, J. A. & Gorman, M. R. (2010). Time-dependent effects of dim light at night on re-entrainment and masking of hamster activity rhythms. *Journal of Biological Rhythms* **25**, 103–112.

Futsaether, C., Vollsnes, A., Kruse, O. M. O., Otterholt, E., Kvaal, K. & Eriksen, A. B. (2009). Effects of the Nordic photoperiod on ozone sensitivity and repair in different clover species studied using infrared imaging. *Ambio* **38**, 437–443.

Garber, S. D. (1978). Opportunistic feeding behaviour of *Anolis cristatellus* (Iguanidae: Reptilia) in Puerto Rico. *Transactions of the Kansas Academy of Science* **81**, 19–80.

Gauthreaux, S. A. Jr. & Belser, C. G. (2006). Effects of artificial night lighting on migrating birds. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 67–93. Island Press, Washington.

Gehring, J., Kerlinger, P. & Manville, A. M. II (2009). Communication towers, lights, and birds: successful methods of reducing the frequency of avian collisions. *Ecological Applications* **19**, 505–514.

Gerrish, G. A., Morin, J. G., Rivers, T. J. & Patrawala, Z. (2009). Darkness as an ecological resource: the role of light in partitioning the nocturnal niche. *Oecologia* **160**, 525–536.

Gliwicz, Z. M. (1986). A lunar cycle in zooplankton. *Ecology* **67**, 883–897.

Grémillet, D., Kuntz, G., Gilbert, C., Woakes, A. J., Butler, P. J. & le Maho, Y. (2005). Cormorants dive through the Polar night. *Biology Letters* **1**, 469–171.

Gutman, R. & Dayan, T. (2005). Temporal partitioning: an experiment with two species of spiny mice. *Ecology* **86**, 164–173.

Gwinner, E. (1977). Photoperiodic synchronization of circannual rhythms in the European starling (*Sturnus vulgaris*). *Naturwissenschaften* **64**, 44–45.

Haim, A., Shanas, U., Zubidad, A. E. S. & Scantelbury, M. (2005). Seasonality and seasons out of time—the thermoregulatory effects of light interference. *Chronobiology International* **22**, 59–66.

Hart, N. S. & Hunt, D. M. (2007). Avian visual pigments: characteristics, spectral tuning, and evolution. *American Naturalist* **169**, S7–S26.

Health Council of the Netherlands (2000). *Impact of Outdoor Lighting on Man and Nature.* Publication No. 2000/25E. Health Council of the Netherlands, The Hague.

Heide, O. M. (2006). Daylength and thermal time responses of budburst during dormancy release in some northern deciduous trees. *Physiologia Plantarum* **88**, 531–540.

Heiling, A. M. (1999). Why do nocturnal orb-web spiders (Araneidae) search for light? *Behavioral Ecology and Sociobiology* **46**, 43–49.

Hogg, C., Neveu, M., Stokkan, K.-A., Folkow, L., Cottrill, P., Douglas, R., Hunt, D. M. & Jeffery, G. (2011). Arctic reindeer extend their visual range into the ultraviolet. *Journal of Experimental Biology* **214**, 2014–2019.

Holden, A. (1992). Lighting the night: technology, urban life and the evolution of street lighting. *Places* **8**, 56–63.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., Hänel, A., Kappeler, P. M., Völker, S., Schwope, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C. & Tockner, K. (2010a). The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society* **15**, 13.

Hölker, F., Wolter, C., Perkin, E. K. & Tockner, K. (2010b). Light pollution as a biodiversity threat. *Trends in Ecology and Evolution* **25**, 681–682.

Horváth, G., Kriska, G., Malik, P. & Robertson, B. (2009). Polarized light pollution: a new kind of ecological pollution. *Frontiers in Ecology and Environment* **7**, 317–325.

Howell, J. C., Laskey, A. R. & Tanner, J. T. (1954). Bird mortality at airport ceilometers. *Wilson Bulletin* **66**, 207–215.

Imber, M. J. (1975). Behaviour of petrels in relation to the moon and artificial lights. *Notornis* **22**, 302–306.

Jakle, J. A. (2001). *City Lights: Illuminating the American Night*. Johns Hopkins University Press, Baltimore.

Johnson, K. (1979). Control of Lampenflora at Waitomo Caves, New Zealand. In *Cave Management in Australia III: Proceedings of the 3rd Australasian Cave Tourism and Management Conference, Mount Gambier*, pp. 105–122. South Australian National Parks and Australian Speleological Federation, Adelaide.

Jones, J. & Francis, C. M. (2003). The effects of light characteristics on avian mortality at lighthouses. *Journal of Avian Biology* **34**, 328–333.

Kappeler, P. M. & Erkert, H. G. (2003). On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). *Behavioral Ecology and Sociobiology* **54**, 359–369.

Kelber, A., Balkenius, A. & Warrant, E. J. (2002). Scotopic colour vision in nocturnal hawkmoths. *Nature* **419**, 922–925.

Kelber, A. & Roth, L. S. V. (2006). Nocturnal colour vision- not as rare as we might think. *Journal of Experimental Biology* **209**, 781–788.

Kelber, A., Vorobyev, M. & Osario, D. (2003). Animal colour vision – behavioural tests and physiological concepts. *Biological Reviews* **78**, 81–118.

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E. & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology* **20**, 1735–1739.

Kolb, H. H. (1992). The effect of moonlight on activity in the wild rabbit (*Oryctolagus cuniculus*). *Journal of Zoology* **228**, 661–665.

Kotler, B. P. (1984). Effects of illumination on the rate of resource harvesting in a community of desert rodents. *American Midland Naturalist* **111**, 383–389.

Kramer, K. M. & Birney, E. C. (2001). Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. *Journal of Mammalogy* **82**, 535–544.

Kristiansen, K. (1988). Light quality regulates flower initiation, differentiation and development of *Campanula carpatica* Jacq. 'Karl Forster'. *Scientia Horticulturae* **35**, 275–283.

Kronfeld-Schor, N. & Dayan, T. (2003). Partitioning of time as an ecological resource.*Annual Review of Ecology. Evolution and Systematics* **34**, 153–181.

Kuijper, D. P. J., Schut, J., van Dullemen, D., Toorman, H., Goossens, N., Ouwehand, J. & Limpens, H. J. G. A. (2008). Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). *Lutra* **51**, 37–49.

Kyba, C. C. M., Ruhtz, T., Fischer, J. & Hölker, F. (2011*a*). Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. *PLoS ONE* **6**, e17307.

Kyba, C. C. M., Ruhtz, T., Fischer, J. & Hölker, F. (2011*b*). Lunar skylight polarization signal polluted by urban lighting. *Journal of Geophysical Research* **116**, D24106.

Kyba, C. C. M., Ruhtz, T., Fischer, J. & Hölker, F. (2012). Red is the new black: how the colour of urban skyglow varies with cloud cover. *Monthly Notices of the Royal Astronomical Society* **425**, 701–708.

Land, M. F. & Nilsson, D.-E. (2002). Animal Eyes. Oxford University Press, Oxford.

van Langevelde, F., Ettema, J. A., Donners, M., WallisDeVries, M. F. & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation* **144**, 2274–2281.

Larsen, L. O. & Pedersen, J. N. (1982). The snapping response of the toad *Bufo bufo*, towards prey dummies at very low light intensities. *Amphibia-Reptilia* **2**, 321–327.

Lashbrook, M. K. & Livezey, R. L. (1970). Effects of photoperiod on heat tolerance in *Sceloporus occidentalis occidentalis*. *Physiological Zoology* **43**, 38–46.

Le Corre, M., Olliver, A., Ribes, S. & Jouventin, P. (2002). Light-induced mortality of petrels: a 4-year study from Réunion Island (Indian Ocean). *Biological Conservation* **105**, 93–102.

Lefèvre, M. (1974). La maladie verte de Lascaux. *Studies in Conservation* **19**, 126–156.

Lewis, T. & Taylor, L. R. (1964). Diurnal periodicity of flight by insects. *Tansactions of the Royal Entomological Society of London* **116**, 393–476.

Lin, C. (2000). Photoreceptors and regulation of flowering time. *Plant Physiology* **123**, 39–50.

Lloyd, J. E. (2006). Stray light, fireflies and fireflyers. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 345–364. Island Press, Washington.

Lockwood, R. (2011). *A Review of Local Authority Road Lighting Initiatives Aimed at Reducing Costs, Carbon Emissions and Light Pollution.* Department for Environment, Food and Rural Affairs, London.

Longcore, T. & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and Environment* **2**, 191–198.

Longcore, T. & Rich, C. (2006). Synthesis. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 413–430. Island Press, Washington.

Lorne, J. K. & Salmon, M. (2007). Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the océan. *Endangered Species Research* **3**, 23–30.

Lyytimäki, J., Tapio, P. & Assmuth, T. (2012). Unawareness in environmental protection: the case of light pollution from traffic. *Land Use Policy* **29**, 598–604.

Marshall, N. J. & Oberwinkler, J. (1999). The colourful world of the mantis shrimp. *Nature* **401**, 873–874.

Martin, G. (1990). *Birds by Night*. T & A D Poyser, London.

Matzke, E. B. (1936). The effect of street lights in delaying leaf-fall in certain trees. *American Journal of Botany* **23**, 446–452.

McFarlane, R. W. (1963). Disorientation of loggerhead hatchlings by artificial road lighting. *Copeia* **1963**, 153.

Megdal, S. P., Kroenke, C. H., Laden, F., Pukkala, E. & Schernhammer, E. S. (2005). Night work and breast cancer risk: a systematic review and meta-analysis. *European Journal of Cancer* **41**, 2023–2032.

Menaker, M. (1968). Extraretinal light perception in the sparrow. I. Entrainment of the biological clock. *Proceedings of the National Academy of Sciences of the United States of America* **59**, 414–421.

Metcalfe, N. B., Valdimarsson, S. K. & Fraser, N. H. C. (1997). Habitat profitability and choice in a sit-and-wait predator: juvenile salmon prefer slower currents on darker nights. *Journal of Animal Ecology* **66**, 866–875.

Miller, M. W. (2006). Apparent effects of light pollution on singing behavior of American robins. *Condor* **108**, 130–139.

Milson, T. P. (1984). Diurnal behaviour of lapwings in relation to moon phase during winter. *Bird Study* **31**, 117–120.

Mills, A. M. (2008). Latitudinal gradients of biologically useful semi-darkness. *Ecography* **31**(5), 578–582.

Montevecchi, W. A. (2006). Influences of artificial light on marine birds. In Ecological Consequences of Artificial Night Lighting (eds C. Rich and T. Longcore), pp. 94–113. Island Press, Washington.

Moore, C. B. & Siopes, T. D. (2000). Effects of lighting conditions and melatonin supplementation on the cellular and humoral immune responses in Japanese quail *Coturnix coturnix japonica*. *General and Comparative Endocrinology* **119**, 95–104.

Moore, M. V., Pierce, S. M., Walsh, H. M., Kvalvik, S. K. & Lim, J. D. (2000). Urban light pollution alters the diel vertical migration of *Daphnia*. *Verhandlungen des Internationalen Verein Limnologie* **27**, 779–782.

Morrison, D. W. (1978). Lunar phobia in a Neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Animal Behaviour* **26**, 852–855.

Mougeot, F. & Bretagnolle, V. (2000). Predation risk and moonlight avoidance in nocturnal seabirds. *Journal of Avian Biology* **31**, 376–386.

Muheim, R., Phillips, J. B. & Akesson, S. (2006). Polarized light cues underlie compass calibration in migratory songbirds. *Science* **313**, 837–839.

Navara, K. J. & Nelson, R. J. (2007). The dark side of light at night: physiological, epidemiological and ecological consequences. *Journal of Pineal Research* **34**, 215–224.

Neff, M. M., Fankhauser, C. & Chory, J. (2000). Light: an indicator of time and place. *Genes and Development* **14**, 257–271.

Negro, J. J., Bustamante, J., Melguizo, C., Ruiz, J. L. & Grande, J. M. (2000). Nocturnal activity of lesser kestrels under artificial lighting conditions in Seville, Spain. *Journal of Raptor Research* **34**, 327–329.

Niva, C. C. & Takeda, M. (2003). Effects of photoperiod, temperature and melatonin on nymphal development, polyphenism and reproduction in *Halyomorpha halys* (Heteroptera: Pentatomidae). *Zoological Science* **20**, 963–970.

Niven, J. E. & Laughlin, S. B. (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *Journal of Experimental Biology* **211**, 1792–1804.

Nowinsky, L. & Puskás, J. (2010). Light trapping of *Helicoverpa armigera* in India and Hungary in relation with the moon phases. *Indian Journal of Agricultural Sciences* **81**, 152–155.

Osorio, D. & Vorobyev, M. (2008). A review of the evolution of animal colour vision and visual communication signals. *Vision Research* **48**, 2042–2051.

Outen, A. R. (1998). *The Possible Ecological Implications of Artificial Lighting*. Hertfordshire Biological Records Centre, Hertfordshire.

Packer, C., Swanson, A., Ikanda, D. & Kushnir, H. (2011). Fear of darkness, the full moon and the nocturnal ecology of African lions. *PLoS ONE* **6**, e22285.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Lourenço, R. & Campioni, L. (2011). Individual status, foraging effort and need for conspicuousness shape behavioural responses of a predator to moon phases. *Animal Behaviour* **82**, 413–420.

Penteriani, V., del Mar Delgado, M., Campioni, L. & Lourenço, R. (2010). Moonlight makes owls more chatty. *PLoS ONE* **5**, e8696.

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C. & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* **2**, 122.

Perry, G. & Fisher, R. N. (2006). Night lights and reptiles: observed and potential effects. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 169–191. Island Press, Washington.

Peters, A. & Verhoeven, K. J. F. (1994). Impact of artificial lighting on the seaward orientation of hatchling loggerhead turtles. *Journal of Herpetology* **28**, 112–114.

Polak, T., Korine, C., Yair, S. & Holderied, M. W. (2011). Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. *Journal of Zoology* **285**, 21–27.

Poot, H., Ens, B. J., de Vries, H., Donners, M. A. H., Wernand, M. R. & Marquenie, J. M. (2008). Green light for nocturnally migrating birds. *Ecology and Society* **13**, 47.

Price, M. V., Waser, N. M. & Bass, T. A. (1984). Effects of moonlight on microhabitat use by desert rodents. *Journal of Mammology* **65**, 353–356.

Queval, G., Issakidis Bourguet, E., Hoeberichts, F. A., Vandorpe, M., Gakière, B., Vanacker, H., Miginiac-Maslow, M., Van Breusegem, F. & Noctor, G. (2007). Conditional oxidative stress responses in the *Arabidopsis* photorespiratory mutant *cat2* demonstrate that redox state is a key modulator of daylength-dependent gene expression, and define photoperiod as a crucial factor in the regulation of H2O2-induced cell death. *The Plant Journal* **52**, 640–657.

Ragni, M. & D'Alcalà, M. R. (2004). Light as an information carrier underwater. *Journal of Plankton Research* **26**, 433–443.

Raven, J. A. & Cockell, C. S. (2006). Influence on photosynthesis of starlight, moonlight, planetlight and light pollution (reflections on photosynthetically active radiation in the universe). *Astrobiology* **6**, 668–676.

Reed, J. R., Sincock, J. L. & Hailman, J. P. (1985). Light attraction in endangered procellariiform birds: reduction by shielding upward radiation. *Auk* **102**, 377–383.

Reiter, R. J., Tan, D.-X., Korkmaz, A., Erren, T. C., Piekarski, C., Tamura, H. & Manchester, L. C. (2007). Light at night, chronodisruption, melatonin suppression, and cancer risk: a review. *Critical Reviews in Oncogenesis* **13**, 303–328.

Reiter, R. J., Tan, D. X., Sanchez-Barcelo, E., Mediavilla, M. D., Gitto, E. & Korkmaz, A. (2011). Circadian mechanisms in the regulation of melatonin synthesis: disruption with light at night and the pathophysiological consequences. *Journal of Experimental and Integrative Medicine* **1**, 13–22.

Rich, C. & Longcore, T. (2006a). Introduction. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 1–13. Island Press, Washington.

Rich, C. & Longcore, T. (eds) (2006*b*). *Ecological Consequences of Artificial Night Lighting*. Island Press, Washington.

Riegel, K. W. (1973). Light pollution. *Science* **179**, 1285–1291.

Riley, W. D., Bendall, B., Ives, M. J., Edmonds, N. J. & Maxwell, D. L. (2012). Street lighting disrupts the diel migratory pattern of wild Atlantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture* **330**, 74–81.

Rivera, G., Elliot, S., Caldas, L. S., Nicolossi, G., Coradin, V. T. R. & Borchert, R. (2002). Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees* **16**, 445–456.

Rodríguez, A., Rodríguez, B. & Lucas, M. P. (2012). Trends in numbers of petrels attracted to artificial lights suggest population declines in Tenerife, Canary Islands. *Ibis* **154**, 167–172.

Rojas, L. M., McNeil, R., Cabana, T. & Lachapelle, P. (1999). Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. *Brain, Behavior and Evolution* **53**, 29–43.

Rotics, S., Dayan, T. & Kronfeld-Schor, N. (2011*a*). Effect of artificial night lighting on temporally partitioned spiny mice. *Journal of Mammalogy* **92**, 159–168.

Rotics, S., Dayan, T., Levy, O. & Kronfeld-Schor, N. (2011*b*). Light masking in the field: an experiment with nocturnal and diurnal spiny mice under semi-natural field conditions. *Chronobiology International* **28**, 70–75.

Rydell, J. (1991). Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssoni*. *Holarctic Ecology* **14**, 203–207.

Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology* **6**, 744–750.

Rydell, J. (2006). Bats and their insect prey at streetlights. In *Ecological Consequences of Artificial Night Lighting* (eds C. Rich and T. Longcore), pp. 43–60. Island Press, Washington.

Rydell, J., Entwistle, A. & Racey, P. A. (1996). Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* **76**, 243–252.

Salmon, M., Tolbert, M. G., Painter, D. P., Goff, M. & Reiners, R. (1995). Behavior of loggerhead sea turtles on an urban beach. II. Hatchling orientation. *Journal of Herpetology* **29**, 568–576.

Santos, C. D., Miranda, A. C., Granadeiro, J. P., Lourenço, P. M., Saraiva, S. & Palmeirim, J. M. (2010). Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecologica* **36**, 166–172.

Schreuder, D. (2010). *Outdoor Lighting: Physics, Vision and Perception*. Springer-Verlag, New York.

Sharma, V. K., Chandrashekaran, M. K. & Nongkynrih, P. (1997). Daylight and artificial light phase response curves for the circadian rhythm in locomotor activity of the field mouse *Mus booduga*. *Biological Rhythm Research* **28**(Suppl. 1), 39–40.

Shuboni, D. & Yan, L. (2010). Nighttime dim light exposure alters the responses of the circadian system. *Neuroscience* **170**, 1172–1178.

Sinha, R. P. & Häder, D.-P. (2002). UV-induced DNA damage and repair. *Photochemical and Photobiological Sciences* **1**, 225–236.

Skutelsky, O. (1996). Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. *Animal Behaviour* **52**, 49–57.

Smit, B., Boyles, J. G., Brigham, R. M. & McKechnie, A. E. (2011). Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *Journal of Biological Rhythms* **26**, 241–248.

Smith, H. (2000). Phytochromes and light signal perception by plants – an emerging synthesis. *Nature* **407**, 585–591.

Speakman, J. R. (1991). Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology* **5**, 518–524.

Stevens, R. G. (1987). Electric power use and breast-cancer – a hypothesis. *American Journal of Epidemiology* **125**, 556–561.

Stevens, R. G. (2009). Light-at-night, circadian disruption and breast cancer: assessment of existing evidence. *International Journal of Epidemiology* **38**, 963–970.

Stone, E. L., Jones, G. & Harris, S. (2009). Street lighting disturbs commuting bats. *Current Biology* **19**, 1123–1127.

Sutherland, B. M. (1981). Photoreactivation. *Bioscience* **31**, 439–444.

Sutherland, W. J., Armstrong-Brown, S., Armsworth, P. R., Brereton, T., Brickland, J., Campbell, C. D., Chamberlain, D. E., Cooke, A. I., Dulvy, N. K., Dusic, N. R., Fitton, M., Freckleton, R. P., Godfray, H. C. J., Grout, N., et al. (2006). The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology* **43**, 617–627.

Svensson, A. M. & Rydell, J. (1998). Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera* spp.; Geometridae). *Animal Behaviour* **55**, 223–226.

Sweeney, B. M. (1963). Biological clocks in plants. *Annual Review of Plant Biology* **14**, 411–440.

Takemura, A., Ueda, S., Hiyakawa, N. & Nikaido, Y. (2006). A direct influence of moonlight intensity on changes in melatonin production by cultured pineal glands of the golden rabbitfish, *Siganus guttatus*. *Journal of Pineal Research* **40**, 236–241.

Tanner, J. E. (1996). Seasonality and lunar periodicity in the reproduction of pocilloporid corals. *Coral Reefs* **15**, 59–66.

Tarling, G. A., Buchholz, F. & Matthews, J. B. L. (1999). The effect of a lunar eclipse on the vertical migration behaviour of *Meganyctiphanes norvegica* (Crustacea: Euphausiacea) in the Ligurian Sea. *Journal of Plankton Research* **21**, 1475–1488.

Taylor, M. H., Leach, G. J., DiMichele, L., Levitan, W. M. & Jacob, W. F. (1979). Lunar spawning cycle in the mummichog, *Fundulus heteroclitus* (Pisces: Cyprinodontidae). *Copeia* **1979**, 291–297.

Taylor, E. L., Taylor, T. N. & Cúneo, N. R. (1992). The present is not the key to the past: a polar forest from the Permian of Antarctica. *Science* **257**, 1675–1677.

The Royal Commission on Environmental Pollution (2009). *Artificial Light in the Environment*. The Stationery Office, London.

Thorington, L. (1985). Spectral, irradiance, and temporal aspects of natural and artificial light. *Annals of the New York Academy of Sciences* **453**, 28–54.

Thresher, R. J., Vitaterna, M. H., Miyamoto, Y., Kazantsev, A., Hsu, D. S., Petit, C., Selby, C., Dawut, L., Smithies, O., Takahashi, J. S. & Sancar, A. (1998). Role of mouse cryptochrome blue-light photoreceptor in circadian photoresponses. *Science* **282**, 1490–1494.

Tigar, B. J. & Osborne, P. E. (1999). The influence of the lunar cycle on ground-dwelling invertebrates in an Arabian desert. *Journal of Arid Environments* **43**, 171–182.

Tin, T., Fleming, Z. L., Hughes, K. A., Ainley, D. G., Convey, P., Moreno, C. A., Pfeiffer, S., Scott, J. & Snape, I. (2009). Impacts of local human activities on the Antarctic environment. *Antarctic Science* **21**, 3–33.

Topping, M. G., Millar, J. S. & Goddard, J. A. (1999). The effects of moonlight on nocturnal activity in bushy-tailed wood rats (*Neotoma cinerea*). *Canadian Journal of Zoology* **77**, 480–485.

Tuxbury, S. M. & Salmon, M. (2005). Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation* **121**, 311–316.

Ugolini, A., Boddi, V., Mercatelli, L. & Castellini, C. (2005). Moon orientation in adult and young sandhoppers under artifical light. *Proceedings of the Royal Society B* **272**, 2189–2194.

Urbanski, J., Mogi, M., O'Donnell, D., DeCotiis, M., Toma, T. & Armbruster, P. (2012). Rapid evolution of photoperiodic response during invasion and range expansion across a climatic gradient. *American Naturalist* **179**, 490–500.

Vásquez, R. A. (1994). Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behavioral Ecology and Sociobiology* **34**, 375–381.

Vepsäläinen, K. (1974). Lengthening of illumination period is a factor in averting diapause. *Nature* **247**, 385–386.

Verheijen, F. J. (1958). The mechanisms of the trapping effect of artificial light sources on animals. *Archives Néerlandaises de Zoologie* **13**, 1–107.

Verheijen, F. J. (1985). Photopollution: artificial light optic spatial control systems fail to cope with. Incidents, causations, remedies. *Experimental Biology* **1985**, 1–18.

Vollsnes, A. V., Eriksen, A. B., Otterholt, E., Kvaal, K., Oxaal, U. & Futsaether, C. M. (2009). Visible foliar injury and infrared imaging show that daylength affects short-term recovery after ozone stress in *Trifolium subterraneum*. *Journal of Experimental Botany* **60**, 3677–3686.

Warrant, E. (2004). Vision in the dimmest habitats on Earth. *Journal of Comparative Physiology A* **190**, 765–789.

Warrant, E. & Dacke, M. (2010). Visual orientation and navigation in nocturnal arthropods. *Brain, Behavior and Evolution* **75**, 156–173.

Warrant, E. & Dacke, M. (2011). Vision and visual navigation in nocturnal insects. *Annual Review of Entomology* **56**, 239–254.

Wiltschko, W., Munro, U., Ford, H. & Wiltschko, R. (1993). Red light disrupts magnetic orientation of migratory birds. *Nature* **364**, 525–527.

Wiltschko, R., Stapput, K., Bischof, H.-J. & Wiltschko, W. (2007). Light-dependent magnetoreception in birds: increasing intensity of monochromatic light changes the nature of the response. *Frontiers in Zoology* **4**, 5.

Wiltschko, R., Stapput, K., Thalau, P. & Wiltschko, W. (2010). Directional orientation of birds by the magnetic field under different light conditions. *Journal of the Royal Society Interface* **7**, S163–S177.

Witherington, B. E. & Bjorndal, K. A. (1991). Influences of artificial lighting on the seaward orientation of hatchling loggerhead turtles *Caretta caretta*. *Biological Conservation* **55**, 139–149.

Wolff, R. J. (1982). Nocturnal activity under artificial lights by the jumping spider *Sitticus fasciger*. *Peckhamia* **2**, 32.

Woods, C. P. & Brigham, R. M. (2008). Common poorwill activity and calling behavior in relation to moonlight and predation. *Wilson Journal of Ornithology* **120**, 505–512.

Zhang, S., Wei, J., Guo, X., Liu, T.-X. & Kang, L. (2010). Functional synchronization of biological rhythms in a tritrophic system. *PLoS ONE* **5**, e11064.

Zubidat, A. E., Ben-Shlomo, R. & Haim, A. (2007). Thermoregulatory and endocrine responses to light pulses in short-day acclimated social voles (*Microtus socialis*). *Chronobiology International* **24**, 269–288.

(*Received 11 May 2012; revised 16 February 2013; accepted 27 February 2013; published online 8 April 2013*)

Folio N° 965

Volumen 35, Nº 4. Páginas 87-95
IDESIA (Chile) Diciembre, 2017

Estudio comparativo de diferentes trampas de luz (LEDs) con energía solar para la captura masiva de adultos polilla del tomate *Tuta absoluta* en invernaderos de tomate en la Provincia de Entre Ríos, Argentina

Comparative study among a variety of solar-powered LED traps to capture tomato leafminers *Tuta absoluta* adults by mass trapping in tomato greenhouses in the Province of Entre Ríos, Argentina

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RESUMEN

Existen a nivel mundial una gran variedad de artrópodos plaga que causan perjuicios en cultivos hortícolas. Entre estos se encuentra la polilla del tomate *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) la cual ha sido considerada como una de las principales plagas que afectan al cultivo de tomate bajo cubierta. La polilla del tomate produce daño directo por medio de sus larvas que realizan galerías en las hojas, brotes y cáliz de frutos inmaduros, en su proceso alimenticio interfiriendo en la fotosíntesis y el aspecto estético del fruto lo cual provoca graves pérdidas económicas.

El trabajo se realizó con el objetivo de evaluar la efectividad de diferentes tipos de trampas caseras con diodos emisores de luces (LEDs) alimentadas con energía solar en combinación con feromona para la captura de adultos de polilla del tomate como alternativa ecológica de control en un cultivo protegido de tomate en Concordia, Argentina. Se probaron diferentes trampas: con luces LEDs 430, 470 nm solas o en combinación con feromona sexual, los cuales fueron comparados con una trampa testigo de feromona sexual. Para ello se realizó una un diseño en bloques completamente al azar con dos repeticiones (invernaderos). Las trampas fueron distribuidas en forma aleatoria y colocadas en los caminos a una distancia equidistante entre ellas parte las cuales fueron rotadas quincenalmente para no producir sesgos en las capturas. Se evaluó el número promedio de capturas totales (adultos de polilla de tomate). Los resultados mostraron que la trampa con LEDs de 470 nm combinada con feromona sexual registró un mayor número de capturas de polilla del tomate respecto al resto de las trampas.

Palabras clave: polilla del tomate, trampas, LEDs, captura masiva, tomate.

ABSTRACT

A wide variety of arthropod pests that cause damage in agricultural crops can be found worldwide. The tomato leafminer (Meyrick) (Lepidoptera: Gelechiidae) is considered to be one of the most significant pests which affects greenhouse tomato crops. The tomato leafminer causes direct damage when larvae produce galleries in leaves, shoots and calix of immature fruits throughout their feeding process, which affects the photosynthesis and makes the fruit unattractive resulting in serious economic loss. This research was carried out to investigate the efficacy of a variety of handmade mass trapping equipped with solar-powered Light Emitting Diodes (LEDs) and combined with pheromones, as an alternative biological control, in order to capture tomato leafminers adults in greenhouse tomato crops in Concordia, Argentina. Different types of traps were tested, namely, traps supplemented with LEDs 430, 470 nm with or without sex pheromones, which were compared to a witness trap of sex pheromone. The study was designed as a randomized complete block design replicated 2 times (greenhouses). These traps were placed at random and along the corridor at an even distance among one another changed on a two-weekly basis in order to eliminate bias from the capture results. These results showed that the total average number of tomato leafminer adults caught in the trap equipped with LEDs 470 nm in combination with sex pheromone was higher compared to the other traps.

***Key words**: tomato leafminer, traps, LEDs, massive trapping, tomato.*

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Fecha de Recepción: 29 Junio, 2017.
Fecha de Aceptación: 20 Septiembre, 2017.

DOI:

Introducción

Entre las principales plagas del cultivo de tomate *Lycopersicon esculentum* Mill. en América del Sur se encuentra *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Pican ço *et al*., 2007). Este insecto es originario de América del Sur y se distribuye en un estrecho territorio limitado por Ecuador, Cordillera de los Andes, Norte de Chile y litoral del Océano Pacífico, incluyendo el archipiélago de las islas Galápagos (Giordano & Silva, 1999). La polilla del tomate fue introducida en Europa vía España (2006) y, por su gran capacidad de dispersión, ha llegado prácticamente a todo el continente. Recientemente fue introducida en África y Asia, donde ha causado grandes perjuicios (Desneux *et al*., 2010). Está presente en los cultivos de tomate bajo cubierta en la Provincia de Entre Ríos, Argentina. Los daños causados por las larvas de este insecto afectan la productividad, ya que reducen el área fotosintética al alimentarse del mesófilo foliar (Bogorni *et al*., 2003) como así también afectan el crecimiento vertical al minar, tallo, brote apical, los botones florales, las flores y, principalmente, los frutos (Leite *et al*., 2004; Potting *et al*., 2009). Las pérdidas ocasionadas por este insecto varían entre los estadios fenológicos del tomate y a lo largo del año (Castelo Branco, 1992). En ataques severos, a causa de su alimentación, pueden destruir completamente las hojas del tomate, los brotes tiernos y comprometer los frutos en todas sus etapas (EPPO, 2011), preferentemente en los frutos inmaduros penetrando por el extremo del pedúnculo, lo cual favorece la entrada de patógenos que da como resultado un deterioro en su calidad para la comercialización (Potting *et al*., 2009). Es una plaga que exhibe un alto potencial de multiplicación, ya que los adultos son nocturnos y durante el día pueden encontrarse escondidos entre las hojas (Hariza nova, 2009). Si bien *T. absoluta* vuela a poca altura (30 - 60 cm), sobre la planta huésped (Al-Zaidi, 2009a), pueden desplazarse con gran facilidad varios kilómetros a la deriva con la ayuda del viento (van Deventer, 2009).

En Argentina esta plaga se controla exclusivamente a través del uso de insecticidas. La alta densidad de población de polilla del tomate en el cultivo requiere la aplicación reiterada de tratamientos con insecticidas de síntesis química (organofosforados y piretroides), cuyos resultados son tan poco eficaces (Siquiera *et al*., 2000) y, tan importantes en un en cultivo bajo cubierta, que es necesario intensificar los tratamientos que inexorablemente conducen a un uso indiscriminado de estos productos de síntesis química. Ésto ocasiona los siguientes perjuicios: 1) destrucción del complejo de enemigos naturales, 2) incremento de costos de producción, 3) aumento del desarrollo de resistencia de poblaciones de la polilla a insecticidas; y 4) riesgos para la salud de productores, consumidores y contaminación ambiental.

En los cultivos de tomate bajo cubierta de la Provincia de Entre Ríos, el uso indiscriminado de insecticidas de síntesis química es el principal y casi exclusiva forma de control de la polilla del tomate. Entre los o dificultades que se presentan es, por una parte, que sólo algunos productores tienen acceso a utilizar insecticidas selectivos con principios activos para su control con bajo impacto, compatibles con la fauna auxiliar existente y, por otro lado, la falta de precaución en alternar el uso de las materias activas con diferentes formas de actuación, formulaciones y aplicaciones adecuadas.

La utilización de feromona sexual es una alternativa de control para la *T. absoluta* que reduce el uso de insecticidas. Esta feromona puede ser colocada en dos tipos de trampas. 1) trampa delta, con el propósito de realizar captura de adultos para hacer un seguimiento de la plaga. En este caso se puede determinar el riesgo para el cultivo (Cabello *et al.* 2010) teniendo en cuenta que no siempre el hecho de no capturar adultos se relaciona con la ausencia de la plaga, por lo tanto, debe monitorearse periódicamente el cultivo para detectar la presencia de orugas en folíolos. (Cabello *et al.* (2010), 2) trampa de agua, con la finalidad de realizar una captura masiva de adultos de polilla del tomate (Martí *et al*., 2010). Ambos tipos de trampas son complementos fundamentales en el marco del manejo integrado de plagas (MIP). Con respecto a la captura masiva, si bien existen varios estudios a campo realizados, éstos resultan tener una alta eficacia únicamente para la captura de machos temprano en la mañana (Ferrara *et al*., 2001). Considerando que cada hembra fecundada tiene una longevidad de días (24) y puede poner más de 250 huevos en los brotes como en el envés de las hojas, una pequeña proporción de éstas vivas podría generar graves daños al cultivo.

Sobre la premisa que los ojos compuestos de los insectos en general perciben el color por medio

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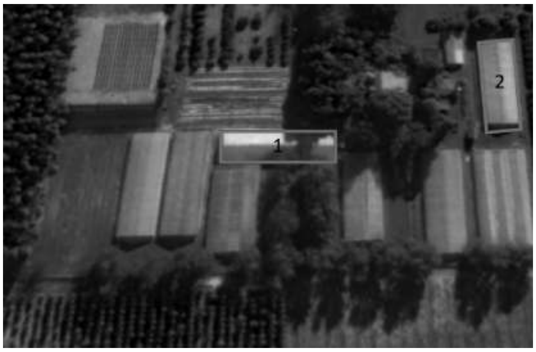

Figura 1. Vista aérea de la zona del ensayo en contorno verde, superficie del estudio.

de tres diferentes tipos de células fotorreceptores sensibles al espectro de la luz con picos en la región del ultravioleta, azul y verde, (370-390 nm, 450 - 470 nm, y 530 - 550 nm), respectivamente, los cuales se han conservado a través de su evolución. (Briscoe & Chittka, 2001), se han llevado a cabo estudios en los cuales varias especies de polillas son atraídas por iluminación nocturna artificial, especialmente, con alta emisión de luz en la región del UV (Frank, 2006). Esta atracción está posiblemente determinada por la sensibilidad a la luz, lo cual se supone está relacionada con el tamaño del cuerpo y el de los ojos, concluyendo que los más grandes serían más sensibles a la luz que los pequeños (Yack *et al.,* 2004). Con respecto a los microlepidópteros, estudios realizados por de Oliveira *et al*., (2008) demostraron que los adultos machos y hembras de *Tuta absoluta* fueron atraídos en forma eficiente por lámparas de luz negra (BLB) y lámparas de UV, las cuales tienen una longitud de onda entre (365 - 400 nm).

En cuanto a los diodos emisores de luz (LEDs), éstos están en estado sólido y son fuentes de luz de semiconductores con algunas propiedades específicas, es decir, son pequeños, de alta estabilidad mecánica, alta confiabilidad, largo tiempo de vida operacional, utilizan poca energía y son de bajo costo y ecológicos (Schubert, 2003). Estos LEDs han sido también utilizados en algunas aplicaciones de la vida cotidiana como el control remoto, pantallas numéricas, indicador de estados, pantallas planas, comunicaciones ópticas etc… (Schubert & Yao, 2002). En general pocos estudios han sido llevados a cabo para evaluar la respuesta de insectos a la luz emitida por LEDs. A su vez, teniendo en cuenta las siguientes características: 1) su monocromía, 2) la amplia variabilidad de colores, 3) el rango de longitud de onda típico se encuentra comprendido entre 20 nm y 60 nm, con lo cual podemos elegir aquella longitud de onda del color requerido. Por lo anteriormente expuesto, se plantea como objetivo de esta investigación determinar la mejora en la eficiencia de la captura de adultos machos colocando en trampas de agua utilizadas para la captura masiva diodos emisores de luz (LEDs) de diferentes longitudes de onda con la finalidad de poder desarrollar las bases para futuras estrategias integradas a las ya existentes para la prevención y el tratamiento de la plaga.

Objetivo

Comparar distintos tipos de trampas caseras con luces LEDs en combinación con feromona para la captura de adultos de polilla del tomate (*Tuta absoluta*).

Materiales y métodos

Manejo de los invernaderos y del cultivo de tomate

El ensayo se llevó a cabo en un establecimiento hortícola de producción comercial situado en la localidad de Concordia, localizado en las coordenadas GPS 31º 20’ 28,46’’ S; 58º 2’ 0,29” O; 516 (s.n.m), Departamento de Concordia, Provincia de Entre Ríos, Argentina.

Los muestreos de adultos de polilla del tomate se realizaron en un periodo desde el 15 de agosto de 2016 hasta el 29 de diciembre de 2016. El ensayo se llevó a cabo en dos invernaderos con estructura de madera tipo a Dos Aguas (DA) con una superficie total de 800 m^2 cada uno, orientación este-oeste, con las siguientes dimensiones: 16 m de frente por 50 m de lateral, con una altura de 2,2 m en los laterales y 3,5 m en la parte central con un total de 10 surcos apareados a 1 m entre sí y 0,25 m entre plantas de tomate (c.v., “ELPIDA”, Enza Zaden) (redondo híbrido indeterminado), logrando una densidad de plantas de 4 plantas/ m^2. Las plantas se condujeron a un sólo tallo y el tutorado se realizó con hilo plástico. En el momento que las plantas alcanzaron la altura de 1,70 m se bajaron y se apoyó el tallo en el acolchado plástico del surco. El riego y la fertilización se realizaron según las necesidades del cultivo. No se aplicaron hormonas para el cuaje de las flores.

Los estadios fenológicos del cultivo durante el período que se desarrolló el ensayo fue de crecimiento del fruto, comienzo de maduración, maduración y, finalmente, cosecha. Este establecimiento fue seleccionado por la disposición del productor a que se realice y además por la incidencia de la polilla del tomate en campañas anteriores.

Condiciones climáticas de la zona de muestreo

En la Figura 2 se observan los valores medios de temperatura y humedad relativa en el período del ensayo.

Tratamientos

Las trampas que se evaluaron fueron las siguientes:

- Trampa casera con piso engomado y sin feromona (TA) (Figura 3).
- Trampa casera con piso engomado con feromona (TF) (Figura 3).
- Trampa casera con dispositivo LED de 430 nm superior, piso engomado y sin feromona LBL - F (Figura 4).
- Trampa casera con dispositivo LED de 430 nm superior, piso engomado y con feromona LBL + F (Figura 4).
- Trampa casera con dispositivo LED de 470 nm superior, piso engomado y sin feromona LBH - F (Figura 5).
- Trampa casera con dispositivo LED de 470 nm superior, piso engomado y con feromona LBH + F (Figura 5).

Figura 3. Trampa casera sin luz LED.

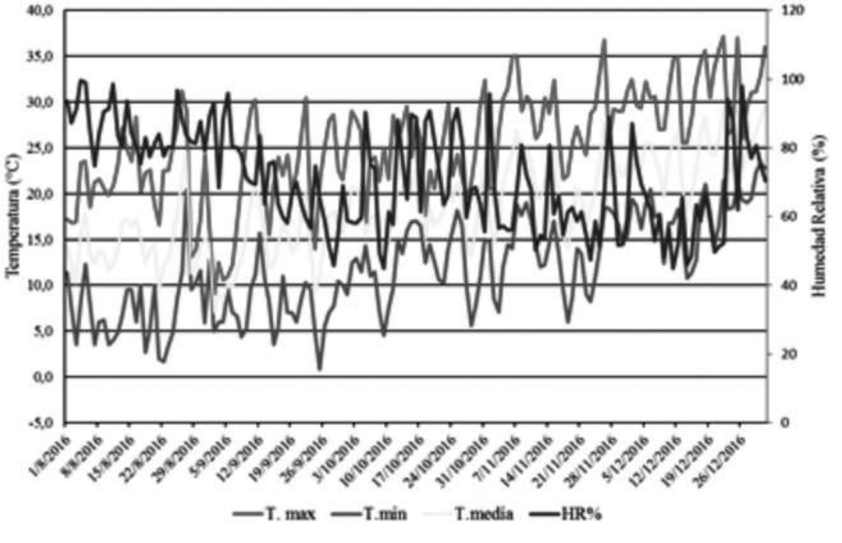

Figura 2. Datos meteorológicos registrados por la estación meteorológica situada en la EEA INTA Concordia durante el periodo del ensayo de agosto de 2016 hasta diciembre del 2016 (valores de temperatura máxima, mínima y media y de humedad relativa).

Figura 4. Trampa casera con luz LED 430 nm.

Figura 5. Trampa casera con luz LED 470 nm.

La trampa casera consiste en un bidón de plástico transparente reciclado de 5 litros de capacidad. Para el caso de los tratamientos trampa testigo absoluto sin feromona (TA) y trampa testigo con feromona (TF) en la parte superior del bidón queda cerrado con la misma tapa. Asimismo, en la parte media del bidón se abrieron dos ventanas laterales de 20 cm. de ancho y 20 cm. de alto para permitir el ingreso de los adultos de polilla del tomate y además situar el piso engomado sobre el cual, dependiendo del tratamiento que se utilice, es cebada o no con una feromona como atrayente sexual. Cabe destacar la originalidad de estas trampas por la simplicidad en la confección, su bajo costo y la alimentación a traves de luz solar respecto de las ya conocidas trampas de luz utilizadas para la captura masiva de adultos de la polilla del tomate en invernadero como a campo.

Todas las trampas equipadas con LEDs fueron alimentadas con una fuente de baja tensión proveniente de un panel solar que transforma la energía solar en eléctrica que, a su vez, es acumulada en una batería recargable que está incluida. Asimismo, este dispositivo posee un fotosensor y carga automática (encendido y apagado automático), cuya energía se almacena en una batería AA recargable de 1.2 volts Ni-MH de 2900 mah incluida, lo que permite mantener encendido el LED desde el anochecer hasta el amanecer.

Las trampas LBL- F y LBL + F son trampas TA y TF a las que se les realizó un corte transversal en la parte superior para montar la lámpara LED de 1 Watts de potencia con una longitud de onda de 430nm (SHENZEN SEALAND OPTOELECTRONICS CO., LTD).

Las trampas LBH - F y LBH + F son trampas TA y TF a las que se les realizó un corte transversal en la parte superior para montar la lámpara LED de 1 Watt de potencia con una longitud de onda de 470 nm (SHENZEN SEALAND OPTOELECTRONICS CO., LTD).

Diseño del ensayo

El diseño del ensayo fue en bloques (DBCA) al azar con 5 tratamientos y 2 repeticiones o bloques (invernadero). Las repeticiones estuvieron separadas entre ellas como mínimo 12 metros.

Las trampas se mantuvieron durante aproximadamente 5 meses en invernadero, desde el 1 de agosto al 29 de diciembre de 2016 y fueron colocadas sobre del suelo en los caminos que separan a los camellones para capturar la mayor parte de polillas que emergen del suelo como así también para favorecer la difusión de la feromona y la fuente de luz. Ésta última permaneció encendida desde el anochecer hasta el amanecer y estuvo ubicada por debajo de la altura de los zócalos laterales del invernadero para evitar atraer polillas del exterior.

Las trampas se rotaron en el invernadero cada 25 días, según indica la Figura 6, de manera que, al cabo de 6 rotaciones, todas las trampas habían pasado por todas las ubicaciones. Esto se realizó de esta manera con el fin de eliminar el efecto de cualquier foco que pudiera existir dentro del invernadero y pudiera influir en las capturas. Asimismo, se decidió cambiar quincenalmente los pisos engomados como así también la feromona sexual de cada una de las trampas en las que fue colocada.

Sistema de evaluación

Las trampas se colocaron el 15 de agosto de 2016 y se retiraron el 29 de diciembre del mismo año. Para la evaluación de la comparación de las trampas se efectuaron un total de 8 registros quincenales y, posteriormente, se contabilizaron sobre cada una el número total de adultos de polilla del tomate (machos y hembras) que habían quedado adheridas en el piso engomado en laboratorio mediante una lupa estereoscópica de 10 a 40 x de magnificación. Además, semanalmente se monitorearon distintas plagas y enfermedades en las plantas de tomate en ambos invernaderos para observar si alguna de éstas había llegado a un umbral de intervención, así como también para corroborar la carga de las pilas que alimentaban las lámparas LEDs con un multímetro portátil para mantener su funcionamiento desde el amanecer hasta el anochecer.

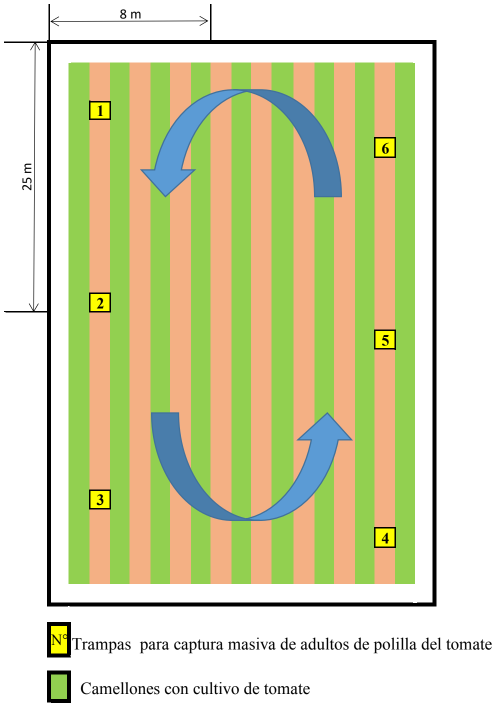

Figura 6. Croquis de la distribución las trampas en invernadero.

Los datos del número de capturas de adultos de polillas del tomate que se obtuvieron durante el período del ensayo mostraron un patrón de distribución muy alejado de la distribución Normal con signos de fuerte asimetría. Se observó muy alta frecuencia de valores bajos del número de adultos (0-14 adultos) y poca frecuencia de valores más altos (130-160 adultos). Por esta razón se decidió utilizar un modelo lineal generalizado mixto (Zuur *et al.*, 2009; Di Rienzo *et al.*, 2015), el cual permitió utilizar la distribución Poisson de acuerdo con la naturaleza de la variable respuesta. El modelo contaba con los tratamientos y los invernáculos, como efectos fijos, y las fechas de muestreo, como efecto aleatorio. Las medias de los distintos tratamientos se compararon con la prueba LSD de Fisher con un nivel de significación del 5%. Se utilizó el paquete estadístico InfoStat.

Resultados

Registros de capturas de la polilla del tomate

Los resultados estadísticos obtenidos durante el período del ensayo permitieron detectar diferencias significativas del número de adultos de polilla del tomate capturados por tipo de trampa ($X^2_{tratamiento}$=3135,86; df=5: p<0.0001).

En la Tabla 1 y Figura 7 se observan dos grupos de significación bien diferenciados, los constituidos por los tipos de trampa que combinan lámparas LEDs con feromona sexual y el otro grupo con los tipos de trampas con LEDs y feromona sin combinar, siendo las trampas del primer grupo las que mayor capturas promedio registraron (76,68 adultos de polilla del tomate/LBH+F) y (70,37 adultos de polilla del tomate/LBL+F). En el caso de las trampas no combinadas, la trampa equipada con feromona fue la que obtuvo mayores capturas (34,62 adultos de polilla del tomate/TF) y le seguían por un amplio margen las trampas con fuente de luz (5.75 polillas del tomate/ LBH-F), (4.56 polilla del tomate/LBL-F 4.56) y, por último, la trampa sin feromona (2.06 polillas del tomate/ TA).

Tabla 1. Resultados de test de comparación de medias ajustadas del número de capturas de *Tuta absoluta* (media ± Error Standard) para cada uno de los tratamientos evaluados.

Tipo de trampa	(Medias ± D.S.)
Trampa casera en bidón con LED 470 nm con feromona (LBH+F)	35.16 ± 22.59 a
Trampa casera en bidón con LED 430 nm con feromona (LBL+F)	33.60 ± 21.59 a
Trampa casera en bidón con feromona (TF)	17.07 ± 10.98 b
Trampa casera en bidón con LED 470 nm sin feromona (LBH-F)	2.64 ± 1.71 c
Trampa casera en bidón con LED 430 nm sin feromona (LBL-F)	2.09 ± 1.36 c
Trampa casera en bidón sin feromona (TA)	1.02 ± 0.68 d

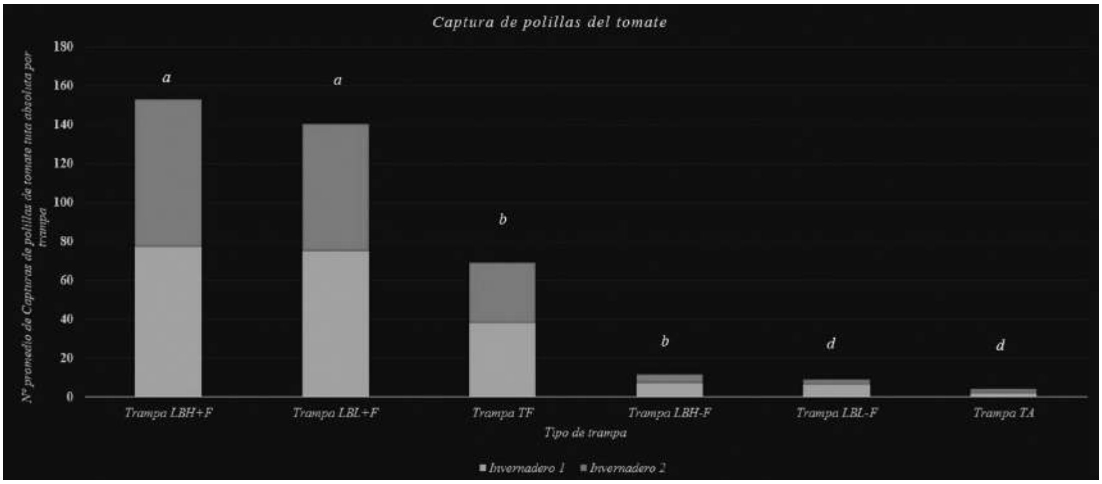

Figura 7. Número promedio de polillas del tomate por trampa y por tipo de trampa durante el periodo del ensayo.

Discusión y conclusión

Los datos presentados en la Tabla 1 muestran que la *T. absoluta* es atraída por fuente de luz de longitudes de onda de 430nm y 470 nm como señal de orientación luego de observar un mayor número de capturas en trampas sólo cuando éstas estaban en combinación con atrayentes, en este caso feromona sexual. Estos datos son coincidentes con los obtenidos por (Matos *et al.*, 2012), quienes evaluaron diferentes tipos de trampas para captura masiva de adultos de *T. absoluta* tomate y registraron mayor captura en las que se combinaba una señal química, en este caso feromona sexual, con un dispositivo lumínico. Asimismo, es conocido que en el orden Lepidoptera en general tienen receptores con sensibilidad espectral en la región del azul con picos cercanos a los 460nm (Briscoe & Chittka, 2001). Dentro de los lepidópteros, la polilla del tabaco (*Manduca sexta*) ha sido durante mucho tiempo un insecto experimental utilizado para diferentes estudios referidos a los potenciales eléctricos en respuesta al estímulo lumínico, que permitieron conocer que su ojo contiene tres diferentes tipos de fotorreceptores con sensibilidad espectral, en el pico del espectro UV (370 nm - 390 nm), azul (450 - 470 nm) y la región verde del espectro (370 a (530 - 550 nm), provocando así la estimulación de cada uno de los fotorreceptores a diferentes respuestas en su comportamiento (Cutler *et al.*, 1995). Sobre la base de los resultados y las citas anteriormente mencionadas, podemos concluir que las trampas de feromonas en combinación con los dispositivos LEDs de longitudes de onda de 430 nm y 470 nm produjeron un sinergismo que funcionó como orientación o señal de navegación que dio como resultado el máximo de las capturas en ambos invernaderos.

De los 6 tipos de trampas evaluadas, las que tenían montadas luces LEDs (LBH+F y LBL+F) fueron las que obtuvieron un número significativamente mayor de capturas de polilla del tomate, seguida por la trampa con feromona

(TF) la cual registró una captura de polillas significativamente menor con respecto a las anteriores pero mayor al resto de las trampas (LBH-F, LBL-F, TA). Éstas últimas no contabilizaron caídas de adultos de polilla significativamente diferentes entre sí.

En la comparación entre los tipos de trampas con LEDs (LBH+F y LBL+F) no se obtuvieron diferencias significativas. A continuación, se exponen las ventajas y desventajas de las trampas LEDs:

Ventajas:

1) Su bajo costo al igual que el de los paneles solares para el armado del dispositivo de captura masiva;
2) Alimentación autónoma, lo cual no exige ningún tipo de alimentación de red eléctrica y además brinda mayor seguridad en su manipulación por su bajo voltaje.
3) Su bajo mantenimiento y la adaptabilidad de su funcionamiento a diferentes condiciones meteorológicas, incluso a campo bajo la lluvia.

Desventajas:

1) Su colocación debe realizarse de manera tal que el cultivo no obstaculice la emisión de luz ni en los lugares sin sombra para permitir la carga completa de la batería.
2) Su ubicación en lugares donde no emita señal de llamada a insectos externos al invernadero, en nuestro caso particular, en los cuales los invernaderos no estén cerrados herméticamente por mallas por debajo de la altura del zócalo.

Tomando en consideración que es una técnica no contaminante para el medio ambiente y que su utilización adecuada puede ser una valiosa herramienta como complemento de otras que constituyen el manejo integrado de plagas (MIP), esto plantea la necesidad de seguir investigando este tipo de trampas con la finalidad de aumentar su eficacia para realizar la captura de polilla de tomate.

Agradecimientos

Este trabajo pudo ser realizado gracias al apoyo de:

1) Proyecto específico INTA - PNHFA 1106082. “Tecnología apropiada para la sustentabilidad con énfasis en sistemas hortiflorícolas con énfasis en cultivos protegidos”.
2) Red de Agroecologia INTA - REDAE 1136021
3) Proyecto Regional con Enfoque Territorial INTA - PRETERIOS 1263305.” Contribuir al desarrollo socio económico del noreste de Entre Ríos, en un marco de competitividad, salud ambiental y equidad social”.
5) A la familia del productor Víctor Campeglia, que siempre me recibió con buena disposición, durante los muestreos.
4) A la traductora Pública en Inglés Mónica Castresana, por sus aportes, observaciones y correcciones.
6) A los Ingenieros en electrónica Gonzalo Castresana y Jorge Jones, por sus aportes en la parte electrónica.
7) Al Ing. Agr. Javier Rosenbaum por el uso del vehículo asignado a PROHUERTA en los momentos en que no había disponibilidad de otros.

Literatura Citada

Al-Zaidi, S.
2009. Recommendations for the Detection and Monitoring of *Tuta absoluta*. Russell IPM. Disponible en http://www.russellipm-agriculture.com/case-studies/tuta-absoluta/ Consultado: 19/ene/2017.

Bogorni, P.C.; da Silva, R.A. &G.S. Carvalho.
2003. Consumo de mesofilo foliar por *Tuta absoluta* (Meyrick, 1971) (Lepidoptera: Gelechidae) em tres cultivares de *Lycopersicon esculentum* Mill. Ciencia Rural, 33 (1): 7-11.

Briscoe, A.D., & L. Chittka.
2001. The evolution of color vision in insects. Annual Review of Entomology, 46: 471-510.

Cabello, T., Gallego, J.R., Fernández, F.J., Vila, E., Soler, A. & A. Parra.
2010. Aplicación de parasitoides de huevos en el control de *Tuta absoluta en* España. *Phytoma* España, 217: 53-59.

Castelo-Branco, M.
1992. Flutuação populacional da traça-do-tomateiro na região do Distrito Federal. Horticultura Brasileira, 10: 33-34.

Cutler, D.E., Bennett, R.R., Stevenson, R.D & R.H. White.
1995. Feeding-behavior in the nocturnal moth *Manduca sexta* is mediated mainly by blue receptors, but where are they located in the retina. *Journal of Experimental Biology,* 198: 1909-1917.

Desneux, N., Wajnberg, E., Wyckhuys, K.A.G., Burgio, G. & S. Arpaia.
2010. Biological invasion of European tomato crops by *Tuta absoluta*: ecology, geographic expansion and prospects for biological control. *Journal of Pest Science,* 83:197-215.

Di Rienzo J.A., Casanoves F., Balzarini M.G.; Gonzalez L.; Tablada M., Robledo C.W.
2015. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.

de Oliveira, A.C.R., Veloso, V.R.S., Barros, R.G., Fernandes, P.M. & E.R.B., de Souza.
2008. Captura de *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) com armadilha luminosa na cultura do tomateiro tutorado. *Pesquisa Agropecuária Tropical*, 38: 153-157.

EPPO.
2011. *Tuta absoluta* continues to spread around the Mediterranean Basin (2011/076). EPPO Reporting Services 4 (076). 30 p.

Ferrara, F.A., Vilela, E.F., Jham, G.N., Eiras, A.E., Picanço, M.C., Attygalle, A.B., Svatos, A., Frighetto, R.T.S. & J. Meinwald.
2001. Evaluation of the synthetic major component of the sex pheromone of *Tuta absoluta* (Myerick) (Lepidoptera: Gelechiidae). *Journal of Chemical Ecology,* 27 (5): 907-917.

Frank, K.D.
2006. Effects of artificial night lighting on moths. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press. Washington DC, Us. pp. 305-344.

Giordano, L., Silva, C.
1999. Hibridação em tomate. In: BORÉM, A. (Ed.). Hibridação artificial de plantas. UFV. Viçosa, Brasil. pp. 463-480.

Harizanova, V., Stoeva A., Mohamedova M.
2009. "Tomato Leaf Miner, *Tuta absoluta* (Povolny) (Lepidoptera: Gelechiidae) - First Record in Bulgaria", *Agricultural Science and Technology,* 1 (3): 95-98.

Leite, G.L.D., Picanço, M., Jham, G.N., & Marquini, F.
2004. Intensity of *Tuta absoluta* (Meyrick, 1917) (Lepidoptera: Gelechiidae) and *Liriomyza* spp. (Diptera: Agromyzidae) attacks on *Lycopersicum esculentum* mill. Leaves. *Ciência e Agrotecnologia*, 28: 42-48.

Martí Martí S., Muñoz Celdrán, Casagrande E.
2010. El uso de feromonas para el control de *Tuta absoluta*: primeras experiencias en campo. *Phytoma España*, 217: 35-40.

Matos, T., Figueiredo, E. & A. Mexia.
2012. Sexual pheromone traps with light for mass trapping of *Tuta Absoluta* (Meyrick), yes ou no?. *Revista de Ciências Agrárias,* 35, (2): 282-286.

Picanço, M.C., Bacci, L., Crespo A.L., Miranda M.M. & J.C. Martins.
2007. Effect of integrated pest management practices on tomato production and conservation of natural enemies. *Agricultural and Forest Entomology*, 9, (4): 327-335.

Potting, R.; van der Gaag, D.J.; Loomans, A.; van der Straten, M.; Anderson, H.; MacLeod, A.; Guitián Castrillón, J.M.; Cambra, G.V.
2013. *Tuta absoluta*, tomato leaf miner moth or South American tomato moth, Ministry of Agriculture, Nature and Food Quality, Plant Protection Service of the The Netherland.Wageningen,The Netherlands. 28 pp.

Schubert, E.F.
2003. Light-Emitting Diodes. Cambridge University Press, Cambridge, New York. 313 p.

Siqueira, H.A.A., Guedes, R.N.C. & M.C. Picanço.
2000. Cartap resistance and synergism in populations of *Tuta absoluta* (Lep., Gelechiidae). *Journal Applied Entomology*, 124: 233-238.

Van Deventer, P.
2009. Leaf miner threatens tomato growing in Europe. *Fruit and Vegetal Technology,* 9: 10-12.

Yack, J.E., Johnson, S.E., Brown, S.G. & E.J. Warrant.
2007. The eyes of *Macrosoma sp.* (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. *Arthropod Structure & Development,* 36; 11-22.

Zuur, A.F.; Ieno, E.N.; Walker, N.J.; Saveliev, A.A. y Smith, G.M.
2009. Zero-truncated and zero-inflated models for count data. Mixed effects models and extensions in ecology vith R. ED Springer New York, US. pp. 261-293.

Ecological Entomology

Ecological Entomology (2014), DOI: 10.1111/een.12174

Folio N° 975

INVITED REVIEW

Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review

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Abstract. 1. Moths (Lepidoptera) are the major nocturnal pollinators of flowers. However, their importance and contribution to the provision of pollination ecosystem services may have been under-appreciated. Evidence was identified that moths are important pollinators of a diverse range of plant species in diverse ecosystems across the world.

2. Moth populations are known to be undergoing significant declines in several European countries. Among the potential drivers of this decline is increasing light pollution. The known and possible effects of artificial night lighting upon moths were reviewed, and suggest how artificial night lighting might in turn affect the provision of pollination by moths. The need for studies of the effects of artificial night lighting upon whole communities of moths was highlighted.

3. An ecological network approach is one valuable method to consider the effects of artificial night lighting upon the provision of pollination by moths, as it provides useful insights into ecosystem functioning and stability, and may help elucidate the indirect effects of artificial light upon communities of moths and the plants they pollinate.

4. It was concluded that nocturnal pollination is an ecosystem process that may potentially be disrupted by increasing light pollution, although the nature of this disruption remains to be tested.

Key words. Agro-ecosystems, artificial night lighting, ecological networks, ecosystem services, flowering plants, food-webs, moths, population declines.

Introduction

Pollinating insects have been undergoing significant declines for several decades in many parts of the world (Williams, 1982; Potts *et al.,* 2010; Carvalheiro *et al.,* 2013). This is of concern because pollination represents a critical ecosystem service (Costanza *et al.,* 1997; Ollerton *et al.,* 2011; Garibaldi *et al.,* 2013), and declines in pollinators have been linked with declines in the plants that they interact with (Biesmeijer *et al.,* 2006; Pauw, 2007; Potts *et al.,* 2010). However, most studies to date have focused on diurnal pollinating insects, largely ignoring nocturnal insects, many of which have also undergone significant declines. In Great Britain, two-thirds of widespread larger moth species populations declined over a 40-year period (Fox *et al.,* 2013), with probable detrimental cascading effects on ecosystem functioning: the nature of these is considered a priority, policy-relevant question (Sutherland *et al.,* 2006). Recent work suggests that nocturnal moths (Lepidoptera) may perform an important, although often overlooked, functional role as plant pollinators (Philipp *et al.,* 2006; Devoto *et al.,* 2011; LeCroy *et al.,* 2013), but little is known about the scale and importance of nocturnal pollination services. Here, we review the scientific literature for evidence of the importance of nocturnal Lepidoptera (moths) as plant pollinators.

Nocturnal insect pollinators, including moths, face many of the same threats as diurnal pollinators, including habitat fragmentation, climate change, and agrochemical use

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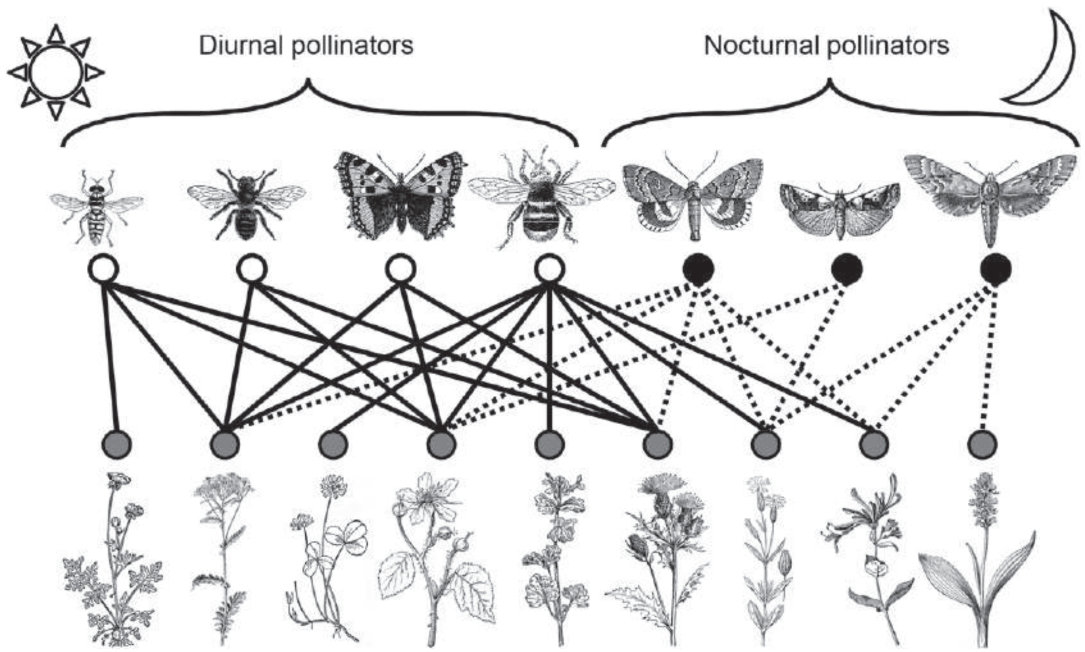


Fig. 1. An illustrative temperate grassland network combining diurnal and nocturnal pollination. Combined networks may reveal the extent of redundancy and complementarity of pollination interactions in ecosystems. Some apparently specialist plants in diurnal networks may be generalist with nocturnal visitors included. Thus, nocturnal visitors may provide redundancy to plants pollinated by diurnal visitors, and vice versa. Nocturnal interactions are derived from Table S1.2, Appendix S2 and diurnal interactions from Pocock *et al.* (2012). Nodes represent species: white = diurnal insects, black = nocturnal insects, grey = plants. Pollinators (from left): hoverfly (Diptera), leaf-cutter bee (Hymenoptera), butterfly (Lepidoptera), bumblebee (Hymenoptera), noctuid moth, pyralid moth, sphingid moth (all Lepidoptera); plants (from left): *Ranunculus* sp. (Ranunculaceae), *Jacobaea vulgaris* (Asteraceae), *Trifolium* sp. (Fabaceae), *Rubus* sp. (Rosaceae), *Lamium* sp. (Lamiaceae), *Cirsium* sp. (Asteraceae), *Silene latifolia* (Caryophyllaceae), *Lonicera* sp. (Caprifoliaceae), *Gymnadenia conopsea* (Orchidaceae). Links represent hypothetical pollination interactions: solid = diurnal, dashed = nocturnal. Drawings of pollinators and plants are for illustration only and may not precisely represent the named plant or animal. Drawings are used under license from ClipArt ETC (see Appendix S1 for full acknowledgements).

(Fox *et al.,* 2014). They may also be affected by increasing light pollution (Hölker *et al.,* 2010a), but the effects of artificial night lighting on nocturnal pollinator communities have not yet been established. We examine how the known effects of artificial light upon moths may potentially affect pollination processes. We also consider how recent advances in network ecology can be used to examine the impacts of light pollution on moth communities and their interactions with plants.

Nocturnal pollination

The experimental methods used in the majority of field studies of plant–pollinator interactions involve observations of insect visitors to flowers. Such observations almost always take place during daylight hours (e.g. Forup *et al.,* 2008; Bosch *et al.,* 2009; Popic *et al.,* 2013), because conducting surveys in the dark is difficult (Martinell *et al.,* 2010). However, to fully understand plant–pollinator networks, we must also understand the role played by nocturnal pollinators (Fig. 1). In addition to some bats (Chiroptera), beetles (Coleoptera), and flies (Diptera), moths are important nocturnal pollinators (Willmer, 2011); in particular, nectarivorous species from the families Sphingidae, Noctuidae, and Geometridae (Winfree *et al.,* 2011) and probably also the newly defined Erebidae (LeCroy *et al.,* 2013).

To determine the importance of moths as providers of nocturnal pollination services, and which plants are pollinated, we searched ISI Web of Knowledge for papers containing the terms ‘moth’ and ‘pollinat*’ (30 January 2014) and searched the bibliography of each relevant publication for further citations. Any paper demonstrating the existence of a moth–plant pollination interaction or providing evidence for such an interaction was considered relevant and included in the review. Levels of evidence supporting pollination interactions varied from observed flower visitation alone to proven dependence of the flower on moths for pollination (Table 1). Eight studies only inferred moth pollination from floral characteristics and did not present further evidence. While a high proportion of flower visitors at any particular flower species may not be effective pollinators (King *et al.,* 2013), flower visitation or pollen transfer by insects is frequently used as a proxy for insect-pollination. Therefore, for simplicity, we hereafter use the terms ‘pollination’ and ‘pollinator’ where there was reasonable evidence that moths acted as pollinators, although we note that in many cases pollination was not strictly proven. Using this method, we identified 168 studies from between 1971 and 2013 detailing examples of nocturnal moths involved in pollination (this search was comprehensive, but we recognise that some additional published examples may exist).

Table 1. Types of evidence for moth pollination given by studies reviewed (see Table S1.2, Appendix S2).

Evidence	Types of evidence	No. studies
Only flower visitation recorded	VF, VO, VR, VT	52
Flower visitation and moths observed making contact with floral reproductive organs	C + (VF, VO, VR, VT)	11
Only pollen found on moths	P	15
Flower visitation recorded and pollen found on moths	P + (VF, VO, VR, VT)	49
Flower visitation recorded with other additional evidence	(VF, VO, VR, VT) + X	9
Pollen found on moths with other additional evidence	P + X	2
Flower visitation and pollen found on moths with other additional evidence	P + (VF, VO, VR, VT) + X	8
Other	X	4
Only inferred from floral syndrome	I	8
Unspecified/unknown	U	5

In column 2: C = contact with anthers and/or stigmas observed, D = pollen deposited on stigmas and/or removed from anthers, E = plants pollinated when experimentally exposed only to visits by moths, I = inferred from pollination syndrome, P = pollen present on captured moths, S = moth scales or hairs present on stigmas, VF = flower visitation determined by fluorescent markers transferred by visiting moths, VO = flower visitation determined by observations, VR = flower visitation determined by video recordings, VT = flower visitation determined by flower-visitor trapping, U = unspecified/unknown; X = any combination of C, D, E, and S.

Fourteen of these studies examined complete pollinator communities, finding moths to be of general importance to pollination in a variety of ecosystems (Table S1.1, Appendix S2), including tropical rainforest and savannah, temperate coniferous forest and meadow, and oceanic islands, and including examples from all continents except Antarctica. In several studies, moths were considered to be second in importance only to bees, in terms of pollination provision (Bawa *et al.,* 1985; Kato & Kawakita, 2004; Ramirez, 2004; Chamorro *et al.,* 2012).

Moth pollination was important for a wide range of plant species. We found representatives of 75 different plant families (Table 2), including 289 species and some wider taxa, reported to be partially or exclusively pollinated by moths (Table S1.2, Appendix S2) of 21 families (Table S3, Appendix S2). The majority of plants were angiosperms; the one exception was the gymnosperm *Gnetum gnemon* Linne var. *tenerum* Markgraf (Gnetaceae), reportedly pollinated by moths of Geometridae and Pyralidae (Kato *et al.,* 1995). Many species within the angiosperms were dicotyledons, especially from the orders Caryophyllales, Ericales, Gentianales, and Lamiales, but moth-pollinated plants in the monocotyledons included many in the order Asparagales (including Orchidaceae, Amaryllidaceae, Asparagaceae, and others), and the economically important species *Elaeis guineensis* Jacq. oil palm (Arecaceae), visited by large numbers of moths in the genus *Pyroderces* (Cosmopterigidae; Syed, 1979). These observed patterns may be a function of both real effects and bias in recorder effort, so we treat them with caution.

Traditionally, pollination by moths has been subdivided into two ‘pollination syndromes’ (Willmer, 2011): sphingophily (pollination by hovering moths of the Sphingidae) and phalaenophily (pollination by settling moths of other families). The best-known examples of moth pollination are of sphingophilous plants (e.g. Wasserthal, 1997). To examine if this has led to a bias towards sphingophily in studies of moth pollination, we categorised all studies in Table S1.2, Appendix S2 according to whether they made any explicit or implicit prediction of sphingophily. In general, we did not find evidence of bias towards sphingophily leading to other pollination interactions being overlooked. Fifty-six studies (35% of those reviewed) made a prediction of sphingophily. Of these, 53 (95%) found Sphingidae and 18 (32%) found non-sphingid moths to be pollinators, even although the experimental methods in all but two studies were sufficient to detect both sphingid and non-sphingid pollinators. From the 103 studies not predicting sphingophily, 82 (80%) found non-sphingid moths and 50 (49%) found Sphingidae to be pollinators; the experimental methods in all but nine were sufficient to detect both sphingid and non-sphingid pollinators (Table S2, Appendix S2).

Moths primarily visit flowers to obtain nectar, which is an energy-rich food source and the main adult food source in the majority of moth species that feed as adults (Willmer, 2011). Several studies have also documented moths acting as pollinating seed parasites (Table S1.3, Appendix S2). In these specialised interactions, moths both pollinate and lay eggs in flowers, so providing a food supply for their larvae, which feed on developing seedheads.

Pollination by moths may be an advantageous strategy for plants in some examples. Several studies evaluate aspects of pollination in generalist plants pollinated both by moths (both Sphingidae and other families) and diurnal pollinators; for example, *Lonicera japonica* Thunb. (Caprifoliaceae; Miyake & Yahara, 1998), *Asclepias* spp. (Apocynaceae; Bertin & Willson, 1980; Morse & Fritz, 1983; Jennersten & Morse, 1991) and *Silene* spp. (Caryophyllaceae; Young, 2002; Barthelmess *et al.,* 2006). Compared with diurnal pollinators, the moths in these examples provided benefits including: greater interpopulation gene flow, shown by movement of genetic markers between experimental populations of plants (Barthelmess *et al.,* 2006); longer-distance dispersal of dye-marked pollen (Miyake & Yahara, 1998; Young, 2002); higher quality pollination, causing equal or greater seed set in spite of transferring fewer pollinia (Bertin & Willson, 1980; Jennersten & Morse, 1991; but see Morse & Fritz, 1983); and more efficient pollination, having a lower ratio of pollen removed to pollen deposited after visits by single pollinators (Miyake & Yahara, 1998). In the latter example, moths visiting *L. japonica* were thought to be more efficient pollinators than bees because the latter actively collect pollen to provision their larvae, and so must remove substantially more pollen than moths for the same level of pollen deposition to occur (Miyake & Yahara, 1999). As a result,

Table 2. Studies of moth-pollinated plants by family (see Table S1.2, Appendix S2).

Plant family	No. known moth-pollinated species or wider taxa	Known pollinating moth families	Plant family	No. known moth-pollinated species or wider taxa	Known pollinating moth families
Adoxaceae	1	N	Liliaceae	4	G, N, P, S
Amaranthaceae	1	–	Linaceae	1	–
Amaryllidaceae	10	E, N, S	Loasaceae	1	S
Anacardiaceae	1	–	Loganiaceae	2	–
Apiaceae	1	–	Malvaceae	2	Ct, E, G, N, P, Se, S, U
Apocynaceae	20	E, G, N, P, S, T	Meliaceae	1	S
Arecaceae	1	C	Myrtaceae	2	Ct, S
Asparagaceae	7	N, Pr, S	Nepenthaceae	1	–
Asteraceae	13	G, N, P, S	Nyctaginaceae	5	N, S
Balsaminaceae	2	S	Oleaceae	3	S
Bignoniaceae	3	E, G, L, N, S	Onagraceae	8	E, G, N, P, S
Boraginaceae	4	N, P, S	Orchidaceae	45	G, N, Pr, Pt, P, Se, S, T
Brassicaceae	3	S	Orobanchaceae	2	S
Cactaceae	7	G, N, P, Sa, S	Passifloraceae	2	S
Capparaceae	1	P	Phrymaceae	1	S
Caprifoliaceae	3	N, S	Phyllanthaceae	10	Ge, Gr
Caricaceae	1	–	Plantaginaceae	1	–
Caryocaraceae	1	S	Polemoniaceae	1	S
Caryophyllaceae	12	Cr, G, N, P, S	Polygonaceae	1	–
Cleomaceae	1	S	Primulaceae	2	–
Convulvulaceae	4	S	Proteaceae	2	S
Crassulaceae	1	G	Ranunculaceae	5	S
Cucurbitaceae	1	N, S	Rhamnaceae	1	–
Dipterocarpaceae	2	G, N, S	Rosaceae	2	–
Ebenaceae	1	–	Rubiaceae	16	Ct, N, S
Ericaceae	4	G, N, P, S	Rutaceae	1	G
Escalloniaceae	1	G	Santalaceae	2	–
Euphorbiaceae	4	S	Sapotaceae	2	–
Fabaceae	12	E, G, N, P, S, U	Saxifragaceae	3	Pr
Geraniaceae	1	–	Scrophulariaceae	2	G, N, P, T
Gesneriaceae	1	–	Solanaceae	6	S
Gnetaceae	1	G, P	Thymelaeaceae	8	E, G, L, N, No, P, Th
Hyacinthaceae	1	N	Urticaceae	1	–
Hypericaceae	1	N	Verbenaceae	3	P, S
Iridaceae	3	G, N, S	Violaceae	1	S
Lamiaceae	2	S	Vochysiaceae	5	S
Lecythidaceae	1	Gl	Winteraceae	2	M
Lentibulariaceae	1	N, P, S, U	–	–	–

In column 2, ‘known’ moth-pollinated taxa are those identified in this review as having evidence of being moth-pollinated; ‘wider taxa’ includes any named group at a hierarchical level above species and below family. In column 3: C = Cosmopterigidae, Cr = Crambidae, Ct = Ctenuchidae, E = Erebidae, Ge = Gelechiidae, G = Geometridae, Gl = Glyphipterigidae, Gr = Gracillariidae, L = Lasiocampidae, M = Micropterigidae, N = Noctuidae, No = Nolidae, Pr = Prodoxidae, Pt = Pterophoridae, P = Pyralidae, Sa = Saturniidae, Se = Sesiidae, S = Sphingidae, Th = Thyrididae, T = Tortricidae, U = Uranidae.

moth-pollinated plants could perhaps invest fewer resources into producing pollen without compromising reproductive success (Cruden, 1973); however, analysis of pollen–ovule ratios for diurnally and nocturnally pollinated members of Caryophyllaceae does not support this (Jürgens *et al.,* 2002).

The literature, therefore, contains numerous examples of moths serving as pollinators which, in many cases, are of considerable importance to individual species and to communities. A diverse selection of plant taxa in an equally wide range of ecosystems benefit from pollination by moths. It is important to consider how environmental change may threaten this ecosystem service.

Artificial light as a driver of environmental change

There are many drivers of environmental change, but artificial night lighting is one which is uniquely important for nocturnal organisms, through direct interaction with a light source such as a streetlamp, increased background illumination at night, and altered perception of photoperiod (Hölker *et al.,* 2010b; Lyytimäki, 2013; Lewanzik & Voigt, 2014). Light pollution has increased considerably and continues to increase worldwide, often associated with urban development (Cinzano *et al.,* 2001; Bruce-White & Shardlow, 2011), although levels may be declining in some economically developed regions (Bennie *et al.,* 2014). The predominant types of artificial lighting in use are also changing; lights emitting a broader spectrum of wavelengths are increasingly favoured because they facilitate human discernment of colours at night and, in the case of light-emitting diodes (LEDs), are more energy-efficient (Bruce-White & Shardlow, 2011; Gaston *et al.,* 2012).

Artificial night lighting, even at low levels, exerts an influence at every level of biological organisation (Gaston *et al.,* 2013), from cell (Navara & Nelson, 2007) to organism (Longcore & Rich, 2004) and community (Davies *et al.,* 2012). However, little is currently known about the effects of light pollution on species population dynamics, whole communities, and networks of interacting species, or ecosystem functioning.

Long-term declines in populations and distributions of many moth species have been found in Great Britain (Conrad *et al.,* 2004, 2006; Fox *et al.,* 2011, 2013), the Netherlands (Groenendijk & Ellis, 2011), and Finland (Mattila *et al.,* 2006, 2008). Habitat degradation and climate change are likely drivers of these declines (Fox *et al.,* 2014), as with diurnal pollinators (Potts *et al.,* 2010); however, artificial night lighting has also been proposed as a potential contributing factor (Fox, 2013; Fox *et al.,* 2013). Conrad *et al.* (2006) found no significant correlation between a change in light pollution and a change in light-trap catches from 1992 and 2000, but short-term trends in moth (and other insect) populations can be difficult to detect, as large inter-annual fluctuations are normal (Conrad *et al.,* 2004).

Below, we describe a range of mechanisms by which artificial night lighting could impact negatively upon moths. Many such impacts are not empirically proven. Therefore, we describe first the well-established mechanisms, followed by those unproven, but for which some evidence exists. Even where negative impacts have been demonstrated, their effects at the population level are mostly unknown.

Established effects of artificial light on moths

Individual moths are certainly affected by artificial night lighting, famously appearing to be attracted to artificial lights, sometimes in huge numbers (Howe, 1959). Numerous theories have been put forward to explain flight-to-light behaviour (Robinson & Robinson, 1950; Mazokhin-Porshnyakov, 1961; Callahan, 1965; Hsiao, 1973; Sotthibandhu & Baker, 1979; Hamdorf & Höglund, 1981), although the debate is inconclusive. Nevertheless, this observation has led to the popularity of using light-baited traps to survey many families of moths.

The extent to which moths are attracted to light varies according to a number of factors. It has been recognised for many years that shorter wavelengths are, in general, more attractive to moths (Frank, 2006, and references therein); attractiveness appears to peak around wavelengths of 400 nm (violet light; Cowan & Gries, 2009). The degree of attraction and preferred wavelengths both vary between moth taxa (Merckx & Slade, 2014); typically, larger-bodied moths with larger eyes are more likely to be attracted to light dominated by smaller wavelengths (van Langevelde *et al.,* 2011; Somers-Yeates *et al.,* 2013). Variation also appears to exist between sexes; males of some species are significantly more likely to be recorded at light traps than females (Garris & Snyder, 2010), but it is not clear if this is due to stronger male attraction to lights, or males being more active and therefore more likely to move into the zone of influence of a given light (Altermatt *et al.,* 2009).

Aside from flight-to-light behaviour, moths may be further affected by artificial night lighting through other mechanisms, related to direct interaction with lights, increased ambient light at night, and locally altered perception of photoperiods in the vicinity of artificial lights. Contact with hot components of lamps or radiant energy from bright lights can kill insects or damage their wings, legs, and antennae (Eisenbeis, 2006; Frank, 2006). Insects killed by light-baited electric traps, primarily targeting biting Diptera, contain a high proportion of nocturnal Lepidoptera (Frick & Tallamy, 1996).

Reproduction

Reproductive success of moths could also be negatively affected by artificial night lighting. Low levels of artificial light inhibited the release of sex pheromones by female moths of a Geometridae species (Sower *et al.,* 1970). Artificial light can suppress oviposition (Nemec, 1969) or act as an ecological trap, causing females to lay eggs at an unusually high density and/or in unsuitable locations near to lights (Pfrimmer *et al.,* 1955; Brown, 1984), either of which could increase larval competition for limited food resources.

Artificial light may also have an effect on larvae, which are nocturnal in many Lepidopteran species, including some that are diurnal as adults (butterflies and day-flying moths). Even at a low intensity, light caused reductions in age and mass at pupation in males and inhibited diapause in both sexes of a Noctuidae species in the laboratory (van Geffen *et al.,* 2014). However, few studies have investigated the effects of artificial night lighting on Lepidopteran larvae.

Predation

Predators of moths have been observed to hunt at artificial lights, exploiting above-average prey densities caused by flight-to-light behaviour (Frank, 2006). This includes both active hunters, such as bats (Rydell, 1992) and predatory insects (Warren, 1990), and sit-and-wait predators, such as spiders (Heiling, 1999), reptiles, and amphibians (Henderson & Powell, 2001). Artificial light also interferes with the anti-bat defensive behaviour of moths, increasing their vulnerability to predation (Svensson & Rydell, 1998; Acharya & Fenton, 1999).

Possible further effects of artificial light on moths

In addition to the known mechanisms described above, a number of other mechanisms have the potential to affect moths but have not yet been conclusively demonstrated.

Reproduction

Changes in photoperiod disrupted the pheromone release behaviour of females of a Pyralidae species (Fatzinger, 1973), which could disrupt mating. Competition in male moths between light traps and pheromone traps (Delisle *et al.,* 1998) suggests that artificial lighting could distract males from female pheromone signals and thus reduce mating frequency. More severely, radiant energy from bright lights can sterilise other insects in the laboratory (Riordan, 1964; Eisenbeis, 2006); this could occur with moths in the wild. Artificial lights have been observed to divert dispersing or migrating moths to locations that are unsuitable for breeding (Frank, 2006, and references therein), potentially creating an ecological trap.

A reduction of the dark scotophase of the photoperiod prevented diapause in the larval stage of a Tortricidae species in the laboratory (Berlinger & Ankersmit, 1976); however, this result could not be replicated in field trials. In addition, moth larvae may be attracted to artificial lights in much the same way as adults (Gillett & Gardner, 2009).

Predation

Artificial light may also increase the risk of predation by disrupting crypsis, both by causing moths to rest in unsuitable locations where their wing patterns are an ineffective disguise, and by concentrating moths in a small area, assisting predators in establishing a search image of cryptic wing patterns (Frank, 2006). Similarly, repeat exposure can habituate predators to stimuli that elicit startle reactions, such as patterned hindwings or bodies (Schlenoff, 1985; Ingalls, 1993); highly visible aggregations of moths around lights could accelerate the habituation process (Frank, 2006).

Vision

Artificial light affects the sensitivity of the compound eyes of moths (Frank, 2006). Screening pigment reduces ocular sensitivity within 23 min of exposure to light (Hamdorf & Höglund, 1981); the return to full ocular sensitivity is far slower, taking around 30 min (Bernhard & Ottoson, 1960). To what extent these effects may be exerted by exposure to artificial lights in natural settings is unclear. However, moths attracted to a light will often rest on vegetation or the ground for a period of time, sometimes before even reaching the light (Hartstack *et al.,* 1968; Hsiao, 1973); this behaviour could represent a period of readjustment to full ocular sensitivity.

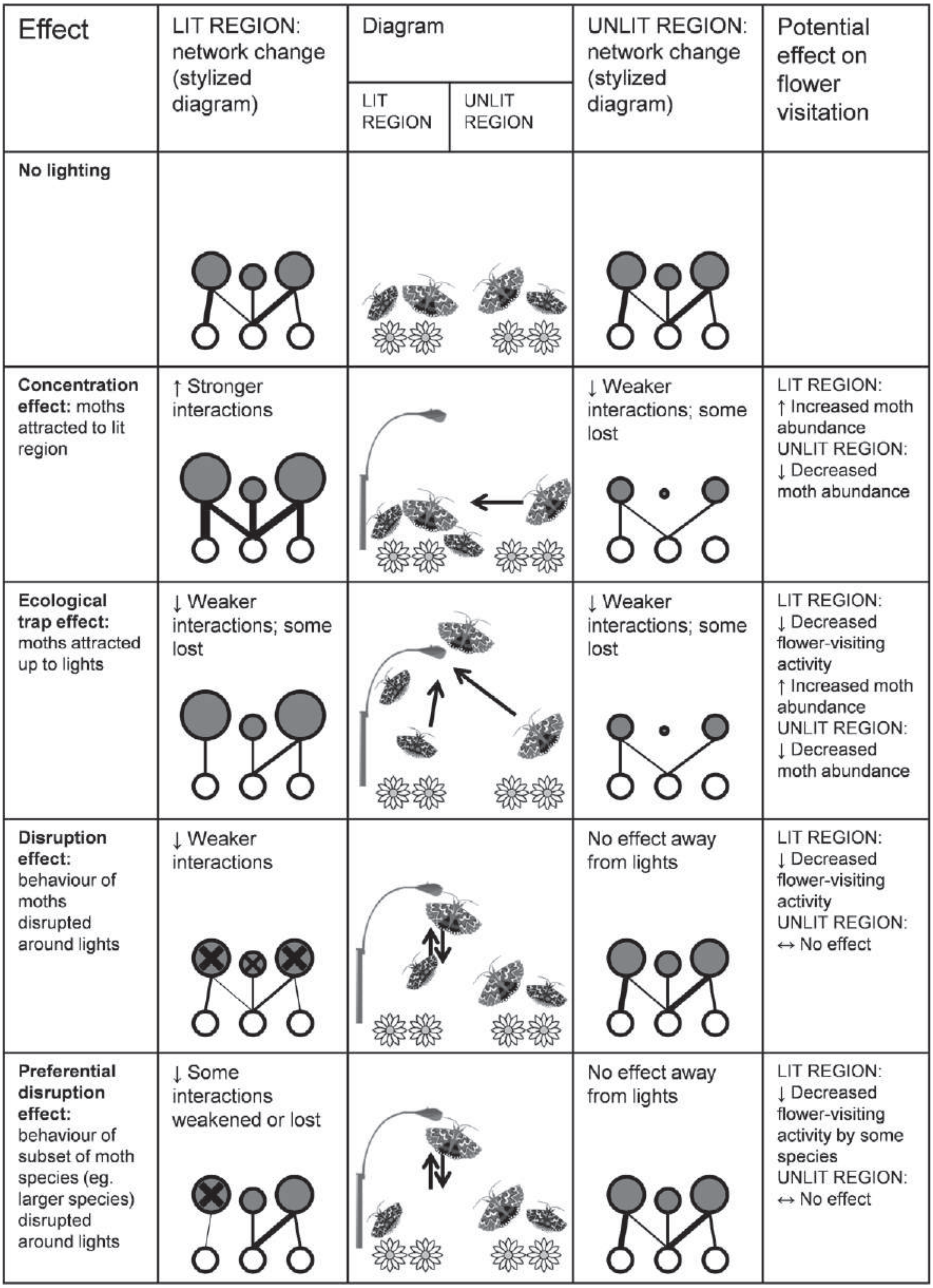
In addition to compound eyes, most insects (including moths) have simple eyes (dorsal ocelli) that are sensitive to changes in light intensity (Mizunami, 1995), and appear to have a role in timing flight initiation at dusk in moths (Eaton *et al.,* 1983). It is possible that artificial night lighting could delay or even prevent the onset of nocturnal activity. While this effect is likely to be localised to the immediate vicinity of light sources, it could negatively affect moth fitness (and hence population growth) and nocturnal pollination.

The visual capacity of moths could also be indirectly affected by artificial night lighting altering the spectrum of background illumination. Ultraviolet (UV) radiation (10–400 nm), predominantly at longer wavelengths close to visible light (Eguchi *et al.,* 1982), is particularly important to pollinating moths, as moths orient themselves to flowers by a combination of olfactory and visual cues (Raguso & Willis, 2005) including UV-reflecting markers on flowers (Barth, 1985). The spectral content of artificial night lighting will therefore determine its effect upon flower-visiting moths (Davies *et al.,* 2013): UV-rich lighting (e.g. from mercury vapour lights) could accentuate these nectar guides, whereas UV-poor lighting (e.g. from low-pressure sodium lights), by illuminating other parts of the nocturnal environment relatively more brightly, could cause nectar guides to stand out less clearly (Frank, 2006).

Moths and pollination: an ecological network approach

The studies above considered the direct effects of artificial light upon moths, mostly at the level of the individual. Whether artificial night lighting, through these effects, is a contributing factor in declines in moth populations remains a key research question. It is also necessary to consider the indirect effects of artificial light mediated by moth pollination, as can be demonstrated with an ecological network approach. Ecological networks describe the structure of communities as the occurrence (and frequency) of interactions between species, such as plants and pollinators (Montoya *et al.,* 2006; Bascompte, 2007). From descriptions of the network's structure, its function can be inferred (Tylianakis *et al.,* 2010); for example, its robustness to perturbations such as species extinction and their cascading effects (Bascompte, 2009; Ings *et al.,* 2009; Evans *et al.,* 2013). It has been demonstrated that drivers of environmental change, such as climate change, can alter the composition and balance of networks (Tylianakis *et al.,* 2008), including plant–pollinator networks (Rathke & Jules, 1993; Memmott *et al.,* 2007). Removal of pollinator species can cause plant species diversity to suffer (Memmott *et al.,* 2004; Fontaine *et al.,* 2006), while loss of plants can likewise affect pollinators (Wallis De Vries *et al.,* 2012).

Two attributes of networks are particularly important. First, many pollinator networks have a nested structure, in which specialist species (with few connections in the network) tend to interact with generalists (with many connections) more frequently than with other specialists (Dicks *et al.,* 2002; Bascompte *et al.,* 2003). Nested systems have high tolerance to the random loss of species from the community but are sensitive to the removal of certain highly connected species (Solé & Montoya, 2001; Memmott *et al.,* 2004). Second, these systems are also modular, in which sets of species within modules interact strongly with each other; these modules are akin to pollination syndromes (Olesen *et al.,* 2007), and increase overall robustness because impacts cascade less quickly between modules and through the whole system. Some modules are as a result of close co-evolutionary relationships; in extreme examples, plants are entirely reliant on a single or few species of moth [eg. *Oxyanthus pyriformis* (Hochst.) Skeels (Johnson *et al.,* 2004)]. In such cases, minor disruption of the pollinator will directly impact the reproductive success of the plant (Pauw, 2007). The modules themselves may be nested within the whole system, and species will often be nested within modules.



Effect	LIT REGION: network change (stylized diagram)	Diagram		UNLIT REGION: network change (stylized diagram)	Potential effect on flower visitation
		LIT REGION	UNLIT REGION		
No lighting					
Concentration effect: moths attracted to lit region	↑ Stronger interactions			↓ Weaker interactions; some lost	LIT REGION: ↑ Increased moth abundance UNLIT REGION: ↓ Decreased moth abundance
Ecological trap effect: moths attracted up to lights	↓ Weaker interactions; some lost			↓ Weaker interactions; some lost	LIT REGION: ↓ Decreased flower-visiting activity ↑ Increased moth abundance UNLIT REGION: ↓ Decreased moth abundance
Disruption effect: behaviour of moths disrupted around lights	↓ Weaker interactions			No effect away from lights	LIT REGION: ↓ Decreased flower-visiting activity UNLIT REGION: ↔ No effect
Preferential disruption effect: behaviour of subset of moth species (eg. larger species) disrupted around lights	↓ Some interactions weakened or lost			No effect away from lights	LIT REGION: ↓ Decreased flower-visiting activity by some species UNLIT REGION: ↔ No effect

Fig. 2. Possible scenarios for change in plant–moth pollination networks as a result of artificial night lighting, with predictions for effects on local flower-visitation activity by moths. In network representations, nodes represent species (lower = flowering plants, upper = moths) and links represent pollination interactions. Node width represents relative species abundance and link thickness represents interaction strength. Crosses indicate disruption of behaviour.

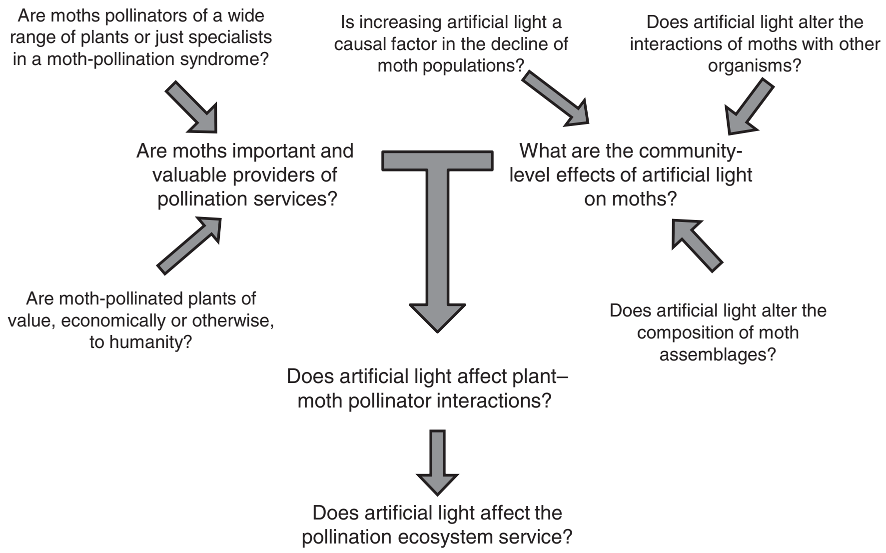


Fig. 3. Future research directions raised in this review.

Most studies of plant–pollinator networks to date have focused on diurnal interactions. Two exceptions considering nocturnal plant–pollinator networks are Devoto *et al.* (2011) and Banza (2011); these authors identified nocturnal moth–flower interactions by sampling pollen on captured moths. Combining nocturnal pollination networks with diurnal ones could lead to increased modularity (if there are distinct sets of flowers visited by diurnal and nocturnal pollinators), such that the effects of environmental change (e.g. artificial night lighting) could be substantial in one part of the network but not cascade through the whole network. It could also lead to increased redundancy (if flowers share diurnal and nocturnal pollinators), such that the plants in the network may be robust to the disruption of one set of pollinators (e.g. moths). Testing for differences in the structure of plant–moth pollinator networks between unlit and artificially lit sites will begin to empirically reveal the functional impact of artificial night lighting on wider communities through indirect, as well as direct, effects.

Potential effects of artificial light on moth pollination

A variety of changes in moth abundance, composition of moth assemblages, and moth behaviour are all possible results of artificial lighting at night, but the overall effect on the whole community via disruption of pollination remains to be tested (Fig. 2). Moths may be drawn in towards a light from several metres away (Baker & Sadovy, 1978; Truxa & Fiedler, 2012; van Grunsven *et al.,* 2014); this might alter local moth abundance and the composition of moth assemblages both in the vicinity of lights, and in the source habitats from which attracted moths are drawn (Fig. 2: concentration and ecological trap effects). Interactions could also be weakened or lost through behavioural changes in moths, even if their abundance is unchanged (Fig. 2: disruption effect). The level and nature of disruption might vary between moth species (van Langevelde *et al.,* 2011; Somers-Yeates *et al.,* 2013), leading to some interactions being more strongly affected than others (Fig. 2: preferential disruption effect). If reproduction is affected, some moth species may decline in abundance or go extinct, leading to further loss of interactions. Therefore, the effects of increasing artificial light may be positive for some moth or plant species and negative for others in any given community, leading to cascading changes in the system that are difficult to predict prior to empirical, experimental research.

Discussion

Future research directions

We believe that our findings in this review highlight a number of key priorities for future research (Fig. 3). While we have described evidence that moths are pollinators of a diverse range of plant species, the extent of their role as pollinators in maintaining botanical diversity, in agro-ecosystems, and especially of commercially valuable crops demands attention.

The effects of artificial night lighting on moths, too, should be investigated further. Many of the individual-level effects summarised above have not been empirically demonstrated to occur under natural conditions. Moreover, there are no published studies into the community-level effects of artificial night lighting on moths; this is a major research gap (Fox, 2013; Gaston *et al.,* 2013). The impacts of lighting on plant–moth pollination networks are difficult to predict (Fig. 2) and also require empirical testing. It is worth noting that moths are a food source for many other organisms including birds and bats (Fox, 2013); therefore, a similar approach with trophic networks may also be worthwhile.

Conclusion

In this review, we show the importance of moths as pollinators for a diverse range of plant species in ecosystems worldwide and, hence, their role in ecosystem functioning. We discuss the many ways in which moths are known to be affected by artificial night lighting, and suggest how these effects may, in turn, impact pollination interactions between moths and plants.

The effects of artificial night lighting may go beyond simple declines in moth populations, with potential changes in the composition of moth assemblages and in the nature and frequency of interspecies interactions between moths and other taxa; this justifies an ecological network approach to the problem (Fig. 2).

Artificial night lighting may negatively affect a range of ecosystem services (Lyytimäki, 2013; Lewanzik & Voigt, 2014). Based on the evidence summarised in this review, we consider pollination to be one such ecosystem service that may be disrupted by increasing ecological light pollution. The research directions outlined will help develop an understanding of what form that disruption may take, and may direct ways to mitigate the negative effects of artificial night lighting upon moths and the ecosystem processes that rely upon them.

Acknowledgements

This work was supported by the Natural Environment Research Council and Butterfly Conservation (Industrial CASE studentship awarded to C.J.M., Project Reference: NE/K007394/1). We thank Mark Parsons, Herbert Macgregor, and three anonymous reviewers for their helpful comments on the manuscript. All authors contributed to the literature review and manuscript writing.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12174

Appendix S1. References for Fig. 1.

Appendix S2. Further tables summarising results of the moth-pollination review.

References

Acharya, L. & Fenton, M.B. (1999) Bat attacks and moth defensive behaviour around street lights. *Canadian Journal of Zoology*, **77**, 27–33.

Altermatt, F., Baumeyer, A. & Ebert, D. (2009) Experimental evidence for male biased flight-to-light behaviour in two moth species. *Entomologia Experimentalis et Applicata*, **130**, 259–265.

Baker, R.R. & Sadovy, Y. (1978) The distance and nature of the light-trap response of moths. *Nature*, **276**, 818–821.

Banza, P. (2011) *Investigating the importance of nocturnal Lepidoptera as pollinators: a network approach*. MSc thesis, Universidade de Évora, Portugal.

Barth, F.G. (1985) *Insects and Flowers: The Biology of a Partnership*. Princeton University Press, Princeton, New Jersey.

Barthelmess, E.L., Richards, C.M. & McCauley, D.E. (2006) Relative effects of nocturnal vs diurnal pollinators and distance on gene flow in small *Silene alba* populations. *New Phytologist*, **169**, 689–698.

Bascompte, J. (2007) Networks in ecology. *Basic and Applied Ecology*, **8**, 485–490.

Bascompte, J. (2009) Disentangling the web of life. *Science*, **325**, 416–419.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, **100**, 9383–9387.

Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E. & Grayum, M.H. (1985) Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany*, **72**, 346–356.

Bennie, J., Davies, T.W., Duffy, J.P., Inger, R. & Gaston, K.J. (2014) Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Scientific Reports*, **4**, 3789.

Berlinger, M.J. & Ankersmit, G.W. (1976) Manipulation with the photoperiod as a method of control of *Adoxophyes orana* (Lepidoptera, Torticidae). *Entomologia Experimentalis et Applicata*, **19**, 96–107.

Bernhard, C.G. & Ottoson, D. (1960) Studies on the relation between the pigment migration and the sensitivity changes during dark adaptation in diurnal and nocturnal Lepidoptera. *Journal of General Physiology*, **44**, 205–215.

Bertin, R.I. & Willson, M.F. (1980) Effectiveness of diurnal and nocturnal pollination of two milkweeds. *Canadian Journal of Botany*, **58**, 1744–1746.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T. *et al.* (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Bosch, J., Gonzalez, A.M.M., Rodrigo, A. & Navarro, D. (2009) Plant–pollinator networks: adding the pollinator's perspective. *Ecology Letters*, **12**, 409–419.

Brown, L.N. (1984) Population outbreak of Pandora moths *(Coloradia pandora* Blake) on the Kaibab plateau, Arizona (Saturniidae). *Journal of the Lepidopterists' Society*, **38**, 65.

Bruce-White, C. & Shardlow, M. (2011) *A Review of the Impact of Artificial Light on Invertebrates*. Buglife, U.K.

Callahan, P.S. (1965) Intermediate and far infrared sensing of nocturnal insects. Part I. Evidences for a far infrared (FIR) electromagnetic theory of communication and sensing in moths and its relationship to the limiting biosphere of the corn earworm. *Annals of the Entomological Society of America*, **58**, 727–745.

Carvalheiro, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R. *et al.* (2013) Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecology Letters*, **16**, 870–878.

Chamorro, S., Heleno, R., Olesen, J.M., McMullen, C.K. & Traveset, A. (2012) Pollination patterns and plant breeding systems in the Galápagos: a review. *Annals of Botany*, **110**, 1489–1501.

Cinzano, P., Falchi, F. & Elvidge, C.D. (2001) The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, **328**, 689–707.

Conrad, K.F., Woiwod, I.P., Parsons, M., Fox, R. & Warren, M.S. (2004) Long-term population trends in widespread British moths. *Journal of Insect Conservation*, **8**, 119–136.

Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S. & Woiwod, I.P. (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, **132**, 279–291.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.

Cowan, T. & Gries, G. (2009) Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*. *Entomologia Experimentalis et Applicata*, **131**, 148–158.

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Cruden, R.W. (1973) Reproductive biology of weedy and cultivated Mirabilis (Nyctaginaceae). *American Journal of Botany*, **60**, 802–809.

Davies, T.W., Bennie, J. & Gaston, K.J. (2012) Street lighting changes the composition of invertebrate communities. *Biology Letters*, **8**, 764–767.

Davies, T.W., Bennie, J., Inger, R., de Ibarra, N.H. & Gaston, K.J. (2013) Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Global Change Biology*, **19**, 1417–1423.

Delisle, J., West, R.J. & Bowers, W.W. (1998) The relative performance of pheromone and light traps in monitoring the seasonal activity of both sexes of the eastern hemlock looper, *Lambdina fiscellaria fiscellaria*. *Entomologia Experimentalis et Applicata*, **89**, 87–98.

Devoto, M., Bailey, S. & Memmott, J. (2011) The 'night shift': nocturnal pollen-transport networks in a boreal pine forest. *Ecological Entomology*, **36**, 25–35.

Dicks, L.V., Corbet, S.A. & Pywell, R.F. (2002) Compartmentalization in plant–insect flower visitor webs. *Journal of Animal Ecology*, **71**, 32–43.

Eaton, J.L., Tignor, K.R. & Holtzman, G.I. (1983) Role of moth ocelli in timing flight initiation at dusk. *Physiological Entomology*, **8**, 371–375.

Eguchi, E., Watanabe, K., Hariyama, T. & Yamamoto, K. (1982) A comparison of electrophysiologically determined spectral responses in 35 species of Lepidoptera. *Journal of Insect Physiology*, **28**, 675–682.

Eisenbeis, G. (2006) Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. *Ecological Consequences of Artificial Night Lighting* (ed. by C. Rich and T. Longcore), pp. 281–304. Island Press, Washington, District of Columbia.

Evans, D.M., Pocock, M.J.O. & Memmott, J. (2013) The robustness of a network of ecological networks to habitat loss. *Ecology Letters*, **16**, 844–852.

Fatzinger, C.W. (1973) Circadian rhythmicity of sex pheromone release by *Dioryctria abietella* (Lepidoptera: Pyralidae (Phycitinae)) and the effect of a diel light cycle on its precopulatory behaviour. *Annals of the Entomological Society of America*, **66**, 1147–1153.

Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. (2006) Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, **4**, e1.

Forup, M.L., Henson, K.S.E., Craze, P.G. & Memmott, J. (2008) The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology*, **45**, 742–752.

Fox, R. (2013) The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity*, **6**, 5–19.

Fox, R., Randle, Z., Hill, L., Anders, S., Wiffen, L. & Parsons, M.S. (2011) Moths count: recording moths for conservation in the UK. *Journal of Insect Conservation*, **15**, 55–68.

Fox, R., Parsons, M.S., Chapman, J.W., Woiwod, I.P., Warren, M.S. & Brooks, D.R. (2013) *The State of Britain's Larger Moths 2013*. Butterfly Conservation and Rothamsted Research, U.K.

Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D. & Roy, D.B. (2014) Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, **51**, 949–957.

Frank, K.D. (2006) Effects of artificial night lighting on moths. *Ecological Consequences of Artificial Night Lighting* (ed. by C. Rich and T. Longcore), pp. 305–344. Island Press, Washington, District of Columbia.

Frick, T.B. & Tallamy, D.W. (1996) Density and diversity of nontarget insects killed by suburban electric insect traps. *Entomological News*, **107**, 77–82.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.

Garris, H.W. & Snyder, J.A. (2010) Sex-specific attraction of moth species to ultraviolet light traps. *Southeastern Naturalist*, **9**, 427–434.

Gaston, K.J., Davies, T.W., Bennie, J. & Hopkins, J. (2012) Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, **49**, 1256–1266.

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.

van Geffen, K.G., van Grunsven, R.H.A., van Ruijven, J., Berendse, F. & Veenendaal, E.M. (2014) Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, **4**, 2082–2089.

Gillett, M.P.T. & Gardner, A.S. (2009) An unusual observation – attraction of caterpillars to mercury vapour light in the Abu Dhabi desert (Lepidoptera: Pyralidae). *Tribulus*, **18**, 56–59.

Groenendijk, D. & Ellis, W.N. (2011) The state of the Dutch larger moth fauna. *Journal of Insect Conservation*, **15**, 95–101.

van Grunsven, R.H.A., Lham, D., van Geffen, K.G. & Veenendaal, E.M. (2014) Range of attraction of a 6-W moth light trap. *Entomologia Experimentalis et Applicata*, **152**, 87–90.

Hamdorf, K. & Höglund, G. (1981) Light induced retinal screening pigment migration independent of visual cell activity. *Journal of Comparative Physiology*, **143**, 305–309.

Hartstack, A.W. Jr., Hollingsworth, J.P. & Lindquist, D.A. (1968) A technique for measuring trapping efficiency of electric insect traps. *Journal of Economic Entomology*, **61**, 546–552.

Heiling, A.M. (1999) Why do nocturnal orb-web spiders (Araneidae) search for light? *Behavioral Ecology and Sociobiology*, **46**, 43–49.

Henderson, R.W. & Powell, R. (2001) Responses by the West Indian herpetofauna to human-influenced resources. *Caribbean Journal of Science*, **37**, 41–54.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D. *et al.* (2010a) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, **15**, 13.

Hölker, F., Wolter, C., Perkin, E.K. & Tockner, K. (2010b) Light pollution as a biodiversity threat. *Trends in Ecology & Evolution*, **25**, 681–682.

Howe, W.H. (1959) A swarm of noctuid moths in southeastern Kansas. *Journal of the Lepidopterists' Society*, **13**, 26.

Hsiao, H.S. (1973) Flight paths of night-flying moths to light. *Journal of Insect Physiology*, **19**, 1971–1976.

Ingalls, V. (1993) Startle and habituation responses of Blue Jays *(Cyanocitta cristata)* in a laboratory simulation of anti-predator defenses of *Catocala* moths (Lepidoptera: Noctuidae). *Behaviour*, **126**, 77–96.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F. *et al.* (2009) Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.

Jennersten, O. & Morse, D.H. (1991) The quality of pollination by diurnal and nocturnal insects visiting Common Milkweed, *Asclepias syriaca*. *American Midland Naturalist*, **125**, 18–28.

Johnson, S.D., Neal, P.R., Peter, C.I. & Edwards, T.J. (2004) Fruiting failure and limited recruitment in remnant populations of the hawkmoth-pollinated tree *Oxyanthus pyriformis* subsp. *pyriformis* (Rubiaceae). *Biological Conservation*, **120**, 31–39.

Jürgens, A., Witt, T. & Gottsberger, G. (2002) Pollen grain numbers, ovule numbers and pollen–ovule ratios in Caryophylloideae: correlation with breeding system, pollination, life form, style number, and sexual system. *Sexual Plant Reproduction*, **14**, 279–289.

Kato, M. & Kawakita, A. (2004) Plant–pollinator interactions in New Caledonia influenced by introduced honey bees. *American Journal of Botany*, **91**, 1814–1827.

Kato, M., Inoue, T. & Nagamitsu, T. (1995) Pollination biology of *Gnetum* (Gnetaceae) in a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany*, **82**, 862–868.

King, C., Ballantyne, G. & Willmer, P.G. (2013) Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution*, **4**, 811–818.

van Langevelde, F., Ettema, J.A., Donners, M., Wallis De Vries, M.F. & Groenendijk, D. (2011) Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, **144**, 2274–2281.

LeCroy, K.A., Shew, H.W. & van Zandt, P.A. (2013) Pollen presence on nocturnal moths in the Ketona Dolomite glades of Bibb County, Alabama. *Southern Lepidopterists' News*, **35**, 136–142.

Lewanzik, D. & Voigt, C.C. (2014) Artificial light puts ecosystem services of frugivorous bats at risk. *Journal of Applied Ecology*, **51**, 388–394.

Longcore, T. & Rich, C. (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, **2**, 191–198.

Lyytimäki, J. (2013) Nature's nocturnal services: light pollution as a non-recognised challenge for ecosystem services research and management. *Ecosystem Services*, **3**, e44–e48.

Martinell, M.C., Dötterl, S., Blanché, C., Rovira, A., Massó, S. & Bosch, M. (2010) Nocturnal pollination of the endemic *Silene sennenii* (Caryophyllaceae): an endangered mutualism? *Plant Ecology*, **211**, 203–218.

Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J.S. & Päivinen, J. (2006) Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology*, **20**, 1161–1168.

Mattila, N., Kotiaho, J.S., Kaitala, V. & Komonen, A. (2008) The use of ecological traits in extinction risk assessments: a case study on geometrid moths. *Biological Conservation*, **141**, 2322–2328.

Mazokhin-Porshnyakov, G.A. (1961) Why insects fly to light by night. *Anzeiger für Schädlingskunde*, **34**, 47.

Memmott, J., Waser, N.M. & Price, M.V. (2004) Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B*, **271**, 2605–2611.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant–pollinator interactions. *Ecology Letters*, **10**, 710–717.

Merckx, T. & Slade, E.M. (2014) Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes. *Insect Conservation and Diversity*, **7**, 453–461. DOI: 10.1111/icad.12068.

Miyake, T. & Yahara, T. (1998) Why does the flower of *Lonicera japonica* open at dusk? *Canadian Journal of Botany*, **76**, 1806–1811.

Miyake, T. & Yahara, T. (1999) Theoretical evaluation of pollen transfer by nocturnal and diurnal pollinators: when should a flower open? *Oikos*, **86**, 233–240.

Mizunami, M. (1995) Functional diversity of neural organization in insect ocellar systems. *Vision Research*, **35**, 443–452.

Montoya, J.M., Pimm, S.L. & Solé, R.V. (2006) Ecological networks and their fragility. *Nature*, **442**, 259–264.

Morse, D.H. & Fritz, R.S. (1983) Contributions of diurnal and nocturnal insects to the pollination of common milkweed *(Asclepias syriaca* L.) in a pollen-limited system. *Oecologia*, **60**, 190–197.

Navara, K.J. & Nelson, R.J. (2007) The dark side of light at night: physiological, epidemiological and ecological consequences. *Journal of Pineal Research*, **43**, 215–224.

Nemec, S.J. (1969) Use of artificial lighting to reduce *Heliothis* spp. populations in cotton fields. *Journal of Economic Entomology*, **62**, 1138–1140.

Olesen, J.M., Bascompte, J., Dupont, Y.L. & Jordano, P. (2007) The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, **104**, 19891–19896.

Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.

Pauw, A. (2007) Collapse of a pollination web in small conservation areas. *Ecology*, **88**, 1759–1769.

Pfrimmer, T.R., Lukefahr, M.J. & Hollingsworth, J.P. (1955) *Experiments with Light Traps for Control of the Pink Bollworm.* ARS-33-6. U.S. Department of Agriculture, Agricultural Research Service, Washington, District of Columbia.

Philipp, M., Böcher, J., Siegismund, H.R. & Nielsen, L.R. (2006) Structure of a plant–pollinator network on a pahoehoe lava desert of the Galápagos Islands. *Ecography*, **29**, 531–540.

Pocock, M.J.O., Evans, D.M. & Memmott, J. (2012) The robustness and restoration of a network of ecological networks. *Science*, **335**, 973–977.

Popic, T.J., Wardle, G.M. & Davila, Y.C. (2013) Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, **38**, 76–86.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**, 345–353.

Raguso, R.A. & Willis, M.A. (2005) Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, *Manduca sexta*. *Animal Behaviour*, **69**, 407–418.

Ramirez, N. (2004) Pollination specialization and time of pollination on a tropical Venezuelan plain: variation in time and space. *Botanical Journal of the Linnean Society*, **145**, 1–16.

Rathke, B.J. & Jules, E.S. (1993) Habitat fragmentation and plant–pollinator interactions. *Current Science*, **65**, 273–277.

Riordan, D.F. (1964) High-intensity flash discharge as a source of radiant energy for sterilizing insects. *Nature*, **204**, 1332.

Robinson, H.S. & Robinson, P.J.M. (1950) Some notes on the observed behavior of Lepidoptera in flight in the vicinity of light sources. *Entomologist's Gazette*, **1**, 3–20.

Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, **6**, 744–750.

Schlenoff, D.H. (1985) The startle responses of blue jays to *Catocala* (Lepidoptera: Noctuidae) prey models. *Animal Behaviour*, **33**, 1057–1067.

Solé, R.C. & Montoya, M. (2001) Complexity and fragility in ecological networks. *Proceedings of the Royal Society B*, **268**, 2039–2045.

Somers-Yeates, R., Hodgson, D., McGregor, P.K., Spalding, A. & ffrench-Constant, R.H. (2013) Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, **9**, 20130376.

Sotthibandhu, S. & Baker, R.R. (1979) Celestial orientation by the large yellow underwing moth, *Noctua pronuba* L. *Animal Behaviour*, **27**, 786–800.

Sower, L.L., Shorey, H.H. & Gaston, L.K. (1970) Sex pheromones of noctuid moths. XXI. Light : dark cycle regulation and light inhibition of sex pheromone release by females of *Trichoplusia ni*. *Annals of the Entomological Society of America*, **63**, 1090–1092.

Sutherland, W.J., Armstrong-Brown, S., Armsworth, P.R., Brereton, T., Brickland, J., Campbell, C.D. *et al.* (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology*, **43**, 617–627.

Svensson, A.M. & Rydell, J. (1998) Mercury vapour lamps interfere with the bat defence of tympanate moths *(Operophtera* spp.; Geometridae). *Animal Behaviour*, **55**, 223–226.

Syed, R.A. (1979) Studies on oil palm pollination by insects. *Bulletin of Entomological Research*, **69**, 213–224.

Truxa, C. & Fiedler, K. (2012) Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology*, **109**, 77–84.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Tylianakis, J.M., Laliberté, E., Nielsen, A. & Bascompte, J. (2010) Conservation of species interaction networks. *Biological Conservation*, **143**, 2270–2279.

Wallis De Vries, M.F., Van Swaay, C.A.M. & Plate, C.L. (2012) Changes in nectar supply: a possible cause of widespread butterfly decline. *Current Zoology*, **58**, 384–391.

Warren, A.D. (1990) Predation of five species of Noctuidae at ultraviolet light by the western yellowjacket (Hymenoptera: Vespidae). *Journal of the Lepidopterists' Society*, **44**, 32.

Wasserthal, L.T. (1997) The pollinators of the Malagasy star orchids *Angraecum sesquipedale, A. sororium* and *A. compactum* and the evolution of extremely long spurs by pollinator shift. *Botanica Acta*, **110**, 343–359.

Williams, P.H. (1982) The distribution and decline of British bumble bees *(Bombus* Latr.). *Journal of Apicultural Research*, **21**, 236–245.

Willmer, P. (2011) *Pollination and Floral Ecology*. Princeton University Press, Princeton, New Jersey.

Winfree, R., Bartomeus, I. & Cariveau, D.P. (2011) Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 1–22.

Young, H.J. (2002) Diurnal and nocturnal pollination of *Silene alba* (Caryophyllaceae). *American Journal of Botany*, **89**, 433–440.

Accepted 19 October 2014

Environmental Pollution 221 (2017) 459–469

Contents lists available at ScienceDirect

Environmental Pollution

journal homepage: www.elsevier.com/locate/envpol

An environmental index of noise and light pollution at EU by spatial correlation of quiet and unlit areas☆

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ARTICLE INFO

Article history:
Received 15 April 2016
Received in revised form
9 December 2016
Accepted 11 December 2016
Available online 15 December 2016

Keywords:
Quiet areas
Unlit areas
Wilderness
Naturalness
Environmental index

ABSTRACT

Quietness exists in places without human induced noise sources and could offer multiple benefits to citizens. Unlit areas are sites free of human intense interference at night time. The aim of this research is to develop an integrated environmental index of noise and light pollution. In order to achieve this goal the spatial pattern of quietness and darkness of Europe was identified, as well as their overlap. The environmental index revealed that the spatial patterns of Quiet and Unlit Areas differ to a great extent highlighting the importance of preserving quietness as well as darkness in EU. The spatial overlap of these two environmental characteristics covers 32.06% of EU surface area, which could be considered a feasible threshold for protection. This diurnal and nocturnal metric of environmental quality accompanied with all direct and indirect benefits to human well-being could indicate a target for environmental protection in the EU policy and practices.

1. Introduction

Noise is one of the dominant contemporary environmental problems affecting human health and wellbeing (EEA, 2014; Fyhri and Aasvang, 2010; WHO, 2002; Zaharna and Guilleminault, 2010), as well as wildlife conservation (Barber et al., 2010). In an attempt to mitigate noise pollution the European Commission introduced in 2002theDirective 2002/49/EC regarding the assessment and management of environmental noise (END). According to END environmental noise is the unwanted or harmful outdoor sound created by human activities, including noise emitted by means of transport and sites of industrial activity. END served as a platform to boost research on environmental noise and led to the development of new tools and methodologies to achieve environmental noise mapping. The END interim report recommended computation methods of assessment, common for all Member States (Manvell and van Banda, 2011). Still, noise pollution continues to threaten about 40 million people living in cities and 25 million people in open-country (EC, 2011), without excluding others exposed at lower sound levels, than the ones documented to cause health problems (WHO, 2011).

The designation and protection of Quiet Areas (QAs) constitute a major policy initiative to confront noise pollution. QAs could be considered as sites where people can recover from harmful noise pollution effects (Brambilla and Maffei, 2006) and wildlife is protected (Barber et al., 2011; Hatch and Fristrup, 2009; Reed and Merenlender, 2008). Focusing on open country, QAs are places without human-induced noise sources (i.e. traffic, agglomerations, industries, constructions, recreational activities), constituting refuges of noise pollution. END, as well as recent studies (De Coensel and Botteldooren, 2006; Licitra et al., 2011; Shepherd et al., 2013) have underscored the role of open country QAs for safeguarding environmental quality. And outside EU, research documented that QAs could form an indicator of remoteness and potential wilderness (Carver et al., 2013; Landres et al., 2008). Hereafter in this paper QAs refer to QAs in open country.

Light pollution, on the other hand, forms another important environmental problem affecting 37% of the European population (Cinzano et al., 2001; Marin, 2009). Considering the role of light as a resource (photosynthesis, diurnal activities, repair and recovery), as well as an information source (visual perception, spatial orientation), the impacts of artificial lights are manifold for human well-being and for wildlife (Davies et al., 2013; Gaston et al., 2013). Among them the increase of mortality and decrease of fecundity resulting in changes in species composition and trophic structure are the most significant for a wide range of plants and animals (Lyytimäki et al., 2012; Rodrigues et al., 2012). As far as human

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☆ This paper has been recommended for acceptance by Eddy Y. Zeng.

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http://dx.doi.org/10.1016/j.envpol.2016.12.015
0269-7491/

effects are concerned, many researchers have recorded sleep, asthma, even cancer related problems (Bephage, 2005; Kloog et al., 2009; Lin et al., 2001). While noise pollution is usually associated with diurnal activities and only rarely with nocturnal activities, artificial light pollution refers primarily (if not exclusively) to nocturnal activities.

Recently various initiatives to measure and mitigate light pollution have been developed [e.g.2009/125/EC,International Dark Sky Association, Albers and Duriscoe (2001), Aubé, and Roby, 2014, Duriscoe (2016), Kyba et al. (2013, 2015), Pun and So (2012)]. In environmental studies, however, it is rather difficult to measure light pollution impacts adopting standard methods (Longcore and Rich, 2004). An alternative and easy to implement approachto quantify the effects of light pollution on humans and the environment is to identify artificial lights and isolate them afterwards, so as to define theUnlit Areas (UAs), i.e. areas without artificial light. Hölker et al. (2010), and Gaston et al. (2012) suggest to study the implications of Darkness as this would significantly contribute to future conservation efforts. These unlit refuges are characterized by lack of intense human interference, thus composing areas where naturalness prevails (Carver et al., 2013; Gaston et al., 2012; Landres et al., 2008).

To sum up, noise and artificial light constitute human induced environmental pollutions, whereas QAs as well as UAs could potentially offer the desired tranquility for human societies and nature conservation (Carver et al., 2013; Chalkias et al., 2006; Hölker et al., 2010). Noise pollution reduces human wellbeing and disturbs the wildlife, while light pollution has similar effects only at nighttime. The objective of this paper is to investigate the pattern of noise and light pollution aiming to develop an integrated diurnal and nocturnal index of these two forms of environmental pollution. This environmental index includes 4 different cases: a) areas free of noise and light pollution, b) areas with noise pollution but no light pollution, c) areas with light pollution but no noise pollution and d) areas with noise and light pollution. To prove this concept, we applied the environmental index at the member-States of the EU in order to contribute in a preliminary time and cost effective way to conserving high ecological value areas as well as ensuring human wellbeing.

2. Material and methods

2.1. Study area

All spatial data, their investigation, as well as their interpretation included the 27 Member-States of the EU, before Croatia' joining. Europe is a continent with a long history of human activities. It is densely populated, with high degree of light and noise pollution, and complex, vastly fragmented landscapes (Jaeger et al., 2011).

2.2. Identifying areas without noise & light pollution

Noise mapping software is, today, a professional well-developed and commonly used tool based on specific standards for various purposes (Manvell and van Banda, 2011; Ramis et al., 2003; WGAEN, 2007). Nevertheless our goal was to identify QAs at a coarse scale, i.e. quiet areas in open country. QAs assessment requires specialized methodology (Clarke, 2011; MacFarlane et al., 2004; Morgan et al., 2006; Symonds, 2003; SWS, 2000; Waugh et al., 2003). Under this framework EEA proposes a multi-dimensional methodological approach of QAs suitability which is based, among others, on distance-based criteria. Indeed, EEA proposes the adoption of different criteria for QAs in cities and in open country (EEA, 2016). For QAs in agglomerations, noise mapping is the recommended approach, even recognizing its limitations, i.e. noise mapping does not distinguish pleasant (water falling, birds singing) from annoying (cars, airplanes) sounds, just records sound pressure levels (EEA, 2014). But this approach is demanding in man power and time and its level of accuracy is not necessary at coarse continental scales (as in the present study).

Here, we applied the methodological designation of QAs in open country based on distance criteria (Votsi et al., 2012, 2015), also supported by EEA (2014; 2016). In this approach, the basic human induced noise sources are located using several spatial datasets [Corine Land Cover (2000), Open Street Map (daily updated), Urban Atlas (2006)], and each noise source is associated with recorded energy equivalent sound pressure levels at the noise source based on calculating the average noise source for each category of existing literature reviews. The model also includes the computation of the cumulative effect of noise sources, as well as the noise source standardization to human response according to the dose-response relationship (Schomer, 2005). The next step comprised buffering each noise source, taking into account the mean radius value that is needed for the sound pressure level of each source to fall below the critical threshold of Quietness (50 dB of Lden). Noise propagation was calculated following the basic principles of Acoustics, according to which sound pressure level decreases in inverse proportion to the distance from source, meaning that doubling the distance from a noise source the sound pressure is reduced to half of the initial value (Pierce, 1989). For a thorough documentation of the input data layers and the methodological approach to define QAs please consult Table 1. By overlaying the buffered noise sources onto a map of EU, we defined QAs (Fig. 1a). Of course this is a simplification, which limits the accuracy of the QA delineation, but it is proposed as a fast and economic first approximation to estimate the QAs.

Our methodological approach is based on the assumption that the different databases used provide data about the distribution of the sound sources referring to the previous decade. This was because the required information (of both noise and light pollution) was available only for that time period. This means that the analysis refers to that dates, and it remains an open question for future research, if and where conditions changed significantly enough in the intervening time. Some first indications from the Noise Observation and Information Service for Europe indicate that there are significant changes in countries such as the UK and France (http://noise.eionet.europa.eu/viewer.html), but the degree to which they affect the continental scale patterns of quiet areas or are more limited and localized remains open question for future research.

Though in the case of noise pollution, no available noise mapping of the EU territory exists, a database on lights observed by satellite images was derived from NOAA (F15 2003 Nighttime Lights Composite) (NOAA, 2015) in the format of raster data. This data also refer to the same time period as the noise data. A number of constraints were used to select the highest quality data. The cleaned up dataset includes city lighting as well as other sites with persistent lighting, including gas flares. There are no ephemeral events and the background noise was identified and replaced with values of zero (DM Duriscoe et al., 2013). (available at: http://ngdc.noaa.gov/eog/dmsp/downloadV4composites.html).

In the case of noise pollution we had to determine and calculate the expansion of each noise source, whereas in the case of light pollution the influenced area around each light source is delineated directly using satellite images. The NOAA data depict the actual area influenced by artificial lighting, with an efficient accuracy for a coarse scale research (Elvidge et al., 2013; Bruehlmann, 2014), enabling use to derive the UAs. We then reclassified the observed data into a binary raster map depicting with value one the lights of

Table 1
The main categories anthropogenic noise sources along with the implemented buffer zones based on emitted sound levels, as these have been recorded to relevant bibliography.

Anthropogenic noise source (input data layer)	Recordings of Sound pressure level (Leq) at the noise source (dB)	Buffer zone (m)
Primary roads (www.openstreetmap.org)	85 (i.e. Miller, 1982; Jackson et al., 2008; Fritschi et al., 2012)	1000
Secondary roads (www.openstreetmap.org)	68 (i.e. Jackson et al., 2008; DIER, 2011)	650
Tertiary roads (www.openstreetmap.org)	60 (i.e. Jackson et al., 2008)	400
Railway (www.openstreetmap.org)	75 (Moritoh et al., 1996; Krylov, 2001; Pahalavithana and Sonnadara, 2009)	750
Agglomerations (http://www.eea.europa.eu/dataandmaps/data/urban-atlas)	87(Bacria et al., 2007; Şchiopu and Bardac, 2012) + 5 dB[a]	1200
Industrial centers (http://land.copernicus.eu/pan-european/corine-land-cover)	100 (Ntalos and Papadopoulos, 2006; Australia, 2011)	1500
Local industries (http://land.copernicus.eu/pan-european/corine-land-cover)	66 (Jackson et al., 2008; City of Williams, 2012)	500
Airports (http://land.copernicus.eu/paneuropean/corine-land-cover)	110 (Pritchett et al., 1976; http://www.pbcgov.com/airport/terminology.htm) + 6 dB[a]	2000
Ports (http://land.copernicus.eu/pan-european/corine-land-cover)	85 (Good Practice Guide on port area noise mapping and management, 2008; Clark and Petersen 2012) + 4 dB[a]	1000
Construction sites (http://land.copernicus.eu/pan-european/corine-land-cover)	90 (Sharma et al., 1998; McMullan and Seeley, 2007) + 12 dB[a]	1250
Recreational activities (http://land.copernicus.eu/pan-european/corine-land-cover)	80 (Clark, 1991; Jiménez et al., 2010) + 5 dB[a]	850
Cumulative effect (Pierce, 1989)	combination (dB) = 10 log(10a/10 + 10b/10 + … + 10n/10)	where a, b, …, n: noise sources with various noise levels

[a] Noise source standardization to human response (Schomer, 2005).

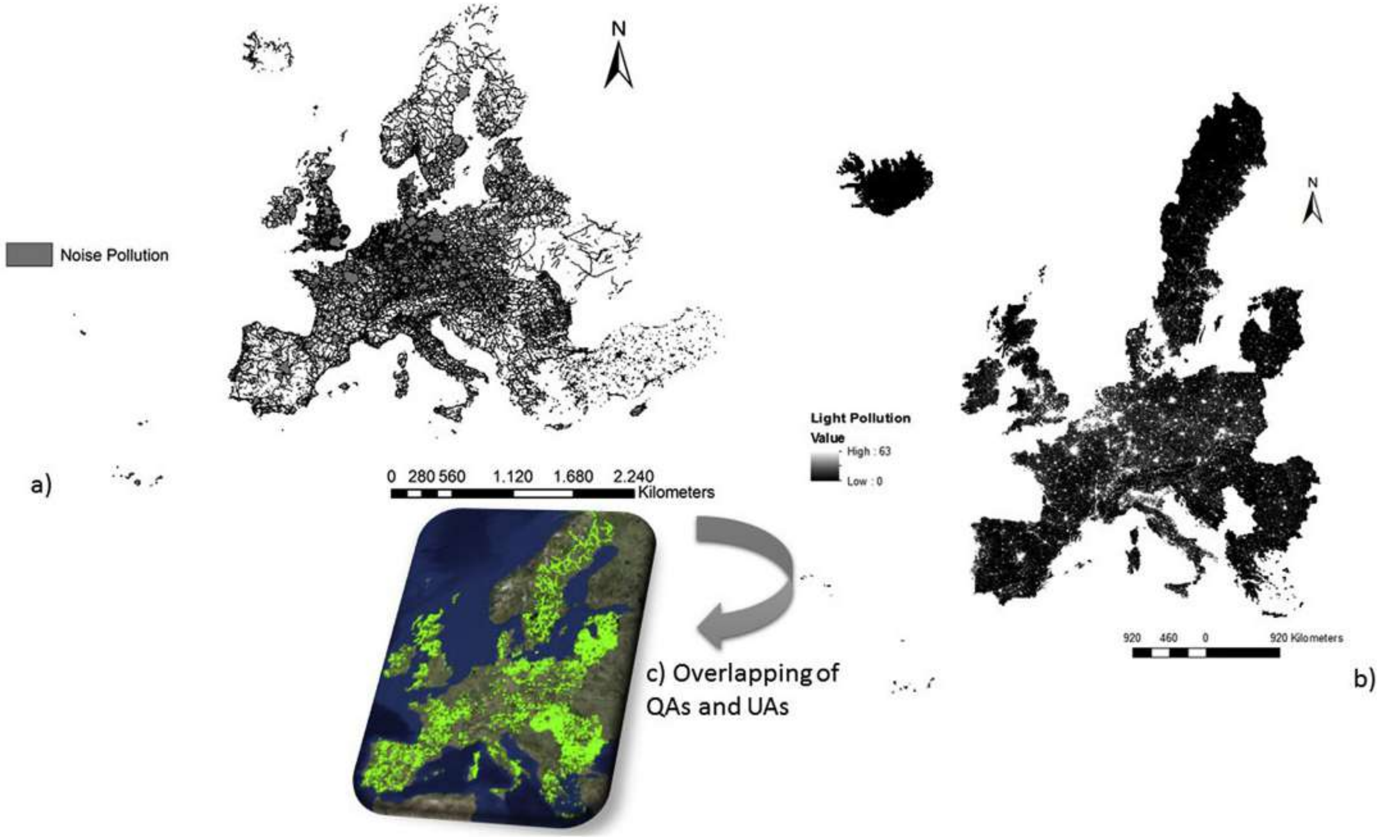

Fig. 1. The methodological approach to result in the integrated network of QAs and UAs. All a) noisy areas as well as b) technically enlightened areas (Image and data processing by NOAA's National Geophysical Data Center. DMSP data collected by US Air Force Weather Agency) were defined and then extracted form a map of Europe to result in QAs and UAs, respectively. c) their spatial overlap, meaning areas with no light and noise pollution were also identified and analyzed.

EU and value zero the areas with no light pollution, meaning UAs of EU. The next step of our methodological approach included the isolation of UAs by selecting only UAs from the raster file. With view to spatially combining UAs with QAs we converted UAs map into a vector format (Fig. 1b).

Initially we recorded the sum and mean area of Quietness and Darkness in each Member-State. Though our datasets included Iceland and Norway (Fig. 1), we excluded them from further analysis since our study area was EU. Then we checked the spatial overlap between QAs and UAs, meaning the sites in the EU which at the same time are characterized as QAs and UAs (Fig. 1c).

2.3. Spatial analysis

We developed a grid with cell size 1 km^2 extending to the entire study area and we recorded the number of grids covered by QAs and UAs respectively in order to compute the distributional density of the two networks.

Band Collection Statistics provides statistics for the multivariate analysis of a set of raster bands. Apart from the basic statistical parameters (minimum, maximum, mean, and standard deviation), Band Collection Statistics calculate the covariance and correlation matrix between QAs and UAs, giving the opportunity to investigate how much dependency exist in our datasets. The covariance of two layers is the intersection of the appropriate row and column while the correlation matrix shows the values of the correlation coefficients that depict the relationship between two datasets.

We measured the spatial autocorrelation based on surface area values of the two examined data sets using the Global Moran's I statistic with view to testing whether QAs in open country, UAs and their spatial overlap are randomly distributed.

Based on Geographically Weighted Regression (GWR)tool spatially calibrated regression models can be generated. This tool enables the investigation of the spatial variation for both QAs, UAs network, as well as their spatial overlap.

All calculations were performed in GIS 10.1 (ArcGIS® software by ESRI) (Scott and Janikas, 2010).

3. Results

Taking into account the surface area of each Member State and the total area of EU (3 963 144 km^2) we recorded total surface area, the mean area size and the relative percentages of QAs, UAs and their spatial overlap resulting in the four different values of the index. The integrated environmental index included: a) 74.56% of the EU territory (2955252 km^2) constitutes QAs, meaning areas free of noise pollution, b) 36.82% of the EU (1 459 182 km^2) is composed of UAs, areas without light pollution, c) 32.06% of the EU is free of noise and light pollution (spatial overlap of QAs and UAs) and d) 71.87% of the EU is polluted by noise and light. The results for each Member State are listed in Table 2 and depicted in Fig. 2.

3.1. Spatial analysis

According to the distributional density results France encompasses the highest surface area of contiguous (i.e. a single united and not fragmented surface area) UAs (3873 km^2) followed by Sweden (3072 km^2), Greece (2982 km^2), Romania (2898 km^2), Spain (2838 km^2), Slovakia (2620 km^2), Portugal (2609 km^2), Bulgaria (2587 km^2), Slovenia (2576 km^2), Hungary (2543 km^2), and Poland (2093 km^2). France is also the country containing the highest surface of QAs followed by the UK.

Based on our findings there are differences within and between the examined countries in the spatial overlap of QAs and UAs, posing several implications on setting a standard of the proposed environmental index. For instance, in the case of Finland 88% of the country is covered by QAs and UAs revealing the prevalence of the natural environment and wilderness of the area. On the other hand Slovakia is covered by QAs as well as UAs only by 5.7% of the total surface area of the country underscoring the necessity for natural areas' protection and restoration. When focusing on the spatial overlap of UAs with noise pollution we can observe that Czech Republic as well as Cyprus cover the highest area percentages, while Estonia, Bulgaria, France, Germany, Poland, Portugal, Spain, Sweden and United Kingdom demonstrate the lowest percentages meaning that special attention should be drawn to countries like Czech Republic and Cyprus as far as the noise pollution is concerned. It seems that even in UAs, where wilderness is expected to prevail, environmental noise is prevalent in a considerable degree. On the other hand countries like Sweden, Spain and Estonia face mostly light pollution related problems, and thus environmental strategies should be directed accordingly. Light pollution does not constitute a problem for Cyprus, Czech Republic, Latvia, Lithuania and Romania. Last but not least in the case of countries with high percentages of the spatial overlap of QAs and UAs, like Lithuania, Latvia and Finland the main environmental problem is noise pollution indicating the priorities in policy designation whereas light pollution is revealed as the prevalent environmental problem in countries with a small spatial overlap of QAs and UAs (for instance Slovakia and Estonia). But, according to our findings, this is not always the case revealing a more complicated spatial pattern of the proposed environmental index. At any rate, it becomes obvious that differences among countries due to several topographic, socioeconomic, legislative reasons form a complicated framework where limits and standards of an environmental index are very difficult to be implemented. Policy initiatives should always take into account the local, regional and national differentiations of each case study, when international, coarse environmental strategies are adopted.

Matching the spatial pattern of contiguous areas in the two cases it is obvious that UAs comprise a more connected network, with high percentage of the surface area being adjacent to other UAs. Nevertheless the more adjacent areas covered by either QAs or UAs are found in the center of the EU (Fig. 3).

The covariance matrix of QAs and UAs did not demonstrate any statistically significant variance between the two layers (7.128161e+005, −1.997032e+005). Moreover the correlation matrix revealed a weak dependency between QAs and UAs (−0.18) indicating that QAs and UAs follow different not correlated spatial patterns. All the basic statistical parameters of the Band Collection Statistics are mentioned in Table 3.

According to the Global Moran's I statistic results QAs as well as UAs are randomly distributed across the EU ($zscore = 0.21$, $p = 0.83$ for QAs, and $zscore = 0.33$, $p = 0.74$ for UAs, respectively). However in the caseof high area values in UAs network, the spatial distribution is more clustered than would be expected under random conditions. In the case of QAs and UAs spatial overlapping an even more clustered distributional pattern due to high area values was revealed ($zscore = 35.42$, $p < 0.01$). In other words, large areas that are quiet and unlit at the same time demonstrate spatial autocorrelation broadening the perspectives for effective management initiatives.

LocalR2, which forms an indicator of the fitness of the local regression model revealed that in both cases models fit in same areas, which include Portugal, Spain, Sweden, and considerable parts of U.K. Bulgaria and Romania, while the fitness is weak in the central EU. Differences are observed in the case of Mediterranean countries, where the model fits well for QAs but not for the case of UAs. The same goes for Moldova. As far as the spatial overlapping of QAs and UAs is concerned, the model fits well in the vast majority of

Table 2
The spatial characteristics of QAs, UAs as well as their spatial overlap in the EU.

Member State	QAs total surface area (km^2)	UAs total surface area (km^2)	QAs average surfaces area (km^2)	UAs average surfaces area (km^2)	Areas free of noise and light pollution(km^2)	% percentage of QAs in relation to member state surface area	% percentage of UAs in relation to member state surface area	% percentage of areas with noise pollution but no light pollution	% percentage of areas with light pollution but no noise pollution in relation to member state surface area	% percentage of spatial overlap in relation to member state surface area
Austria	54 852	58 423	155	8	54 125	65.50	69.77	5.13	0.86	64.64
Belgium	11 746	10 572	31	2	10 489	38.54	34.69	0.28	4.13	34.41
Bulgaria	81 497	60 893	1273	10	60 879	73.55	54.96	0.02	18.61	54.94
Cyprus	3970	6040	136	5	3789	42.91	65.29	24.33	0.01	40.91
Czech Republic	33 403	58 854	101	10	33 329	42.55	74.98	32.52	0.09	42.46
Denmark	18 303	25 100	101	7	18 143	42.89	58.82	16.30	0.37	42.52
Estonia	31 626	5685	445	18	31 589	69.44	6.36	0.01	63.08	6.36
Finland	300 050	326 254	533	15	298 364	88.66	96.40	8.24	0.50	88.16
France	370 390	68 104	269	8	67 856	67.75	12.46	0.05	55.34	12.41
Germany	158 154	57 262	76	11	57 028	44.41	16.08	0.07	28.40	16.01
Greece	102 367	49 821	191	9	48 796	77.64	37.79	0.78	40.63	37.01
Hungary	59 090	56 209	249	12	55 634	63.69	60.58	0.62	3.73	59.96
Ireland	48 564	48 205	220	9	48 089	69.99	69.48	0.17	0.68	69.31
Italy	196 726	50 542	197	8	49 856	65.36	16.79	0.23	48.80	16.56
Latvia	45 616	58 760	345	35	45 489	70.94	91,39	20.64	0.19	70.75
Lithuania	44 693	55 935	647	13	44 589	68.92	86,25	17.49	0.16	68.76
Netherlands	8143	6984	5	3	6897	22.94	19.68	0.25	3.51	19.43
Poland	196 049	61 840	391	12	61 698	63.10	19.90	0.04	43.24	19.86
Portugal	69 853	48 028	513	8	48 000	75.85	52.15	0.03	23.73	52.12
Romania	18 622	57 198	744	6	18 234	7.87	24.17	16.47	0.17	7.70
Slovakia	28 920	2863	190	9	2789	58.98	5.84	0.15	54.29	5.69
Slovenia	12 572	10 472	246	11	10 136	62.10	51.72	1.66	12.04	50.06
Spain	397 182	66 346	859	18	66 148	78.55	13.12	0.04	65.47	13.08
Sweden	368 245	68 905	503	19	68 759	82.98	15.53	0.04	67.49	15.49
United Kingdom	127 003	60 086	71	16	60 000	52.24	24.71	0.03	27.56	24.68
EU	2 955 252	1 459 181	225	12	1 270 705	74.56	36.82	4.76	42.50	32.06

Table 3
Band Collection Statistics of the two examined networks: Dark and Quiet Areas. The units of the two matrices arekm^2.

Layer	Min	Max	Mean	Std
Unlit Areas	38.00	8277.00	4674,96	3119,98
Quiet Areas	3.00	13 089.00	6866.33	3941.94

the EU Member States, excluding Romania, again central EU, the north part of Italy and Greece as well as Denmark. Condition number in all cases ranges from 1.01 to 2.17 indicating that our results are reliable (Fig. 4).

4. Discussion

The approach of defining sites free from noise and light pollution could result in an effective environmental indicator. Areas free of anthropogenic disturbance would be located and it would be feasible to implement various strategic initiatives at multiple administrative and executive levels, opening new dimensions in policy makers. And even though noise and light pollution has been considered independently, their integrated effect has not been explicitly considered. Many studies have highlighted the impact of artificial lighting on nocturnal activities of many organisms, as well as humans (Lyytimäki et al., 2012), its role in environmental planning is still limited (Holker et al., 2010; Longcore and Rich, 2004). Moreover, while noise pollution has been investigated and many policy initiatives consider noise mitigation as a priority step, results of decreasing this problem are still lacking (Shelton, 2016). Remote sensing offers useful and accurate methods of recording light pollution (Chalkias et al., 2006; Liang and Weng, 2011). In this paper we made a preliminary attempt to simultaneously identify Quiet Areas (QAs) and Unlit Areas (UAs), as well as examine their spatial relation at a coarse continental scale based on existing relevant datasets and on distance based calculations about noise and light propagation, as an application of our approach. Next research steps should include field observations to verify on the ground the outcomes of this study. A combination of these approaches could offer options to decision makers for planning and implementing an effective strategy of integrated environmental management that would contribute to an improved environmental policy. In this framework QAs and UAs are based on the concept of areas of human sensory perception of good environmental quality (Hölker et al., 2010).

4.1. *Identifying areas without noise & light pollution*

While noise pollution is associated with diurnal and to a lesser degree nocturnal activities, artificial light pollution is associated almost exclusively with nocturnal activities, thus their spatial pattern across EU differ. According to our findings, UAs are considerably fewer than QAs, indicating that light pollution is much more propagated along Europe, underlying the serious environmental problem of artificial lighting. It goes without saying that future research should not focus only on describing light pollution but should also look into of controlling and limiting light pollution. On the other hand QAs occupy a large percentage of EU, meaning that Quietness still exists in many sites of the EU. Nevertheless and taking into account the remaining unaffected areas of the EU, it seems that QAs are not necessarily natural areas. Defining areas of high ecological value would require the combination of two environmental assets, Quietness and Darkness, which need protection, as it is also suggested by Chalkias et al. (2006) and Lyytimäki et al. (2012). In this paper we investigated UAs and QAs by spatially overlapping them to determine sites without human disturbance, thus potential areas of high ecological value, where naturalness

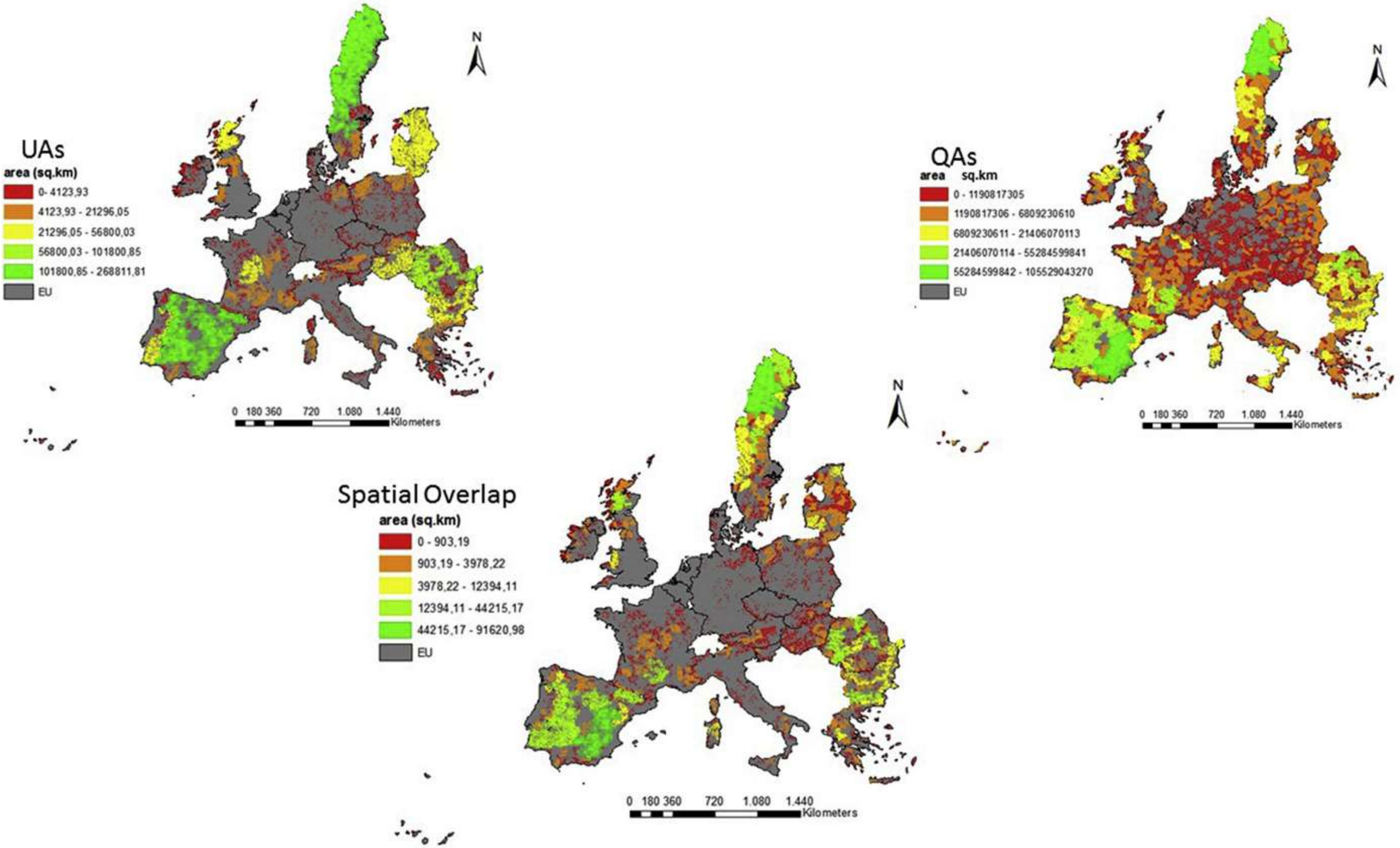

Fig. 2. The spatial pattern of the surface area of UAs, QAs as well as their spatial overlap in the EU. Color range depicts the surface size in 5 categories in an ascending order of area measured in km^2 from red to green. EU is depicted on grey color. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

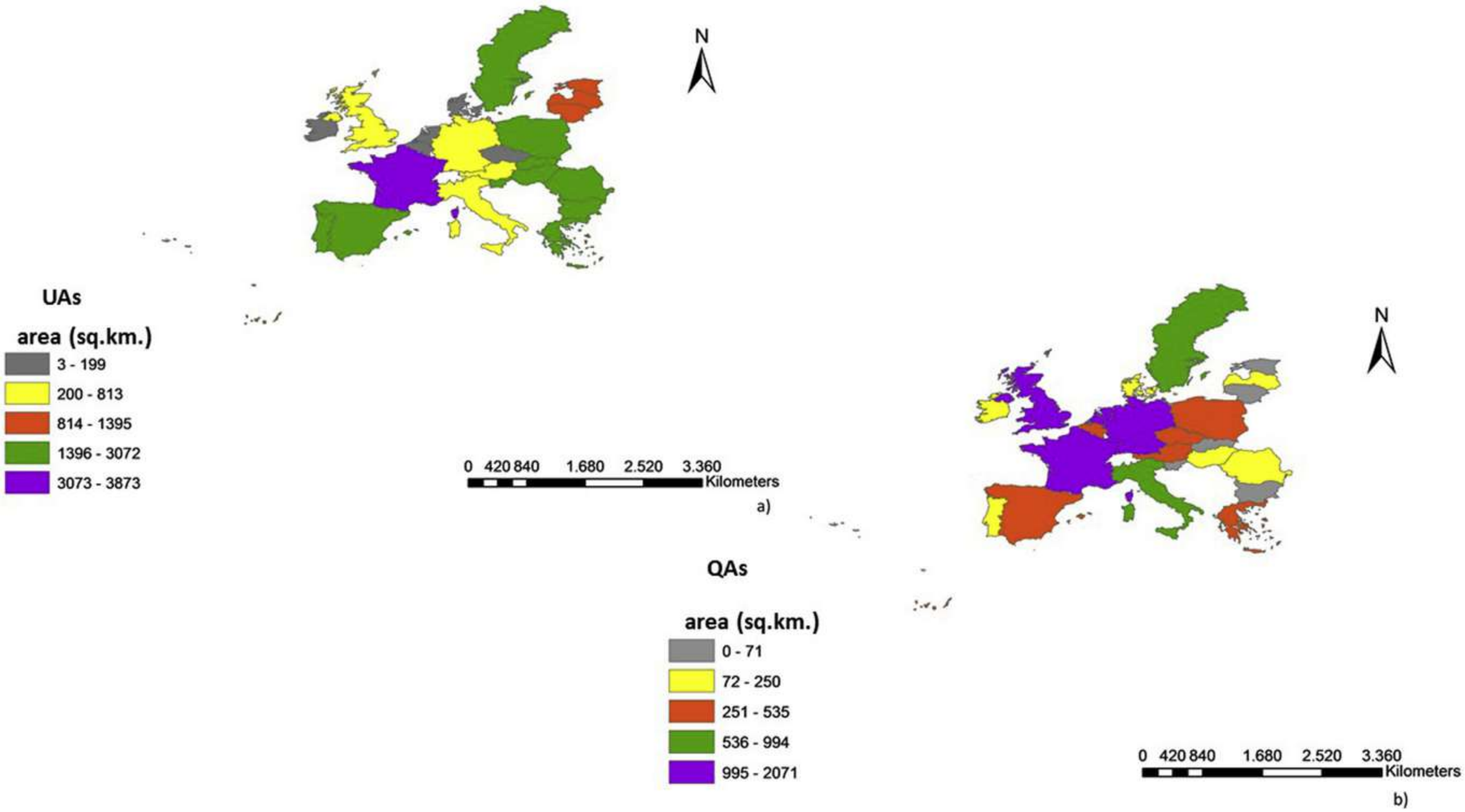

Fig. 3. The relative spatial coverage of UAs and QAs according to the number of 1 km^2 cell size grids they occupy.

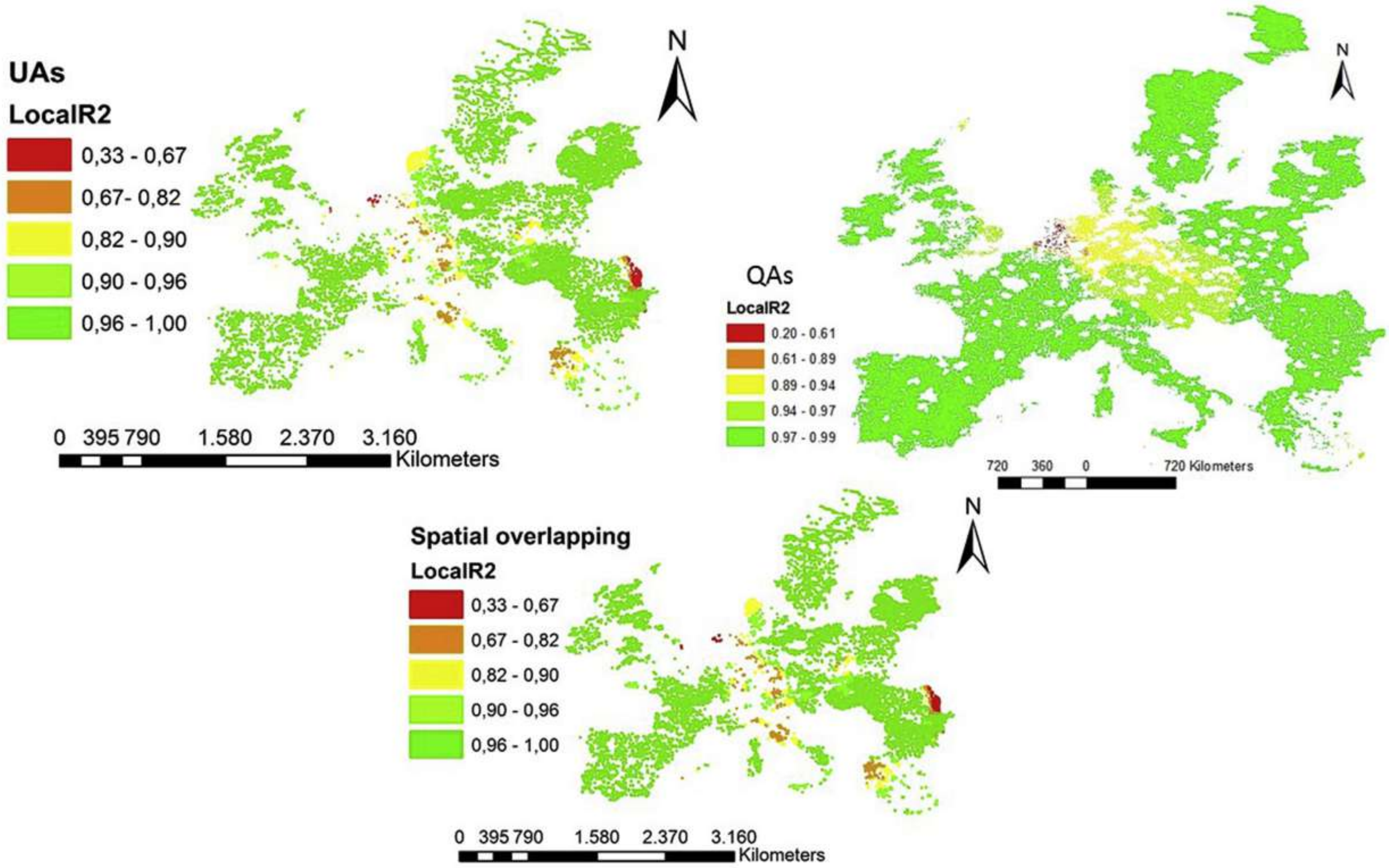

Fig. 4. The model fitness of UAs, QAs and their spatial overlapping according to LocalR2 values (in ascending order with different colors ranging from red to green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prevails. According to our findings the spatial overlap of QAs and UAs covers a considerable percentage of the EU territory, which though it does not extinguish the threat for the remaining natural areas, it constitutes a feasible goal to be incorporated in nature conservation policy initiatives resulting in the protection of these free of anthropogenic disturbance quiet and unlit sites.

The area size of both QAs and UAs demonstrates high variance and includes large, contiguous areas without noise or light pollution, which might also be natural areas. Though in the case of QAs more large areas are identified at the examined coarse scale case study, and the majority of UAs are found in small are sizes, even UAs cover areas of thousands of km^2. On the contrary and thus reinforcing its critical value, the spatial overlap of QAs and UAs shows a small range with surface areas that barely exceed 8 km^2.

4.2. Spatial analysis

QAs network is widely spread while UAs distribution is more aggregated. The diverse spatial characteristics of the two networks indicate that different environmental characteristics are captured by Quietness and Darkness identification. As a consequence, a combined network that would include QAs in open country as well as UAs could highlight areas of high ecological value under multiple criteria.

What is more, QAs and UAs distributional pattern is denser strangely enough, in central Europe, since these areas are the most human dominated places of EU (Prach and Pyšek, 2001). This status reveals the necessity and potential of environmental policy initiatives on protection of QAs and UAs, which due to their concentration could become an easy preservation target to indirectly achieve nature conservation. It's also worth mentioning that UAs form a better connected network, comprised of smaller but numerous contiguous areas, whereas in the case of QAs the network is dispersed formed by large but fewer adjacent areas.

The Band Collection Statistics confirmed the objectives of wilderness preservation in the U.S. regarding QAs and UAs (Landres et al., 2008; Carver et al., 2013). More precisely the two networks have a weak correlation, highlighting the need for an integrated methodological approach and management Implementation.

According to geographically weighted regression QAs' UAs' patterns resemble, the two features are correlated in spatial terms enabling the development and adoption of an environmental policy protecting both of them. In this way, a specific framework is outlined opening up multiple perspectives in policy and management plans. EU strategic actions, regarding noise and light pollution, could adopt an environmental policy that would take into account the observed differences in central and the rest of the EU, under an integrated approach.

The identification of Quietness and Darkness all over the EU could result in the designation of priority sites for further study and perhaps preservation, where QAs overlap with UAs. In the case that one of the two characteristics is missing the sites could be characterized as potentially threatened, and thus identify areas of restoration priorities. Under this concept a combined socio-ecological monitoring and evaluation of the landscape could offer pioneer means of improving environmental quality, giving the opportunity for further research about the impacts of these two environmental problems and their potential solutions, but also a cost and time effective means of defining sites of priority to be protected by policy makers.

4.3. Caveats and future perspectives

In this paper an integrated environmental index of noise and light pollution has been developed. Accurate measurements of noise and light pollution would require high cost, which is difficult to obtain (Jabben et al., 2015). As a proof of concept we chose simple and cost effective methods to estimate quiet and unlit areas, making simplifications for calculating noise propagation in the EU level. We should point out that our index is based on the spatial correlation of unlit and quiet areas and not on the specific methodology used to delineate those areas. So future research using more accurate sound mapping tools may produce more precise maps, where to examine the properties of our index. Having said that, we should mention the simplifications of the approach applied here, such as that free field sound propagation is expanded over a flat ground with no obstacles, as well as the hypothesis that the same topographic, traffic conditions exist in every Member State.

Thus further research is needed to study the expansion of light and noise pollution at finer scales (national, regional, or even local) and consider the factors varying among countries. Moreover future studies should take into account the indirect light and noise pollution (Chalkias et al., 2006), by means of defining more classes on lit/unilt areas. Overall a more detailed and on the ground research is required in order to verify in specific case-studies the coarse-scale outcomes of our study. Noise measurements or acoustical computation methods should also be conducted not only to validate the proposed methodology, but also to compare the outcomes derived from different scales and locations. Under this concept impacts on flora and fauna could also be investigated with view to determining the direct but also indirect consequences of light and noise pollution. It should also be noticed that though the methodological approach of defining QAs has been adopted in a National scale (Votsi et al., 2012), the originality and novelty of this research relies on the modifications made to adjust to the European scale for addressing two of the most significant environmental pollution issues. Last but not least we should mention that the divergence of our results from those reported by EEA (2016) is mostly due to the simplified methodology proposed in this paper, which focuses only in QAs and does not take into account factors like the degree of naturalness which is considered by EEA.

The aim of our study is to offer policy-makers with an index to help plan environmental policies that benefit nature conservation and human well-being Votsi et al. (2014). To this end, this is a first approximation of the index and its value should be tested using epidemiological research examining the association of the index with mental health and physical health outcomes. Similarly ecological research could associate the distribution of biodiversity and endangered species with this index to document its efficiency for nature conservation.

After having defined the conceptual framework of this combined environmental index, it could be applied to finer scales accompanied with accurate field measurements in order to study its effectiveness in urban design. It should be underscored that the integrated environmental index is not based on QAs or UAs identification and mapping. The applied methodological approach was a first easy to implement approach to demonstrate the effectiveness of the index without excluding the adoption of other methodological approaches in the future.

5. Conclusions

Environmental quality forms a demanding element of the contemporary world. Recent policy initiatives and research attempts underscore the effects of noise and light pollution on nature conservation and human wellbeing. However direct mitigation measures of noise and light pollution are economically and administratively difficult to implement. This research revealed an innovative, alternative and combined approach of confronting with these serious environmental problems by developing an integrated environmental index, as well as evaluating its ecological role.

The combination of QAs and UAs forms a nocturnal and diurnal metric which could indicate sites of environmental quality. Needless to say the method outlined in this paper offers a first approximation of how QAs and UAs interact, and future studies are needed to verify the results by field observations. Taking into account other senses, apart from the common visual one, seems a promising and revealing interdisciplinary research objective.

Acknowledgements

IKY FELLOWSHIPS OF EXCELLENCE FOR POSTGRADUATE STUDIES IN GREECE – SIEMENS PROGRAM.

References

Albers, S., Duriscoe, D., 2001. Modeling light pollution from population data and implications for National Park Service lands. George Wright Forum 18 (4), 56–68.

Aubé, M., Roby, J., 2014. Sky brightness levels before and after the creation of the first international Dark sky reserve, Mont-Mégantic observatory, Québec, Canada. J. Quantitative Spectrosc. Radiat. Transf. 139, 52–63.

Australia, S.W., 2011. Australia: Safe Work Australia. Managing Noise and Preventing Hearing Loss at Work. Code of Practice, vol. 46.

Bacria, V., Toader, M., Herisanu, N., Opritescu, C., Dragan, N., 2007. Noise reduction in urban environment. Children 75, 70.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25 (3), 180–189.

Barber, J.R., Burdett, C.L., Reed, S.E., Warner, K.A., Formichella, C., Crooks, K.R., Theobald, D.M., Fristrup, K.M., 2011. Anthropogenic noise exposure in protected natural areas: estimating the scale of ecological consequences. Landsc. Ecol. 26 (9), 1281–1295.

Bephage, G., 2005. Promoting quality sleep in older people: the nursing care role. British J. Nurs. 14, 205–210.

Brambilla, G., Maffei, L., 2006. Responses to noise in urban parks and in rural quiet areas. Acta Acustica united Acustica 92 (6), 881–886.

Bruehlmann, S.M., 2014. Measuring and Mapping Light Pollution at a Local Scale. Dissertation. Vrije Universiteit Amsterdam, The Netherlands.

Carver, S., Tricker, J., Landres, P., 2013. Keeping it wild: mapping wilderness character in the United States. J. Environ. Manag. 131, 239–255.

Chalkias, C., Petrakis, M., Psiloglou, B., Lianou, M., 2006. Modelling of light pollution in suburban areas using remotely sensed imagery and GIS. J. Environ. Manag. 79 (1), 57–63.

Cinzano, P., Falchi, F., Elvidge, C.D., 2001. The first world atlas of the artificial night sky brightness. Mon. Notices R. Astronomical Soc. 328, 689–707.

City of Williams, Califormia, 2012. Noise Chapter 6, 2010 General Plan.

Clark, W.W., 1991. Noise exposure from leisure activities: a review. J. Acoust. Soc. Am. 90 (1), 175–181.

Clark, D., Petersen, B., 2012. Isua Iron Ore Project Annex 5 of the EIA Noise Assessment (London Mining).

Clarke, L., 2011. Is Quiet the New Loud? Developing a Framework for Valuing Quiet Areas Liz. In: http://www.iaia.org/conferences/iaia11/proceedings/presentations/The%20Value%20of%20Quiet%20(IAIA_v1).pdf.

Davies, T.W., Bennie, J., Inger, R., Gaston, K.J., 2013. Artificial light alters natural regimes of night-time sky brightness. Sci. Rep. 3.

De Coensel, B., Botteldooren, D., 2006. The quiet rural soundscape and how to characterize it. Acta Acustica united Acustica 92 (6), 887–897.

DIER (Department of Infrastructure, Energy and Resources), 2011. Tasmanian State Road Traffic Noise Management Guidelines.

Duriscoe, D.M., 2016. Photometric indicators of visual night sky quality derived from all-sky brightness maps. J. Quantitative Spectrosc. Radiat. Transf. 181, 33–45.

DM Duriscoe, D.M., Luginbuhl, C.B., Elvidge, C.D., 2013. The relation of outdoorlighting characteristics to sky glow from distant cities. Light. Res. Technol. 2013 (0), 1–15.

EC, 2011. Report from the Commission to the European Parliament and the Council on the Implementation of the Environmental Noise Directive in Accordance with Article 11 of Directive 2002/49/EC. COM (2011)321 final. http://eur-lex.europa.eu/LexUriServ/LexUriServ.do?uri=COM:2011:0321:FIN: EN:PDF (accessed 10.04.16).

EEA, 2014. Noise in Europe 2014 (Report No. 10/2014). European Environment Agency. http://www.eea.europa.eu/publications/noise-in-europe-2014 (accessed 10.04.16).

EEA, 2016. Quiet Areas in Europe. The Environment Unaffected by Noise Pollution (Report No 14/2016. European Environment Agency. http://www.eea.europa.eu/highlights/mapping-europe2019s-quiet-areas (accessed 17.11.16).

Elvidge, C.D., Baugh, K., Zhizhin, M., Chi Hsu, F., 2013. Why VIIRS data are superior to DMSP for mapping. Proc. Asia-Pacific Adv. Netw. 2013, 62–69.

Fritschi, L., Brown, L., Kim, R., Schwela, D., Kephalopolos, S., 2012. Introduction Burden of Disease from Environmental Noise: Quantification of Healthy Years Life Lost in Europe. World Health Organisation.

Fyhri, A., Aasvang, G.M., 2010. Noise, sleep and poor health: modeling the relationship between road traffic noise and cardiovascular problems. Sci. Total Environ. 408 (21), 4935–4942.

Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. Review: reducing the ecological consequences of night-time light pollution: options and developments. J. Appl. Ecol. 49 (6), 1256–1266.

Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol. Rev. 88 (4), 912–927.

Good Practice Guide on Port Area Noise Mapping and Management, 2008. Noise Management in European Ports (NoMEPorts).

Hatch, L.T., Fristrup, K.M., 2009. No barrier at the boundaries: implementing regional frameworks for noise management in protected natural areas. Mar. Ecol. Prog. Ser. 395, 223–244.

Hölker, F., Wolter, C., Perkin, E.K., Tockner, K., 2010. Light pollution as a biodiversity threat. Trends Ecol. Evol. 25 (12), 681–682.

Jabben, J., Weber, M., Verheijen, E., 2015. A framework for rating environmental value of urban parks. Sci. Total Environ. 508, 395–401.

Jackson, S., Fuller, D., Dunsfold, H., Mowbray, R., Hext, S., MacFarlane, R., Haggett, C., 2008. Tranquility mapping: developing a robust methodology for planning support. Report to the campaign to protect rural England. Centre for Environmental& Spatial Analysis. Northumbria University, Bluespace Environments and theUniversity of Newcastle upon on Tyne.

Jaeger, J.A.G., Soukup, T., Madriñán, L.F., Schwick, C., Kienast, F., 2011. Landscape Fragmentation in Europe (Report No.2/2011). European Environment Agency. http://www.eea.europa.eu/publications/landscape-fragmentation-in-europe (accessed 10.04.16).

Jiménez, S., Romeu, J., Pàmies, T., Majó, M., 2010. Agglomeration Noise Strategic Maps in Catalonia. Lisbon, Portugal. In InterNoise2010, Noise and Sustainability, Lisbon, Portugal, June, vol. 1, pp. 3–16.

Kloog, I., Haim, A., Stevens, R.G., Portnov, B.A., 2009. Global co-distribution of lightat night (LAN) and cancers of prostate, colon, and lung in men. Chronobiology Int. 26, 108–125.

Krylov, V.V., 2001. Noise and Vibration from High-speed Trains. Thomas, Telford.

Kyba, C.C., Wagner, J.M., Kuechly, H.U., Walker, C.E., Elvidge, C.D., Falchi, F., et al., 2013. Citizen Science Provides Valuable Data for Monitoring Global Night Sky Luminance. Scientific reports, 3.

Kyba, C.C., Tong, K.P., Bennie, J., Birriel, I., Birriel, J.J., Cool, A., et al., 2015. Worldwide Variations in Artificial Skyglow. Scientific reports, 5.

Landres, P., Barns, C., Dennis, J.G., Devine, T., Geissler, P., McCasland, C.S., Merigliano, L., Seastrand, J., Swain, R., 2008. Keeping it Wild: an Interagency Strategy to MonitorTrends in Wilderness Character Across the National Wilderness Preservation System. General Technical Report RMRS-GTR-212. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO, 77 pp.

Liang, B., Weng, Q., 2011. Assessing urban environmental quality change of Indianapolis, United States, by the remote sensing and GIS integration. Sel. Top. Appl. Earth Observations Remote Sens. IEEE J. 4 (1), 43–55.

Licitra, G., Chiari, C., Ascari, E., Palazzuoli, D., 2011. Quiet area definition in the implementation of European directive 2002/49/EC. N. Z. Acoust. 24, 20–26.

Lin, R.S., Sung, F.C., Huang, S.L., Gou, Y.L., Ko, Y.C., Gou, H.W., Shaw, C.K., 2001. Role of urbanization and air pollution in adolescent asthma: a mass screening in Taiwan. J. Formos. Med. Assoc. 100, 649–655.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2 (4), 191–198.

Lyytimäki, J., Tapio, P., Assmuth, T., 2012. Unawareness in environmental protection: the case of light pollution from traffic. Land Use Policy 29 (3), 598–604.

MacFarlane, R., Haggett, C., Fuller, D., Dunsford, H., Carlisle, B., 2004. Tranquility Mapping: Developing a Robust Methodology for Planning Support. Report to the Campaign to Protect Rural England, Countryside Agency, North East Assembly, Northumberland Strategic Partnership, Northumberland National Park Authority and Durham County Council. Centre for Environmental & Spatial Analysis, Northumbria University, 190 pp.

Manvell, D., van Banda, E.H., 2011. Good practice in the use of noise mapping software. Appl. Acoust. 72 (8), 527–533.

Marin, C., 2009. Starlight: a Common Heritage. Proceedings of the International Astronomical Union, Volume 5/Symposium S260/January 2009, pp. 449–456.

McMullan, R., Seeley, I.H., 2007. Environmental Science in Building. Palgrave Macmillan, Basingstoke, UK.

Miller, P.H., 1982. Children's and adults' integration of information about noise and interest levels in their judgements about learning. J. Exp. Child Psychol. 33 (3), 536–546.

Morgan, P.A., Abbott, P.G., Watts, G.R., Burke, C.A., Harmer, C., 2006. Research into Quiet Areas: Recommendations for Identification. http://randd.defra.gov.uk/Document.aspx?Document=NO01109_4629_FRP.doc.

Moritoh, Y., Zenda, Y., Nagakura, K., 1996. Noise control of high speed Shinkansen. J. Sound Vib. 193 (1), 319–334.

NOAA (National Centers for Environmental Information), 2015. http://ngdc.noaa.gov/eog/ (accessed 10.04.16).

Ntalos, G.A., Papadopoulos, A.N., 2006. Noise emission levels in Greek wood and furniture processing industry. J. Inst. Wood Sci. 17, 99–130.

Pahalavithana, N.S., Sonnadara, D.U.J., 2009. Measurement of noise within passenger trains on a costal railway line. Sri Lankan J. Phys. 10, 25–37.

Pierce, A.D., 1989. Acoustics: an Introduction to its Physical Principles and

Applications. Acoustical Society of America, Woodbury, NY.

Prach, K., Pyšek, P., 2001. Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. Ecol. Eng. 17 (1), 55–62.

Pritchett, J.F., Caldwell, R.S., Chesser, R.K., Sartin, J.L., 1976. Effect of jet aircraft noise upon in vitro adrenocortical responseto ACTH in feral Mus musculus. Life Sci. 18 (4), 391–396.

Pun, C.S.J., So, C.W., 2012. Night-sky brightness monitoring in Hong Kong a city-wide light pollution assessment. Environ. Monit. Assess. 184 (4), 2537–2557.

Ramis, J., Alba, J., Garcia, D., Hernàndez, F., 2003. Noise effects of reducing traffic flow through a Spanish city. Appl. Acoust. 64, 343–364.

Reed, S.E., Merenlender, A.M., 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conserv. Lett. 1 (3), 146–154.

Rodrigues, P., Aubrecht, C., Gil, A., Longcore, T., Elvidge, C., 2012. Remote sensing to map influence of light pollution on Cory's shearwater in São Miguel Island, Azores Archipelago. Eur. J. Wildl. Res. 58 (1), 147–155.

Şchiopu, N., Bardac, D.I., 2012. Noise and its E ECTS. Acta Medica Transilv. 17 (1).

Schomer, P.D., 2005. Criteria for assessment of noise annoyance. Noise Control Eng. J. 53 (4), 125–137.

Scott, L.M., Janikas, M.V., 2010. Spatial Statistics in ArcGIS. In Handbook of Applied Spatial Analysis. Springer, Berlin Heidelberg, pp. 27–41.

Sharma, O., Mohanan, V., Singh, M., 1998. Noise emission levels in coal industry. Appl. Acoust. 54, 1–7.

Shelton, D., 2016. Environmental pollution: a human rights perspective. In: Environmental Influences on the Immune System. Springer, Vienna.

Shepherd, D., Welch, D., Dirks, K.N., McBride, D., 2013. Do quiet areas afford greater health-related quality of life than noisy areas? Int. J. Environ. Res. Public Health 10 (4), 1284–1303.

SWS, 2000. Noise in Quiet Areas (2000-MS-14-M1). Synthesis Report Prepared for the Environmental Protection Agency by SWS Environmental Services. http://www.epa.ie/downloads/pubs/research/land/epa_noise_in_quiet_areas_ertdi17_synthesis.pdf.

Symonds, 2003. Definition, Identification and Preservation of Urban & Rural Quiet Areas. http://circa.europa.eu/Public/irc/env/noisedir/library?l=/quietsareas/finalsreports3s10s2003pd/_EN_1.0_%26a%3dd.

Votsi, N.E.P., Drakou, E.G., Mazaris, A.D., Kallimanis, A.S., Pantis, J.D., 2012. Distance-based assessment of open country quiet Areas in Greece. Landsc. Urban Plan. 104 (2), 279–288.

Votsi, N.E.P., Kallimanis, A.S., Mazaris, A.D., Pantis, J.D., 2014. Integrating environmental policies towards a network of protected and quiet areas. Environ. Conserv. 41 (04), 321–329.

Votsi, N.E.P., Kallimanis, A.S., Pantis, J.D., 2015. The Distribution and Importance of Quiet Areas in the EU (Under Review at European Planning Studies).

Waugh, D., Durucan, S., Korre, A., Hetherington, O., O'Reilly, B., 2003. Environmental Quality Objectives. Noise in Quiet Areas. Synthesis Report 2000-MS- 14–M1. Environmental Protection Agency (EPA), 25 pp.

WGAEN, 2007. *Good practice* Guide for Strategic Noise Mapping and the Production of Associated Data on Noise Exposure. Final Draft. Position paper.

WHO, 2002. Guidelines for Community Noise. World Health Organization, Geneva. http://whqlibdoc.who.int/hq/1999/a68672.pdf (accessed 10.04.16).

WHO, 2011. Burden of Disease from Environmental Noise, Quantification of Healthy Life Years Lost in Europe. http://www.euro.who.int/__data/assets/pdf_file/0008/136466/e94888.pdf (accessed 10.04.16).

Zaharna, M., Guilleminault, C., 2010. Sleep, noise, and health: review. Noise Health 12 (47), 64–69.

Journal for Nature Conservation 28 (2015) 105–111

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.de/jnc

How to reduce the impact of artificial lighting on moths: A case study on cultural heritage sites in Slovenia

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ARTICLE INFO

Article history:
Received 19 March 2015
Received in revised form 3 September 2015
Accepted 3 September 2015

Keywords:
Ecological light pollution
Moth diversity
flight-to-light
Artificial illumination
Lepidoptera

ABSTRACT

In an ever more artificially illuminated world, common moth behaviour, flight-to-light, causes declines in their abundance and diversity that can have severe impacts on ecosystems. To test if it is possible to reduce the number of moths attracted to artificially illuminated objects, the original lighting of 15 cultural heritage buildings in Slovenia was substituted with blue or yellow lighting. These three illumination types differed in the amount of luminance, percentage of UV and short-wavelength light which are known to affect flight-to-light of moths. During our three-year field study approximately 20% of all known moth species in Slovenia were recorded. The blue and yellow illumination type attracted up to six times less specimens and up to four times less species compared to the original illumination type. This was true for all detected moths as well as within separate moth groups. This gives our study a high conservation value: usage of alternative, environmentally more acceptable illumination can greatly reduce the number of moths attracted to artificially illuminated objects.

1. Introduction

A large part of our planet is being artificially illuminated in hours of darkness, and the proportion of illuminated territory continues to increase (Cinzano, Falchi, & Elvidge, 2001; Hölker et al., 2010). Excessive artificial lighting has several negative effects on ecosystems, and has commonly been referred to as “ecological light pollution” (Longcore & Rich, 2004). Moths, predominantly nocturnal insects, are among the most severely affected animal groups (Frank, 1988), whose declines in diversity (i.e., species richness) and abundance have already been detected in parts of northern Europe (Conrad et al., 2006; Mattila et al., 2006; Groenendijk & Ellis, 2010; Fox, 2013). As moths present a major food source for numerous other animals and act as important pollinators, such declines represent a major threat to local ecosystems (see Macgregor et al., 2014). Moreover, as moths are one of the most species rich animal groups, this threat transcends to the global scale and urges immediate and serious conservation actions (van Langevelde et al., 2011; Fox, 2013).

Considering the importance of its consequences, this phenomenon has so far received insufficient attention (see Gaston, Visser, & Holker, 2015 for review). It is well known that moths are strongly attracted to lights emitting wavelengths that correspond with peak sensitivities of their visual systems (Cowan & Gries, 2009) and that the degree of attraction differs between species and families (van Langevelde et al., 2011; Truxa & Fiedler, 2012; Somers-Yeates et al., 2013). It is also known that lamps emitting light at shorter wavelengths, especially ultra-violet light, attract more and larger individuals as well as more species compared to lamps emitting light at longer wavelengths (Rydell, 1992; Eisenbeis, 2006; van Langevelde et al., 2011; Barghini, Augusto, & Medeiros, 2012). The explicit causes of moth declines due to excessive artificial lighting are however still not properly understood, although it has been demonstrated that artificial lights increase mortality through direct interaction between moths and lamps (Frank, 1988), influence life history traits (van Geffen et al., 2014) and disrupt natural behaviour, particularly dispersal, foraging and breeding (Altermatt, Baumeyer, & Ebert, 2009; Frank, 2006; van Geffen et al., 2015a,b). On the other hand, a recent study by Spoelstra et al. (2015) did not show any negative effects of artificial lighting on moth populations. Unfortunately, field studies testing practical solutions to reduce impact of artificial lighting on moths are completely lacking.

According to Luginbuchl et al. (2009), the major sources of artificial lighting are sport fields, commercial and industrial buildings and street lights. These are mostly concentrated in urban areas,

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http://dx.doi.org/10.1016/j.jnc.2015.09.002
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where moth diversity is already expected to be low due to absence of suitable habitats and diversity of habitats. On the other hand, the majority of cultural heritage buildings that are illuminated at night are, particularly churches, often located at exposed positions (e.g., on top of small hills) in relatively dark rural areas where they are often the only source of light. This is the case in Slovenia (and some other European countries), where almost 3000 churches are illuminated during the whole night. Therefore, illumination of cultural heritage buildings could represent an important source of light pollution and a threat to local moth populations.

We conducted a field study, in which a practical solution for moth conservation was tested for the first time. Our aim was to determine if we can decrease the abundance and diversity of moths attracted to illuminated cultural heritage buildings by changing the type of illumination. Thus, we selected fifteen churches and recorded moth abundance and diversity under three different types of illumination. In addition to illumination type changes, custom blinds preventing the scattering of light away from the object were also used. We predicted that changing the existing light type to a longer wavelength type will result in decreased abundance and diversity of moths around churches. As these two measures are also dependent on habitat quality and suitability, we additionally measured the percentage of woodland around churches as an approximation for suitable moth habitat. We predicted that the abundance and diversity of moths will be positively correlated with habitat quality in the close surroundings of the churches.

2. Materials and methods

2.1. Design of the field study

For the purpose of our study, fifteen illuminated churches across three biogeographic regions in Slovenia were selected as representative illuminated cultural heritage buildings (Fig. 1A, Table A1). More precisely, we selected five geographically distant groups of three adjacent churches (hereafter referred to as “church triplets”). Churches in each group were chosen close to each other to offset the effect of geographic position on sampling. All churches considered were located in relatively dark rural areas and outside larger settlements to avoid interference with other artificial sources of light (e.g., street lights and light from residential buildings).

The field study was carried out in three consecutive years (2011–2013). In the first year each church in a church triplet was illuminated with one of the three illumination types in such a way, that all three types were present concurrently at a church triplet. In the next two years illumination types were rotated among the churches in the triplet, so that by the end of the study, each church was illuminated with all three illumination types (Fig. 1B). Characteristics and details about illumination types are thoroughly described below.

Each year six surveys (for survey protocol see below) were carried out at every church during the period of adult moths main activity i.e., (from mid-May until mid-September). Surveys at churches from the same church triplet were done on the same night, always in the same order. Over the three years this summed up to 18 surveys per church altogether.

2.2. Illumination types

Three illumination types were studied:

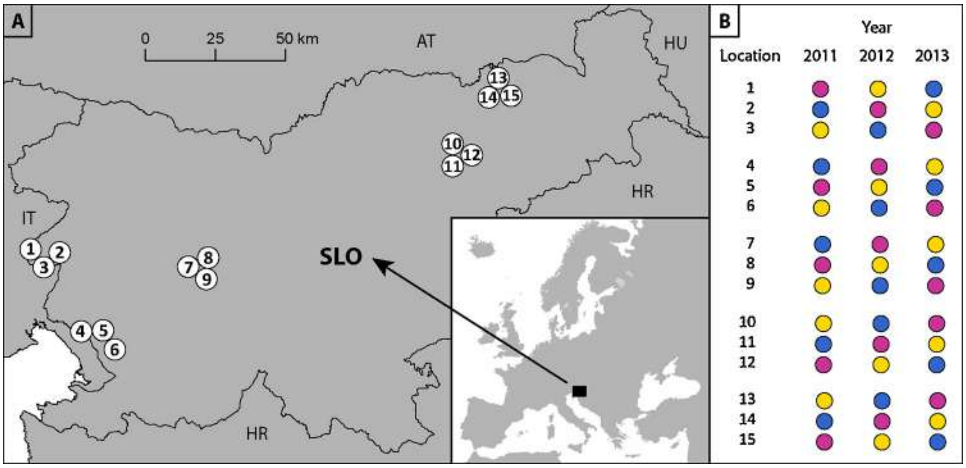
(1) Original—existing illumination type on the church before we started the study. This illumination was very variable in terms of lamp type (including metal halide and high pressure sodium vapour lamps), power, and the amount of UV and short-wavelength light (see Fig. 2; see Fig. A1 for examples of spectrograms).

(2) Blue—metal halide lamps (PHILIPS Master Color CDM-T 70–150 W/830), 70 W or 150 W, with a custom-made filter cutting off wavelengths shorter than 400 nm and with a custom blind unique for each church preventing the scattering of light away from the building (see Fig. A1 for examples of spectrograms).

(3) Yellow—metal halide lamps (PHILIPS Master Color CDM-T 70–150 W/942), 70 W or 150 W, with a custom-made filter cutting off wavelengths shorter than 470 nm and with a custom blind unique for each church preventing the scattering of light away from the building (see Fig. A1 for examples of spectrograms).

2.3. Sampling plot

A 10 m wide and 3 m high sampling plot was determined on the facade of each church. Surveys (for survey protocol see below) were confined to this area. The average luminance of sampling plots was obtained by photographing them with Canon EOS 5D + 16 mm lens, F8, ISO 800 (night images in RAW format) and subsequent image analyses with EcoCandela software developed for the purpose of LIFE at Night project (Mohar Andrej, pers. comm.). Spectral composition of light emitted from sampling plots was



Location	2011	2012	2013
1	🟣	🟡	🔵
2	🔵	🟣	🟡
3	🟡	🔵	🟣
4	🔵	🟣	🟡
5	🟣	🟡	🔵
6	🟡	🔵	🟣
7	🔵	🟣	🟡
8	🟣	🟡	🔵
9	🟡	🔵	🟣
10	🟡	🔵	🟣
11	🔵	🟣	🟡
12	🟣	🟡	🔵
13	🟡	🔵	🟣
14	🔵	🟣	🟡
15	🟣	🟡	🔵

Fig. 1. (A) A map of sampling localities. In five distant geographic regions three adjacent churches (a “church triplet”) were chosen for the purpose of the study. Locality numbers match with numbers on the right and with locality IDs in Table A1. (B) An illumination scheme shows illumination types at each church in three consecutive years of the study. At each church triplet all three illumination types were present in each year. Every church was illuminated with all three illumination types during the study. Purple, blue and yellow colored circles represent the original, blue and yellow illumination type. (Country abbreviation codes: SLO = Slovenia, IT = Italy, AT = Austria, HR = Croatia, HU = Hungary). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

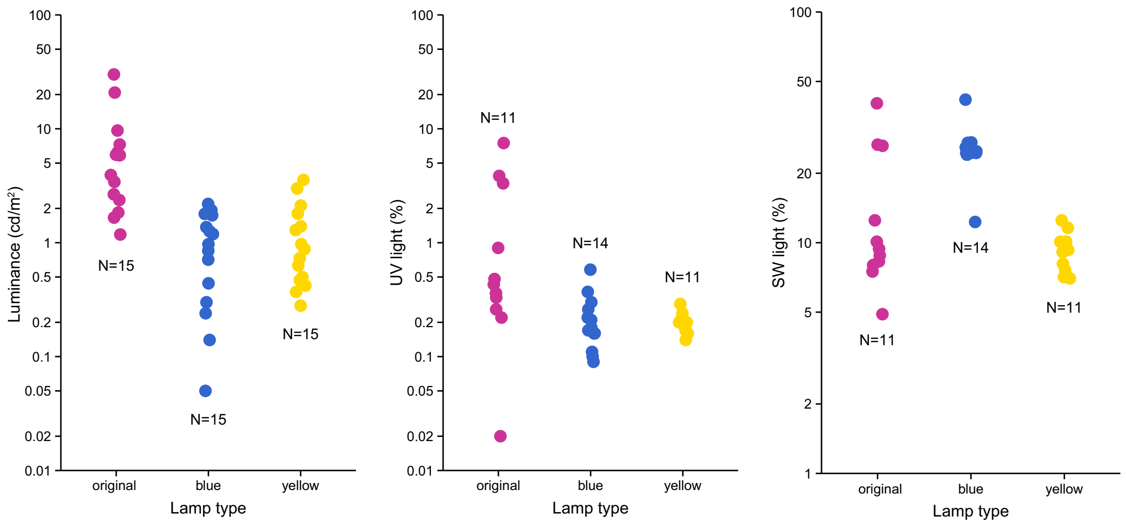


Fig. 2. Light characteristics of sampling plots illuminated with three illumination types. A) luminance, B) percentage of UV, C) percentage of SW light. Because of technical difficulties 9 sampling plots lack measurements of UV and SW light from the first year of the study.

determined using a spectroradiometer SpectriLight ILT950. The percentage of irradiance of UV (<380 nm) and short-wavelength (380–504 nm, hereafter abbreviated as SW) light was calculated from these spectrograms as defined by van Langevelde et al. (2011). In the first year of the study (2011), the percentage of UV and SW light could not be measured at 9 out of 15 localities due to technical difficulties (see Table A1; ID = 3, 5, 6, 7, 8, 9, 12, 13, and 15).

2.4. *Survey protocol and moth identification*

Surveys consisted of counting the number of moth specimens and species attracted to the illuminated sampling plot. The counts were limited to 45 min and performed at least one hour after nautical twilight. As moth activity can be highly influenced by weather conditions (Bowden, 1982; Frank, 2006), surveys were made only in the absence of rain and strong wind (Butler et al., 1999). Nevertheless, we measured temperature, estimated cloud cover, wind speed and its direction during each survey. Full-moon periods were avoided, as moths are significantly less attracted to artificial light at these times (Bowden, 1982). To get an overview of moth fauna in the surroundings of the sampling plot, entire church facade and areas around reflectors were checked for the presence of additional moth species (number of individuals was not counted).

Whenever possible, moth specimens were identified already during the survey. If reliable determination could not be done on site, specimens were collected for later inspection. Identifications were based on moth and micro-moth identification keys (e.g., Fajčik & Slamka, 1998; Belin, 2003; Fajčik, 2003) and personal moth voucher collections of the team experts. Faunistic data collected during the study will be published separately (Jež et al., in preparation).

2.5. *Estimating habitat quality*

Habitat quality in the surroundings of each church was estimated using percentage of area covered by woodland as a proxy; the higher the percentage, the higher the quality of the habitat. This was estimated in ArcGIS 10.1 (ESRI) using maps of land-use types in Slovenia (MKGP, 2014). The percentage of woodland was measured at a 50 m and 600 m radius from the church (zones of attraction according to Eisenbeis, 2006). As estimations of other habitat types turned out to be problematic due to high fragmentation and poor identification, we did not include them in further analyses.

2.6. *Data analysis*

All data manipulation and statistical analyses were conducted in R 3.0.3 (R Core Team, 2014) and graphs were drawn using R package ggplot2 (Wickham, 2009). Model outputs presented in all tables herein were back transformed to the original scale for easier interpretation. The number of moth species and specimens from all six surveys observed at a certain illumination type and church were summed and these values were used in all subsequent analyses unless stated differently. Correlation between species richness and abundance was tested using Spearman's rank test implemented in agricolae R package (de Mendiburu, 2014).

The effect of illumination type (a categorical explanatory variable) on moth abundance and diversity (two distinct response variables which were modelled separately) was estimated with generalized linear mixed models (GLMM) with a negative binomial error distribution and a logarithm link function using the *glmer.nb* function implemented in R package lme4 (Bates et al., 2014). Localities and region were modelled as a random effect. To check if the effect of Illumination type on moth abundance and diversity differs between the three main groups of moths (Noctuidea, Geometridae, and Microlepidoptera) a model with two explanatory variables (illumination type and moth group) was fit. The existence of an interaction between both explanatory variables was tested by comparing a model with interaction and a model without interaction using *anova* function implemented in R. Multiple comparisons tests within all models were performed using the *glht* function implemented in R package multcomp (Hothorn, Bretz, & Westfall, 2008) and *p*-values were adjusted with the single step method.

To estimate which of the measured factors (luminance, percentage of UV, percentage of SW, woodland at 50 m, and woodland at 600 m) effects the number of moth specimens and species attracted to the sampling plot, we performed a multiple regression analysis using a negative binomial GLMM with localities modelled as a random effect. Explanatory variables luminance and percentage of UV were $\log_{10}$ transformed, whereas percentage of SW, woodland at 50 m and woodland at 600 m were left on the original scale. The two response variables (number of specimens and number of species) were modelled separately. By applying a multiple regression to our data, we controlled for correlation and confounding among the explanatory variables.

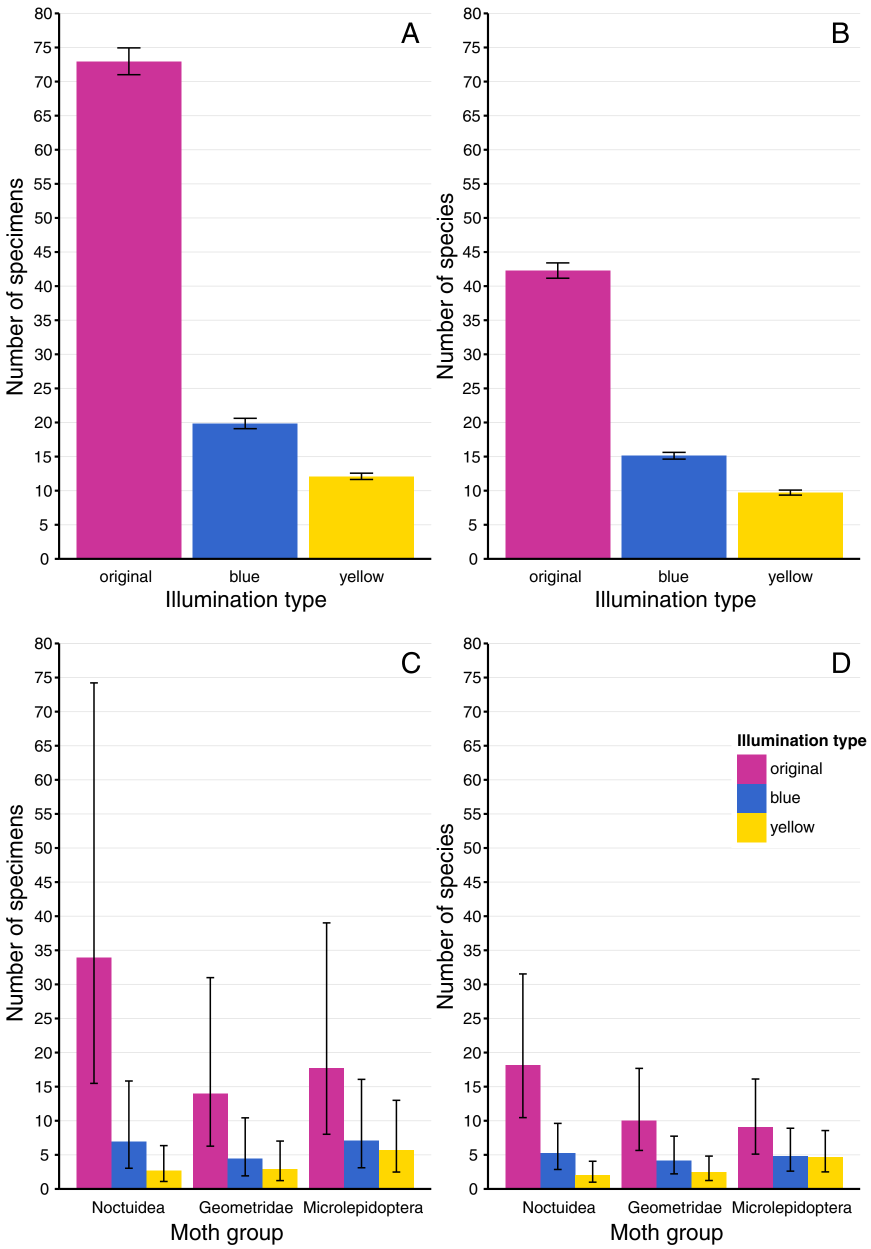


Fig. 3. (A) Effect of illumination type on number of all moth specimens (abundance) and (B) number of all moth species (species richness and diversity) attracted to sampling plots. All three illumination types attracted a significantly different number of specimens and species. (C) Effect of illumination type on number of specimens and (D) number of species of the three main groups of moths attracted to sampling plots. Error bars indicate 95% confidence intervals.

3. Results

3.1. An overview of surveys

Summing data from sampling plots and data from sampling plot surrounding, 548 moth species were recorded during the study, which is about 20% of all known moth species in Slovenia. The total number of species detected at a single church across all three years varied from 25 (church in Gornje Cerovo, ID = 2 and church in Šmarje, ID = 6) to 214 (church in Koritno, ID = 10). Weather conditions measured at each survey (see survey protocol) were within acceptable limits for normal moth activity and were not included in analyses.

3.2. Moth abundance and species richness at three illumination types

Moth abundance and species richness were found to be strongly positively correlated ($\rho = 0.982$, $p < 0.001$), therefore no significant differences between models with either of these two response variables were expected. All three illumination types attracted a significantly different number of specimens and species (Fig. 3A and B, Table 1). The original illumination turned out to be the strongest attractor for moths and attracted almost four times more specimens and almost three times more species as the blue illumination. It also attracted six times more specimens and more than four times more species as the yellow illumination. Inclusion of geographic region among the random effects of models did

Table 1
Results of multiple comparisons tests based on a GLMM fitted to all data using one explanatory variable (illumination type).

Type of illumination	Number of specimens			Number of species		
	estimate	95% CI	*P*-value[c]	estimate	95% CI	*P*-value[c]
original	72.95[a]	[71.01, 74.94]	**<0.001**	42.27[a]	[41.16, 43.41]	**<0.001**
blue	19.84[a]	[19.10, 20.61]	**<0.001**	15.12[a]	[14.63, 15.62]	**<0.001**
yellow	12.10[a]	[11.65, 12.57]	**<0.001**	9.71[a]	[9.35, 10.09]	**<0.001**
original vs. blue	3.68[b]	[3.58, 3.78]	**<0.001**	2.80[b]	[2.74, 2.85]	**<0.001**
original vs. yellow	6.03[b]	[5.87, 6.20]	**<0.001**	4.35[b]	[4.24, 4.47]	**<0.001**
blue vs. yellow	1.64[b]	[1.58, 1.70]	**<0.001**	1.56[b]	[1.51, 1.60]	**<0.001**

[a] Model prediction for the number of specimens or species attracted to a certain illumination type.

[b] Difference between two types of illumination. Estimates of these values indicate how many times more specimens or species are predicted to be attracted to the first illumination type compared to the second illumination type.

[c] *P*-values were adjusted using the single step method. *P*-values lower than 0.05 are bolded and underscored.

not significantly improve them (abundance: $\chi^2 = 0.303$, $p = 0.582$; species richness: $\chi^2 = 0.043$, $p = 0.836$).

Most of the recorded species belonged to one of the three main groups of moths: Noctuidea, Geometridae and Microlepidoptera. The effect of illumination type on abundance and species richness turned out to be very similar among the three moth groups (Fig. 3C and D, Table A2) and in agreement with results of the previous two models that also included other moth groups. In Noctuidea all three illumination types attracted significantly different number of specimens and species, while in Geometridae and Microlepidoptera the difference in attraction to blue and yellow illumination type was significant. The interaction between variables illumination type and moth group was found to be significant (abundance: $\chi^2 = 11.1$, $p = 0.025$; species richness: $\chi^2 = 19.3$, $p = 0.0007$) and is a consequence of a significantly greater difference in abundance and species richness between the original and yellow illumination in Noctuidea compared to the same difference in Microlepidoptera. Inclusion of geographic region among the random effects of models once again resulted in non-significant improvements (abundance: $\chi^2 = 0.437$, $p = 0.508$; species richness: $\chi^2 = 0.128$, $p = 0.721$).

3.3. Which factors affect moth abundance and species richness?

The results of multiple regression analyses show that moth abundance and species richness are significantly affected by luminance, percentage of UV light and woodland coverage at 50 m but not by the percentage of SW light and woodland coverage at 600 m (Table 2). More accurately, while controlling for the effects of all other variables: (A) an increase in woodland at 50 m by 1% results in an 2.3% increase in moth abundance and an 1.4% increase in moth species richness, (B) an increase in luminance by 10% results in an 2.53 fold increase in moth abundance and an 2.12 fold increase in moth species richness, (C) an increase in the percentage of UV light by 10% results in an 2.77 fold increase in moth abundance and an 2.20 fold increase in moth species richness. Luminance and percentage of UV light appear to have a similar and much greater impact on moth abundance and species richness compared to woodland at 50 m radius. Statistical non-significance of of SW light is probably a consequence of its correlation with UV light.

4. Discussion

4.1. Moth diversity and different illumination types

For the first time, we demonstrated in a field study the effectiveness of simple solutions for reducing the number of moth specimens and species attracted to artificially illuminated surfaces of buildings. Significantly more species and specimens were attracted to the original illumination type compared to the blue or yellow illumination type. This was true for all detected moths as well as within the three different groups of moths. Moreover, this was also the case irrespective of whether we used moth abundance or species richness as a response variable. The diminished attraction of moths is a consequence of the joint effects of lower luminance and lower percentage of UV and SW light emitted by the modified illumination compared to the original illumination. Although results of the multiple regression analysis fall a bit short due to a low number of replicates, it seems that the percentage of UV has the greatest impact on moth attraction. Previous studies which indicated that UV and SW light are likely to have a greater impact on moth behaviour than longer wavelength light (Frank, 1988; Rydell, 1992; Eisenbeis & Eick, 2011; van Langevelde et al., 2011; Somers-Yeates et al., 2013) are in agreement with our results.

When comparing effects of the three different illumination types on main moth groups (Noctuidea, Geometridae and Microlepidoptera) significantly more specimens and species were observed at churches with the original illumination within all three groups. A significant difference detected between the response of Noctuidea and Geometridae to different illumination types is in line with the study of Somers-Yeates et al. (2013), where a significantly higher attraction to UV and SW light was observed in Noctuidae over Geometridae in a controlled experiment at a single site. Possible explanations mentioned in their paper are a higher sensitivity of Geometridae to light of 597 nm compared to UV, Noctuidae mis-

Table 2
Results of multiple regression analysis.

	Number of specimens			Number of species		
	estimate	95% CI	*P*-value[a]	estimate	95% CI	*P*-value[a]
Intercept	33.33	[9.86, 112.61]	**<0.001**	22.40	[7.93, 63.28]	**<0.001**
Slope						
woodland at 50 m	1.023	[1.009, 1.038]	**0.002**	1.014	[1.002, 1.026]	**0.017**
woodland at 600 m	0.988	[0.969, 1.007]	0.227	0.994	[0.978, 1.010]	0.435
$\log10_{10}$ (luminance)	2.528	[1.669, 3.829]	**<0.001**	2.120	[1.482, 3.032]	**<0.001**
$\log_{10}$ (UV)	2.767	[1.649, 4.642]	**<0.001**	2.197	[1.389, 3.473]	**<0.001**
SW light	1.009	[0.986, 1.033]	0.450	1.005	[0.985, 1.027]	0.611

[a] *P*-values lower than 0.05 are bolded and underscored.

taking the emitted UV light as a cue to a source of nectar (Penny, 1983), and stronger flight ability in Noctuidae.

Our results clearly show that moth abundance and species richness at the illuminated cultural heritage buildings are positively dependent on the percentage of woodland at the 50 m radius, but not at the 600 m radius around the buildings. Therefore, the ″vacuum cleaner″ effect of illumination (Eisenbeis, 2006) was once again confirmed to be effective at short distances only. This is in agreement with results of recent and detailed mark-release-recapture studies showing that the attraction radius for moths is very short—up to 30 m only (Truxa & Fiedler, 2012; Merckx & Slade, 2014; van Grunsven et al., 2014). In other studies, the reported attraction distances are even shorter (e.g., 3 m in Baker & Sadovy, 1978), but also much longer (e.g., 750 m in Bowden, 1982). It is difficult to accurately compare these results as many uncontrolled factors, such as moon phase, type of lamp and its position, could have strongly affected the outcome.

During the field work for our study cases of moth mortality were observed due to contact with lights, especially as a result of heat emitted by reflectors, and due to bat predation around lights. In most cases, moths were caught in flight, but at one site bats collected also inactive moths directly from the illuminated church walls. If we add the changes in behaviour induced by artificial lighting (e.g., inactivity after initial circling around the light source), that directly affect reproductive success of moths (e.g., field based evidence by van Geffen et al., 2015a,b), observed predation is an ample evidence of the negative effects of artificial lighting on diversity of moths and insects in general (Eisenbeis, 2006).

4.2. Conservation implications

Slovenia is one of the European hotspots of Lepidoptera diversity, with a number of species estimated between 3500 and 3700 (Gomboc & Lasan, 2006). Approximately one fifth of all moth species in Slovenia were recorded in our study, indicating a possible high overall effect of illuminated churches on moth diversity. Among the attracted species, 13 are considered endangered in Slovenia (UL RS, 2002). For example, the Jersey Tiger *Euplagia quadripunctaria* (Poda, 1761), an EU Habitats Directive species, was observed at three sites. Although, an extensive Natura 2000 network covering all major areas of high butterfly diversity is established in Slovenia (Verovnik, Govedič, & Šalamun, 2011), its regulations do not address light pollution despite artificial illumination of churches is very common in these areas. However, if the existing Slovenian legislation would be followed consistently, such anomalies could be prevented and effects of light pollution in many sensitive environments could be significantly reduced.

We confirmed the effectiveness of the modified illumination—it reduces the number of moth individuals up to six times and the number of moth species up to four times. Although, a complete withdrawal of exterior illumination of cultural heritage outside urban areas would be the best possible ecological solution, we consider that an adoption of the yellow and even blue illumination type tested in our study is a tolerable compromise and a good step forward. As the yellow light illumination had a smaller impact on moths than the blue light illumination, it should be favored in the illumination of cultural heritage buildings. It should not be neglected, that when we used yellow and blue illumination, custom blinds were preventing the scattering of light away from buildings. An additional improvement could be achieved by turning off the illumination during late night hours. This would enable a retreat of the attracted moths to their natural environment.

At a global level, artificial lighting is rapidly increasing in many areas (Hölker et al., 2010) and causing increasing effects of light pollution on moths. Nevertheless, a recent study published by Bennie et al. (2014) highlighted an existing opportunity to constrain and even reduce the environmental impact of artificial light pollution while delivering cost and energy-saving benefits. Our results illustrate that an alternative, environmentally more acceptable illumination of cultural heritage buildings could be used worldwide. However, to achieve a wider usage of alternative illumination, support and collaboration among decision makers, lighting designers, lighting planners and the wider public will be mandatory.

Acknowledgements

We are indebted to moth experts Matjaž Jež, Radovan Štanta, Bojan Zadravec and Mojmir Lasan, for their help during field work and moth identification. We wish to express our thanks to Andrej Mohar, Barbara Bolta Skaberne and Mojca Stojan Dolar for providing data on light characteristics and illumination of churches. This study was conducted as a part of a LIFE+ project ‘Improving the conservation status of nocturnal animals (moths and bats) by reducing the effect of artificial lighting at cultural heritage sites or shortly LIFE at night (LIFE09 NAT/SI/000378) and the preparation of paper was partially funded by Slovenian Research Agency, program P1-0184.

We are grateful to reviewers and editor whose valuable comments helped to improve the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jnc.2015.09.002.

References

Altermatt, F., Baumeyer, A., & Ebert, D. (2009). Experimental evidence for male biased flight-to-light behaviour in two moth species. *Entomologia Experimentalis et Applicata*, *130*, 259–265.

Baker, R. R., & Sadovy, Y. (1978). The distance and nature of the light-trap response of moths. *Nature*, *276*, 818–821.

Barghini, A., Augusto, B., & Medeiros, S. D. (2012). UV radiation as an attractor for insects. *Leukos*, *9*, 47–56.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1. 1-7. <http://CRAN.R-project.org/package=lme4>.

Belin, V. (2003). *Nachtfalter der Tschechischen und Slowakischen Republik*. Zlin: Kabourek.

Bennie, J., Davies, T. W., Duffy, J. P., Inger, R., & Gaston, K. J. (2014). Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Scientific Reports*, *4*(3789)

Bowden, J. (1982). An analysis of factors affecting catches of insects in light-traps. *Bulletin of Entomological Research*, *72*, 535–556.

Butler, L., Kondo, V., Barrows, E. M., & Townsend, E. C. (1999). Effects of weather conditions and trap types on sampling for richness and abundance of forest macrolepidoptera. *Environmental Entomolology*, *28*, 795–811.

Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, *132*, 279–291.

Cinzano, P., Falchi, F., & Elvidge, C. D. (2001). The first world atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, *328*, 689–707.

Cowan, T., & Gries, G. (2009). Ultraviolet and violet light: attractive orientation cues for the Indian meal moth, *Plodia interpunctella*. *Entomologia Experimentalis et Applicata*, *131*, 148–158.

Eisenbeis, G. (2006). Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In T. Longcore, & C. Rich (Eds.), *Ecological Consequences of Artificial Night Lighting* (pp. 281–304). Washington, DC: Island Press.

Eisenbeis, G., & Eick, K. (2011). Studie zur anziehung nachtactiver insekten an die strassenbeleuchtung unter einbeziehung von LEDs. *Natur und Landschaft*, *86*, 298–306.

Fajčik, J. (2003). *Die schmetterlinge mittel- und nordeuropas, band I* (2nd ed.). J. Fajčik: Bratislava.

Fajčik, J., & Slamka, F. (1998). *Die schmetterlinge mitteleuropas, band II*. Bratislava: J. Fajčik.

Fox, R. (2013). The decline of moths in Great Britain: a review of possible causes. *Insect Conservation and Diversity*, *6*, 5–19.

Frank, K. D. (1988). Impact of outdoor lighting on moths: an assessment. *Journal of the Lepidopterists Society*, *42*, 63–93.

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Frank, K. D. (2006). Effects of artificial night lighting on moths. In T. Longcore, & C. Rich (Eds.), *Ecological consequences of artificial night lighting* (pp. 305–344). Washington, DC: Island Press.

Gaston, K. J., Visser, M. E., & Holker, F. (2015). The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *370*, 20140133.

Gomboc, S., & Lasan, M. (2006). List of Lepidoptera from Slovenia—review and open questions. In J. Prešern (Ed.). *1st Slovenian entomological symposium. Book of abstracts*, 20–21 (in Slovene).

Groenendijk, D., & Ellis, W. N. (2010). The state of the Dutch larger moth fauna. *Journal of Insect Conservation*, *15*, 95–101.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, *50*, 346–363.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., & Tockner, K. (2010). The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, *15*, 13.

Jež, M., Štanta, R., Zadravec, B., Zakšek, V., Verovnik, R. (2015). Moth fauna (Lepidoptera) at selected illuminated churches in Slovenia. (in preparation).

Luginbuhl, C. B., Wesley Lockwood, G., Davis, D. R., Pick, K., & Selders, J. (2009). From the ground up I: light pollution sources in Flagstaff, Arizona. *Publications of the Astronomical Society of the Pacific*, *121*, 185–203.

Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Enviroment*, *2*, 191–198.

Macgregor, C. J., Pocock, M. J., Fox, R., & Evans, D. M. (2014). Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology*, http://dx.doi.org/10.1111/een.12174

Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J. S., & Päivinen, J. (2006). Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology*, *20*, 1161–1168.

de Mendiburu, F. (2014). Agricolae: statistical procedures for agricultural research. R package version 1. 2-1. <http://CRAN.R-project.org/package=agricolae>.

Merckx, T., & Slade, M. E. (2014). Macro-moth families differ in their attraction to light: implications for light-trap monitoring programs. *Insect Conservation and Diversity*, *7*, 453–461.

MKGP (2014). Dejanska raba kmetijskih zemljišč (RABA, 13.1.2014). Ministry of agriculture, forestry and food. (in Slovene). <http://rkg.gov.si/GERK/>.

Penny, J. H. (1983). Nectar guide colour contrast: a possible relationship with pollination strategy. *New Phytologist*, *95*, 707–721.

R Core Team. (2014). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, *6*, 744–750.

Somers-Yeates, R., Hodgson, D., McGregor, P. K., Spalding, A., & ffrench-Constant, R. H. (2013). Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, *9*, 20130376.

Spoelstra, K., van Grunsven, R. H. A., Donners, M., Gienapp, P., Huigens, M. E., Slaterus, R., et al. (2015). Experimental illumination of natural habitat—an experimental set-up to assess the direct and indirect ecological consequences of artificial light to different spectral composition. *Philosophical Transactions of the Royal Society of London*, *370*, 20140129.

Truxa, C., & Fiedler, K. (2012). Attraction to light—from how far do moths (Lepidoptera) return to weak artificial sources of light? *European Journal of Entomology*, *109*, 77–84.

UL RS. (2002). Pravilnik o uvrstitvi ogroženih rastlinskih in živalskih vrst v rdeči seznam. *Uradni List Republike Slovenije—Uredbe*, *82*, 8893–8975 (in Slovene)

van Geffen, K. G., van Grunsven, H. A., van Ruijven, J., Berendse, F., & Veenendaal, E. M. (2014). Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, *4*, 2082–2089.

van Geffen, K. G., van Eck, E., de Boer, R. A., van Grunsven, R. H. A., Salis, L., Berendse, F., & Veenendaal, E. M. (2015). Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity*, *8*, 282–287.

van Geffen, K. G., Groot, A. T., van Grunsven, R. H. A., Donners, M., Berendse, F., & Veenendaal, E. M. (2015). Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology*, *40*, 401–408.

van Grunsven, R. H. A., Lham, D., Van Geffen, K. G., & Veenendaal, E. M. (2014). Range of attraction of a 6-W moth light trap. *Entomologia Experimentalis et Applicata*, *152*, 87–90.

van Langevelde, F., Ettema, J. A., Donners, M., Wallis DeVries, M. F., & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, *144*, 2274–2281.

Verovnik, R., Govedič, M., & Šalamun, A. (2011). Is the Natura 2000 network sufficient for conservation of butterfly diversity? A case study in Slovenia. *Journal of Insect Conservation*, *15*, 345–350.

Wickham, H. (2009). *ggplot2: Elegant graphics for data analysis*. New York: Springer.

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Proc. R. Soc. B (2006) **273**, 661–667
doi:10.1098/rspb.2005.3369

Light on the moth-eye corneal nipple array of butterflies

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The outer surface of the facet lenses in the compound eyes of moths consists of an array of excessive cuticular protuberances, termed corneal nipples. We have investigated the moth-eye corneal nipple array of the facet lenses of 19 diurnal butterfly species by scanning electron microscopy, transmission electron microscopy and atomic force microscope, as well as by optical modelling. The nipples appeared to be arranged in domains with almost crystalline, hexagonal packing. The nipple distances were found to vary only slightly, ranging from about 180 to 240 nm, but the nipple heights varied between 0 (papilionids) and 230 nm (a nymphalid), in good agreement with previous work. The nipples create an interface with a gradient refractive index between that of air and the facet lens material, because their distance is distinctly smaller than the wavelength of light. The gradient in the refractive index was deduced from effective medium theory. By dividing the height of the nipple layer into 100 thin slices, an optical multilayer model could be applied to calculate the reflectance of the facet lenses as a function of height, polarization and angle of incidence. The reflectance progressively diminished with increased nipple height. Nipples with a paraboloid shape and height 250 nm, touching each other at the base, virtually completely reduced the reflectance for normally incident light. The calculated dependence of the reflectance on polarization and angle of incidence agreed well with experimental data, underscoring the validity of the modelling. The corneal nipples presumably mainly function to reduce the eye glare of moths that are inactive during the day, so to make them less visible for predators. Moths are probably ancestral to the diurnal butterflies, suggesting that the reduced size of the nipples of most butterfly species indicates a vanishing trait. This effect is extreme in papilionids, which have virtually absent nipples, in line with their highly developed status. A similar evolutionary development can be noticed for the tapetum of the ommatidia of lepidopteran eyes. It is most elaborate in moth-eyes, but strongly reduced in most diurnal butterflies and absent in papilionids.

Keywords: eye reflectance; multilayer theory; refractive index gradient; butterfly evolution

1. INTRODUCTION

Insects have facetted, compound eyes, consisting of numerous anatomically identical units, the ommatidia. The eyes are classified according to the optical system that is used to efficiently focus light onto the light-sensitive parts of the photoreceptors. In apposition eyes, employed by butterflies, a facet lens together with its crystalline cone channels light into a fused rhabdom, a long, cylindrical structure, which contains the photoreceptors' visual pigment molecules. In optical superposition eyes, used by moths, light reaches the photoreceptive rhabdom via several facet lenses (Exner 1891, 1989; Nilsson 1989). Moths thus realize a much higher light sensitivity than butterflies, allowing a nocturnal instead of diurnal lifestyle (Warrant *et al.* 2003).

Well over four decades ago, Bernhard & Miller (1962) discovered that the outer surface of the facet lenses in moth-eyes consists of an array of cuticular protuberances termed corneal nipples (Bernhard & Miller 1962; Bernhard *et al.* 1965; Miller 1979). The optical action of the corneal nipple array is a severe reduction of the reflectance of the facet lens surface. Accordingly, it increases the transmittance, and therefore the initial interpretation of the nipple array was that it helps to enhance the light sensitivity of the light-craving moths (Miller 1979). In other words, the corneal nipple array functions as an impedance matching device that improves vision. However, although the nipple array considerably reduces the reflectance of a smooth facet lens surface, from about 4 to less than 1%, this means only a very minor transmittance increase, from 96 to more than 99%. A more adequate consideration hence could be that moths are inactive in the daytime and therefore are vulnerable for predation. A moth with large, glittering eyes will be quite conspicuous, and therefore its visibility is reduced by the eye reflectance decreasing corneal nipple arrays (Miller 1979). This latter camouflage hypothesis seems to be plausible, but direct experimental proof has so far not been obtained.

Further research demonstrated that corneal nipple arrays are widespread among insects. In a comparative survey, Bernhard *et al.* (1970) inspected the corneal facet lenses of 361 insect species. They distinguished three classes of nipple arrays, depending on the height of the nipples. The corneas of class I have minor protrusions, less than 50 nm high, class II corneas have low-sized nipples,

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Received 2 September 2005
Accepted 13 October 2005

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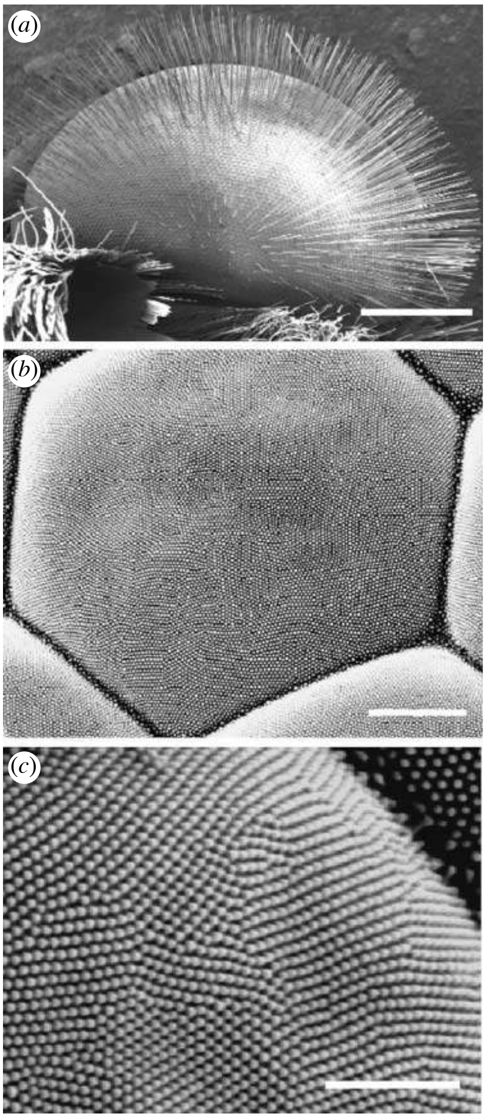

Figure 1. Corneal nipple arrays in the peacock (*Inachis io*), a nymphalid butterfly, as revealed by SEM. (*a*) The complete eye. (*b*) The nipple array in one facet lens. (*c*) Detail, showing the local arrangement of domains with highly ordered nipple arrays. The scale bar is in (*a*) 500, (*b*) 5 and (*c*) 2 μm.

with height between 50 and 200 nm, and class III corneas have full-sized nipples, with amplitude about 250 nm. Full-sized nipples were only found among the Trichoptera and Lepidoptera. The distribution over the three classes of the Trichoptera investigated was 5 : 5 : 5 (15 species in total). The distribution for the 170 lepidopteran species other than rhopalocerans (butterflies) was 42 : 26 : 102, and for the Hesperiidae 7 : 2 : 1, Papilionidae 10 : 0 : 0, Pieridae 2 : 8 : 1, Lycaenidae 0 : 11 : 2 and Nymphalidae 1 : 9 : 20. The Papilionidae, where the corneal nipples are virtually non-existent, differed remarkably from the Nymphalidae, which have large or full-sized nipples. The latter feature is difficult to reconcile with the functional interpretations given for the moths, because the members of both Papilionidae and Nymphalidae are generally only active at bright light conditions and also advertise themselves with conspicuous colourations.

The optical properties of moth-eyes have received considerable biological as well as physical interest (Wilson & Hutley 1982; Parker *et al.* 1998). The operation of a moth-eye surface may be understood most easily in terms of a surface layer in which the refractive index varies gradually from unity to that of the bulk material (Wilson & Hutley 1982). The insight that nipple arrays can strongly reduce surface reflectance has been widely technically applied, e.g. in window panes, cell phone displays and camera lenses (rev. Palasantzas *et al.* 2005; for further information and explanatory figures, see, for example http://www.funktionale-oberflaechen.de/english/a1_ent_f.html, http://www.ntt-at.com/products_e/motheye/, http://www.motheye.com/Index.swf). In fact, some moth species (e.g. *Cephonodes hylas*) apply nipple arrays to reduce the reflectance of their scaleless and transparent wings (Yoshida *et al.* 1997).

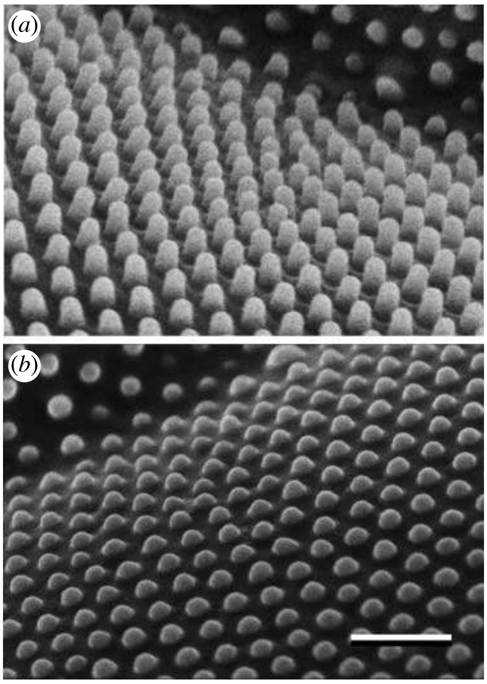

Figure 2. Corneal nipple arrays in the nymphalid *Polygonia c-aureum* (*a*) and the lycaenid *Pseudozizeeria maha* (*b*), showing differences in nipple height and shape. Bar, 500 nm.

In the course of our studies of butterfly vision, we have investigated the corneal nipple arrays of a number of butterfly species. We present novel data, calculate the reflectance for a number of nipple geometries using a simple multilayer modelling approach, and discuss the relevance of nipple arrays for vision and visibility.

2. MATERIAL AND METHODS

(a) *Experimental animals*

Butterflies of the families Papilionidae, Pieridae, Lycaenidae and Nymphalidae were captured in the Netherlands, Taiwan, Japan and Uganda. Two nymphalid species (*Bicyclus anynana* and *Heliconius melpomene*) were obtained from a laboratory culture maintained by Prof. P. Brakefield (Leiden University). The investigated eyes of dead butterflies were often slightly deteriorated, but the nipple structures appeared to be unaffected (see Bernhard *et al.* 1970).

(b) *Electron microscopy*

The corneal nipple arrays were studied by standard scanning electron microscopy (SEM, Philips XL30 ESEM), using palladium sputtering of heads severed from dead specimens (figures 1 and 2). For transmission electron microscopy (TEM), isolated eyes were prefixed overnight at 4 °C in 2%

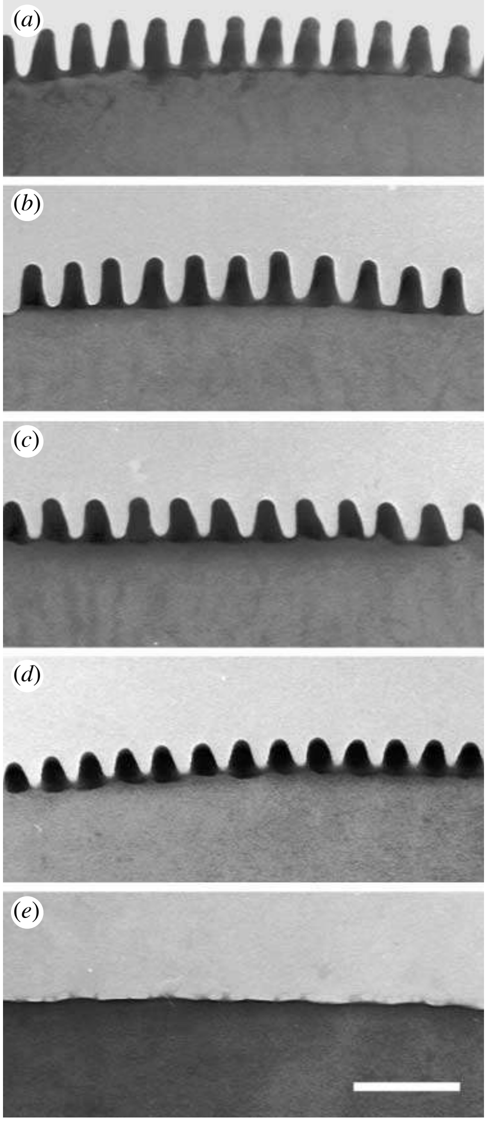

Figure 3. Corneal nipple arrays in the nymphalids *Bicyclus anynana* and *Polygonia c-aureum* (*a*,*b*), the pierid *Pieris rapae* (*c*), the lycaenid *Pseudozizeeria maha* (*d*) and the papilionid *Papilio xuthus* (*e*). Bar, 500 nm.

glutaraldehyde and 2% paraformaldehyde in 0.1 M sodium cacodylate buffer (CB, pH = 7.4). After being washed with CB briefly, the tissues were postfixed in 2% osmium tetroxide in CB for 2 h at room temperature. The tissues were then dehydrated with a graded series of acetone and embedded in Epon. Ultrathin sections cut with a diamond knife were observed with a transmission electron microscope (JEM 1200EX, JEOL Tokyo Japan) without staining (figure 3).

(c) *Atomic force microscopy*

An atomic force microscope (AFM, Dimension 3100) was used in tapping mode, to avoid sample damage, on a few butterfly species. Sputtered as well as non-sputtered corneas yielded reliable results, confirming the estimates obtained by SEM, but only when the nipples were low-or medium-sized. AFM on full-sized nipple arrays appeared to be problematic, presumably due to the high aspect ratio of the nipple arrays.

(d) *Optical modelling*

The reflectances of three types of nipple arrays, with cone, paraboloid and Gaussian-shaped nipples, were calculated with a multilayer model. A coordinate system was used with Z-axis perpendicular to the corneal surface, so that the nipple array troughs were at $z=0$ and the nipple peaks at $z=h$. The z-coordinate relative to the peak value, h, is $z^*=z/h$, and the distance r to the nipple axis relative to the distance of two adjacent nipples, d, is $r^*=r/d$. The three nipple types then are described by $z^*=1-r^*/p$ (cone), $z^*=1-(r^*/p)^2$ (paraboloid), and $z^*=\exp(-4\ln 2(r^*/p)^2)$ (Gaussian), with the condition that $z^*\geq 0$ for all r^*; the parameter p determines the width of the nipple. The nipple lattice is assumed to be hexagonal (figures 1 and 2), and thus the area taken up by a nipple equals $A_\mathrm{n}=\sqrt{3}d^2/2$. The area of the cone and paraboloid at their base, where $z^*=0$ (or $r^*=p$) is πp^2, and this area equals A_n when the width parameter p equals $p_0=\sqrt{(\sqrt{3}/2\pi)}=0.53$. A plane at level z^* contains a fraction $f(z^*)=\pi r^2/A_\mathrm{n}=2\pi r^{*2}/\sqrt{3}$ of corneal material, with refractive index n_c, and the remaining fraction, $1-f(z^*)$, then is air, with refractive index 1. Because the distance of the nipples is small with respect to the wavelength of light, light propagation is governed by the effective refractive index of the nipple array, which can be calculated from effective medium theory (Bruggeman 1935). At height z^*, the effective refractive index, $n_\mathrm{e}(z^*)$, then is $n_\mathrm{c}=[g+(g^2+8n_\mathrm{c})^{1/2}]^{1/2}/2$, with $g=(3f-1)n_\mathrm{c}^2-3f+2$. We note here that for $n_\mathrm{c}=1.52$ (Vogt 1974), $n_\mathrm{e}(f)$ is well approximated by $n_\mathrm{e}=[fn_\mathrm{c}^q+(1-f)]^{1/q}$, with $q=2/3$, and that this function yields values that only slightly deviate from values given by the simple weighting formula $n_\mathrm{e}=fn_\mathrm{c}+(1-f)$. In the case of paraboloid nipples, the volume fraction is therefore very approximately a linear function of z^*, and consequently the refractive index profile of the nipple array is then very approximately a linear function of z^*. The corneal reflectance was calculated from the refractive index gradient by first dividing the transition layer of the nipples, between $z=0$ and h, in 100 layers with thickness $h/100$, and calculating the effective refractive index value for each layer. The stack of 100 layers then can be treated as a multilayer system where the layers have different refractive indices. The reflectance of such a system can be calculated with a matrix multiplication procedure for a stack of thin layers (Macleod 1986). The calculations were performed for five nipple heights: 50, 100, 150, 200 and 250 nm.

3. RESULTS

The set of facet lenses of a butterfly eye, the cornea, is approximately a hemisphere (figure 1*a*). The convex outer surface of the facet lenses of a peacock (*Inachis io*) consists of protuberances, the corneal nipples, which locally are arranged in a highly regular, hexagonal lattice (figure 1*b*,*c*). The nearest-neighbour distance of the nipples, d, is about 210 nm, and their height, h, is *ca* 200 nm.

The dimensions of the nipples, estimated by SEM, TEM as well as AFM, appeared to vary among the butterfly species (figures 2–4; table 1). The five investigated papilionid species, having facet lenses with an average diameter of 29 ± 3 μm, had very minor nipples, with height less than or equal to 30 nm. When visible, the nipples were arranged in an irregular pattern with distance $d=235\pm10$ nm. The non-papilionid species had clear nipples arranged regularly in a hexagonal pattern, in domains with a diameter of roughly 2 μm (about 10 nipple distances; figure 1). The nipple distance was 200 ± 20 nm in the (small-sized) lycaenids, with facet lens diameter 19 ± 2 μm (figure 2*b*, 3*d* and 4), and 210 ± 10 nm in the

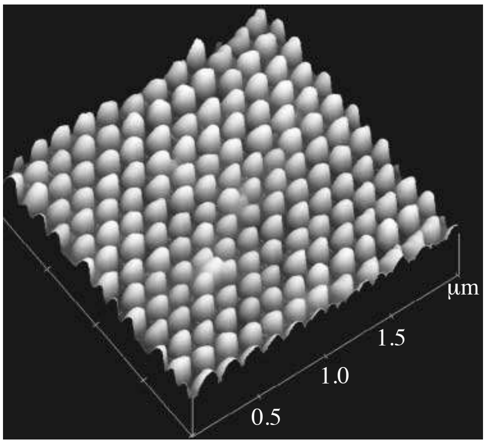

Figure 4. AFM image of the nipple array in a facet lens of the lycaenid *Pseudozizeeria maha*. The nipple distance is $d=170\pm10$ nm and the height is $h=130\pm15$ nm.

Table 1. Dimensions of the corneal nipple array of butterflies. (Average values of measurements by SEM, TEM and AFM. *D*, facet diameter; *d*, nipple distance; *h*, nipple height; n.d., not determined. Errors: $\Delta D=3$ µm, $\Delta d=10$ nm, $\Delta h=10$ nm.)

	D (µm)	*d* (nm)	*h* (nm)
Papilionidae			
Graphium sarpedon	28	230	30
Papilio memnon	31	n.d.	(10
Papilio protenor	33	240	20
Papilio xuthus	25	230	20
Pachliopta aristolochiae	26	235	20
Pieridae			
Pieris rapae	22	210	210
Anthocharis cardamines	24	215	170
Lycaenidae			
Everes argiades	17	215	140
Pseudozizeeria maha	21	180	120
Narathura japonica	17	200	90
Nymphalidae			
Inachis io	23	210	200
Heliconius melpomene	27	205	180
Bicyclus anynana	23	205	210
Mycalesia francisca	28	205	130
Polygonia c-aureum	29	200	190
Polygonia c-album	24	215	165
Euphaedra sp.	35	215	160
Euxanthe wakefieldii	28	220	230
Charaxes fulvescens	30	205	40

(larger) nymphalids, where the facet lens diameter was 26 ± 3 µm (figure 1, 2*a* and 3*a*,*b*). The nipple height, *h*, was in the pierid species 185 ± 20 nm (figure 3*c*), in the lycaenids 120 ± 20 nm (figure 2*b*, 3*d* and 4), and in the nymphalids 180 ± 30 nm (figure 1, 2*a* and 3*a*,*b*), except for one species with $h\approx40$ nm (see table 1).

The shape of the nipples appeared to be somewhat variable and, therefore, we performed reflectance calculations for a few model shapes, a cone, paraboloid and Gaussian bell, respectively (figure 5), assuming a hexagonal nipple lattice. The height was increased from 50 to 250 nm in steps of 50 nm. Two nipple widths, given by the parameter *p*, were taken: $p=0.40$ (figure 5) and 0.53; for the latter value the cone and paraboloid nipples have a base area equal to that of the lattice unit cell (see §2). Incident light faces a gradually increasing effective refractive index, from $n_e=1$ at $z^*=1$ to $n_e=1.52$ at $z^*=0$ (Vogt 1974). The cone and paraboloid-shaped nipples have a base area smaller than that of the lattice unit cell when $p=0.40$ (figure 5*a*), and hence the effective refractive index value suddenly jumps to 1.52 at $z^*=0$ (figure 5*b*).

A thin-film multilayer model was used to calculate the reflectance of the three types of nipple array for normally incident light. The data of the effective refractive index profiles for the three nipple shapes, the two widths and the five heights yielded the reflectance spectra of figure 6. When the nipples are small, with height 50 nm, the refractive index gradient is steep, and accordingly the reflectance approximates the value of 0.043, predicted by the Fresnel equations for light in air normally incident on a medium with refractive index 1.52. The reflectance decreases with increasing nipple height, becoming minimal when the height is about 250 nm. The height-induced changes in the reflectance somewhat depend on the wavelength, especially for the non-touching nipples (figure 6*a*,*c*,*e*). The strongest reduction in reflectance occurs for paraboloid nipples with $p=0.53$ that is for nipples that approximately touch each other in the troughs (figure 6*d*).

At normal incidence the degree of polarization is irrelevant. The reflectance, however, depends on the polarization when the angle of incidence is non-zero. Figure 7*a*,*b* show how the reflectance for 500 nm light depends on the angle of incidence for different nipple heights, that is for TE (s-) polarized and TM (p-) polarized light, respectively. The nipples were taken here to be touching paraboloids (cf. figure 6*d*). Again, for low nipples the angle dependence of the reflectance approximates that predicted by the Fresnel equations for a smooth surface. The reflectance for TE waves decreases monotonically with nipple height at all angles of incidence. A similar reduction occurs for TM waves when the angle of incidence is smaller than *ca* 50°, but the reflectance for TM waves hardly changes at angles above 50°. Qualitatively very similar angle and polarization dependences of the reflectance follow from calculations for the other nipple shapes. No striking differences occurred for wavelengths within the visible range.

4. DISCUSSION

We investigated the corneal nipple arrays on the facet lenses of 19 species of butterflies with SEM, TEM and AFM (table 1). The nipple distance is, generally, about 210 nm. Slightly lower values occur in small facets, with diameter around 20 µm, and larger distances correlate with large facets, around 30 µm. The nipples are created during growth by secretions from regularly spaced microvilli in the corneagenous cells (Gemne 1971). Possibly the number of microvilli per ommatidium is about constant, resulting in a larger separation of the nipples in the bigger facet lenses.

The nipple height is much more variable. Bernhard *et al.* (1970) classified the nipples in classes I–III, with heights $h<50$ nm, $50\text{ nm}<h<200$ nm, and $h>200$ nm, respectively. According to that classification, the distribution of the five investigated papilionid species was 5 : 0 : 0, of the two pierids 0 : 1 : 1, of the three lycaenids 0 : 3 : 0 and of the nine nymphalids 1 : 5 : 3. The corresponding values obtained by Bernhard *et al.* (1970)

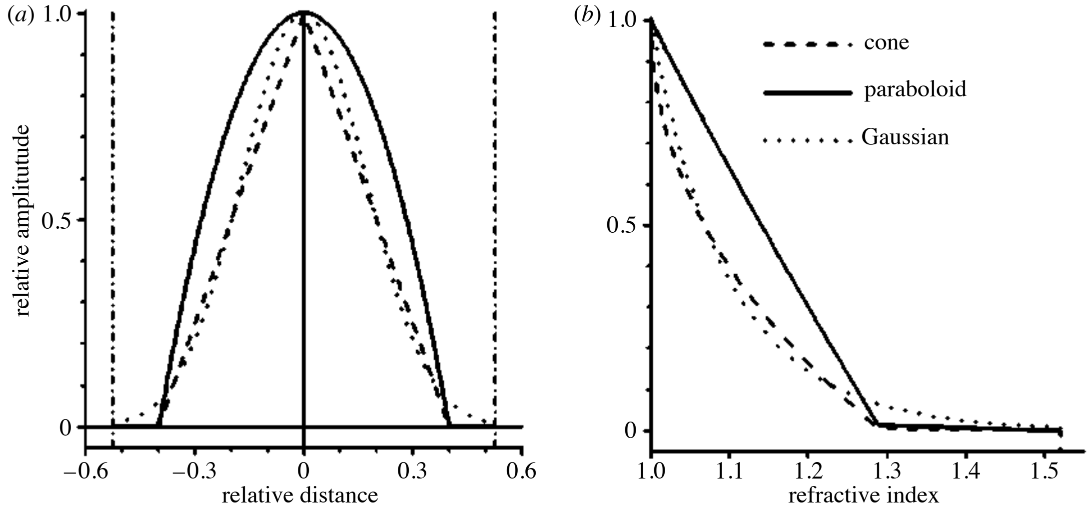

Figure 5. Three model nipple types with a cone, paraboloid and Gaussian-bell shape, and the resulting effective refractive index. (*a*) The amplitude of the three types of nipples relative to the peak value, z^*, shown as a function of the distance relative to the distance of two adjacent nipples, r^*. The boundary value for the width parameter, $p_0=0.53$ (see §2), is given by vertical, dot-dashed lines. For the nipples shown in (*a*), $p=0.40$. (*b*) Effective refractive index values at level z^* for arrays of the three nipples of (*a*); note that the relative amplitude, z^*, is the independent variable here; the refractive index is the dependent variable. When $z^*<0$, the refractive index is that of the facet lens medium, $n_c=1.52$, and when $z^*>1$ the refractive index is 1, that of air. The refractive index for $0<z^*<1$ follows from effective medium theory (see §2). Paraboloid nipples yield a nearly linear refractive index gradient. Cone and paraboloid nipple arrays with $p=0.40$ yield an effective refractive index jump at $z^*=0$ from 1.29 to 1.52.

are 10 : 0 : 0 (papilionids), 2 : 8 : 1 (pierids), 0 : 11 : 2 (lycaenids), and 1 : 9 : 20 (nymphalids). The distribution that we obtained for the nymphalids was close to the boundary of 200 nm, which according to Bernhard *et al.* (1970) should not be taken as very sharp. We, therefore, conclude that our data are in good agreement with those of the earlier workers.

Using microwave models, Bernhard *et al.* (1965) experimentally demonstrated the strong reflectance reduction by a nipple array with cone-shaped nipples. The optical properties of moth-eye antireflection surfaces in the visible wavelength range have been firstly investigated on nipple arrays produced in photoresist by Wilson & Hutley (1982). The early work has induced many technical applications, known as 'moth-eye' arrays, which are widely applied for glare reduction as well as transmittance enhancement (review Palasantzas *et al.* 2005). Recently, Yoshida *et al.* (1997) investigated the effect of the nipple array discovered on the scaleless wings of a hawkmoth. The reflectance of the native wing was *ca* 1.5%, but removing the nipples by scraping resulted in a distinct reflectance increase to 4%, showing that the nipple array on the wings indeed functions as an impedance matching system. A similar prominent nipple array exists in cicada wings (SEM, Wagner *et al.* 1996; AFM, Watson & Watson 2004).

Although several theoretical treatises have been given for the effect of specific nipple profiles on the reflectance for light at normal incidence (e.g. Southwell 1991), quantitative data can be easily obtained by treating the nipple array as an interface with a gradient effective refractive index. The reflectance of such a medium can be straightforwardly calculated with matrix multiplication procedures for thin-film multilayers. It thus appeared that the precise shape of the nipples is rather unimportant for the reduction of the reflectance, that the nipple width plays a secondary role, and that the height of the nipples is the crucial factor (figure 6). An extreme reduction to nearly zero is realized by tall paraboloids, touching each other at

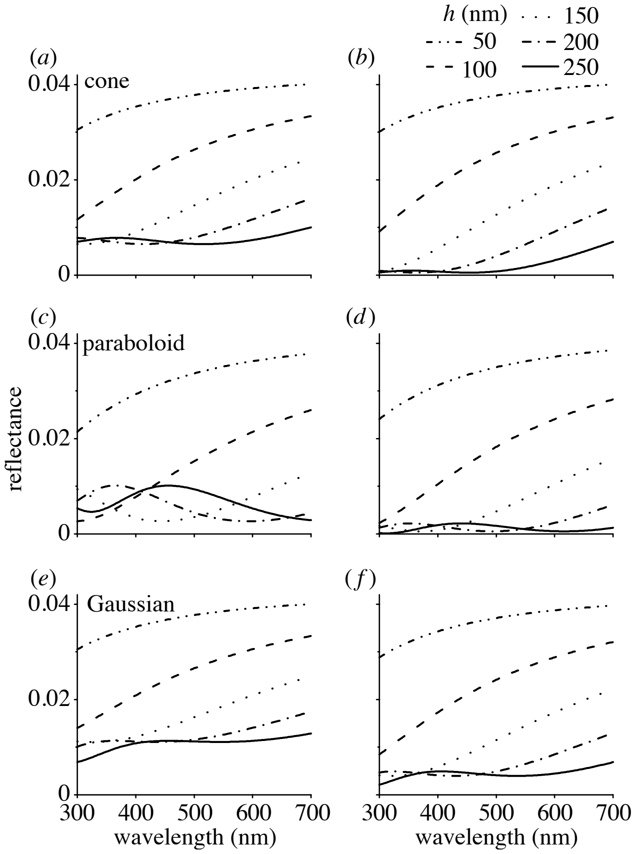

Figure 6. Reflectance of nipple arrays with the three types of nipples for normally incident light. The spectra were calculated with a model multilayer, consisting of 100 layers with thickness $h/100$, where h is the height of the cone (*a*,*b*), paraboloid (*c*,*d*) or Gaussian-shaped (*e*,*f*) nipples. The height was varied from 50 to 250 nm in steps of 50 nm. The width parameter p was taken to be 0.40 (*a*,*c*,*e*) or 0.53 (*b*,*d*,*f*). The reflectance for 50 nm high nipples approximates the value 0.043, predicted by the Fresnel equations, at the longer wavelengths. The reflectance is strongly reduced at nipple heights of *ca* 250 nm, notably when the nipples are paraboloids.

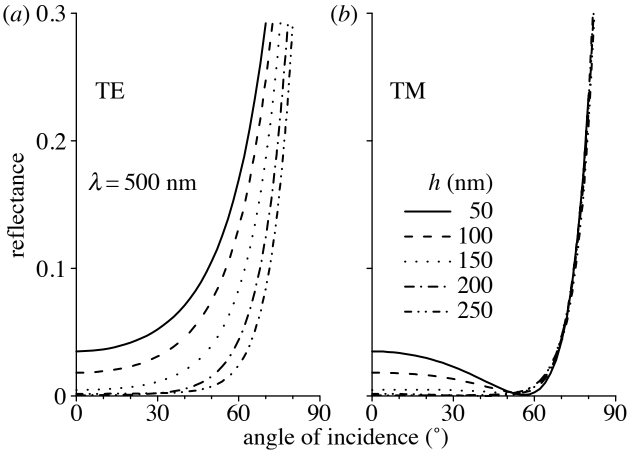

Figure 7. Dependence of the reflectance on polarization and angle of incidence. The corneal nipples were assumed to be paraboloids that touch each other at their base ($p=0.53$; see figure 6*d*), and the nipple height was varied from 50 to 250 nm. The light wavelength was 500 nm. (*a*) The reflectance of TE (s-) polarized light is strongly reduced with increasing nipple height. (*b*) With TM (p-) polarized light, the strong reflectance reduction only occurs at angles of incidence below 50°.

the base (figure 6*d*). This situation is well approximated by the classical moth cases (Bernhard & Miller 1962; Bernhard *et al.* 1965).

A system of regular, radial ridges was reported to exist in the corneal surface of the tiny moth *Leucoptera coffeella* by Meyer-Rochow & Stringer (1993). They also found the same arrangement of microridges in the strongly curved facets of 'other species of tiny flying insects', with spatial dimensions similar to those of the nipple arrays of the larger insects. Parker *et al.* (1998) provided further data for extant flies as well as for an Eocene dolichopodid fly. The latter authors reproduced the ridge structures in photoresist and thus demonstrated a severe reflectance reduction of light incident over a large range of angles of incidence, to about 60°, especially for TE waves. The reported results correspond well with the calculations of figure 7. Many extant dolichopodid flies have facet lenses with minor nipples, however, and in fact have in the distal region of the facet lens alternating layers of high and low refractive index material (Bernard & Miller 1968). The multilayer structure acts as a spectrally selective reflector, which possibly functions to improve colour discrimination (Trujillo-Cenóz 1972; Stavenga 2002*a*). Extant brachyceran flies have facet lenses with front surface curvature slightly smaller than the lens diameter (Stavenga *et al.* 1990). The maximal angle of incidence is then at most 40°. The reflectance for light incident at this extreme angle does not severely deviate from that for normal incidence (figure 7), causing some doubt about the effect of the corneal ridges of flies. Furthermore, the corneal facets of the tiny insects investigated by Meyer-Rochow & Stringer (1993) and Parker *et al.* (1998) are remarkably flat in the centre and, therefore, reflectance reduction will there be minimal. Nevertheless, in some cases the facets appear to be very strongly curved at the lens periphery, so that the ridge structures could serve as an effective impedance matching device there. This may indeed be an important factor in mosquitoes, which have about 200 nm high, hexagonally packed nipples (Brammer 1970) in a virtually hemispherical facet surface (Land *et al.* 1997). All the same, the resulting light sensitivity increase due to the corneal corrugations in dipterans will presumably be no more than a few per cent. This could still be useful, of course, as several mechanism are known that enhance the sensitivity of insect eyes by only a small amount, e.g. the afocal optics of butterfly eyes compared to the conventional focal optics (van Hateren & Nilsson 1987), the tapetum basal to the butterfly rhabdom (Stavenga, unpublished work), or the sensitizing pigment in fly eyes (Stavenga 2004).

Nipple-like structures have been encountered in several insects that are evolutionary ancestral to moths and butterflies; for instance, Thysanura (Parker *et al.* 1998), Collembola (Bernhard *et al.* 1970; Barra 1971) and Trichoptera (Bernhard *et al.* 1970), and their presence hence must be considered a potential property of all insect facet lenses. We temporarily conclude that the most likely biological function of the nipple arrays is glare reduction, especially in the scaleless, transparent wings. An additional consequence of the nipple arrays in insect corneal facet lenses will be a slight improvement of the transmittance, which cannot be disadvantageous (Miller 1979). Neither of both functions seems to be crucial for butterfly eyes, however, as numerous species have low nipples or even have completely discarded them, as for example all known papilionids. This raises again the question of which eye type is ancestral in the Lepidoptera, and inextricably linked to this is the question whether the first moths were diurnal or crepuscular/nocturnal (Warrant *et al.* 2003).

The most likely evolutionary scenario for the corneal nipple arrays of butterflies is that the diurnal butterflies descended from nocturnal moths (Yack & Fullard 2000; Grimaldi & Engel 2005; Wahlberg *et al.* 2005). Most nymphalids, considered to be the least evolved butterflies, thus have retained the full-grown nipples of the moths, but the highly developed papilionids have completely lost the nipple trait.

A similar reasoning can be erected for the lepidopteran tapetum. Moth-eyes have extremely well developed tapeta, created by tracheoles that surround the fat rhabdoms. They form efficient reflectors that enhance light sensitivity as well as visual acuity (Warrant *et al.* 2003). Most diurnal butterflies have an intricate tapetal reflector proximally to each ommatidial rhabdom, which is formed by tracheoles, as in moths. The function of the tapetum is that light which travelled through the length of the rhabdom and reached the proximal end without having been absorbed is reflected back into the rhabdom, so having another chance of absorption. The diurnal butterflies thus feature a unique remnant of the extensive moth tapetum. The tapetal reflector is fully absent in papilionids, however, presumably because the gain in sensitivity is very slight. We recently found that this loss of tapetum also has occurred in certain pierids. The orange tip, *Anthocharis cardamines*, as well as the yellow tip, *Anthocharis scolymus*, appear to lack the tracheolar tapetum (Stavenga & Arikawa, unpublished work).

The hypothesis that butterflies developed from nocturnal moths runs somewhat counter to the view that the optical superposition eyes of nocturnal moths gradually developed from the afocal apposition eyes of diurnal butterflies (Nilsson *et al.* 1988). It may be too early yet to decide (Warrant *et al.* 2003), but we note that recently

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studied nocturnal bees have not developed optical superposition eyes. The only major modification is a huge increase of the rhabdom diameter, whereas the apposition optics is essentially unchanged (Greiner *et al.* 2004).

As a final remark, we note that the corneal nipples of butterflies have a favourable consequence for optical studies on butterfly eyes. Epi-illumination of butterfly eyes with tracheolar tapeta reveals beautiful eye shines, which can be studied with large aperture optics when using an adequate set-up (Stavenga 2002*b*). Background light due to the reflecting facet lens surfaces is in many species appreciably suppressed by the corneal nipple arrays.

We thank H. Bron for technical assistance, B. J. Hoenders and J. Th. M. de Hosson for discussions, and the editor and two anonymous referees for valuable criticisms. Financial support was provided by the EOARD to D.G.S.

REFERENCES

Barra, I. A. 1971 Les photorécepteurs des collemboles, étude ultrastructurale. I. L'appareil dioptrique. *Z. Zellforsch.* **117**, 322–353. (doi:10.1007/BF00324808)

Bernard, G. D. & Miller, W. H. 1968 Interference filters in the corneas of Diptera. *Invest. Ophthalmol.* 7, 416–434.

Bernhard, C. G. & Miller, W. H. 1962 A corneal nipple pattern in insect compound eyes. *Acta Physiol. Scand.* **56**, 385–386.

Bernhard, C. G., Miller, W. H. & Møller, A. R. 1965 The insect corneal nipple array. *Acta Physiol. Scand.* **63**(Suppl. 243), 1–25.

Bernhard, C. G., Gemne, G. & Sällström, J. 1970 Comparative ultrastructure of corneal surface topography in insects with aspects on phylogenesis and function. *Z. Vergl. Physiol.* **67**, 1–25. (doi:10.1007/BF00298117)

Brammer, J. D. 1970 Ultrastructure of the compound eye of a mosquito *Aedes aegypti* L. *J. Exp. Zool.* **175**, 181–196. (doi:10.1002/jez.1401750207)

Bruggeman, D. A. G. 1935 Berechnung verschiedener physikalischer Konstanten von heterogenen Substanzen. I. Dielektrizitätskonstanten und Leitfähigkeiten der Mischkörper aus isotropen Substanzen. *Ann. Phys.* **24**, 636–679.

Exner, S. 1891 *Die Physiologie der facittirten Augen von Krebsen und Insecten*. Leipzig: Deuticke.

Exner, S. 1989 *The physiology of the compound eyes of insects and crustaceans (translated by R. C. Hardie)*. Berlin: Springer.

Gemne, G. 1971 Ontogenesis of corneal surface ultrastructure in nocturnal Lepidoptera. *Phil. Trans. R. Soc. B* **262**, 343–363.

Greiner, B., Ribi, W. A. & Warrant, E. J. 2004 Retinal and optical adaptations for nocturnal vision in the halictid bee *Megalopta genalis*. *Cell Tissue Res.* **316**, 377–390. (doi:10.1007/s00441-004-0883-9)

Grimaldi, D. & Engel, M. S. 2005 *Evolution of the insects*. Cambridge, UK: Cambridge University Press.

Hateren, J. H. & Nilsson, D.-E. 1987 Butterfly optics exceed the theoretical limits of conventional apposition eyes. *Biol. Cybern.* **57**, 159–168. (doi:10.1007/BF00364148)

Land, M. F., Gibson, G. & Horwood, J. 1997 Mosquito eye design: conical rhabdoms are matched to wide aperture lenses. *Proc. R. Soc. B* **264**, 1183–1187. (doi:10.1098/rspb.1997.0163)

Macleod, H. A. 1986 *Thin-film optical filters*. Bristol: Adam Hilger.

Meyer-Rochow, V. B. & Stringer, I. A. N. 1993 A system of regular ridges instead of nipples on a compound eye that has to operate near the diffraction limit. *Vision Res.* **33**, 2645–2647. (doi:10.1016/0042-6989(93)90223-J)

Miller, W. H. 1979 Ocular optical filtering. In *Handbook of sensory physiology* vol. VII/6A, (ed. H. Autrum), pp. 69–143. Berlin: Springer.

Nilsson, D.-E. 1989 Optics and evolution of the compound eye. In *Facets of vision* (ed. D. G. Stavenga & R. C. Hardie), pp. 30–73. Berlin: Springer.

Nilsson, D.-E., Land, M. F. & Howard, J. 1988 Optics of the butterfly eye. *J. Comp. Physiol. A* **162**, 341–366. (doi:10.1007/BF00606122)

Palasantzas, G., De Hosson, J. Th. M., Michielsen, K. F. L. & Stavenga, D. G. 2005 Optical properties and wettability of nanostructured biomaterials: moth-eyes, lotus leaves and insect wings. In *Handbook of nanostructured biomaterials and their applications in biotechnology, vol. 1: Biomaterials* (ed. H. S. Nalwa), pp. 273–301. Stevenson Ranch, CA: American Scientific Publishers.

Parker, A. R., Hegedus, Z. & Watts, R. A. 1998 Solar-absorber antireflector on the eye of an Eocene fly (45 Ma). *Proc. R. Soc. B* **265**, 811–815. (doi:10.1098/rspb.1998.0385)

Southwell, W. H. 1991 Pyramid-array surface-relief structures producing antireflection index matching on optical surfaces. *J. Opt. Soc. Am. A* **8**, 549–553.

Stavenga, D. G. 2002*a* Colour in the eyes of insects. *J. Comp. Physiol. A* **188**, 337–348. (doi:10.1007/s00359-002-0307-9)

Stavenga, D. G. 2002*b* Reflections on colourful butterfly eyes. *J. Exp. Biol.* **205**, 1077–1085.

Stavenga, D. G. 2004 Visual acuity of fly photoreceptors in natural conditions-dependence on UV sensitizing pigment and light-controlling pupil. *J. Exp. Biol.* **207**, 1703–1713. (doi:10.1242/jeb.00949)

Stavenga, D. G., Kruizinga, R. & Leertouwer, H. L. 1990 Dioptrics of the facet lenses of male blowflies *Calliphora* and *Chrysomia*. *J. Comp. Physiol. A* **166**, 365–371. (doi:10.1007/BF00204809)

Trujillo-Cenóz, O. 1972 The structural organization of the compound eye in insects. In *Handbook of sensory physiology* vol. VII/2, (ed. M. G. F. Fuortes), pp. 5–62. Berlin: Springer.

Vogt, K. 1974 Optische Untersuchungen an der Cornea der Mehlmotte *Ephestia kühniella*. *J. Comp. Physiol.* **88**, 201–216. (doi:10.1007/BF00695407)

Wagner, T., Neinhuis, C. & Barthlott, W. 1996 Wettability and contaminability of insect wings as a function of their surface sculptures. *Acta Zool.* **77**, 213–225.

Wahlberg, N. *et al.* 2005 Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proc. R. Soc. B* **272**, 1577–1586. (doi:10.1098/rspb.2005.3124)

Warrant, E. J., Kelber, A. & Kristensen, N. P. 2003 Eyes and vision. In *Handbook of zoology, Vol. IV, Part 36, Lepidoptera, moths and butterflies, Vol. 2: Morphology, physiology and development* (ed. N. P. Kristensen), pp. 325–359. Berlin, New York: Walter de Gruyter.

Watson, G. S. & Watson, J. A. 2004 Natural nano-structures on insects—possible functions of ordered arrays characterized by atomic force microscopy. *Appl. Surf. Sci.* **235**, 139–144. (doi:10.1016/j.apsusc.2004.05.129)

Wilson, S. J. & Hutley, M. C. 1982 The optical properties of 'moth eye' antireflection surfaces. *Opt. Acta* **29**, 993–1009.

Yack, J. E. & Fullard, J. H. 2000 Ultrasonic hearing in nocturnal butterflies. *Nature* **403**, 265–266. (doi:10.1038/35002247)

Yoshida, A., Motoyama, M., Kosaku, A. & Miyamoto, K. 1997 Antireflective nanoprotuberance array in the transparent wing of a hawkmoth, *Cephonodes hylas*. *Zool. Sci.* **14**, 737–741.