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SPECIAL ISSUE ARTICLE

Moths are strongly attracted to ultraviolet and blue radiation

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Abstract. 1. We carried out three choice experiments with 6116 nocturnal lepidopteran individuals (95 species, 7 families, 32 075 counts), each replicated 105 times during the seasons of 2 years. Moths were released indoors at the centre of a 10 × 10 m area with different lamps placed at each corner.

2. In experiment 1, lamps emitted ultraviolet (UV) (peak at 365 nm), blue (450 nm), green (520 nm) or cool white (450 and 520 nm) radiation. In experiment 2, UV was replaced by red (640 nm). In experiment 3, we used UV and three mixed radiation lamps of different emission intensities (365–520 nm).

3. We applied a linear mixed effect model to test for differences in attraction to the light sources.

4. Among all counts, 12.2% (males) and 9.2% (females) were attracted to a lamp. Among the lamp counts, 84% were made at the UV lamp in experiment 1. In experiment 2, 63% of the counts were made at the blue lamp. In experiment 3, most counts were made at the strongest mixed radiation lamp (31%), and the UV lamp (28%). Patterns were generally similar across Lepidopteran families, and for both sexes.

5. Moths are clearly preferentially attracted to short-wave radiation. Even small quantities of UV radiation, emitted, for example, by metal halide lamps and certain mercury vapour tubes, will disproportionately contribute to light pollution. Since blue light also attracts moths strongly, lamps with a low proportion of blue light should be given priority in lighting planning.

Key words. Arthropods, conservation, insect decline, Lepidoptera, light pollution, phototaxis.

Introduction

In urban areas, modern street light sources, illuminated buildings, bridges and landmarks, billboards, and numerous other light sources are turning Earth's essentially dark night into day (Falchi *et al*., 2016). Human civilisation's intensive signature of light increasingly leaves only the remotest areas in original night darkness. This rapid development has in recent years been additionally fostered by the availability of energy-efficient LED technology (Davies *et al*., 2017; Desouhant *et al*., 2019) that is responsible for an increased proportion of emitted short-wave radiation as compared to the previously prevailing long-wave emitting sodium vapour technology (Davies & Smyth, 2018). However, the use of white LED light (with a primary blue peak, with radiation partially transformed into a continuous spectrum over the whole range visible for humans) is becoming controversial, as it is suspected to negatively impact on human health and day/night rhythm (Lunn *et al*., 2017). Light pollution not only influences the visibility of dark skies and celestial objects (Wesołowski, 2019), human biological rhythmicity and potentially health, it also severely impacts wildlife, particularly nocturnal insects (e.g. Huemer *et al*., 2011; van Langevelde

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et al., 2011; Somers-Yeates *et al.*, 2013; Pawson & Bader, 2014; van Grunsven *et al.*, 2014; Altermatt & Ebert, 2016; Macgregor *et al.*, 2017; Wakefield *et al.*, 2016, 2018; Davies & Smyth, 2018, Owens & Lewis, 2018).

A large proportion of nocturnal flying insects shows positive phototaxis at night, that is, they move towards a stimulus of light. Most insects have trichromatic vision, with peak receptor sensitivities in the ultraviolet (UV), blue, and green spectral range (Briscoe & Chittka, 2001). Some noctuid moths appear to have an additional sensitivity to red light (Briscoe & Chittka, 2001). UV sources are particularly effective in attracting nocturnal flying insects (van Langevelde *et al.*, 2011), and the trapping of nocturnal insects using light sources with a high UV component has been widely used in taxonomic and ecological research (e.g. Holloway *et al.*, 2001; Brehm, 2017). Quantifying the relative influence of wavelength on the attractiveness of lamps has nonetheless remained difficult, as previous studies comparing different lamp types (such as inorganic LEDs, sodium vapour, mercury vapour, metal halide low- or high-pressure discharge lamps) were hampered by the simultaneous alteration of multiple parameters such as the overall spectral composition or angle, as well as the pattern and luminous flux of emitted light. This renders the interpretation of the resulting data problematic, since observed patterns cannot reliably be linked exclusively to a single parameter like UV content or radiation intensity. Experiments to test the attractiveness of different lamp types to flying insects, using lamp setups standardised with regards to emission quantity, and with tightly defined single wavelength peaks are, to our knowledge, novel approaches.

Furthermore, experiments testing the attraction of insects to different types of lamps have generally been carried out in the field (e.g. Wakefield *et al.*, 2018). Experiments under controlled (indoor) conditions, in contrast, have generally been limited to single or very few insect species, mostly representing agricultural or silvicultural pest species (e.g. Cowan & Gries, 2009). In such experiments, flying insects were also not usually allowed to fly freely in space, and were only given the choice between light sources (mostly two) at very small spatial scales (<2 m, e.g. Park & Lee, 2017).

Here, we present results from a novel experimental approach that combines (i) choice experiments of freely flying moths under controlled conditions at a medium spatial scale (100 m^2), (ii) a large number of individual lepidopterans (6116) representing seven different families, and (iii) standardised radiation sources that allow attraction patterns to be clearly linked to single factors. Moreover, we analyse our data separately for males and females, because different sexes are often not attracted in equal numbers to artificial light sources (Altermatt *et al.*, 2009; Cheng *et al.*, 2016; Degen *et al.*, 2016). Observed sex ratio biases can, for example, be explained by a generally lower flight activity of females as compared to males. Females often 'sit and wait' for males to approach for mating (Umbers *et al.*, 2015). On the other hand, females may possibly become more active later in their adult lifetime when searching for specific hostplants as an egg-laying substrate.

Specifically, we tested the following hypotheses:

1. Short-wave radiation attracts more individuals compared to radiation of longer wavelength.
2. Strong sources of radiation attract more individuals than weaker sources of the same spectral quality.
3. Males are more strongly attracted to radiation than females.

Material and methods

Experimental set-up and study organisms

All experiments were carried out between August and November 2018 (111 experiments) and between April and November 2019 (204 experiments) in a disused lecture hall in the former children's hospital at Jena University, Germany

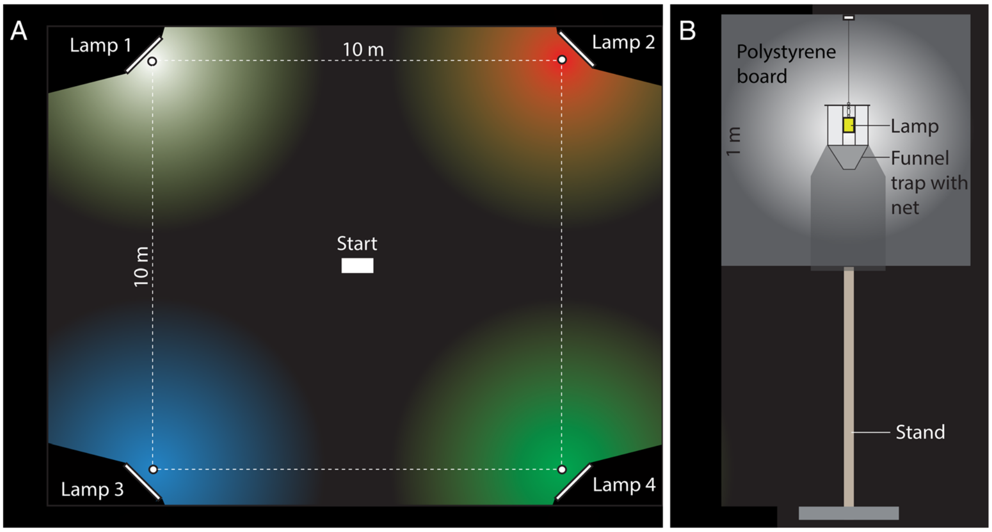

Fig. 1. Schematic presentation of the experimental setup (a) and of the light trap used in the experiments with its 1 m^2 background (b). Position of lamps was changed randomly between every round of experiments. [Color figure can be viewed at wileyonlinelibrary.com]

(Fig. 1, Supporting Information Figs S1 and S2). The hall had a size of about 10.50 m × 15 m, with a wall height of 4 m. It still contained its original wooden seating, allowing moths to potentially find resting places outside the direct influence of the radiation sources. Windows were carefully blinded with oriented strand boards, resulting in a completely dark room. During natural daytime, the centre of the room was illuminated with 2 × 36 W mercury vapour white light tubes (Osram Lumilux, Fig. S2) to imitate a day–night rhythm. During the night, these lamps were switched off and one of the three experiments was started. Day–night rhythm was approximately matched to the natural conditions in Jena and moths were usually observed resting during daytime.

Four different LED lamps were installed at the corners of a 10 m × 10 m central area, with a distance of 7.1 m from each lamp to the centre of this square area (Fig. 1a). Funnel traps (Insects & Light, Jena, Germany) were installed below the lamps at a height of 1.50 m (Fig. 1b) (design: see Brehm & Axmacher, 2006). Moths were released in the centre of the hall, and insects attracted to lamps were caught alive in a cylindrical net (Supporting Information Figs S1 and S2). In order to standardise reflection, each lamp was installed in front of a 1 × 1 m wooden panel covered with an aluminium foil and 15 mm thick polystyrene plates to reflect light towards the centre of the hall. Measurements with a photospectrometer (Jeti Blue Spec Cube, 300–1000 nm range) confirmed that the polypropylene materials used for the trap and the polystyrene reflective plate reflected both visible light and UV radiation equally well.

Most moths were collected in the field prior to usage in our experiments. Overall, 48% of the species (29% of the specimens) were collected by light-trapping with LepiLED lamps (see below) in the wider vicinity of Jena, avoiding areas with direct light pollution. A further 32% of the species (43% of the specimens) were baited with a mixture of rotten fruits and red wine (Niermann & Brehm, 2019). These specimens were collected in the Saale floodplains within built-up areas in the vicinity of street lighting, but at a location not experiencing direct light exposure. Nonetheless, we cannot rule out that the ambient light pollution at this location might have affected the strength of the phototaxis response of the specimens sampled here (Altermatt & Ebert, 2016; van Grunsven *et al*., 2019). The remaining 20% of the species (28% of the specimens) were reared from early life stages (Supporting Information Table S1). The latter category included both native European species as well as species from outside the Western Palaearctic region, such as *Spodoptera littoralis*, *Samia wangi*, *Actias luna*, and the Asian box moth *Cydalima perspectalis*. This invasive species had already been recorded from Jena in 2018 before our experiments started. However, all specimens were strictly kept inside the hall (two-door entrance) to prevent any escape.

Moths were individually numbered on their wing surfaces using felt-tip pens (Stabilo OH Pen Universal). Every day, any new as well as re-captured individuals were put into a gauze cage (80 × 40 × 40 cm) positioned in the centre of the hall (Fig. 1), but fully opened at the top so they could move freely within the lecture hall in the evening/night. At the beginning of each day, moths at each lamp were counted and their respective position was noted. Specimens were counted as having been attracted to a lamp if they were caught in the trap or were encountered within a radius of 2 m around the lamp. We chose this approach because our own field observations strongly imply that moths are regularly attracted to lamps, but only come to rest in close vicinity to the lamps rather than directly flying into them. Since not all insects were recovered each morning, we estimated the total number of moths in the room for each day of the experiment based on an estimation of the species' lifespan. This was calculated based on the recorded lifespans of individuals (in 84% of the species, data of ≥3 individuals were available for analysis; see also Supporting Information Table S10).

Radiation sources

Brehm (2017) developed a lamp with a spectral range strongly tailored towards the known peak sensitivity of insect eye receptors. For our experiments, we used this multi-chromatic 'LepiLED' device (available from Insects & Light) and additionally customised narrow-banded lamps with the same design as the LepiLED mini model, manufactured by K2W Lights (Jena, Germany). The latter lamps were equipped with four narrow-banded LEDs corresponding to the peak sensitivity of photoreceptors commonly present in moths: UV (365 nm), blue (450 nm), green (530 nm), and red (640 nm) (Briscoe & Chittka, 2001) (Supporting Information Fig. S3). In addition, a cool white LED was used with a primary peak at 450 nm and a secondary peak at 520 nm. The four narrow-banded and the white LED lamps were standardised with regards to their radiant flux as far as technically possible, resulting in a radiant flux ranging from 0.39 W (UV LED) to 0.51 W (cool white LED) (Table 1; Supporting Information Fig. S3). Photon flux subsequently increased with wavelength from 7.18×10^{17} photons s^{-1} (UV LED) to 1.62×10^{18} photons s^{-1} (red LED) (Supporting Information Fig. S6).

Given its rectangular geometry, we could not sensibly arrange more than four LED lamps in the hall, and therefore chose to

Table 1. Radiant flux (350–700 nm) of LED lamps used in the experiments during three consecutive nights.

Experiment	Lamp 1	Lamp 2	Lamp 3	Lamp 4
1	UV (0.39 W)	Blue (0.46 W)	Green (0.41 W)	Cool white (0.51 W)
2	Red (0.51 W)	Blue (0.46 W)	Green (0.41 W)	Cool white (0.51 W)
3	UV (0.39 W)	Mixed radiation Mini LepiLED (0.55 W)	Mixed radiation Standard LepiLED (0.96 W)	Mixed radiation Maxi LepiLED (1.34 W)

The position of each lamp was randomly assigned for every new round of experiments. See also Supporting Information Fig. S3 for an illustration and Supporting Information Fig. S6 for photon flux.

carry out three distinct choice experiments during consecutive nights. In the first experiment (night), lamps emitting in the UV, blue, and green range plus the white LEDs were operated simultaneously. During the second experiment (night), the UV-emitting lamp was replaced by a lamp emitting red light. During the third experiment (night), the UV lamp was combined with three multi-chromatic lamps: the three models LepiLED mini, LepiLED standard, and LepiLED maxi. These were composed of identical sets of LEDs (4 UV, 2 blue, 1 green, 1 white, see Brehm, 2017), while each lamp had a distinct radiant flux density (Table 1). On the fourth night, experiments were started again with the first set of lamps, while randomly altering the position of each lamp. Emission spectra of the lamps were recorded at the University of Applied Sciences, Münster, using the light measurement integration sphere system Illumia plus from Labsphere (Herrsching, Germany) equipped with a 1 m Ulbricht sphere. The spectrometer used was a CDS610 model and the light sources were measured in a 4 pi geometry.

Statistical analyses

We firstly calculated the fraction of individuals attracted to the lamps on their first to sixth night after eclosion, based on the estimated total number of specimens present in the room. This threshold of six nights was chosen because few moth specimens survived longer in the experiments (mean average of survival time recorded in 2743 individuals was 5 days, Supporting Information Table S3). For this analysis, only the 18 species reared in captivity were included (Supporting Information Table S1). We used a logit-transformed linear mixed effect model with Gaussian distribution to test for differences in the activity pattern (attracted or not) across time (the first 6 days after eclosion) using the lme4 package (version 1.1-23, Bates *et al*., 2015) in R (version 3.6.3, R Core Team, 2020). The logit-transformation in combination with a Gaussian distribution was preferred over a logistic regression after testing for better fit (Maximum likelihood method, ANOVA, $P < 0.001$), and because of its high interpretability and power for analysing proportions (Warton & Hui, 2011). The night after eclosion (1–6) and sex were fitted as fixed effects, and experiment and lamp source were fitted as random effects. Proportions were then recalculated taking into account taxonomy (moth family). Proportions were analysed as a function of the fixed effect: night after eclosion and phylogeny (family as a factor variable), with experiment and lamp source as random effects. Model diagnostics were performed using the DHARMA package (v. 0.3.3.0, Hartig, 2020).

Secondly, we focused on the proportion of all moth specimens across all species attracted to the different light sources per experiment, considering the respective fractions of moths attracted to light. Differences in attraction between light sources were tested using generalised mixed effect models with binomial error distribution. Proportions were analysed as a function of the fixed effect: type of light source, and the random effect: date. These proportions refer to the percentage of attracted moths per light source per night (four lamps offered summing up to 100% per night). Model diagnostics were performed using the DHARMA package (v. 0.3.3.0, Hartig, 2020), and when encountering overdispersion, an observation-level random effect was included. We performed a multiple comparison test using Tukey contrasts within the multcomp package in R (version 1.4-13, Hothorn *et al*., 2008). We then expanded the generalised mixed effect models further to also discriminate by family, sex, and the interaction with light source as fixed effects, and the random effect: date. We reported the type III Wald χ^2 test results. When sex was included as a model variable, results were based on 92 instead of 95 species, since sex was not determined for three species (*Crambinae* sp., *Eupithecia* sp., and *Idaea humiliata*). To test for a difference in attractiveness among sexes, we tested for the total of attracted individuals using a linear mixed effect model with Gaussian distribution (overdispersion was not detected), using experiment as a random effect.

Results

In total, 6116 moth individuals representing 95 species in seven families were released for our experiments (Supporting Information Tables S1 and S2). We analysed a total of 32 075 valid counts (observations of a moth specimen per night, Supporting Information Table S2). In models differentiated by sex, the number of individuals was reduced to 5948. For 2744 moth individuals, the date of death could be recorded, and accordingly the average lifespan in the experiment was calculated as 5.0 ± 3.7 days for reared and collected individuals (Supporting Information Table S3). The combined fraction of all moths found at the four lamps ranged from 0.3% to 18% in the first six nights. The average was 12.2% for males and 9.2% for females (Supporting Information Table S2). This fraction decreased significantly with time (Supporting Information Figs S6a and S7a) (lmer $F\text{-value}_{1,112} = 22.30$, $P < 0.001$) and was significantly lower for females than males (lmer $F\text{-value}_{1,112} = 16.64$, $P < 0.001$). Additionally, we found significant differences in activity patterns with time between families (lmer $F\text{-value}_{6,251} = 34.24$, $P < 0.001$, Supporting Information Figs S6b and S7b, Table S4).

Focussing exclusively on moths attracted to the lamps, the UV-emitting lamp proved to be the most attractive during experiment 1 (84% of counts) (Figs 2a and 3a; Supporting Information Tables S2 and S5–S7). In experiment 2, the blue lamp attracted the highest number, but at lower absolute and relative numbers than the UV lamp on the previous night (63% of counts) (Figs 2b and 3b; Supporting Information Tables S2 and S5–S7). The distribution of moths in experiment 3 showed smaller, but significant differences between lamps (Figs 2c and 3c; Supporting Information Tables S5 and S6). Post hoc Tukey contrasts showed that the strongest mixed radiation source and the UV lamp were jointly the most attractive light sources (with 31% and 28% of counts, respectively), whereas lamps with a lower mixed radiation intensity attracted fewer moths (with 24% and 16% of counts, respectively) (Supporting Information Tables S2 and S7). Significant differences between families in the response to the lamps were not found in experiment 1 (Supporting Information Table S6), but were found in experiment 2 (Supporting Information Table S6) and experiment 3 (Supporting Information Table S6). No significant interactions between lamp and family were observed. Only individuals of Sphingidae and Erebidae

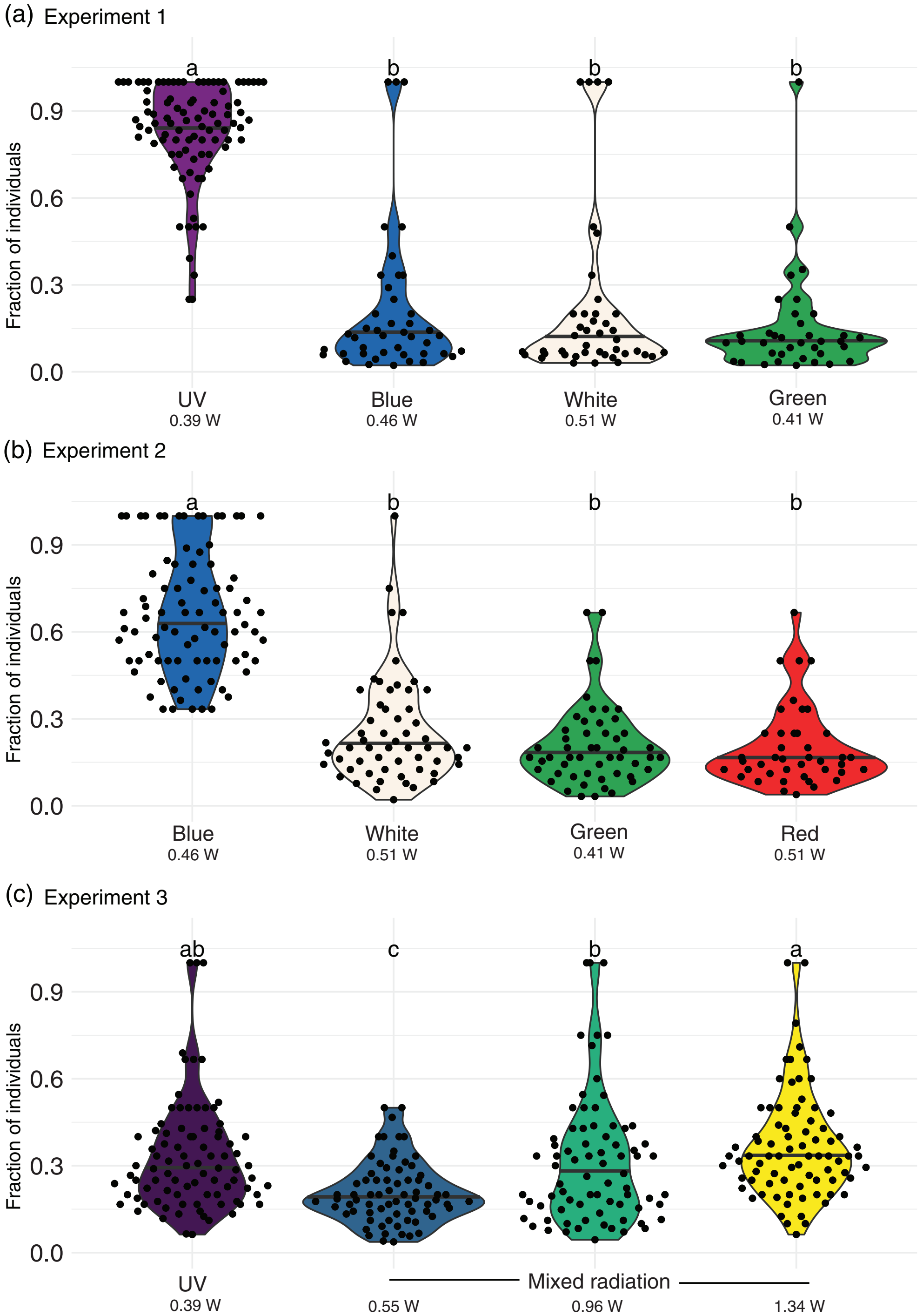

Fig. 2. Violin plots showing the fraction of individuals attracted to the different lamps. Only counts of moths at or near lamps were included. Each dot represents the proportion of individuals at each of the lamps per night. The zero proportions were excluded as we focus on the information from responsive individuals. For example, experiment 1 was carried out in 105 nights with four lamps (420 'lamp nights'), and in 217 of these lamp nights, at least one individual was counted; experiment 2: n = 239, experiment 3: n = 317). Different letters indicate statistical differences from multiple comparisons (Tukey contrasts). Medians of violin plot densities are shown as horizontal lines. Radiant flux (W) of all lamps is shown. [Color figure can be viewed at wileyonlinelibrary.com]

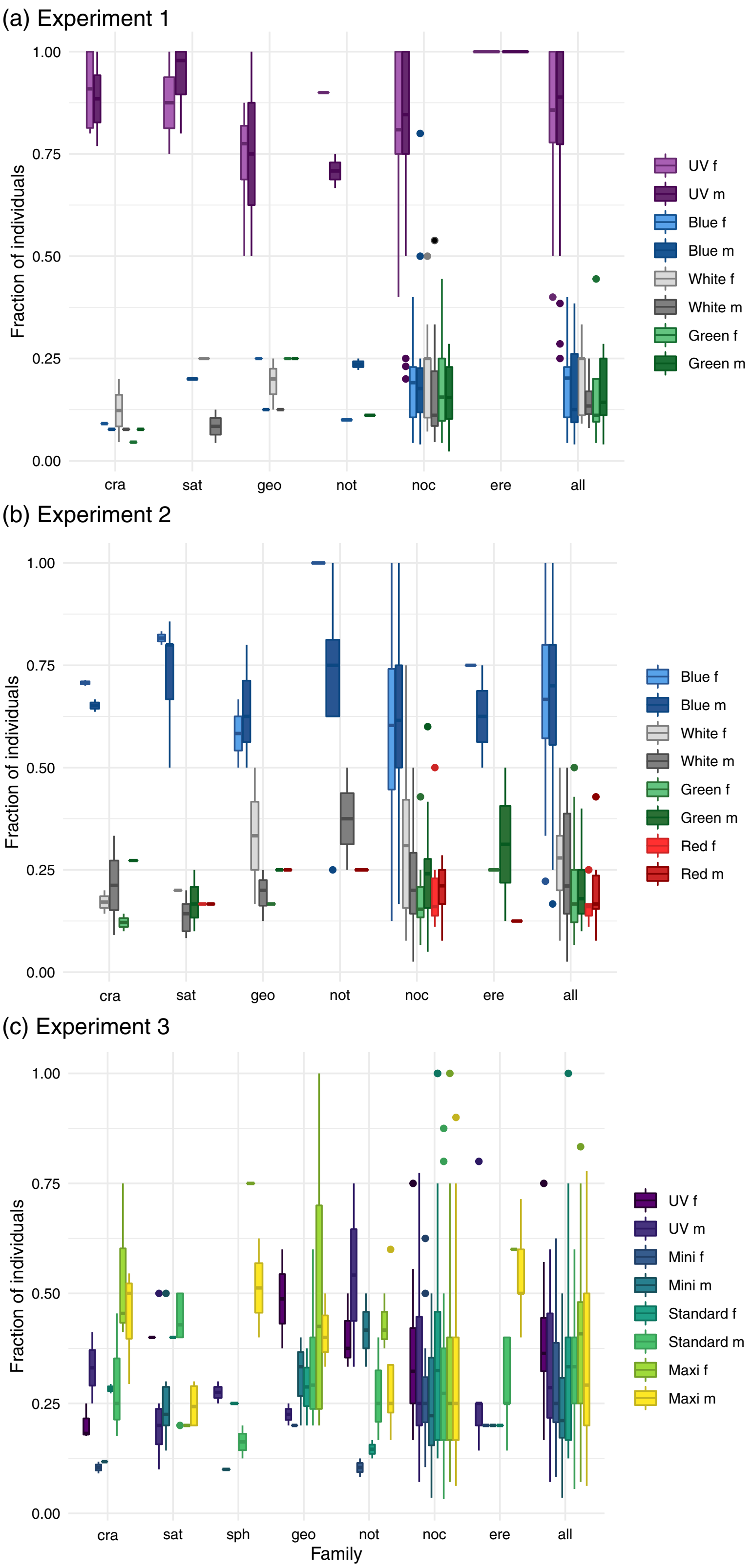

Fig. 3. Legend on next page.

occurred preferentially at the lamp with the highest emission, whereas no consistent patterns were found in the other families – or when all taxa were pooled. Neither did we find significant differences in lamp choice between sexes in any of the experiments, nor a significant interaction between light source and sex (Supporting Information Table S8). Nevertheless, males were significantly more attracted to light sources than were females ($X^2_{1,6} = 19.37$, $P < 0.001$), with males representing 52% of the released individuals. The highest overall rate of attraction to a lamp was found in male saturniid moths, with 27% of the total counts made at the UV lamp. In contrast, saturniid female counts at the UV lamp only accounted for 8% (Supporting Information Fig. S5a).

Across all tested Lepidoptera, the lamps attracted 32% more males than females – with the notable exception of the crambid moth *C. perspectalis*. A separate analysis of the 10 most common species (>197 specimens: 8 Noctuidae, 1 Crambidae, 1 Notodontidae) revealed similar patterns as the analysis at family level (Supporting Information Fig. S8). Only 63 individuals from 27 different species were recorded at the red lamp (experiment 2, Supporting Information Table S9) corresponding to 0.29–20% of all individuals of the species tested.

Discussion

Our phototaxis choice experiments provided key results based on a large number of specimens and species under controlled conditions. They therefore complement both available field studies and small-scale experimental studies that generally focused exclusively on a very small number of species. The use of standardised narrow-banded wavelength lamps with controlled emission intensities provided novel insights into the relative attraction of moths to specific wavelengths. Our study experimentally confirms, for a broad range of Lepidopteran taxa, that (i) short wavelength radiation, particularly UV, attracts far more moth individuals than longer wavelength radiation, (ii) stronger sources of radiation tend to attract more insects than weaker sources, and (iii) there is a clear tendency for male moths to be more strongly attracted to light than females (see also Garris & Snyder, 2010). Results generally correspond well to a model developed by Donners *et al.* (2018) that predicts the attractiveness of different lamps to insects (Supporting Information Fig. S6). However, their model predicts a similar attractiveness for our blue and green lamps whereas in our experiment 2, blue was clearly preferred over green.

The total fraction of moths attracted to any of the lamps was relatively low under the conditions of our indoor experiment (10.7% of all counts). This could indicate that moths can still thrive in urban and light-polluted environments. However, our experimental lamps had a very low radiant (and photon) flux resulting in a small effective sampling range (Merckx & Slade, 2014). Hence, the disturbing effect of artificial light should not be underestimated because of the permanent and year-round pressure it might exert on local nocturnal insect populations. Moreover, we did not feed moths during the experiments. This is likely to have decreased their potential activity (with the exception of species unable to feed, e.g. Saturniidae, which were relatively often attracted to the lamps).

The higher relative attraction of moths to short wavelength radiation was impressively confirmed in experiments 1 and 2. In experiment 1, 84% of moth counts were made at the UV lamp, and in experiment 2, 63% of the moth counts were made at the blue lamp (of all specimens attracted to any of the lamps). It has long been known that UV radiation is extremely attractive for many nocturnal insects (e.g. van Langevelde *et al.*, 2011), and a broad range of UV sources, including specifically developed lamps (Muirhead-Thompson, 2012; Brehm, 2017), has been used to collect moths and other insects at night. In this context, the relatively higher attractiveness of compact fluorescent tubes (CFTs) to Lepidoptera, as compared to LED lamps, can be explained by the presence of emission peaks in CFTs within the UV range at 365 and 400 nm (Wakefield *et al.*, 2016). The high attractiveness of metal halide lamps in field experiments (Wakefield *et al.*, 2018) can be explained in the same way. The higher attractiveness of standardised sources of blue light compared to white, green, and red light sources, has not been explicitly demonstrated by previous studies in a broad range of taxa. A high attractiveness for blue light was nonetheless predicted from theory (Brehm, 2017), and LepiLED entomological lamps were therefore equipped with 25% blue LEDs. The higher attractiveness of blue light is particularly interesting when compared to white LEDs, with the latter benefiting from a slightly higher radiant flux and higher photon flux (Supporting Information Fig. S4). Equally remarkable, blue light was widely ignored by moths in the presence of UV radiation during experiment 1, but became attractive in experiment 2 once the UV lamp was removed. This demonstrates that not only does absolute emission matter, but also suggests the existence of 'light competition'.

The physiological mechanism underlying the positive phototaxis of nocturnal insects, as well as their preference for short wavelengths, is still poorly understood. Light temperature significantly changes in the evenings from the 'Golden Hour' before sunset (low proportion of short-wave radiation) to the 'Blue Hour' after sunset (very high proportion). Later in the night, however, the proportion of UV in moonlight is slightly lower, and in starlight significantly lower, than in daylight (Warrant & Johnsen, 2013; Warrant *et al.*, 2020). Despite these lower levels of UV at night, nocturnal insects find UV light sources highly attractive. This is also true of diurnal insects that are lured out

Fig. 3. Fraction of moths, differentiated by sex, that was attracted to one of the lamps used in experiments 1, 2, and 3 for seven moth families separately and for all specimens combined. The fraction of individuals represents the proportion of individuals of a certain family at a certain lamp in a night, from the total of all individuals of that family released during that night (for experiment 1: $n = 344$, experiment 2: $n = 247$, and experiment 3: $n = 566$; theoretical maximum n in experiment 1 is 105 nights × 4 lamps × 6 families = 2520 'lamp nights'). In experiment 2, Sphingidae were excluded from the analysis because of their low number of records. cra, Crambidae; ere, Erebidae; f, female; geo, Geometridae; m, male; Maxi, LepiLED with radiant flux 1.34 W; Mini, LepiLED with radiant flux 0.55 W; noc, Noctuidae; not, Notodontidae; sat, Saturniidae; sph, Sphingidae; Standard, LepiLED with radiant flux 0.96 W [Color figure can be viewed at wileyonlinelibrary.com]

of hiding by nearby UV-emitting lamps at night (EW, GB, JCA, pers. obs.).

Attraction of moths to lamps with the same radiant spectrum, but different radiant flux differed only slightly. The lamp with the weakest emission tended to attract the smallest fraction of moths for almost all taxa. In Sphingidae and Erebidae, the strongest lamp clearly attracted most individuals. However, differences related to variations in radiant flux between the four offered lamps were overall far less pronounced than differences seen in the other two experiments. At family level, there were no significant differences between a UV lamp and the two larger LepiLED models with mixed radiation. This stresses again the outstanding attraction to UV radiation when compared to longer wavelengths. We explain the overall small differences in experiment 3 as follows: First, the radiant flux and photon flux difference between the lamps was only moderate, that is, only a factor of 2.4 between the models with smallest and highest flux, respectively (Supporting Information Fig. S4). This difference in emission is a very modest intensity difference for an eye to detect. Daily terrestrial light levels vary over eight orders of magnitude, thus stimulus intensity is logarithmically rather than linearly coded (Weber-Fechner law: Mhatre & Robert, 2018). Second, we hypothesize that a stronger lamp *in the field* could attract more insects because the radiation reaches further into the surrounding space and can thus attract insects from longer distances. This effect is not (or hardly) detectable within the given spatial design of our experiment. We assume that all lamps could be detected almost equally well by the test insects within the 100 m^2 quadrat design. This hypothesis should nonetheless be tested in future field experiments.

Finally, in most families, females were less frequently observed at lamps than were males. Since the number of males and females was known in our experiment, we can safely conclude that this observation was not the result of a sex bias in the number of individuals. A very pronounced pattern was recorded for the large Saturniid *S. wangi*, where 29% of the male counts, in contrast to only 8% of the female counts, were made at a lamp. Most *Samia* females simply remained at the place where they were released. A notably different pattern was observed in the box moth, *C. perspectalis* (Crambidae), where a slightly higher proportion of females (12%) than males (9%) was attracted to lamps. While *C. perspectalis* is a typical income breeder (energy for reproduction is largely gained in the adult stage), *S. wangi* is a perfect example of a capital breeder; all eggs are developed upon eclosion from the pupa, and the adults do not take up any food. Typically, females of *S. wangi* will be visited by a male for mating, and they will not spontaneously fly over long distances.

Practical implications

We emphasise that from a conservation perspective, artificial light sources emitting UV radiation should be strictly limited, or even completely banned, from outdoor use, as also argued by Wakefield *et al.* (2016, 2018). Especially UV-emitting low pressure mercury discharge lamps (i.e. many compact or linear fluorescent lamps), as well as metal halide discharge lamps, are highly problematic, but still widely used despite the fact that many emit UV (Bergesen *et al*., 2015). In direct comparison, regular LED light sources hardly emit any UV radiation. However, they do emit far larger proportions of blue light than high-pressure sodium discharge lamps (HPS), which they have regularly replaced in recent years (Bergesen *et al*., 2015). Almost all modern LEDs used for lighting have a primary blue light peak, whereas HPS chiefly emit in the green-red part of the spectrum. Indeed, Wakefield *et al*. (2018) showed that more insects are attracted to LED lighting than to HPS lighting. Theory would also predict that warm-white LEDs attract fewer insects than cool-white LEDs. However, Wakefield *et al*. (2016) and Bolliger *et al*. (2020) found no significant differences in this case, while van Grunsven *et al*. (2020) also reported no long-term differentiation of moth declines according to different wavelengths. Overall, more studies on different LED types are urgently needed, both in the field and under controlled conditions, although well-fitting models already provide appropriate shortcuts (Donners *et al*., 2018). Our study clearly shows that UV emissions at night will attract nocturnal moths to a much larger degree than emissions at longer wavelengths, potentially preventing important pollinator taxa (Walton *et al*., 2020) from providing their ecosystem services, with implications far beyond the conservation of the moth species themselves. These lamps should therefore be totally avoided from outside use, and longer-wave alternative LED types with primary peaks in similar ranges to sodium vapour lamps should be tested and considered as suitable future replacements.

While we strongly argue for the banning of UV-emitting radiation sources from outside use, our study also clearly supports their use in lamps specifically designed to survey and monitor populations of nocturnal insects. It is unsurprising that high pressure mercury-vapour bulbs have remained popular among entomologists for sampling of nocturnal insects due to their high efficiency and strong radiation, including in the UV range. LED and battery technologies have now enabled the development of portable, light-weight and versatile light sources that are well matched to the specific spectral sensitivities of insect eyes (Brehm, 2017). With insects disappearing at alarming rates globally (Bell *et al*., 2020; Wagner 2020) it is becoming imperative to closely monitor their population and community dynamics as a basis for their effective conservation. Our results demonstrate that this can best be achieved by using lamps that emit significant radiation in the UV range, and that take advantage of the many practical advantages of LED lamps over other alternative light sources.

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Data availability statement

All relevant data are published along with this manuscript.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Disused lecture hall of Jena University in panoramic view. Photo credit: J.P. Kasper, FSU Jena.

Figure S2. Centre of hall with release box ("aerarium") and one of the lamps. Lamps at the release box were only operated during daylight hours. Photo credit: G. Brehm.

Figure S3. Radiant flux of lamps used in experiments 1–3. Lamps in experiment 1 were UV, blue, green and white. Lamps in experiment 2 were blue, green, white and red. In experiment 3, one lamp was UV, and the other three lamps ("LepiLED") consisted of 4 UV LEDs, 2 blue LEDs, 1 white LED and 1 green LED.

Figure S4. A) Radiant flux, B) photon flux and C) attractiveness (sensu Donners *et al.*, 2018) of lamps used in experiments 1–3. Since short wave photons have more energy, photon flux in lamps with long wave radiation (e.g. red) is relatively higher. Lamps in experiment 1 were UV, blue, green and white. Lamps in experiment 2 were blue, green, white and red. In experiment 3, one lamp was UV, and the other three lamps ("LepiLED") consisted of 4 UV LEDs, 2 blue LEDs, 1 white LED and 1 green LED.

Fig S5. Total records from experiments 1–3. Most specimens were not attracted to any of the lamps (See also Fig. 3.; m = male, f = female. Cra = Crambidae, Sat = Saturniidae, Sph = Sphingidae, Geo = Geometridae, Not = Notodontidae, Noc = Noctuidae, Ere = Erebidae).

Fig S6. Linear models showing the relationship between the logit-transformed fraction of individuals recorded at each light source in the nights after first release (1st to 6th night), differentiated by sex (a) and by family (b). Each dot represents the proportion of moths attracted to a lamp in one of the three experiments. We considered 12 replicates per night (4 lamps in each experiment) per sex. Most moths were not attracted to any of the lamps (m = male, f = female. Cra = Crambidae, Sat = Saturniidae, Sph = Sphingidae, Geo = Geometridae, Not = Notodontidae, Noc = Noctuidae, Ere = Erebidae.)

Fig S7. Relationship between the logit-transformed fraction of individuals recorded at each light source in the nights after first release (1st to 6th night), differentiated by sex (a) and family (b). A smooth spline was used to fit the data. Each dot represents the proportion of moths attracted to a lamp in one of the three experiments. We considered 12 replicates per night (4 lamps in each experiment) per sex. Most moths were not attracted to any of the lamps. (m = male, f = female). No noctuids or crambids living longer than 5 days were tested. 92 species were included (3 species excluded because of unknown sex, see Table S6). Family abbreviations: see legend of Fig. S4.

Figure S8. Attraction of the ten most common species to lamps in experiments 1–3.

Table S1. Number of specimens per species included in the entire experimental set-up. A total of 6116 specimens representing 95 species were tested. Specimens were either light-trapped or baited in the field (rotten fruit + red wine) in Jena and vicinity, or reared from early life stages (Cra = Crambidae, Sat = Saturniidae, Sph = Sphingidae, Geo = Geometridae, Not = Notodontidae, Noc = Noctuidae, Ere = Erebidae).

Table S2. (separate file: Table_S2_raw-data.xlsx). First sheet: Individual observation points (32075 valid points). At the beginning of the day after an experiment, specimens were counted and their respective position noted: (1) starting place ("a"), (2) one of the four traps including the direct vicinity (2 m radius) ("u, b, g, r, w, mi, ma, st") (3) somewhere else in the hall ("s"), or (4) as not found ("x"). Second sheet: Only records made at lamps. Third sheet: List of all 315 nights. Fourth sheet: Legend. Fifth sheet: Basic statistics.

Table S3. (separate file: Table_S3_Lifespan_records.xlsx) The file (one sheet) contains records of 2743 specimens with known life-span.

Table S4. Estimated coefficients on the effect of family in the activity / attraction of the moths in their first six nights after eclosion. A logit-transformed linear mixed effect model with gaussian distribution was performed. Taxonomical family and night after eclosion were fitted as fixed effects. Experiment and lamp source were fitted as random effects.

Table S5. Analysis of Deviance Table to test the difference in the fraction of individuals attracted to the different lamps, for each experiment (Type III Wald chisquare tests). df = Degrees of freedom.

Table S6. Analysis of Deviance Table to test the effect of lamp, family the interaction between lamp and family in the fraction of individuals attracted for each experiment (Type III Wald chisquare tests). df = Degrees of freedom

Table S7. Multiple comparison of means using Tukey contrasts for differences between light sources. All models used a binomial distribution for the description of the unexplained variation. In experiment 1 and 3, an observation-level random effect was included to account for overdispersion. Adjusted P-values reported using the single-step method (Dunnett Method).

Table S8. Analysis of Deviance Table (Type III Wald chi square tests) of the differences from the attracted moths, the proportion of females and males attracted to each light and the interaction between sex and light source.

Table S9. List of the 63 individuals representing 27 species that were attracted to the red lamp (found in or near the trap), sorted by total attracted number. Also given are the total number of individuals in the experiment and the percentage of attracted specimens (Cra = Crambidae, Sat = Saturniidae, Sph = Sphingidae, Geo = Geometridae, Not = Notodontidae, Noc = Noctuidae, Ere = Erebidae).

Table S10. (separate file: Table_S10_Lamp_measurements.xlsx)

First sheet: Raw measurement data of radiation flux of the used lamps, and calculated photon flux data. Second sheet: Sums of radiation flux, photon flux, attractiveness sensu Donners *et al*. (2018) and figures.

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