Insect Conservation and Diversity (2021) doi: 10.1111/icad.12446

SPECIAL ISSUE ARTICLE

Spectral optimization of beacon lights for the protection of night-swarming mayflies

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Abstract. 1. Negative ecological effects of artificial night-time illumination on wildlife are becoming more and more widely investigated. Flight-to-light behaviour of insects is a well-known phenomenon, which becomes really conspicuous when numerous individuals are simultaneously attracted to light. Mass mortality of night-swarming mayflies at lamp-lit urbanized areas, particularly at bridges, is a well-known phenomenon.

2. White beacon lights are able to keep the mayfly swarms above the water surface. Firstly, it is beneficial for the offspring particularly in the case of protected species. Secondly, this method facilitates maintaining traffic safety on the bridge.

3. Our primary aim was to find the optimal emission spectrum for the mayfly-protecting beacons. With equal-intensity quasi-monochromatic light sources, we measured the attraction of *Ephoron virgo* and *Caenis macrura* mayflies to light as a function of wavelength in the 432–744 nm spectral range.

4. We established that phototaxis of these mayflies increases with decreasing wavelength. We also estimated the attractiveness of different light source types widely used in public lighting to *E. virgo*. According to our results, lamp types emitting light rich in short wavelengths (cool white/bluish to the human eye) are noticeably more attractive to *E. virgo* and to other night-swarming mayflies than lamp types with longer-wavelength-dominated emission spectra (warm white/yellowish to the human eye).

5. Finally, we report on the construction of the very first, permanently installed, spectrally optimized mayfly-protecting beacon system on the bridge of Tahitótfalu (Northern Hungary), which was realized as a practical application of our results.

Key words. Bridge, ecological trap, *Ephoron virgo*, LED, light pollution, mayfly, phototaxis, spectral sensitivity.

Introduction

Evidence of the negative impact of nocturnal artificial illumination on the environment came to light one after the other during the past years (Grubisic *et al*., 2018), and a number of strategies have been proposed to minimize these effects (Gaston *et al*., 2012; Longcore *et al*., 2015; Davies *et al*., 2017). Lighting technologies are rapidly developing and due to their energy efficiency, light-emitting diodes (LEDs) are increasingly used in public lighting (Kyba *et al*., 2014), but the impact of white LEDs on wildlife is often higher than that of conventional lighting technologies (Pawson *et al*., 2014; Lewanzik & Voigt, 2017). Besides duration of exposure and light intensity, the emission spectrum of a light source greatly determines the quality of impact on the environment. Light sources with emission spectra dominated by the UV and blue spectral ranges have greater effects on wildlife than light sources with emission spectra shifted towards longer wavelengths (Longcore *et al*., 2018).

Insects are one of the most important groups of animals that are affected by artificial night-time lighting (Grubisic *et al*., 2018). From the aspect of aquatic insects, bridges are the most problematic structures because they are mostly constructed in the vicinity of aquatic habitats and they are usually illuminated. An example for the impact of the artificial lights of a bridge on aquatic insects was provided by Nankoo *et al*. (2019).

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They found that the abundance of various insects has increased in the vicinity of the Jacques Cartier Bridge (Montreal, Canada) just after the installation of the new bridge-lighting.

Ecological traps arise when sudden changes in the environment (e.g., disturbance caused by humans) lead an organism to choose a poor-quality habitat (Robertson & Hutto, 2006). An ecological trap of the night-swarming *Ephoron virgo* (Olivier, 1791) [= *Polymitarcis virgo* (Olivier, 1971)] (protected species in Hungary, conservation value/individual = 10 000 HUF ≈ 30 EUR; Decree No. 66/2015 of the Minister of Agriculture of Hungary, 2015) mayfly was described recently at the Zoltán Tildy Bridge overarching the Danube in Tahitótfalu (Northern Hungary) (Száz *et al*., 2015). Like other river-dwelling mayflies, *E. virgo* females collectively fly upstream after mating to compensate for the downstream drift of eggs and larvae. This is the so-called upstream-directed compensatory flight (Russev, 1973). Urban lights, particularly lamps on bridges, can attract enormous amounts of egg-carrying females (Fig. 1). This spectacular phenomenon may look beautiful for the human observer, but for these mayflies it means death without purpose. On the one hand, mayflies attracted by public lighting easily get exhausted around the lights. On the other hand, the illuminated asphalt surfaces also attract egg-laying *E. virgo* individuals because the road-reflected light is usually horizontally polarized just like the light reflected from the surface of natural water bodies (Száz *et al*., 2015). Finally, mayfly carcasses pile up with their eggs on the road and sidewalks. Such mass mortality of *E. virgo* has been observed throughout Europe on the rivers Rhine (Kureck, 1992), Main (Tobias, 1996), Kura (Kazanci & Türkmen, 2015) and Ebro (National Geographic, 2016), for example. Out of the total number of 95 mayfly species of Hungary (Kovács & Bauernfeind, 2003; Kovács, 2006a, 2006b, 2007a, 2007b), 11 are protected (Decree No. 66/2015 of the Minister of Agriculture of Hungary, 2015). Among the night-swarming species, *E. virgo* is the most conspicuous with its mass swarmings and besides being spectacular, this species is a good indicator of ecological quality of rivers (Kureck & Fontes, 1996).

Fig. 1. Mass swarming of *E. virgo* in 2012 at the bridge of Tahitótfalu (Northern Hungary) (photo: György Kriska). The inset shows a flying female *E. virgo* specimen (photo: Imre Potyó). [Color figure can be viewed at wileyonlinelibrary.com]

In an earlier study, we demonstrated that mayfly swarms can be prevented from perishing on the dry surface of a road when white beacon lights are attached to the bridge structure and are switched on during times when the bridge lights due to traffic safety reasons cannot be switched off (Egri *et al*., 2017a). The mayflies arriving at the bridge get attracted to these beacons instead of to the public lighting and they end up in the river with their eggs. Besides reducing the impact on the offspring, this method is also important from the aspect of traffic safety, because the bridges easily become slippery due to the thick layer of mayfly carcasses (Fremling, 1960; Száz *et al*., 2015).

The aim of our present study was to optimize the emission spectrum of the mayfly-protecting beacon lights by revealing the wavelength dependence of phototaxis in *E. virgo* and other night-swarming mayfly species. In addition, we estimated the attractiveness to *E. virgo* mayflies of typical light source types used in public lighting. Finally, as a practical application of our research, we report on the construction of the first, permanently installed and spectrally optimized mayfly protecting beacon system.

Materials and Methods

Behavioural field experiments with E. virgo

Attraction of *E. virgo* mayflies to light as a function of wavelength was studied in field experiments performed on 30 July 2018, 31 July 2018, 1 August 2019, 5 August 2019 and 8 August 2019 at the Slovakian-Hungarian border on a bridge overarching the river Ipoly near Salka (Slovakia, 47°53′10″N, 18°45′46″E). Seven custom-built LED light sources were built specifically for this project and used for quantifying the attraction of *E. virgo* to different light wavelengths (Fig. 2). Six were equipped with quasi-monochromatic LEDs covering the 378–744 nm spectral region and the last contained 3000K warm white LEDs. Peak wavelength and half bandwidth of the quasi-monochromatic LEDs were 378 nm (±8.6 nm) (UV), 432 nm (±9.1 nm) (blue), 513 nm (±16.5 nm) (green), 599 nm (±7.7 nm) (yellow), 659 nm (±8.7 nm) (red) and 744 nm (±10.5 nm) (IR). Each light source included 4 × 3 W power LEDs driven by the pulse width modulation (PWM) signal of an Arduino Nano development board (http://arduino.cc/en/Main/ArduinoBoardNano) with a frequency of $f_{PWM} \approx 980$ Hz. The structure and electronic circuit of the light sources are displayed in Fig. 2. The electronics were built into a wooden case, the LEDs were mounted on a heatsink at the centre of the case encompassed by a reflector made of aluminium foil, and finally a piece of sandblasted glass (110 mm × 110 mm × 5 mm) was used for covering the LEDs (Fig. 2). The photon flux of the lamps was calibrated with a radiometrically calibrated Ocean Optics STS-VIS spectrometer (Ocean Optics, Largo, FL, USA) and the duty cycle of the PWM signals was used for adjusting the photon flux of the lamps. Lamp photon fluxes were set to the same value of 5.09×10^9 photons/cm^2/s (±1.5%, measured from 1 m in the optical axis of the lamps) for all light sources except for the UV one because the UV LEDs were significantly dimmer than the others (Fig. 3). The photon flux of the UV light

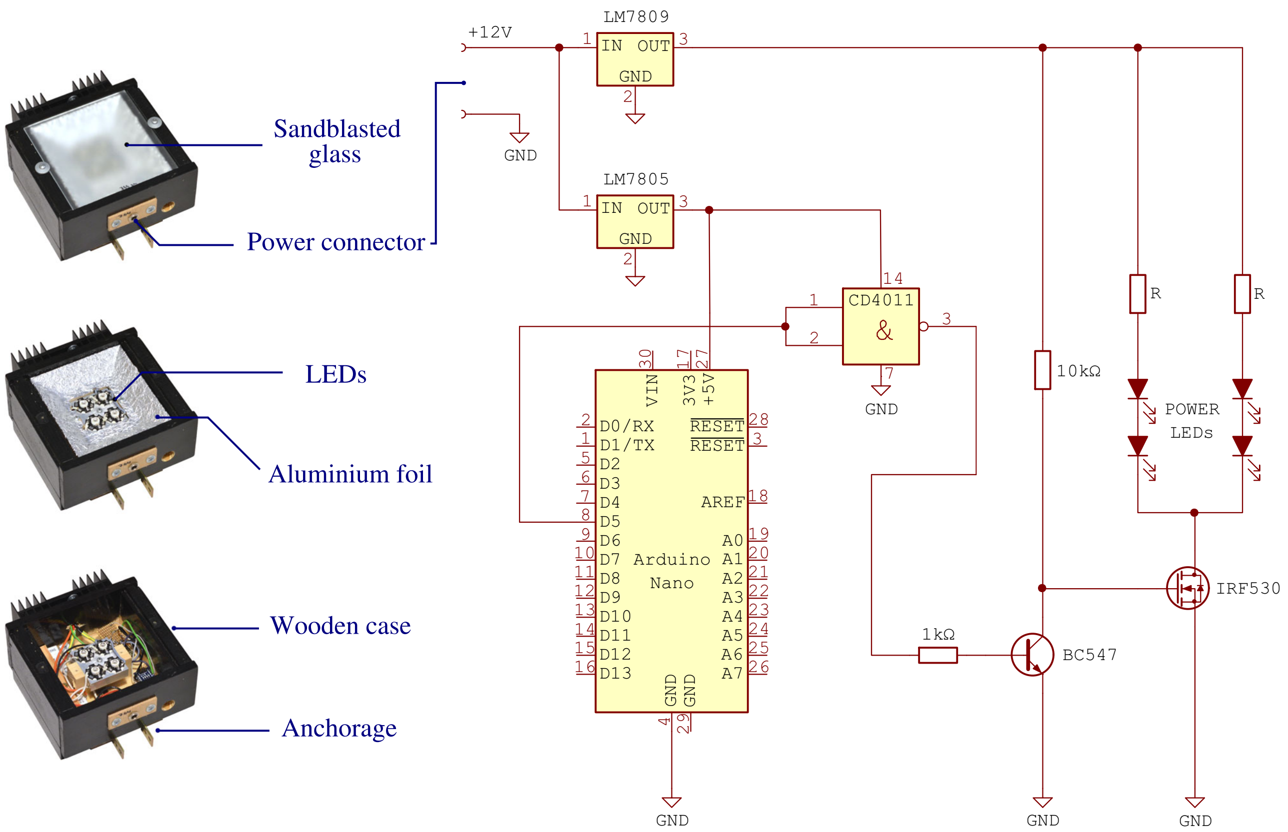

Fig. 2. Structure and electronic circuit of the custom-built light sources. Resistor value *R* was specifically chosen for a given light source, because LED forward voltage varies with LED type ($2.2\Omega \leq R \leq 9.4\ \Omega$). PWM duty cycles for different light sources were set with the analogWrite(5, *d*) function in Arduino IDE with the following 8-bit *d* values: $d_{white} = 65$, $d_{UV} = 255$, $d_{blue} = 73$, $d_{green} = 137$, $d_{yellow} = 255$, $d_{red} = 112$, $d_{IR} = 89$. [Color figure can be viewed at wileyonlinelibrary.com]

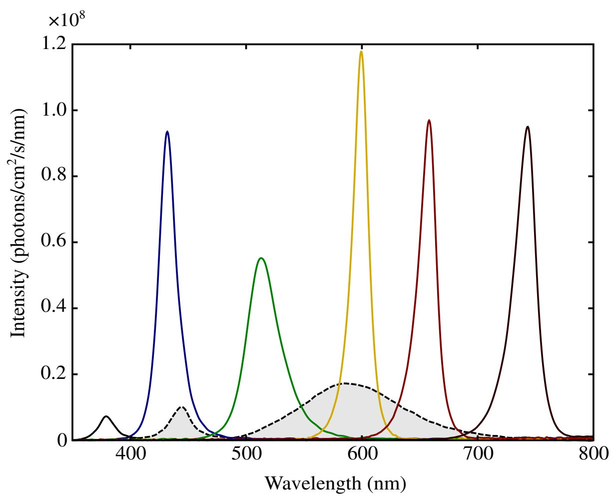

Fig. 3. F Emission spectra of the calibrated custom-built light sources measured from 1 m in the optical axis of the lamps (solid curves from left to right: UV, blue, green, yellow, red and IR; dashed curve: white) Total photon fluxes (area under the curves) are equal (±1.5%) except for the UV light source. [Color figure can be viewed at wileyonlinelibrary.com]

source was 10.2% of the photon flux of the other lamps. The producers and specifications of the LEDs were unknown but their appropriateness for our experiments was verified by the radiometric calibration (Fig. 3).

On each experimental day at around 20:00 (UTC + 2 h), the light sources were fixed 60 cm beneath the asphalt level by wood laths hooked on the bridge rail (Fig. 4). The lamps faced downstream and their arrangement was linear with 2.3 m gaps between them. This gap value was a compromise. Firstly, the lamps must have been spatially well separated to minimize the influence of the neighbouring lamps. On the other hand, the arrival of mayflies was expected mostly at the middle of the 20-m-wide river, thus the total size of the setup was limited. The arrangement of lamps was randomly chosen for each experimental day.

The compensatory swarm of *E. virgo* mayflies arrived in the darkness at around 21:00 (UTC + 2 h) and the swarming lasted 45–60 min. The arriving mayflies formed swarms in front of the light sources and these swarms were documented in photo groups by photographing them with flash one after the other, from above, with a Nikon D3200 camera equipped with a Nikon AF-S DX 18–55 mm f/3.5–5.6G VR objective (Nikon Corporation, Tokyo, Japan). Thus, to avoid the trapping of individuals of the protected *E. virgo*, swarms were only photographed and no specimens were collected. To facilitate further evaluation, the corresponding light source was intentionally included in the bottom of the photographs (Fig. 5a). Each photo group consisted of seven separate photographs of the mayfly swarms in front of each seven light sources taken with the same camera settings. Recording five consecutive photo groups resulted in an experimental replicate. For a given day the whole experiment consisted of five experimental replicates separated by 30-s-long lamp-off periods. The purpose of switching off the light sources was to release the previously accumulated mayflies and allow the initiation of a new experimental replicate. Taking into account all five experimental days, the total number of photos used for evaluation was 5 (days) × 5 (experimental replicates) × 5 (photo groups) × 7 (light sources) = 875.

Fig. 4. Linear arrangement of the seven downstream-facing light sources in the field experiments. The experimental site was located on the Slovakian-Hungarian border near Salka over river Ipoly. [Color figure can be viewed at wileyonlinelibrary.com]

Data evaluation

The numbers of mayflies in front of the different light sources were quantified with image processing of the photographs (Fig. 5). All seven images in a photo group were evaluated in parallel. In the photographs, the width of the light source w was determined in pixels and a cropping rectangle was defined in front of the light source with its shorter edge being parallel with the front side of the light source (Fig. 5a). The cropping rectangle was $2w$ wide, while its height varied between $3w$ and $5w$, but was constant within a photo group. The cropping rectangles were always large enough so that their interior was never saturated by 'mayfly-pixels'. Consequently, all seven rectangles in the photographs in a photo group represented a same sized area calibrated to the standard size of the light sources. The rectangular regions were cropped and converted to greyscale (Fig. 5b). The following step was to standardize the dark background intensity level, because it was not exactly the same value for all images. In the cropped greyscale image, the intensity level of

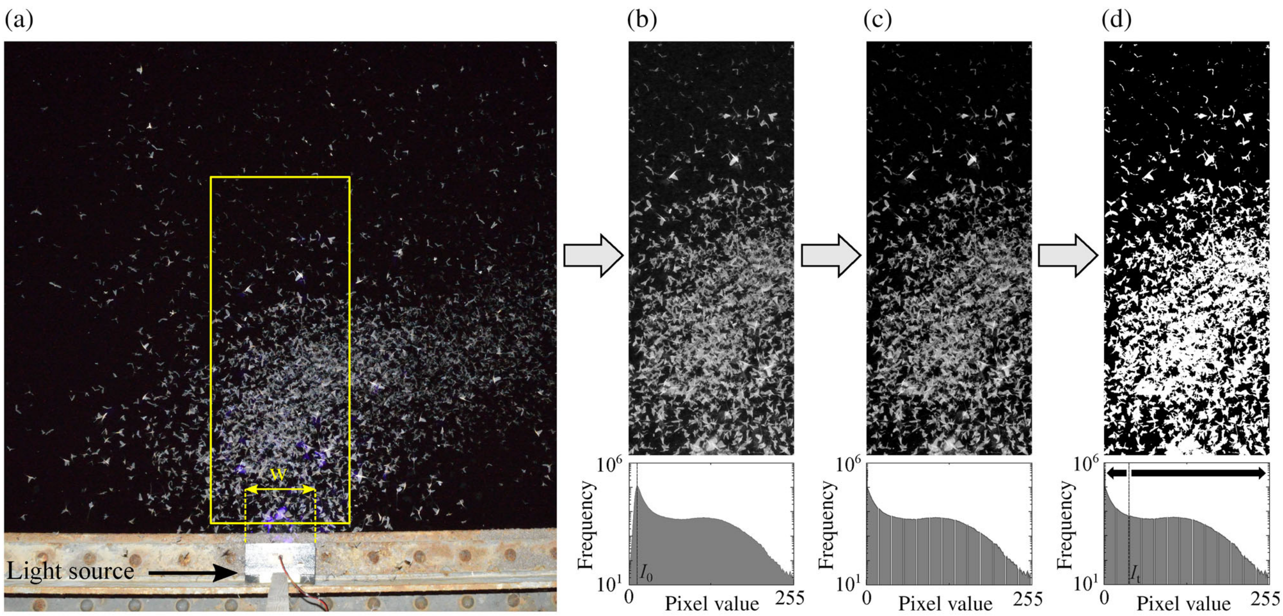

Fig. 5. Image processing for quantifying the attraction of *E. virgo* mayflies to the different light sources. (a) Example photograph of a mayfly swarm formed in front of the blue (432 nm) quasi-monochromatic light source. Yellow rectangle shows the sub-image that was used in further analysis. The apparent width w of the light source was used to standardize the size of the yellow cropping rectangle (width = 2 × w, height = 5 × w). (b) Cropped greyscale sub-image with its histogram. The most frequent intensity I_0 represents the dark background. (c) Sub-image after stretching the histogram between I_0 and 255 to the 0–255 range and assigning zero value to pixels being darker than I_0. (d) Thresholded image with threshold value of $I_t = 40$. [Color figure can be viewed at wileyonlinelibrary.com]

the dark background was obtained by calculating the most frequent pixel intensity value I_0 (intensity at the peak of the histogram). Pixels having intensity values below I_0 were set to zero, while the remaining pixels were adjusted in such a way that the histogram above intensity level I_0 was stretched to the full 0–255 intensity range (Fig. 5c). After this background standardization, the seven images were thresholded simultaneously with the same I_t value that was adjusted manually, making sure not to recognize background regions as mayflies, and vice versa. Pixels with values being less than I_t (dark pixels corresponding to background) were set to black, otherwise (bright pixels corresponding to *E. virgo* specimens) were set to white (Fig. 5d). Then the ratio of number of white pixels to the total number of pixels in the cropped image was calculated, and this procedure was performed for all seven light sources resulting in $A_i = N_{i,\text{white\_pixels}}/N_{i,\text{total\_pixels}}$ ($i = 1\ldots7$), where i refers to the type of the custom-built light sources (i = 1, white; i = 2, UV; i = 3, blue; i = 4, green; i = 5, yellow; i = 6, red; i = 7, IR). These seven numbers were normalized to a total sum of 1 yielding $a_i = A_i/\Sigma A_i (\Sigma a_i = 1)$. Thus, evaluation of one photo group resulted in these seven numbers (a_i) representing the mayfly attraction to our seven different light sources. All five photo groups in each experimental replicate were evaluated as described above and the normalized white pixel to total pixel ratios (five different a_i vectors) were averaged, which resulted in a single, normalized seven-element vector α_i ($i = 1\ldots7$, $\Sigma\alpha_i = 1$) containing quantified attraction of *E. virgo* mayflies to the different light sources for the given experimental replicate. As this calculation was performed for all 5 experimental replicates for all 5 experimental days, 25 different α_i vectors of normalized attraction ($i = 1\ldots7$) were obtained, each containing numbers proportional to the attraction to the 7 different light sources.

Estimating attractiveness of most commonly used light sources to E. virgo

For each experimental replicate, attraction of *E. virgo* to our different light sources was quantified and stored in the previously mentioned seven-element vector α_i, where i refers to the light source type (white, UV, blue, green, yellow, red, IR). Taking into account the equally bright and quasi-monochromatic light sources (blue, green, yellow, red, IR) and omitting the white (wide spectrum) and UV (intensity was 10.2% that of the other lamps) one, we obtain for each experimental day the attraction of *E. virgo* to light as a function of wavelength, that is, the action spectrum of phototaxis in arbitrary dimensionless units in the 432–744 nm range with the resolution of five points.

To estimate the attractiveness of light source types used most frequently in public lighting, we extracted the emission spectra of a 18 W low pressure sodium (LPS) lamp, a 150 W high pressure sodium (HPS) lamp and a 60 W metal halide (MH) lamp from Gaston *et al.* (2012), and extracted the emission spectra of a cool white LED (CW), a warm white LED (WW), a phosphor-converted amber LED (PCA) and a blue LED (B) from the catalogue of Cree® Xlamp® XP-E2 LEDs (Cree Inc., Durham, NC, USA, https://www.cree.com/led-components/media/documents/XLampXPE2.pdf). Although the blue LED is not a typical light source in urban lighting, its significance will be clear when we discuss the optimal emission spectrum for the mayfly protecting beacon lights. These spectra were originally given in power units or arbitrary units being proportional to power. Therefore they were converted to arbitrary units being proportional to photon numbers by multiplying the points of the spectra with the corresponding wavelength (Johnsen, 2012). As the action spectrum of phototaxis was available in the 432–744 nm range, this spectral region was cropped from the emission spectra of the typical light sources (LPS, HPS, MH, CW, WW, PCA, B) and the cropped spectra were normalized with their integral (area under curve = 1) (Fig. 6a–c). This normalization enabled us to consider these light sources being equally bright, that is, emitting the same amount of photons. Emission below 432 and above 744 nm was negligible for all light sources (Fig. 6a–c). Action spectra of phototaxis obtained from each experimental replicate (25 different α_i vectors, $i = 3\ldots7$) were linearly interpolated between the 5 measured points (Fig. 7). Finally, these 25 interpolated action spectra were multiplied with each lamp's spectrum (Fig. 6a–c) and the area under the resulting curves was used as a quantitative measure of estimated attraction of *E. virgo* to the given light source for a given action spectrum. In other words, the attraction was estimated by quantifying the similarity between a given action spectrum of phototaxis and the emission spectrum of the given light source type (LPS, HPS, MH, CW, WW, PCA and B). Since calculations were separately performed for action spectra obtained from all 25 experimental replicates, 25 different values of estimated attraction were calculated for each light sources type. These dimensionless numbers provided information about the relative attractiveness of the LPS, HPS, MH, CW, WW, PCA and B type light sources compared to each other.

Insect samplings with hand net

To collect data about the wavelength dependence of phototaxis in other night-swarming, non-protected mayfly species, we performed hand net samplings in front of the 7 above mentioned light sources from 20:15 to 21:00 (UTC + 2 h) on 31 July 2018, 27 August 2018, 1 August 2019, 5 August 2019 and 8 August 2019. Before the arrival of the first *E. virgo* mayflies, this period was dark enough to ensure the conspicuousness of the light sources. Sampling at a given lamp was performed by manually sweeping 20 times directly in front of the light source with an aquarium fish net (collecting area = 15 cm × 12 cm, mesh size = 0.2 mm). Samples were washed into 50% alcohol and finally, before proceeding to the next lamp, the net was shaken to spill out the incidentally remaining insects. Samples corresponding to a given lamp were pooled together. All light sources were sampled 7–8 times during the approximately 45-min-long period before the arrival of the *E. virgo* compensatory swarm, but the same amount of net sweeping was done at each lamp and the same person did all of the net samplings. Only mayflies were identified to species level, other insects were identified to order or family level. The primary goal of these hand net samplings was to compare the wavelength dependence of phototaxis of

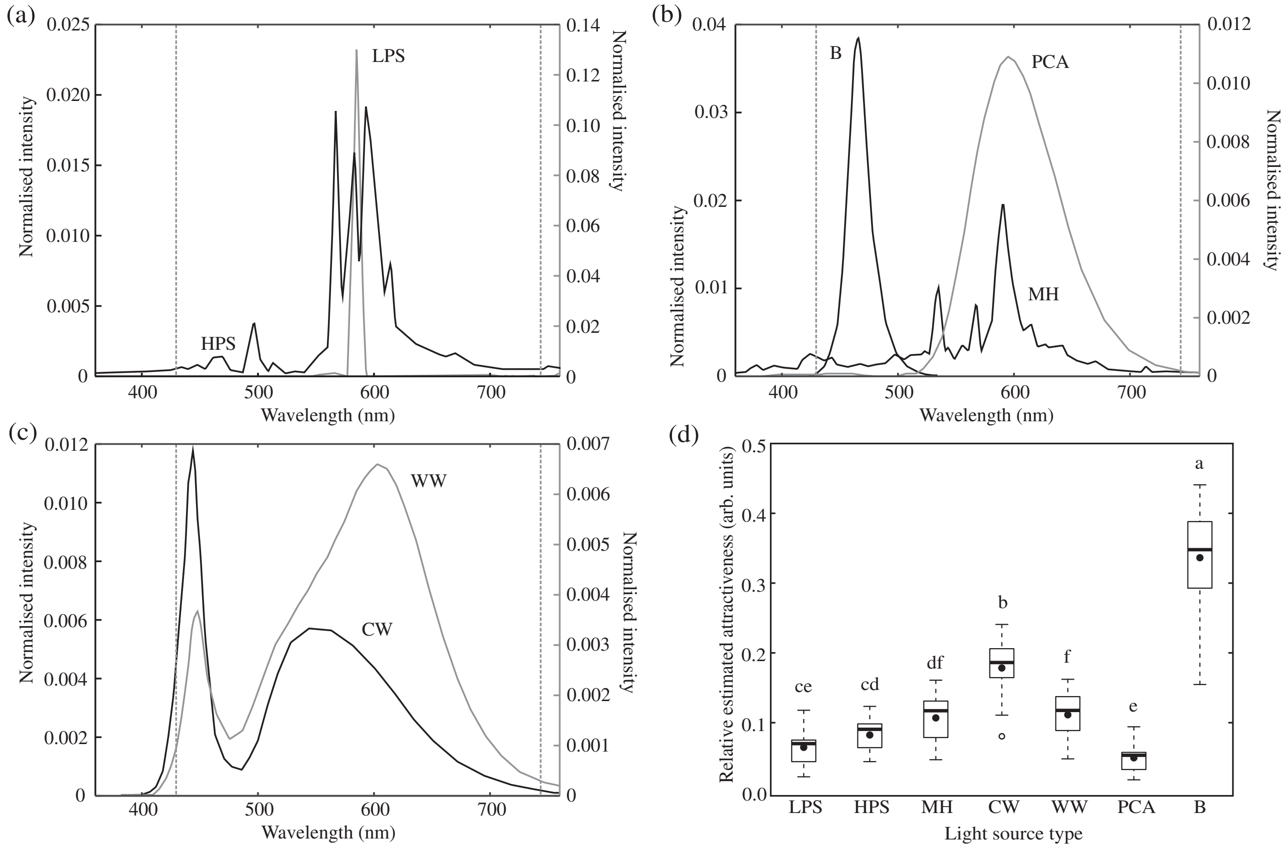

Fig. 6. Normalized emission spectra of light source types widely used in public lighting and estimated attraction of *E. virgo* mayflies to these lamp types. (a) Emission spectrum of a 18 W low pressure sodium (LPS) and a 150 W high pressure sodium lamp (HPS). Spectra are normalized with their integral in the 432–744 nm range, thus the area under each curve between the grey vertical dashed lines equals 1. (b) Normalized emission spectrum of a 60 W metal halide lamp (MH), a phosphor-converted amber (PCA) LED and a blue (B) LED. (c) Normalized emission spectrum of a cool white (CW) and a warm white (WW) LED. (d) Relative estimated attractiveness of the typical light source types to *E. virgo* mayflies. Each box in the boxplot represents 25 points that were calculated by multiplying the 25 action spectra of phototaxis in Fig. 7 with the corresponding emission spectrum (a, b, c) and calculating the integral of the resulting curves. Black dots denote means and groups with same lowercase letter do not significantly differ at $\alpha = 0.05$ significance level according to pairwise Wilcoxon rank-sum test.

E. virgo with that of other mayflies swarming in the same time period.

Statistics

To reveal differences between attractiveness of the equal-intensity light sources to *E. virgo* in the field experiments, a mixed effects model followed by Tukey's post-hoc test with Holm's correction was used. The UV data were intentionally left out from the analysis because of the reduced light intensity of the UV light source. Light source type was considered as a fixed factor, while experimental replicate was nested within day as a random factor. Differences between estimated attractiveness of the LPS, HPS, MH, CW, WW, PCA and B light source types to *E. virgo* were tested with multiple pairwise Wilcoxon signed-rank tests and multiple pairwise Wilcoxon sank-sum tests with Bonferroni *P*-value adjustment. Differences in insect catch numbers in samples collected with hand net in front of the equal-intensity light sources (white, blue, green, yellow, red, IR) were revealed with chi-squared goodness of fit test with the expectation that all light sources were equally attractive. Statistical analyses were made with the R statistical package v3.6.0 (R Core Team, 2019).

Results

Behavioural field experiments with E. virgo

Normalized attractiveness of our custom-built light sources to *E. virgo* in the field experiments is summarized in Fig. 7. The most attractive light source was unequivocally the blue one (432 nm) and attractiveness gradually decreased with increasing wavelength. Mean attractiveness of the green (513 nm), yellow

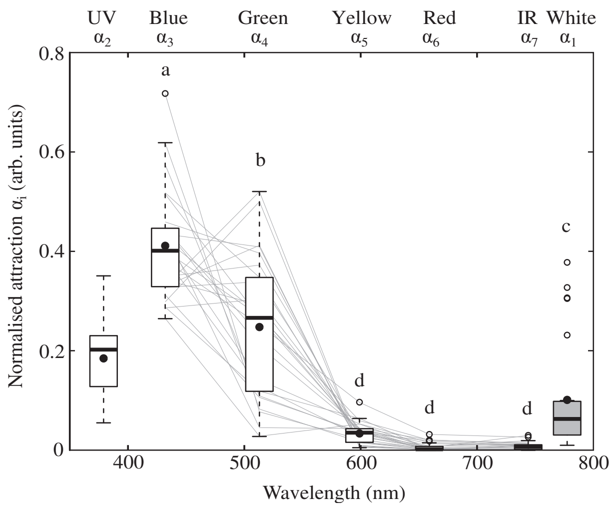

Fig. 7. Boxplot of normalized attraction of *E. virgo* mayflies to light as a function of wavelength/lamp type in the field experiments. The values corresponding to the white, UV, blue, green, yellow, red and IR light sources are, respectively, the α_1, α_2, α_3, α_4, α_5, α_6, α_7 values of all 25 α_i vectors of normalized attraction ($i = 1\ldots7$, $\Sigma\alpha_i = 1$ for all of the 25 cases). The white boxes show results for the quasi monochromatic light sources (UV, blue, green, yellow, red, IR) and the light grey box on the right shows attraction to the white light source. Light intensities apart from the UV light source were equal (Fig. 3). Black dots in boxes denote mean values for each light source. Groups with same lowercase letter do not significantly differ at $\alpha = 0.05$ significance level according to Tukey's post-hoc test. Grey lines in the 432–744 nm range show the 25 linearly interpolated action spectra corresponding to the 25 α_i vectors ($i = 3\ldots7$) obtained from the 25 separate experimental replicates.

(599 nm), red (659 nm), IR (744 nm) and white light sources to *E. virgo* were 60.4%, 8.4%, 1.7%, 2.0% and 24.8% that of the blue light source. Comparison of the attractiveness of the blue light source with that of each of the other equally bright light sources resulted in highly significant differences ($P < 0.0001$). This statement was also true for the green light source. Thus attractiveness of the green lamp was significantly lower than that of the blue one ($P < 0.0001$). The yellow, red and IR light sources elicited statistically similar attraction ($P > 0.7$). Finally, the attractiveness of the yellow and white light sources differed significantly ($P = 0.024$). Mean attractiveness of the UV (378 nm) light source was 18.6% that of the blue light source, but the UV data were excluded from statistical comparisons because in terms of photon number it was one tenth as bright as the other light sources (Fig. 3). Nevertheless, as shown in Fig. 7, the attractiveness of the UV and green light sources to *E. virgo* were qualitatively similar. This may be the indication of high attraction to UV, even higher than attraction to blue. Attractiveness of the white light source, which is shown with grey box on the right side of Fig. 7, was between the attractiveness of the UV and yellow light sources. Grey lines in the 432–744 nm range indicate the 25 linearly interpolated action spectra corresponding to the 25 α_i vectors ($i = 3\ldots7$) obtained from separate experimental replicates.

Estimating attractiveness of most commonly used light sources to E. virgo

Relative estimated attractiveness of LPS, HPS, MH, CW, WW, PCA and B type light sources are displayed in Fig. 6d. Each box in the boxplot represents 25 points, since all 25 separately obtained action spectra of phototaxis (α_i, $i = 3\ldots7$) (Fig. 7) were separately used to calculate an estimated attraction for a given light source type (Fig. 6a–c). These relative estimated attraction values to the different light sources are in arbitrary units, and have meaning only together, but they are very informative and give prediction about attractiveness of the seven light source types (Fig. 6a–c) relative to each other. The mean estimated attractiveness of the LPS, HPS, MH, CW, WW, PCA and B light sources were, respectively, 0.069, 0.087, 0.111, 0.183, 0.116, 0.055 and 0.339 in arbitrary units. Since the same 25 action spectra of phototaxis were used for estimating the attractiveness for all 7 lamp types (Fig. 6a–c), the data are not independent. Therefore, at first, Wilcoxon signed-rank test was performed, which resulted in very high significances ($P < 0.0001$) between all pairs of the seven light source types (Fig. 6a–c). This means that independent of the action spectrum of phototaxis chosen for the calculations, the estimated attractiveness of the different typical light source types relative to each other are very similar. On the other hand, to reveal statistically significant differences in attraction of *E. virgo* that would occur in a real-life situation to these light sources, the pairwise Wilcoxon rank-sum test was applied. Statistically significant differences and similarities between estimated attraction of light source types are displayed by letters in Fig 6d. The blue LED (B) was obviously the most attractive possessing 1.85 times higher attractiveness than the CW LED, which was a significant difference ($P < 0.0001$). The estimated attractiveness of the WW LED and the MH lamp was statistically similar ($P = 1$), but significantly lower than that of the CW LED ($P < 0.0001$). The estimated attractiveness of B and CW LEDs was significantly 2.93 ($P < 0.0001$) and 1.58 ($P < 0.0001$) times higher than that of the WW LED, respectively. Estimated values of attractiveness for the LPS and HPS lamps were statistically similar ($P = 0.083$), as well as for the HPS and MH lamps ($P = 0.116$). Attractiveness of the CW LED was 2.63, 2.10 and 1.64 times higher than that of the LPS, HPS and MH lamps, respectively ($P < 0.0001$ for all three cases). The least attractive light source type was the PCA LED showing statistical similarity only with the LPS lamp ($P = 0.09$). It is clear from Fig. 6, that light sources with emission spectra being rich in short-wavelength components are predictably more attractive to *E. virgo* than light sources with emission spectra dominated by longer wavelengths.

Insect samplings with hand net

The numbers of insects caught during hand net samplings in front of our custom-built light sources are shown in Table 1. Rows represent different taxa and columns correspond to the light sources. Numbers are total catch numbers for the 5 sampling days. Only one mayfly species, *Caenis macrura* (Stephens, 1836) was caught (2664 individuals). The total numbers of

  doi: 10.1111/icad.12446

Table 1. Total number of insects caught by hand net samplings in front of the light sources. Intensity of the UV light source was 10.2% that of the other lamps. Collection of individuals of the protected *E. virgo* was intentionally avoided in these samplings.

	White (3000 K)	UV (378 nm)	Blue (432 nm)	Green (513 nm)	Yellow (599 nm)	Red (659 nm)	IR (744 nm)	Total
Caenis macrura	215	850	1325	261	6	2	5	2664
Chironomidae	406	338	2347	4160	201	14	13	7479
Other Diptera	4	38	75	89	1	2	3	212
Coleoptera	0	19	10	3	0	1	0	33
Auchenorrhyncha	1	13	9	5	1	0	0	29
Heteroptera	1	0	1	1	0	0	0	3
Trichoptera	2	112	28	3	0	0	0	145

trapped *C. macrura* in front of the white, UV, blue, green, yellow, red and IR light sources were 251, 850, 1325, 261, 6, 2 and 5, respectively. According to chi-squared goodness of fit test, these catch numbers show significant inhomogeneity (χ^2 = 4371.3, d.f. = 5, $P < 0.0001$). It is clear from Table 1 that attraction of *C. macrura* to the light sources was qualitatively similar to the attraction of *E. virgo* (Fig. 7). High numbers of individuals were also caught among the order diptera, where chironomids dominated (7479 individuals). Attractiveness of our equal-intensity light sources to diptera also depended on lamp type (chironomids: χ^2 = 12201, d.f. = 5, $P < 0.0001$; other diptera: χ^2 = 294.14, d.f. = 5, $P < 0.0001$). In general, the attraction of diptera to light was highest in the green spectral region. A total number of 145 Trichoptera individuals were also trapped, most of them at the UV light source. Statistical tests were performed only for *C. macrura* and diptera (chironomids + other diptera) being the dominant taxa in the samples.

Discussion

Our results show that attraction of *E. virgo* mayflies to light in the 432–744 nm spectral range was highest for the shortest wavelengths (Fig. 7). Although the highest attraction was elicited by the 432 nm blue light source, it is more than likely that the 378 nm UV light source would have attracted more mayflies if it had the same light intensity as the other light sources used in our experiments. This concept is strongly supported by the fact that compound eyes of certain *Ephemera* mayflies are maximally sensitive to UV (Meyer-Rochow, 1982). According to Table 1, this result might be extended to other night-swarming mayflies. As Fig. 6d shows, estimated attraction of *E. virgo* to the different light source types strongly depend on the spectral composition of the given light source. Lamps emitting high amounts of short wavelength light, like cool white and blue LEDs, are significantly more attractive to *E. virgo* than light sources emitting primarily in the longer wavelength ranges, for example, LPS, HPS and PCA LEDs (Fig. 6). This tendency of insect attraction to light as a function of spectral composition has also been reported by other researchers (Pawson *et al*., 2014; Longcore *et al*., 2018).

Controlling the light intensity of LEDs during the field experiments with pulse width modulation implies flickering, but in the case of our custom-built light sources the PWM frequency was $f_{\mathrm{PWM}} \approx 980$ Hz, which is much higher than the maximal insect flicker fusion frequency (FFF) of 300 Hz (Shields, 1989). Such fast-eyed insects are diurnal, while nocturnal species possess remarkably lower FFF (Inger *et al*., 2014). This suggests that the temporal resolution of the eye of the night-swarming *E. virgo* is also lower and they sensed no flickering during our experiments, although FFF of any mayflies has not been measured yet, as far as we know. Accordingly, effects of light flickering on mayfly phototaxis when flicker frequency is low enough to be visible for mayflies is still an interesting field to study.

A special form of ecological light pollution is polarized light pollution, which occurs when the behavioural patterns of polarization-sensitive animals become altered due to the highly polarized light reflected from artificial surfaces (Horváth *et al*., 2009). Typical victims of polarized light pollution are polarotactic aquatic insects, because they optically locate water bodies by means of the horizontal polarization of water-reflected light (Schwind, 1989). Sources of polarized light pollution are usually shiny and dark surfaces, for example asphalt roads, solar panels, dark plastic surfaces and crude oil lakes (Horváth *et al*., 2009). Like other polarotactic aquatic insects, *E. virgo* also possesses positive polarotaxis which facilitates the following of the river's track during the upstream-directed compensatory flight (Száz *et al*., 2015; Farkas *et al*., 2016). According to Száz *et al*. (2015), *E. virgo* mayflies were not only attracted to the lamps on the bridge of Tahitótfalu (Northern Hungary), but oviposition also occurred on the asphalt of the bridge and the nearby road, which was optically similar to water and reflected horizontally polarized light. Another situation, where mayflies were deceived because of the presence of a bridge, has been reported by Egri *et al*. (2017b). They showed that the creek-dwelling *Ephemera danica* (Müller, 1764) mayflies became deflected at bridges, and they continued their upstream-directed compensatory flight along the asphalt road instead of the creek. To mention another example of deceived mayflies, the compensatory flight of the protected *Palingenia longicauda* (Olivier, 1971) was also interrupted by a bridge overarching the river Tisza (Málnás *et al*., 2011). These two mayfly species typically swarm in daylight, hence night-time lighting does not affect them. Nevertheless, night-swarming mayflies like *E. virgo* must deal with the challenges of illuminated bridges.

The main message of our paper is included in Fig. 6d. In habitats of *E. virgo* and other night-swarming mayflies, for public lighting, the use of CW LEDs should be avoided and PCA LEDs should be used, but the attractiveness of HPS lamps, LPS lamps and WW LEDs are also significantly lower than those of CW LEDs. From the aspect of ecological impact, the similarity of

Fig. 8. Zoltán Tildy Bridge in Tahitótfalu (Northern Hungary) after sunset with the blue mayfly protecting beacon lights permanently installed on the bridge piers (photo: György Kriska). The beacons are equipped with a dusk sensor relay switch and a timer allowing automatic operation restricted to the swarming hours of *E. virgo*. [Color figure can be viewed at wileyonlinelibrary.com]

HPS lamps and PCA LEDs has been reported by Schulte-Römer *et al*. (2019), but the colour rendering of PCA LEDs is better (Aubé & Simoneau, 2018). Longcore *et al.* (2015) also suggested that shifting the emission spectrum towards longer wavelengths results in ecologically more friendly illumination and the use of PCA LEDs has already been successfully tested in protected areas (Maierova, 2018). As another example for reducing light pollution by changing the spectral composition of illumination, the lights of the entire village of Bárdudvarnok (Hungary) has been replaced with PCA LEDs (Kolláth *et al*., 2019). One of the most striking elements of Fig. 6d is the apparently high attractiveness of blue LEDs to *E. virgo*. This suggests that a spectrally optimized mayfly protecting beacon should emit light dominantly in this spectral range. Ultraviolet light would also be effective for keeping mayfly swarms above the water, but the use of UV is hazardous due to public-health-related risk factors (Roberts, 2011).

Our findings about the spectral sensitivity of *E. virgo* presented in this paper have been put into practice in 2019. Cooperation between the Hungarian Public Road nonprofit PLC, the Centre for Ecological Research of the Hungarian Academy of Sciences, the Tahitótfalu Town Council (Northern Hungary) and the Budapest Electricity PLC resulted in the permanent installation of two mayfly protecting beacons (produced by MES-TECH Ltd., Budapest, Hungary) on the Zoltán Tildy Bridge in Tahitótfalu (Fig. 8). Each beacon is a 90 W LED light source composed of blue LEDs (Fig. 8, see normalized emission spectrum in Fig. 6b). After manually enabling the system when the first mayflies of the year appear, on each evening, the beacons are automatically switched on by a dusk sensor relay switch approximately at sunset and after 3 h of operation, a timer deactivates the beacons. According to our former observations (Száz *et al*., 2015; Egri *et al*., 2017a), swarming of *E. virgo* falls within this time window with a high degree of certainty, hence the operation of the beacons are restricted to the swarming hours and the incidental negative impact of the beacons on the environment is minimized. This is a very important issue, because effects of blue lighting at night are not only wildlife-related (Longcore *et al*., 2018; Schulte-Römer *et al*., 2019), but humans can also be affected (West *et al*., 2011; Schulte-Römer *et al*., 2019). Nevertheless, in our case, urbanized areas are separated by a dense line of trees from the beacon-lit section of the river. The public lighting on the bridge consists of 5 pieces of 85 W dimmable 3000K warm white LED lamps (Fig. 8). Every year, on each evening, between 15 August and 15 September, their light intensity is automatically reduced by 30% for the first 3 h of operation to enhance the effectiveness and conspicuousness of the beacons.

According to information at hand, the results of our experiments led to the construction of the very first beacon system for keeping mayfly swarms above the water. Quantitatively testing the effectiveness and possible impact of the beacons in connection with mayflies and other aquatic organisms should be a subject of future investigations.

Acknowledgements

Project no. 131738 has been implemented with the support provided from the National Research, Development and Innovation Fund of Hungary, financed under the PD_19 funding scheme. The work was also supported by the Hungarian Economic Development and Innovation Operational Programme (GINOP-2.3.2-15-2016-00057). Á. Egri was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. Á. Mészáros was supported by the ÚNKP-19-3 New National Excellence Program of the Ministry for Innovation and Technology. We are grateful to Alexandra Farkas and Dénes Száz for their assistance in the field works. We thank Alexandra Farkas for obtaining financial resources for the permanent beacon system in Tahitótfalu. This work was supported by the Scholarship for the Young Talents of the Nation (NTP-NFTÖ-18-B-0074) of the Ministry of Human Capacities received by Alexandra Farkas.

Conflict of Interest

The authors declared no competing or financial interests.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Accepted 24 August 2020

Editor: Alan Stewart; Associate Editor: Christopher Hassall