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The color of artificial light affects mate attraction in the common glow-worm

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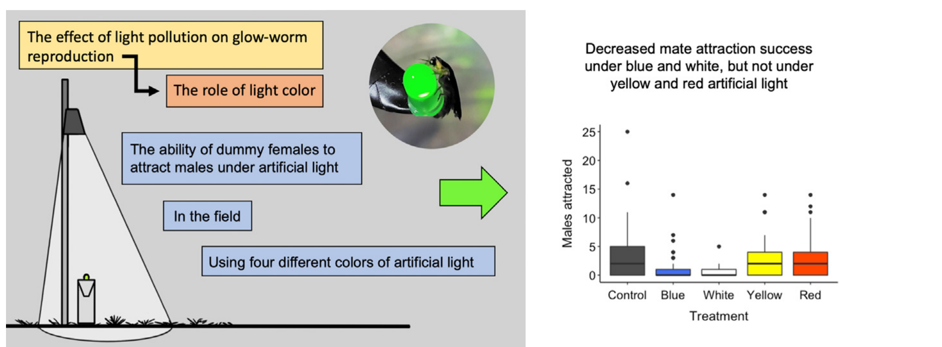
HIGHLIGHTS

- Light pollution is an emerging environmental threat to nocturnal organisms.
- Glow-worms are dependent on darkness for mate finding.
- Dummy female glow-worms were exposed to four colors of light in the field.
- Long wavelength artificial light was less detrimental to mate attraction success.
- Spectral tuning of outdoor lighting is a potential mitigation measure.

GRAPHICAL ABSTRACT



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ABSTRACT

Artificial light at night, often referred to as 'light pollution', is a global environmental problem that threatens many nocturnal organisms. One such species is the European common glow-worm (*Lampyris noctiluca*), in which reproduction relies on the ability of sedentary bioluminescent females to attract flying males to mate. Previous studies show that broad-spectrum white artificial light interferes with mate attraction in this beetle. However, much less is known about wavelength-specific effects. In this study, we experimentally investigate how the peak wavelength (color) of artificial light affects glow-worm mate attraction success in the field by using dummy females that trap males landing to mate. Each dummy was illuminated from above by either a blue (peak wavelength: 452 nm), white (449 nm), yellow (575 nm), or red (625 nm) LED lighting, or light switched off in the control. We estimated mate attraction success as both the probability of attracting at least one male and the number of males attracted. In both cases, mate attraction success depended on the peak wavelength of the artificial light, with short wavelengths (blue and white) decreasing it more than long wavelengths (yellow and red). Hence, adjusting the spectrum of artificial light can be an effective measure for mitigating the negative effects of light pollution on glow-worm reproduction.

1. Introduction

Light pollution, or artificial light at night (ALAN) (Davies and Smyth, 2017), is a potentially severe anthropogenic environmental challenge. Since electric lighting became common in the early 20th century, nighttime environments have become increasingly more illuminated by artificial light, with light pollution continuing to be a rapidly growing problem (estimated global increase of 6 % per year (Hölker et al., 2010b)). Currently, light pollution is estimated to affect 49.5 % of the land surface area between 59°N and 55°S (Gaston et al., 2021). Natural dark-light cycles have, in the time scale of evolution, remained consistent, and therefore their disturbances can have various ecological consequences (Longcore and Rich, 2004; Gaston et al., 2015a; Davies and Smyth, 2017). A wide diversity of organisms, from plants to both terrestrial and aquatic vertebrates and invertebrates, have been impacted, with the effects ranging

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from changes in individual physiology and behavior to those in population ecology and community structure (Gaston and Bennie, 2014; Davies and Smyth, 2017). Nocturnal species, which constitute an estimated 30 % of all vertebrates and 60 % of all invertebrates, are particularly vulnerable to artificial light (Hölker et al., 2010a). Indeed, light pollution has been proposed as a major driver of global insect declines (Owens et al., 2020).

Light pollution may affect behavior by interfering with, for instance, foraging, reproduction, migration, or communication (Longcore and Rich, 2004). For example, positively phototactic insects, such as many moths, are attracted to artificial light sources. This response disrupts their normal behavioral patterns, sometimes with fatal consequences (Boyes et al., 2021). Artificial light at night may also obscure the light from natural light sources, disorienting species that navigate by the moon and stars. Similarly, it can disturb communication in bioluminescent species, such as glow-worms and other fireflies (Owens and Lewis, 2018).

Due to the negative effects of light pollution highlighted by recent research, there is an urgent need for effective mitigation measures. Here, new technologies offer promising opportunities, for example by controlling the artificial light spectrum and intensity with Light Emitting Diode (LED) based lighting infrastructure (Gaston et al., 2015a; Davies and Smyth, 2017). However, increased efficiency and lowered costs of light sources can also result in increased light use (Hölker et al., 2010b). Furthermore, the ecological consequences of the changing spectral landscape of artificial light resulting from the application of these new technologies (Gaston et al., 2015a; Pagden et al., 2020) are poorly known. Given the global increase in light pollution, a better understanding of the ecological impacts of different types (e.g. spectral composition) of artificial light is required, especially for the needs of policy development and strategic planning of lighting systems (Hölker et al., 2010a; Gaston et al., 2015b).

Glow-worms and other fireflies (Lampyridae), which use bioluminescent signals to attract mates, are especially vulnerable to light pollution. Broad spectrum white artificial light has been shown to affect both glow behavior and mate attraction success of female common glow-worms (*Lampyris noctiluca*). For example, females exposed to artificial light glow less and attract fewer males (Bird and Parker, 2014; Elgert et al., 2020a; Stewart et al., 2020; Van den Broeck et al., 2021a). The impact of artificial light on mate attraction increases with light quantity (i.e. intensity) (Elgert et al., 2020b; Van den Broeck et al., 2021a), but we still know little about the influence of light quality (e.g. spectrum). Such knowledge is essential, because the effects of artificial light on glow-worm reproduction and, in the long term, even population viability, may vary depending on the type of light, especially its spectral composition. The use of new technologies should allow adjustment of e.g., public artificial lights accordingly.

In the current study, we investigated the effects of artificial light wavelength spectrum (i.e. color) on mate attraction success in the common glow-worm. In particular, we assessed mate attraction success both in terms of the proportion of successful female dummies and the number of mates they attracted and, based on previous findings, expected that the success is lower under exposure to artificial light than in natural darkness (Ineichen and Rüttimann, 2012; Bird and Parker, 2014; Elgert et al., 2020a; Van den Broeck et al., 2021b). Furthermore, we predicted that mate attraction success is related to the spectrum of artificial light, with light characterized by short wavelengths (white and blue) having a larger impact than long wavelengths (yellow and red). This prediction was based on the previous observations that a light signal is less attractive to males when a blue component is added to it, whereas the addition of a red light component does not have an adverse effect (Booth et al., 2004). In addition, white artificial light has generally been considered more adverse to a range of animals than yellow light (Gaston et al., 2012; Longcore et al., 2018).

2. Materials and methods

2.1. Study species and area

In the common glow-worm, sedentary and larviform females attract flying males by emitting a constant greenish glow at night (Lewis, 2016). The brightness of the glow correlates with female body size, which, in turn, correlates with fecundity (i.e. the number of eggs the female produces) (Hopkins et al., 2015, 2021). Furthermore, brighter females tend to be more successful in attracting males (Hopkins et al., 2015; Elgert et al., 2020b; Lehtonen and Kaitala, 2020). The glow-worm is a capital breeder, with a typical adult lifespan of less than two weeks and females dying after having mated and laid their eggs (Lewis, 2016). Population surveys indicate that glow-worm populations have declined at least locally in the UK and probably also elsewhere (Gardiner, 2009; Gardiner and Didham, 2020). The reasons for the declines are likely to include climate change, habitat fragmentation, and urbanization, including light pollution (Gardiner and Didham, 2020, 2021; Lewis et al., 2020; Lehtonen et al., 2021).

All work was conducted in Southern Finland in the proximity of Tvärminne Zoological Station (N 59°51′, E 23°14′), during the glow-worm breeding season, between 12th June and 4th July in 2020. This period was chosen based on earlier observations of glow-worm reproduction in the same area (e.g. Elgert et al., 2020a; Lehtonen and Kaitala, 2020). The experiment was run only on nights of good weather ($N = 20$ nights), because poor weather conditions (low temperatures, wind and rain) restrict male activity (Dreisig, 1971).

2.2. Experimental setup

We used dummy females (LED lures) that trapped males landing to mate. These were identical to those used in multiple recent studies (Elgert et al., 2020a, 2020b; Lehtonen and Kaitala, 2020), except for the brightness of the LED. In particular, the dummies were equipped with a green 5 mm LED that mimicked the glow of a female. The LED was attached to a halved 1.5 L bottle of transparent, non-glossy plastic, with the top half inserted upside down to form a funnel trap (Fig. 1). The green LED was powered by two AA batteries and wired with resistors (2000 Ω) to adjust the intensity to 0.065–0.075 $\mu Wnm-1$ (microwatts per nanometer), as measured with a spectrophotometer and integrating sphere (Borshagovski et al., 2020). Its peak wavelength was 562 nm, which matches the glow of female glow-worms (550–570 nm) (Schwalb, 1961; De Cock, 2004).

Each dummy female was lit from above by an artificial light that simulated a light source, such as a streetlamp or yard light. The artificial light sources were composed of white LEDs covered with EUROLITE color-foil to alter their light spectra (Table 1). We had five treatments: blue, white, yellow, and red artificial light, and a control (the LED switched off). The

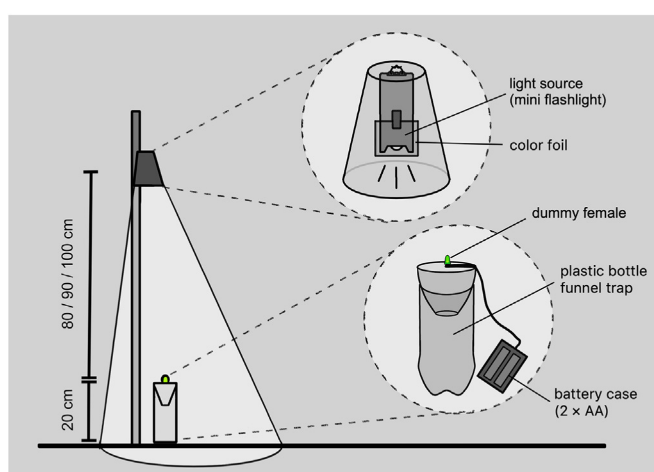

Fig. 1. The experimental setup for investigating the impact of color on mate attraction. A dummy female was placed under either a red, white, yellow, or blue artificial light source. In the control the light was turned off. The height at which the light was attached was customized for each treatment to even out differences in intensity caused by the color-altering foils.

Table 1
Light treatment details. Light intensities were measured at the vertical level of the dummy female.

Color	Filter	Peak wavelength (nm)	Intensity	
			Photons/cm^2/s	Lux
Blue	Color-foil 165 "Daylight blue"	452	$6.45 * 10^{12}$	5.0
White	Diffusion filter 129 "Heavy frost"	449	$5.27 * 10^{12}$	5.6
Yellow	Color-foil 104 "Deep amber"	575	$4.21 * 10^{12}$	6.0
Red	Color-foil 164 "Flame red"	625	$1.27 * 10^{13}$	8.0
Control	None	None	0	0

light source in the blue, white, and yellow light treatments consisted of a Fenix UC01 mini flashlight at medium output. Due to the stronger absorption (i.e. a dimming effect) of the red color foil, the red light source needed to be more powerful to reach a similar intensity of light as that of the other treatments. Therefore, we used a VARTA Indestructible LED x5 headlamp at half output.

We used opaque lampshades (made of plastic cups) to prevent the source of artificial light from being directly visible from the outside, and to direct its cone downwards. Each light source was attached to a pole at 100–120 cm above the ground level, i.e. 80–100 cm above the LED lure. To calibrate the light intensities and counter variation in the color foils' absorption, the light sources were attached at the following heights above the ground: 100 cm (blue), 110 cm (yellow), 120 cm (white), and 120 cm (red) (Fig. 1). We measured the resulting intensity and peak wavelength of the artificial light in each treatment with a spectrophotometer and cosine corrector (Borshagovski et al., 2020) in an otherwise dark room to acquire precise values in the absence of external disturbances (Table 1). These intensities were comparable to the lower range of intensities of artificial lights we measured in the area (but not closer than 50 m from any of the replicates of this study) (Table S1). The spectrophotometer measurements were taken at 20 cm above the ground level, corresponding to the position of the dummy females (in relation to the ground) in the experiment. Such a position is ecologically relevant, with females often perching on vegetation above the ground level (Tyler, 2002).

The dummy females and artificial lights were placed along a 1 km stretch of an unlit, forested road to Tvärminne Zoological Station, at 15 separate sites where glow-worms had been observed in previous years, with the distance between adjacent sites at least 40 m. We randomized which treatment was conducted at a specific site each night. We ran 3 replicates of each of the 5 treatments per night. Over the course of the experiment, we completed 4 replicates of each treatment at each of the 15 sites. This resulted in 60 replicates per treatment (over 20 nights), except for the yellow treatment, in which one replicate was discarded due to battery failure.

We activated the artificial lights and dummy females each night between 23:45 and 00:15 and turned them off between 01:45 and 02:15. We turned off the lights in the same order as we had turned them on, with each light and dummy female being active for two hours. We then inspected the dummy females for any male glow-worms that they had attracted and trapped, which were counted and placed into plastic vials. We kept the males indoors until the following morning. Males were then marked with a small dot of acrylic paint on their pronotum (first exoskeletal shield) and released. The markings allowed us to identify recaptured males. To ensure the independence of data points, recaptured males were not included in the data analyses (detailed below).

2.3. Statistical analysis

All statistical analyses were performed using R v. 4.2.0. (R Core Team, 2022) and RStudio v. 2022.02.3. (RStudio Team, 2022) for macOS. We investigated the effect of the artificial light treatments (blue, white, yellow, red, dark control) on mate attraction success (see below) by using a generalized linear mixed model (GLMM) with a negative binomial distribution (R package *lme4* v. 1.1.29.; Bates et al., 2015), as appropriate for overdispersed count data (Zuur et al., 2013). The number of males attracted into each trap was denoted as a count response variable and the treatment (color of artificial light) as a categorical explanatory variable. To account for the effects of the night and site of each replicate, they were included as random effects. The model was selected based on Akaike information criteria (AIC, Akaike, 1973). The goodness of fit of the model was checked using the R package DHARMa v. 0.4.5. (Hartig, 2022).

As we cannot rule out the possibility that the presence of a male in a trap gives odor cues that might attract other males, or that males move in swarms, we also analyzed the data using male presence/absence data. Here, we used a binomial GLMM (suitable for binary data), with whether the dummy female attracted at least one male as a binary response variable (0/1), the artificial light treatment as an explanatory variable, and each replicate's night and site as random effects.

3. Results

The dummy females attracted a total of 624 male glow-worms during the experiment. Dummy females in the blue and white light treatments attracted significantly fewer males than dummy females in the yellow, red and control treatments (Fig. 2, Table 2). The yellow and red light treatments did not significantly differ from the control treatment and the white and blue treatments did not significantly differ from each other (Fig. 2, Table 2). The median number of males attracted was two in the control, yellow and red light treatments, and zero in the blue and white light treatments (Fig. 2).

Over the whole experiment, 56.9 % (170/299) of the dummy females attracted at least one male. A significantly lower portion of dummies attracted at least one male in the blue and white light than in the yellow and red light treatments, and in the control (Tables 3 and 4). The proportion of attracted males did not significantly differ between the yellow, red, and control light treatments (Tables 3 and 4) or between the blue and white light treatments (Tables 3 and 4). Thus, results from the two analyses were qualitatively the same.

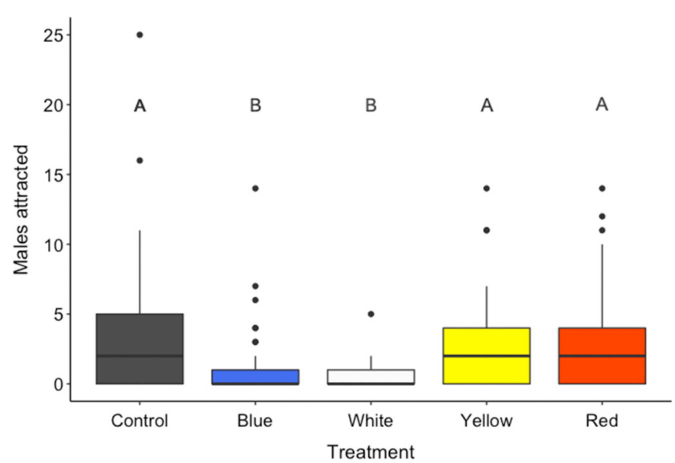

Fig. 2. Number of males attracted by imitation females in the unlit control, and in the blue, white, yellow, and red, artificial light treatments. The box plots show median values (horizontal black lines), interquartile ranges (colored boxes), upper quartiles (whiskers), and extreme values (black dots). Whiskers representing the lower quartiles are not visible, because in all treatments at least 25 % of the imitation females attracted zero males. Treatments with a different letter A-B were significantly different from each other (negative binomial GLMM). N = 60 in all treatments except N = 59 in the yellow light treatment.

Table 2
Estimates, z-values and p-values of pairwise treatment comparisons of numbers of attracted males using a negative binomial GLMM, with replicate night and site included as random factors.

Pairwise comparisons of numbers of attracted males			
Treatment	Estimate	Z	P
Blue vs control	−1.372	−6.601	<0.001
White vs control	−1.891	−7.735	<0.001
Yellow vs control	−0.203	−1.157	0.247
Red vs control	−0.049	−0.287	0.774
White vs blue	−0.519	−1.905	0.057
Yellow vs blue	1.168	5.461	<0.001
Red vs blue	1.3225	6.231	<0.001
Yellow vs white	1.687	6.768	<0.001
Red vs white	1.842	7.435	<0.001
Red vs yellow	0.1542	0.871	0.384

Table 4
Estimates, z-values and p-values of a binomial GLMM assessing whether the dummy female attracted at least one male, with replicate night and site included as random factors. Pairwise comparisons between the different light treatments are shown.

Pairwise comparisons of numbers of attracted males			
Treatment	Estimate	Z	P
Blue vs control	−1.573	−3.769	<0.001
White vs control	−1.491	−3.594	<0.001
Yellow vs control	0.1627	0.386	0.699
Red vs control	0.270	0.636	0.525
White vs blue	0.082	0.202	0.840
Yellow vs blue	1.735	4.075	<0.001
Red vs blue	1.843	4.294	<0.001
Yellow vs white	1.653	3.906	<0.001
Red vs white	1.761	4.128	<0.001
Red vs yellow	0.107	0.249	0.803

4. Discussion

The results show that female glow-worm mate attraction success under artificial light depends on the peak wavelength of the light, independent of whether the success is measured as the number of attracted males or as mate attraction probability. In the field, dummy females exposed to relatively short wavelengths of artificial light (blue and white) had a significantly lower mate attraction success than those exposed to longer wavelengths of artificial light (yellow and red). Moreover, the mate attraction success of dummy females under yellow and red artificial light did not differ significantly from that of dummy females in the control.

Our result that white artificial light hinders the ability of female glow-worms to attract males is in line with previous findings (e.g. Bird and Parker, 2014; Elgert et al., 2020a; Stewart et al., 2020). We also found blue light to have a very similar effect (with its spectrum also being very similar, only narrower, Fig. S1). In contrast to our initial hypothesis, we also found that the mate attraction success of dummy females under yellow and red artificial light was similar to that observed in the control treatment. In particular, due to previous findings of a lower mate attraction success even under sodium lamps (Ineichen and Rüttimann, 2012; Van den Broeck et al., 2021b), we hypothesized that mate attraction success would be lower in all artificial light treatments compared to the control. In particular, Ineichen and Rüttimann (2012) found yellow-tinted artificial light from high-pressure sodium streetlights to prevent mate attraction in the common glow-worm, albeit under streetlights with considerably higher intensity of artificial light than what was used in this experiment (46–64 lx vs 5–8 lx; for comparison, moonlight is typically only 0.01–0.6 lx (Kyba et al., 2017)). Moreover, Van den Broeck et al. (2021b) recently found that female glow-worms took longer to mate when exposed to light from low-pressure sodium streetlights, even when light intensity was relatively low.

Why, then, did we not find a difference between our long wavelength treatments, red and yellow, or between them and the control? First, wavelengths may differ in the extent they interact with the greenish female glow. For example, adding a blue component to a female mimicking stimulus was found to reduce the attractiveness of the stimulus to male glow-worms, whereas adding a red component did not have an effect (Booth et al., 2004). Second, male glow-worms may not be able to perceive longer wavelength artificial light; thus such light might not markedly reduce the visibility of female signals to them. In another lampyrid species, the firefly *Aquatica ficta*, male signaling behavior was altered as a result of exposure to artificial light of short and mid wavelengths, but not too long wavelength (≥597 nm), implying a low visual sensitivity to yellow and red light (Owens et al., 2018). Third, it is possible that yellow, and even red, artificial light did suppress female signal visibility, but to such a low degree that it did not significantly affect the number of males attracted (given the current sample sizes and study design). As in many recent studies (Hopkins et al., 2015; Elgert et al., 2020a; Lehtonen and Kaitala, 2020), the dummy female LEDs in the current study corresponded to the glow of a particularly bright glow-worm female, i.e. dummy females were notably brighter than the glow of an average female (A.-M. Borshagovski 2017–2018, unpublished data). Therefore, under long wavelength artificial light, the apparent brightness of dummy females to males, or other aspects of their detectability or attractiveness, may not have decreased markedly (e.g. under a critical threshold level).

The final potential explanation we provide for the high number of males attracted by dummy females in the long wavelength treatments is that males may be attracted by long wavelength (yellow to red) artificial light. Anecdotal observations suggest that glow-worm males do make approaches towards red light, although to a lesser extent than towards green light (Schwalb, 1961). More generally, positive phototaxis (attraction) in response to artificial light is common in insects, with many moths, beetles, flies, and aquatic insects showing attraction especially to short wavelength (blue and UV) light (Park and Lee, 2017; Owens and Lewis, 2018). However, observations of attraction to long wavelengths of light are rarer. Examples include certain pest insects being attracted to red light, and nymphs of certain aquatic insects showing attraction to mid wavelength (green and yellow) light (Park and Lee, 2017; Kühne et al., 2021). Furthermore, fireflies of the genus *Diaphanes* have been found to be attracted to red LEDs (Pacheco et al., 2016). Hence, if long wavelength light attracts male glow-worms, the high male attraction success of dummy females in the yellow and red light treatments may have been due to males being lured to their vicinity by the light. Being in the proximity may then have increased the probability of males noticing the dummy female within the cone of artificial light. Such a scenario could compensate for any reduction in the visibility (or apparent brightness) of the dummy female under the artificial light.

Previous studies have shown that the intensity of artificial light can also affect glow-worm mate attraction success (Elgert et al., 2020a, 2020b; Van den Broeck et al., 2021a). Here, our treatments had minor differences in light intensity, when measured both as photons/cm2/s and lux (Table 1, Fig. S2). However, these do not explain the differences in mate attraction, because the treatments with both the lowest (yellow) and highest (red) light intensity value attracted the greatest numbers of males (Fig. S2),

Table 3
Male attraction success of dummy females in the different light treatments. Treatments with a different letter (A or B) were significantly different from each other (logistic regression). N = 60 in all treatments except in the yellow-light treatment N = 59.

Number of males attracted (frequency)				
Treatment	0	≥1	Success %	Significance
Control	19	41	68.3 %	A
Blue	39	21	35.0 %	B
White	38	22	36.7 %	B
Yellow	17	42	71.2 %	A
Red	16	44	73.3 %	A

showing the minor light intensity differences did not explain treatment differences in mate attraction.

Spectral tuning of artificial lights has been suggested as a mitigation measure for reducing the harmful impacts of nighttime illumination, with yellow light often presented as a less detrimental alternative to white light (Gaston et al., 2012; Longcore and Rich, 2016). The suggestion is supported by our result that the mate attraction success of dummy females under red and yellow artificial light was not significantly reduced, unlike that of dummy females under blue and white light, indicating a lesser impact of the former on glow-worm reproduction. Nevertheless, we may need to be cautious about recommending yellow artificial lighting instead of blue-white light in areas inhabited by glow-worms (or other firefly species). For example, in the firefly *Photinus obscurellus*, all tested colors of artificial light (cool white, warm white, blue, amber, and red) suppressed the courting activity of both sexes, with bright amber light having the greatest negative impact (Owens and Lewis, 2021). Furthermore, we cannot yet judge with confidence whether long wavelength artificial light is truly innocuous to glow-worm mate finding and attraction. For instance, we do not know how long-wavelength artificial light may affect female signaling behavior or the extent it may attract male glow-worms away from females. Moreover, the impact of artificial light is likely to be more severe when a wide area is illuminated, while our setup was akin to the use of spotlights (e.g. in yards and gardens) that only illuminate a small area. Thus, we need more research into the effectiveness of spectral tuning as a mitigation measure for this species. In addition, other species may differ in their light sensitivities, which poses a challenge to finding a universal solution. Additional measures to consider include reducing light intensity, limiting direct glare through shielding, and decreasing lighting duration, e.g., by using motion detection or timers (Longcore and Rich, 2016).

5. Conclusions

To conclude, we found that long wavelength (yellow and red) artificial light did not significantly reduce mate attraction success in the common glow-worm, whereas short wavelength (blue and white) artificial light did. Hence, artificial light wavelength appears to be an important factor in determining the effects of light pollution on glow-worms, with potential implications for glow-worm conservation. Our findings indicate that favoring yellow over bluish and white lighting in the proximity of glow-worm habitats may be a useful method for mitigating the negative effects of light pollution on glow-worm reproduction. However, further investigation of how glow-worms respond to long wavelength light is still required. By showing that different artificial light spectra can have different effects, this study strengthens our knowledge regarding the ecological effects of light pollution.

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CRediT authorship contribution statement

Linnea Kivelä: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Christina Elgert:** Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Topi K. Lehtonen:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Ulrika Candolin:** Conceptualization, Methodology, Writing – review & editing.

Data availability

The data are available at doi:https://doi.org/10.7910/DVN/QWQPLJ.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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