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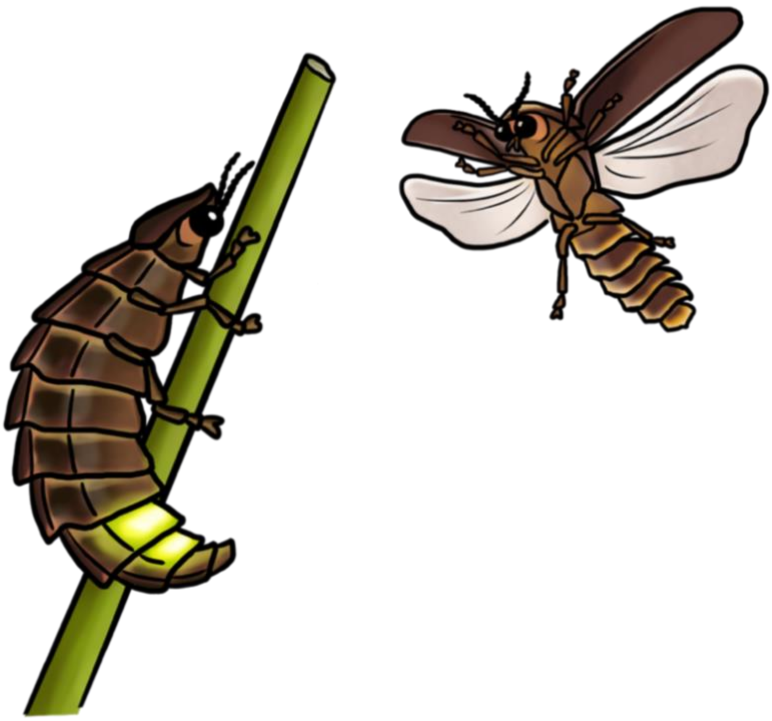
The effect of artificial light spectrum on mate attraction in the common glow-worm, *Lampyris noctiluca*



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Abstract

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Abstract:

Light pollution, or artificial light at night, is a globally increasing environmental problem that threatens especially nocturnal organisms dependent on darkness. Modern lighting technology offers opportunities for mitigation of the ecological impacts of light pollution, but effective implementation requires better understanding of how different artificial light qualities, such as light spectrum, influence its effects on wildlife. The common glow-worm, *Lampyris noctiluca*, is an example of a species believed to be suffering from light pollution. Artificial light has been found to interfere with glow-worm reproduction by decreasing the success of females in attracting males with their glow. In this study, I investigated how the color (spectrum) of artificial light affects the attraction of male glow-worms towards a female mimicking stimulus, in order to find out whether certain colors of artificial light are less detrimental to glow-worm reproduction than others.

I used dummy female traps to capture male glow-worms in the field and compared the catch success of traps in different treatments: illuminated from above with blue, white, yellow or red artificial light, or left unilluminated as a control. I also conducted a laboratory experiment where male glow-worms were given two choices. One of the choices was an unilluminated dummy female, and the other was either a dummy female illuminated with yellow or red light, or a red light illuminated area with no dummy female.

Traps illuminated with short wavelength artificial light (blue and white) caught significantly fewer males than unilluminated traps or traps illuminated with long wavelength artificial light (yellow and red). There was no significant difference in the number of males caught between unilluminated traps and traps illuminated with long wavelength artificial light. In the laboratory, males significantly preferred an unilluminated dummy female over a dummy female illuminated with yellow light. However, the males chose a red light illuminated dummy female or area more often than an unilluminated dummy female, although this difference in preference was not significant.

The results show that mate attraction in the glow-worm is influenced by artificial light color, with short wavelength artificial light decreasing the mate attraction success of female glow-worms more than long wavelength artificial light. This could point to yellow-tinted artificial lighting presenting an ecologically friendly alternative to cool white lighting. However, the specifics of how long wavelength artificial light affects male glow-worm perception of female attractiveness are still unclear. Furthermore, male glow-worms show signs of attraction towards long wavelength artificial light, which could form an evolutionary trap for them. The impacts of artificial light spectrum on organisms are thus not straightforward, but can vary depending on both species and situation.

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Valosaaste eli yöllinen keinovalo on maailmanlaajuisesti lisääntyvä ympäristöongelma, joka uhkaa etenkin pimeydestä riippuvaisia yöaktiivisia organismeja. Moderni valoteknologia tarjoaa mahdollisuuksia valosaasteen ekologisten vaikutusten lieventämiseen, mutta tehokas toteutus vaatii parempaa ymmärrystä siitä, miten keinovalon eri ominaisuudet, kuten valon spektri, vaikuttavat sen seurauksiin luonnolle. Kiiltomato (*Lampyris noctiluca*) on esimerkki lajista, jonka uskotaan kärsivän valosaasteesta. Keinovalon on havaittu häiritsevän kiiltomatojen lisääntymistä heikentämällä naaraiden kykyä houkutella koiraita loisteellaan. Tässä tutkimuksessa tarkastelin miten keinovalon väri (spektri) vaikuttaa kiiltomatokoiraan kiinnostukseen naarasta matkivaa ärsykettä kohtaan. Tarkoituksenani oli selvittää ovatko jotkin keinovalon värit vähemmän haitallisia kiiltomatojen lisääntymiselle kuin toiset.

Pyydystin kiiltomatokoiraita kentällä käyttäen tekonaarasansoja, ja vertailin pyydystysmenestystä eri käsittelyissä olleiden ansojen välillä. Käytetyt käsittelyt olivat valaisu yläpuolelta sinisellä, valkoisella, keltaisella ja punaisella keinovalolla, sekä valaisematon kontrolli. Lisäksi suoritin laboratoriokokeen, jossa kiiltomatokoiraat saivat valita kahden vaihtoehdon välillä. Toinen vaihtoehdoista oli valaisematon tekonaaras, ja toinen joko keltaisella tai punaisella valolla valaistu tekonaaras, tai punaisella valolla valaistu alue ilman tekonaarasta.

Lyhytaaltoisella keinovalolla (sininen ja valkoinen) valaistut ansat pyydystivät merkitsevästi vähemmän koiraita kuin valaisemattomat tai pitkäaaltoisella (keltainen ja punainen) keinovalolla valaistut ansat. Valaisemattomien ja pitkäaaltoisella keinovalolla valaistujen ansojen välillä pyydystettyjen koiraiden määrässä ei ollut merkitsevää eroa. Laboratoriokokeissa koiraat suosivat valaisematonta tekonaarasta merkitsevästi keltaisella keinovalolla valaistua tekonaarasta enemmän. Koiraat kuitenkin valitsivat punaisella keinovalolla valaistun tekonaaraan tai alueen useammin kuin valaisemattoman tekonaaraan, joskin tämä ero ei ollut merkitsevä.

Tulokset osoittavat, että keinovalon väri vaikuttaa kiiltomatojen kumppanin houkutteluun. Lyhytaaltoinen keinovalo heikentää kiiltomatonaaraan menestystä kumppanin houkuttelussa enemmän kuin pitkäaaltoinen keinovalo, mikä voisi tarkoittaa, että keltasävyinen keinovalaistus muodostaisi ekologisesti harmittomamman vaihtoehdon kylmälle valkoiselle valaistukselle. On kuitenkin vielä epäselvää, miten pitkäaaltoinen keinovalo tarkalleen vaikuttaa kiiltomatokoiraan käsitykseen naaraan viehättävyydestä. Lisäksi kiiltomatokoiraat osoittivat merkkejä kiinnostuksesta pitkäaaltoista keinovaloa kohtaan, mikä voisi muodostaa niille evolutiivisen ansan. Keinovalon spektrin vaikutukset organismeihin eivät siten ole suoraviivaisia, vaan voivat vaihdella sekä lajista että tilanteesta riippuen.

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1. Introduction

1.1. Artificial light as an environmental problem

Human activity is known to cause a myriad of environmental problems, some of the most well-known among them habitat destruction and fragmentation, chemical pollution and climate change. However, another potentially serious but still often overlooked anthropogenic environmental problem is that of light pollution, or artificial light at night (ALAN) (Davies & Smyth 2017). Since the use of electric lightning became common in the early 20th century, night-time environments have become increasingly more illuminated with artificial light. Light pollution is still a rapidly growing problem, with artificial lighting increasing on average 6% per year globally as estimated by Hölker et al. (2010b).

Artificial light composing light pollution can be divided into two broad, interlinked categories: direct light and skyglow (Gaston 2018). Skyglow refers to the increased illumination of the night sky as a cumulative result of light from numerous point sources being directed or reflected upwards (Longcore and Rich 2004, Gaston 2018). Light contributing to skyglow is scattered in the atmosphere and reflected back, resulting in a broad-scale phenomenon that can spread vast distances from the urban areas of its origin (Gaston 2018). Skyglow is estimated to affect 23% of the land surface between 75°N and 60°S, including 88% of Europe (Falchi et al. 2016). Direct light is more local and spatially heterogenous, consisting of the direct glare and temporarily fluctuating lights from point sources such as streetlights, lighted buildings, and the lights of vehicles (Longcore & Rich 2004, Gaston 2018).

Obscuration of the night sky to human view due to skyglow has been recognized as a problem by astronomers for decades, with measures taken to curb it over the past 70 years (Smith 2009). However, the potential ecological impacts of illuminated night skies, for example the of obscuration of cues such as lunar cycles that can be used to guide biological activity, have gained less attention until lately (Hölker et al. 2010a, Gaston et al. 2017). Ecological light pollution, as defined by Longcore and Rich (2004), refers to artificial light that alters the natural patterns of light and darkness in ecosystems. Ecological light pollution includes both skyglow and direct light, thus potentially extending to an even wider area than covered by light polluted skies, since even light sources that do not contribute to skyglow, such as shielded lights, can still disturb ecosystems (Longcore & Rich 2004).

Whereas light pollution is theoretically a very easily mitigated form of pollution in the sense that it disappears when the lights are simply turned off (Smith 2009), practical efforts to reduce light pollution are faced with the strong positive associations people commonly have with lighting (Hölker et al. 2010b). Lit environments are associated with an increased sense of wellbeing, safety and enjoyment of a place, although an actual link between artificial lighting and public safety is not clear, and night-time lighting can have negative effects on human health as well, e.g., in the form of melatonin suppression (Gaston et al. 2015a).

Government bodies in many countries are developing new lighting programs with a focus mostly on increased energy efficiency and lowered costs of public lighting, but also on reduction of greenhouse gas emissions (Hölker et al. 2010b, Gaston et al. 2015a). New lighting solutions concerning streetlights include the dimming of lights, part-night lighting, and replacement of old metal-halide and high-pressure sodium (HPS) lamps with more energy efficient light emitting diode (LED) lamps (Gaston et al. 2015a, Pagden et al. 2020). Increasing use of LED lights also means a shift towards whiter lighting, which offers a better rendering for human vision, compared to older lighting types such as high-pressure sodium lamps which have a yellow tint (Gaston et al. 2015a, Pagden et al. 2020). Lighting reforms offer opportunities for mitigating the effects of light pollution, for example through adoption of flexible LED-based lighting infrastructure that allows control over light spectrum and intensity (Gaston et al. 2015a, Davies & Smyth 2017). However, increased efficiency and lowered costs of lighting can have results in the opposite direction and lead to increased light usage and thus increased light pollution (Hölker et al. 2010b).

1.2. Effects of ecological light pollution

Current literature shows that ecological light pollution has demonstrable effects on a wide diversity of organisms, including plants, crustaceans, corals, arachnids, insects, and all the five main groups of vertebrates, with the effects ranging from changes in individual physiology and behavior to population ecology and community structure (Gaston & Bennie 2014, Davies & Smyth 2017). Ecological effects of light pollution derive from alterations in the natural light environment and the cycles of light and darkness that have previously remained mostly consistent over the species' evolutionary history (Gaston et al. 2015a, Davies & Smyth 2017). Artificial light sources also introduce light at brighter intensities and with different spectra than found in nature, with additional unnatural pulsing and flickering (Gaston et al. 2015a). Particularly vulnerable to light pollution are night-active species, which depend on natural day-night cycles, and also constitute a substantial portion of the world's biodiversity. For animals, it has been estimated that around 30% of all vertebrates and over 60% of all invertebrates are nocturnal (Hölker et al. 2010a). Furthermore, due to the evolutionary novelty of artificial light at night as a phenomenon and the rapidity of its increase, the ability of organisms to adapt to it is likely to be limited, and the risk of maladaptive responses relatively high (Robertson et al. 2013).

Ecological light pollution has been found to affect many types of behavior, including foraging, reproduction, migration, and communication (Longcore & Rich 2004). For example, increase in the amount of ambient illumination can affect the ability of animals to navigate in the dark, a well-known example of which is the disorientation of hatchling sea turtles in response to city lights (Salmon et al. 1995). Artificial light sources themselves can cause attraction or repulsion. Many insects, especially moths, are attracted to artificial lights (positive phototaxis), whereas others such as cockroaches and earwigs avoid light (negative phototaxis) (Owens & Lewis 2018). Artificial light also has the potential to cause evolutionary traps, situations, where rapid environmental change of anthropogenic origin causes the environmental cues used by organisms to direct decision making to become disconnected from their historically adaptive outcomes, resulting in maladaptive behavior (Shclaepfer et al. 2002). The term ecological trap refers to a subtype of evolutionary trap, where the habitat choice of an organism is impaired, causing it to prefer a low quality habitat equally to or more than an available habitat of higher quality (Shclaepfer et al. 2002, Robertson & Hutto 2006). A striking example of an ecological trap is water-seeking insects such as mayflies being tricked to lay their eggs *en masse* on polarizing surfaces such as asphalt roads where they perish, an effect to which nearby artificial lighting can also contribute (Kriska et al. 1998, Egri et al. 2017).

The behavior of individual animals is reflected to communities, affecting species interactions, such as competition and predation. For example, increased artificial light at night can result in competitive advantage of light attracted bat species over light avoidant species, granting them better foraging opportunities feeding on insects gathered around streetlights (Polak et al. 2011). Furthermore, artificial light can benefit the bat species foraging around streetlights but damage the populations of the insect prey attracted to the lights (Owens & Lewis 2018). Similarly, diurnal species can gain advantage over nocturnal species if artificial light allows them to continue their activity after nightfall, broadening their presence into the "night light niche", while night active prey species may suffer increased predation due to decreasing protection of the cover of darkness (Longcore & Rich 2004). Generally, ecological light pollution is likely to cause alterations in community structures, by favoring light tolerant species and excluding those dependent on darkness, which can cumulatively disrupt key ecosystem functions (Longcore & Rich 2004, Owens & Lewis 2018).

Although numerous published studies have demonstrated biological impacts of artificial light at night, many challenges for research still remain. Open questions include the impact of the spectral composition of artificial light, the fitness consequences of altered physiological and behavioral responses, and the extent to which documented impacts on individuals translate to impacts on populations, communities and ecosystems (Gaston et al. 2015b). Gaining a better understanding of the effects of ecological light pollution is urgent, due to the rapid global increase and potentially severe ecological impacts of artificial light (Hölker et al. 2010a). The currently ongoing lighting reforms offer opportunity for adjusting artificial light at night to reduce negative environmental impacts. However, in order to effectively inform policy development and strategic planning, better understanding of especially the effects of artificial light intensity and spectral composition are required (Hölker et al. 2010a, Gaston et al. 2015b).

1.3. Study species: the common glow-worm

The common glow-worm, *Lampyris noctiluca*, is a nocturnal beetle in the family Lampyridae (fireflies). Female glow-worms are larviform and sedentary, and attract males by emitting a constant greenish glow in the night (Lewis 2016) (Fig. 1A, B). Male glow-worms resemble typical beetles, and search for females by flying (Fig. 1C). The glow of a female is produced in the lantern, a glow organ located on the undersize of the abdomen, and the brightness of the glow correlates with female body size, which in turn correlates with fecundity (number of eggs) (Hopkins et al. 2015). Male glow-worms prefer females with a brighter glow, which indicates that brightness functions as a reliable sexual signal of female fecundity (Hopkins et al. 2015). The glow-worm is a capital breeder, with an adult lifespan of generally less than two weeks, the females dying after having mated and laid their eggs (Lewis 2016).

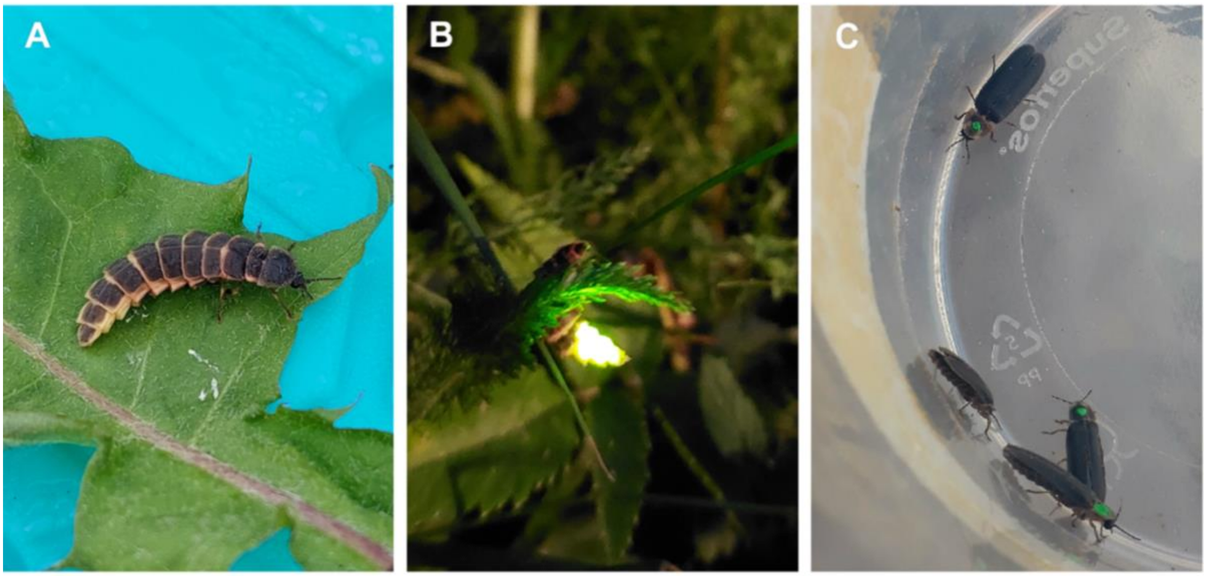

Figure 1. (A) A female common glow-worm (*Lampyris noctiluca)*. (B) A female glow-worm displaying on a piece of vegetation. (C) Male glow-worms in a jar. The males are marked with a green dot of acrylic paint on their pronotum for identification purposes.

The common glow-worm has no official IUCN Red List status (not evaluated), but it is generally considered to be a declining species. Local population declines and lowered numbers of individuals are reported for example in the UK (Gardiner 2009, Gardiner & Didham 2020). Likely reasons for the decline include the warming and drying of climate, habitat fragmentation, and light pollution (Gardiner & Didham 2020, Gardiner & Didham 2021). Light pollution has also been ranked among the most serious threats for firefly populations globally, along with habitat loss and pesticide use (Lewis et al. 2020).

In the common glow-worm, white artificial light has been shown to affect both female glowing behavior and their ability to attract males. Female glow-worms exposed to artificial light have been found to delay the onset of their glowing after natural nightfall and even to refrain from glowing altogether (Elgert et al. 2020a). Furthermore, females appear not to move away from a light source when exposed to a light gradient, showing a maladaptive response to spatial variation in light conditions (Elgert et al. 2020a). Even when they do glow, many studies report female glow-worms suffering decreased mate attraction success when exposed to artificial light (Ineichen & Rüttimann 2012, Bird & Parker 2014, Elgert et al. 2020a, Stewart et al. 2020, Van den Broeck et al. 2021a, Van den Broeck et al. 2021b). The impact of artificial light on mate attraction is dependent on the intensity of the light, with stronger light having a larger negative effect (Elgert et al. 2020b, Van den Broeck et al. 2021a). However, even low intensities of artificial light have been reported to reduce mate attraction success (Bird & Parker 2014). Whether the spectrum of artificial light influences signal visibility and thus mate attraction in the glow-worm is, however, still unknown.

According to Booth et al. (2004) color vision in the common glow-worm is based on chromatic opponency, with the addition of short wavelength (blue) light to a female mimicking stimulus decreasing its attractiveness to males, but the addition of long wavelength (red) light having no such effect. Additionally, in another lampyrid species, the firefly *Aquatica ficta*, the wavelength of artificial light was found to affect signaling. Exposure to short wavelength (blue and green), but not longer wavelength (red), ambient light induced a change in the flashing of males, possibly due to inability of the fireflies to detect long wavelengths of light (Owens et al. 2018).

The effect of artificial light spectral composition on glow-worm reproduction could have important implications for the conservation of the species, as the ongoing lighting reform offers opportunities for adjusting public lighting to favor less damaging lighting types. Furthermore, the lighting reform in itself is changing the spectral landscape of artificial light, as yellow-tinted high-pressure sodium lights are being replaced with whiter LED-based lighting, with wavelengths generally between 400-700nm and peaks in the blue and green (Gaston et al. 2015a).

1.4. Study aims

The aim of this study was to investigate the effect of light spectrum (color) on how artificial light affects mate attraction in the common glow-worm. Namely, I sought to investigate whether certain colors of artificial light interfere with the ability of male glow-worms to locate glowing females, or of glowing females to attract males, to a different degree than others. If certain colors of artificial light were found to interfere with mate attraction less, these findings could be used to mitigate the negative effects of light pollution on glow-worms, by informing policy makers and urban planners of artificial light spectral compositions that have the least detrimental effects on glow-worm reproduction.

Based on previous literature, I hypothesized that dummy females exposed to artificial light would have decreased mate attraction success compared to dummy females in natural darkness, either because artificial light deters males or because artificial light reduces the visibility of female signaling. Furthermore, I hypothesized that decrease in mate attraction success would be connected to artificial light wavelength so that short wavelength light would have a larger detrimental effect than long wavelength light. This could be due to male glow-worms not being able to perceive longer wavelength, especially red, light.

2. Materials and methods

To answer to the questions above, I conducted two experiments. In the first, primary experiment I compared the mate attraction success of glow-worm females in regard to artificial light spectrum, by monitoring male glow-worms attracted to dummy females under different colored artificial lights in the field. The second experiment was decided upon midway through the conducting of the primary experiment, and thus served more as a pilot study than a full experiment of its own. The second experiment aimed to further examine the effect of longer wavelength artificial light on the mate choice of male glow-worms. In a laboratory choice experiment, male glow-worms were set to choose between a dummy female under yellow or red artificial light and an identical dummy female in the dark. The general behavior of the males in regard to the artificial light was also observed. All work was conducted at or nearby Tvärminne Zoological Station (N 59°51’, E 23°14’) in Southern Finland, in June-July 2020 during the glow-worm mating season.

2.1. Attraction of males in the field

Adult male glow-worms were trapped on twenty nights between 12th June and 4th July 2020. The duration of the experiment was based on observations of male glow-worm activity from previous years in the same area (e.g., Elgert et al. 2020a, Lehtonen & Kaitala 2020). Males were trapped only on nights with reasonably good weather, because poor weather conditions (low temperatures, wind and rain) deter male activity (Dreisig 1971).

Males were trapped using light emitting diode (LED) traps constructed following the methods in Hopkins et al. (2015). The traps consisted of a 1,5 L plastic bottle cut into two with the top half inserted into the bottom half to form a funnel, and a green 5 mm LED-light mimicking the glow of a female attached to the top to act as a lure (Fig. 2, Fig. 3). The green LEDs (dummy females) had an intensity of 0.065-0.075 µW nm^{-1} (microwatts per nanometre) as measured with a spectrophotometer and integrating sphere, and a peak wavelength of 562 nm, which is within the natural spectrum observed in real female glow-worms (550-570 nm) (Schwalb 1961, De Cock 2004).

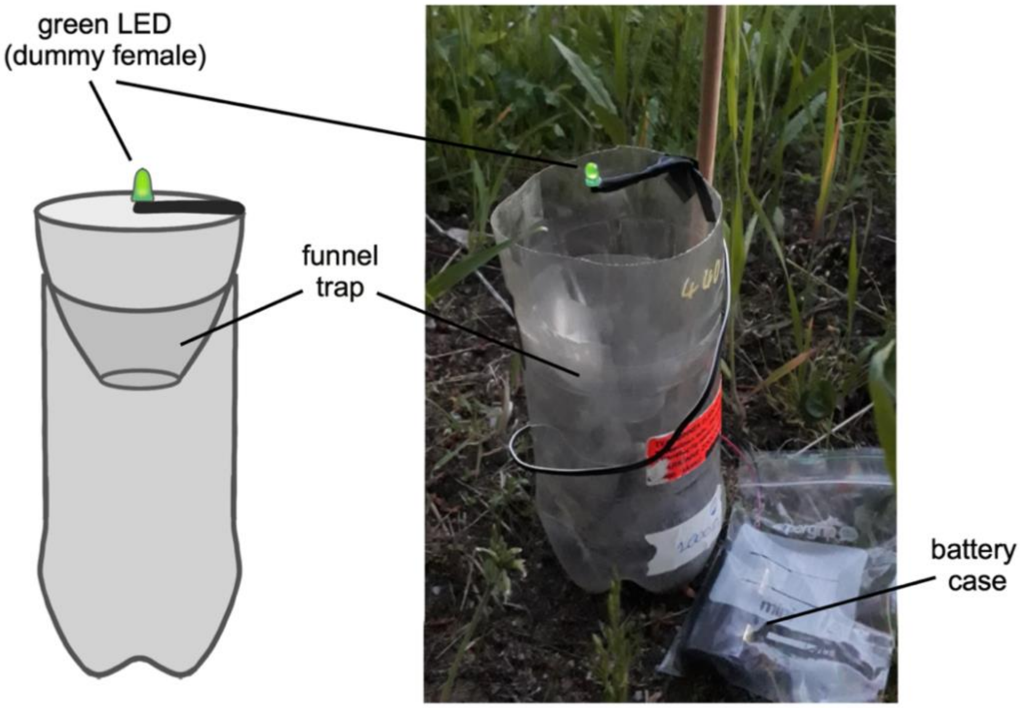

Figure 2. A schematic depiction and a photograph of a dummy female trap used to catch male glow-worms.

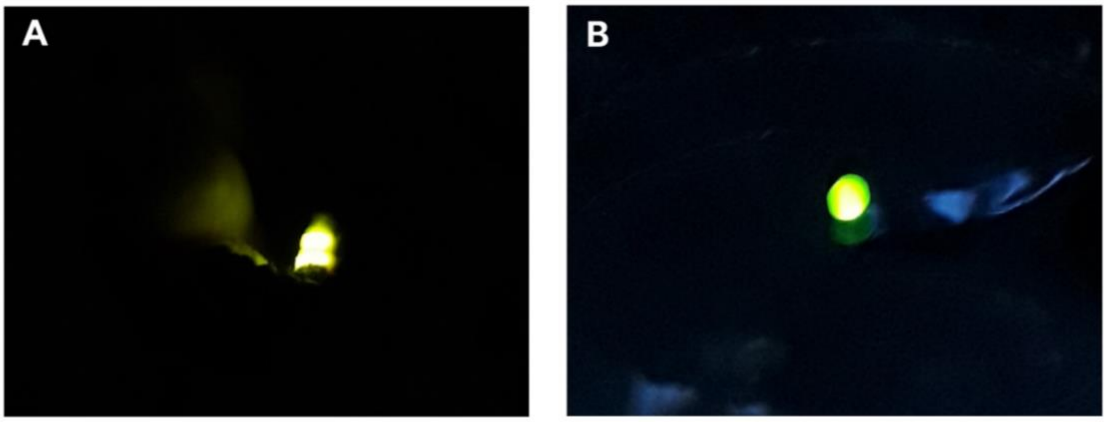

Figure 3. (A) A glowing female glow-worm. (B) A lit dummy female (green 5 mm LED-light).

Each dummy female trap was lit from above by an artificial light, simulating a light pollution source such as a streetlamp or yard light. The artificial lights used were white LED-lights covered with color-foil to alter their spectra. The experiment had five different treatments: blue, white, yellow and red light, and a dark control (Fig. 4). In the case of the blue, white and yellow lights the light was a Fenix UC01 mini flashlight at half output. The red light demanded a more powerful light source (due to the dimming effect of the color-foil), for which a VARTA Indestructible LED x5 headlamp at half output was used. The emission spectra of the lights were manipulated using EUROLITE color-foils attached over the light. The intensities and peak wavelengths of the lights were measured with a spectrophotometer and cosine corrector in an otherwise dark room and are given in Table 1.

Figure 4. The four colored lights used in the study: blue, white, yellow and red.

Table 1. Light treatment details. Light intensities are given at the 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

The lights were covered with opaque lampshades made from plastic cups in order to direct the cone of light downwards and to reduce the visibility of the light source itself. Attached to a pole, the lights were placed 80-100 cm above the dummy females, corresponding to 100-120 cm above the ground, as the traps were around 20 cm high. The height varied slightly between treatments, with blue at 80 cm, yellow at 90 cm, and white and red at 100 cm. This was done in an attempt to achieve more uniform light intensities based on the original lux measurements, as the amount of absorption and thus dimming effect between the different colored filters used varied greatly.

The traps and lights were placed along 1 km of an unlit, forested road leading to Tvärminne Zoological Station (J. A. Palménin tie) in 15 locations where glow-worms had been found in previous years (Fig. 5). The average distance between selected sites was around 50 m. The order of treatments was randomized and altered between nights, so that each site had an equal number of replicates of every treatment over the course of the experiment. Each treatment had three replicates per night, amounting in a total of 15 replicates each night.

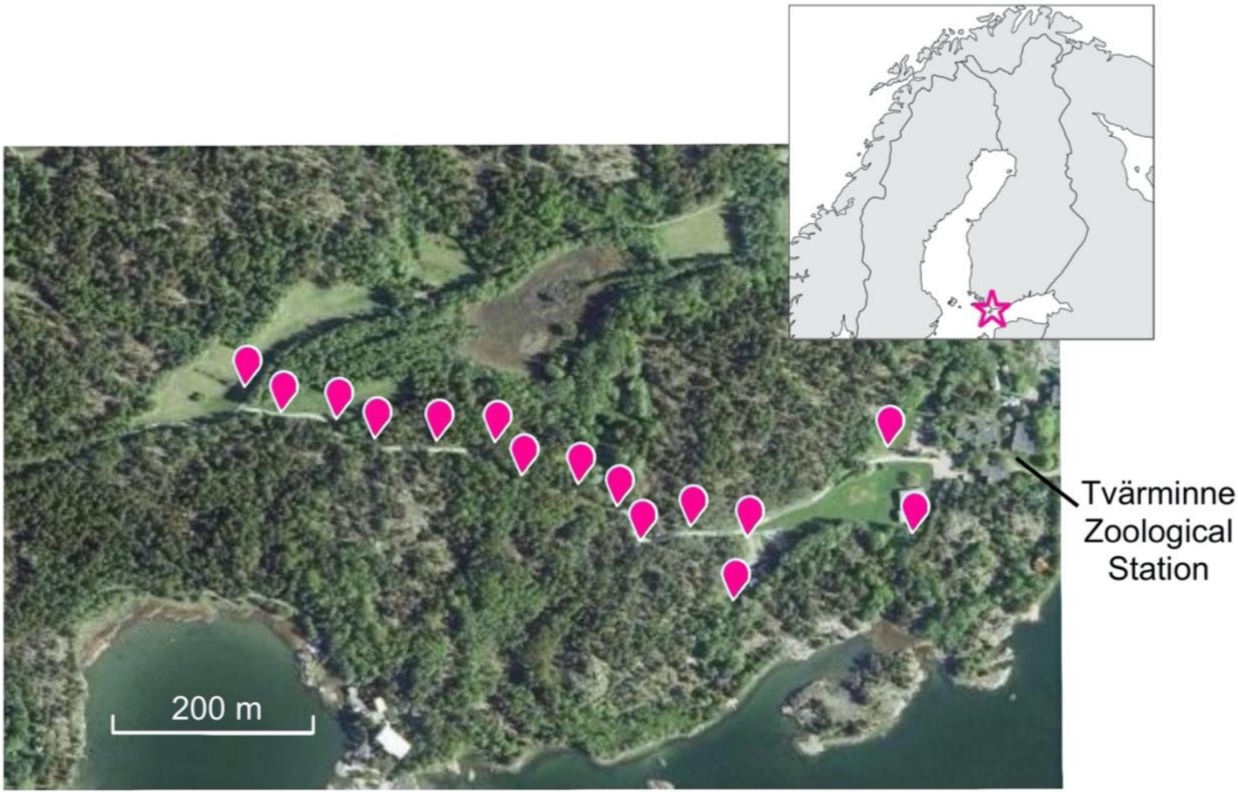

Figure 5. Trap sites. Each of the pink pointers marks one of the 15 sites where traps were set nightly, with the light treatment used varying between the sites each night. The study site was located in the vicinity of Tvärminne Zoological Station, Hanko, Southern Finland. Map data ©Maanmittauslaitos.

The artificial lights and dummy female traps were turned on each night between 23.45 and 00.15 and turned off between 01.45 and 02.15. The lights were turned off in the same order as they were turned on, ensuring that each light was on for two hours. After the lights were turned off, the traps were inspected for male glow-worms, and caught males were counted and collected. The males were held until the following day, when they were marked with a small dot of acrylic paint on their pronotum, in order to be able to tell apart recaptures from new males. Recaptured (marked) males were not counted in the number of captured males in order to ensure the independence of the observations. After being marked the males were released, except for those which would be used in the laboratory choice experiment, which were held for another night.

2.2. Laboratory choice experiment

Laboratory trials were conducted nightly between 00.30 and 01.30, from 26th June to 4th July, using male glow-worms trapped in the field experiment during the previous night. Prior to the trials, the males were housed individually in 8 cm diameter plastic jars with a few pieces of vegetation for cover. Used males were released the following day.

The laboratory experiment was carried out in a room located in an outbuilding. An experimental arena was built to the back of the room facing the outdoor by lining the floor and the left, right and back walls with cardboard (Fig. 6). The “front” of the arena was left open, enabling easy access and clear view to the arena. The arena was 110 cm x 110 cm in size, with 90 cm high walls. The door of the laboratory was left open during the experiment in order to let in natural ambient light, making the light environment of the laboratory more like that in the field.

Two dummy females were placed in the corners of the arena, with 60 cm between them (Fig. 6). As dummy females, the same green LED-lights were used as in the field experiment, but with a slightly higher intensity of 0.088 μW nm^{-1} each. Instead of being attached to traps, the dummy females were attached to 10 cm diameter cardboard discs and were thus at floor level. An artificial light was hung in either the left or right corner of the arena, illuminating the arena on one side. As artificial lights, the same Fenix UC01 mini flashlights as in the field experiment were used, as well as the same color-foils. Two colors of light were used, yellow and red. In the case of yellow light, the light source and height (and thus the brightness of $4.21*10^{12}$ photons/cm^2/s) were the same as in the field experiment. The red light, on the other hand, was also a mini flashlight instead of a headlamp as in the field experiment (because the headlamps were needed in the field and were too bulky to properly hang up), resulting in a slightly dimmer light of $3.75*10^{12}$ photons/cm^2/s. The order of the dummy females and the side of the light were altered between trials to control for any preference towards a certain side or dummy female.

Three experimental set-ups were used. In the first set-up, one side of the arena was illuminated with yellow light and the other left dark, with one dummy female on either side of the arena (experimental set-up 1, Fig. 6A, B). In the second set-up, red light was used instead of yellow (experimental set-up 2, Fig. 6C). In trials conducted with these two set-ups, some males were observed showing apparent interest towards the illuminated walls and the light sources instead of either of the dummy females, and thus a third set-up was used to test whether the males would still be attracted to the illuminated side of the arena even without the dummy female lure. Again, one side of the arena was illuminated with red light, but the dummy female on the illuminated side was switched off, leaving only the control female on the dark side lit (Experimental set-up 3, Fig. 6D).

At the start of each trial, a single male was placed on the arena in a spot 80 cm away from both dummy females, and made to walk through a 3 cm paper tube so that it would see both dummy females at approximately the same time. The behavior of the males was observed from the open side of the arena. The males were recorded as having chosen a given dummy female if they entered on the cardboard disc that the female was attached to. In the case of experimental set-up 3, where the female on the red light illuminated side was switched off, the male was recorded as having chosen the illuminated area if it entered the area after heading straight for it.

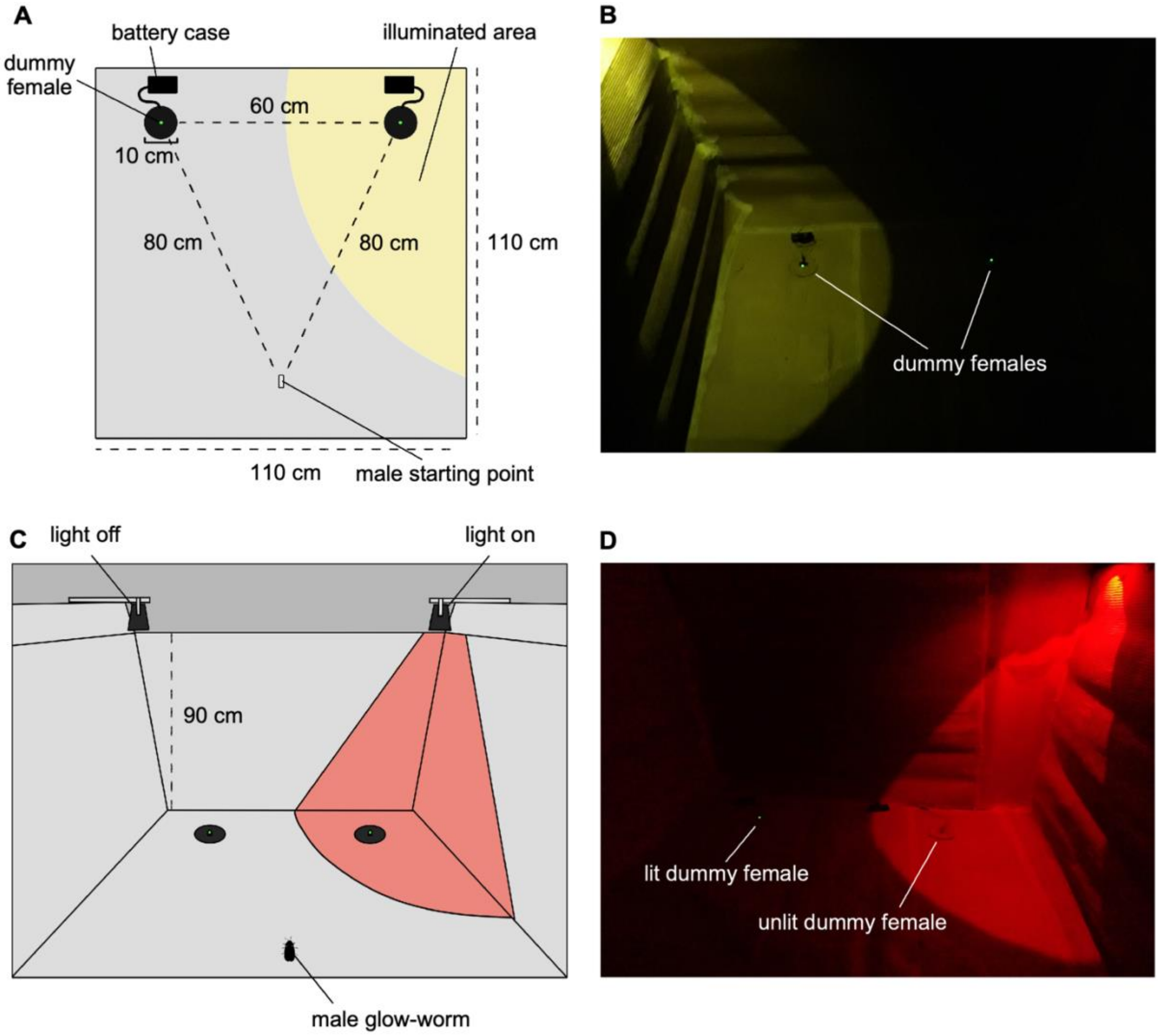

Figure 6. Laboratory set-ups. (A) A schematic depiction of the laboratory arena from above, with yellow light and both dummy females lit, as in experimental set-up 1. (B) A photograph of the laboratory arena from the "front" (researcher perspective), with yellow light and both dummy females lit, as in experimental set-up 1. (C) A schematic depiction of the laboratory arena from the front, with red light and both dummy females lit, as in experimental set-up 2. (D) A photograph of the laboratory arena from the front, with red light and the illuminated dummy female switched off, as in experimental set-up 3.

2.3. Statistical analysis

All statistical analyses were performed using R v. 3.6.1. (R Core Team 2019) and RStudio v. 1.2.5001 (RStudio Team 2019) for macOS. Models were built using functions from the R packages *MASS* v. 7.3.51.4. (Venables & Ripley 2002) and *pscl* v. 1.5.2. (Jackman 2017).

2.3.1. Main data: Attraction of males in the field

I investigated the effect of artificial light spectrum on the number of males attracted using a generalized linear model (GLM) with a negative binomial distribution, with the number of males caught in a trap as a count response variable and the color of artificial light as a categorical explanatory variable. In order to find the statistical model with the best fit, I fitted the data with four different models using the same response and explanatory variables: a linear model, and GLMs with Poisson, zero inflated Poisson, and negative binomial distributions. I compared the performance of the models using model validation plots, dispersion, and Akaike information criteria (AIC, Akaike 1973) scores. I rejected the linear model on the basis of non-normality of residuals, and the Poisson model due to overdispersion (dispersion = 4.04 >> 1). I settled on the generalized linear model with negative binomial distribution as the best alternative to use for having the Q-Q plot with the closest fit, reasonable dispersion (= 1.13) and the smallest AIC-score out of the four (AIC-scores of the linear model, Poisson model, zero inflated Poisson model and negative binomial model 1531.4, 1442.5, 1241.4 and 1087.6, respectively).

However, male glow-worms caught in a trap are not necessarily independent from each other. Although there is no clear evidence of this, is it possible that the presence of one male in a trap might attract others via pheromones, or that the males might move in swarms. To account for this possibility, I repeated the analysis using presence/absence data, comparing the treatments with regard to traps that caught one or more males versus traps that caught no males. Here, I used a logistic regression model (GLM with Bernoulli distribution, suitable for binary data), with the presence or absence of males in a trap as a binary response variable, and the artificial light treatment again as the explanatory variable.

2.3.2. Secondary data: Laboratory choice experiment

To investigate the effect of long wavelength artificial light on male glow-worm preference for a dummy female, I first coded the possible choices as “0” (unilluminated control dummy female) and “1” (artificial light, either an illuminated dummy female or an illuminated area with an unlit dummy female, depending on the experimental set-up). I then conducted two-sided exact binomial tests separately for each of the three experimental set-ups (yellow light, red light, red light with unlit female) to determine whether the choice ratios differed from 0.5.

3. Results

3.1. Attraction of males in the field

<u>3.1.1. Catch size</u>

A total of 624 individual male glow-worms were caught during the experiment. Traps in the blue and white light treatments caught significantly fewer males than traps in the yellow, red and control treatments (Fig.7, Table 2), with fewer males caught in the white than in the blue light treatment (Fig. 7, Table 2). There was no significant difference in the number of caught males between the yellow and red light treatments and the control (Fig. 7, Table 2).

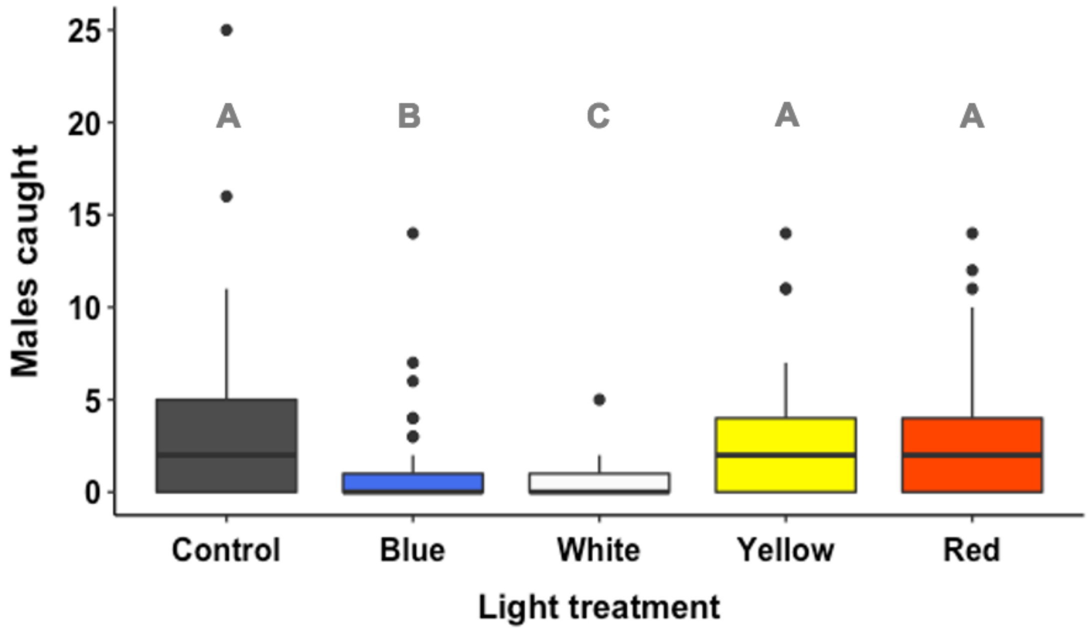

Figure 7. Number of males caught per trap in unilluminated (control) traps and in traps illuminated from above with blue, white, yellow and red artificial light. Box plots show median values (horizontal black lines), interquartile ranges (colored boxes), upper quartiles (whiskers), and extreme values (black dots). Whiskers representing the lower quartiles are not visible, because in all treatments at least 25% of the traps caught zero males. Treatments with a different letter A-C were significantly different from each other (negative binomial GLM). N = 60 in all treatments except the yellow light treatment, where N = 59.

Table 2. Estimates, z-values and p-values of pairwise comparisons of male catch sizes between the different light treatments using a negative binomial GLM. Comparisons are done against the treatments listed in the left side column. Significant p-values are underlined.

TREATMENT	Control	Blue	White	Yellow	Red
Control	–	-1.248 z = -4.818 p < 0.001	-1.975 z = -6.778 p < 0.001	-0.308 z = -1.286 p = 0.198	-0.178 z = -0.749 p = 0.454
Blue	1.248 z = 4.818 p < 0.001	–	-0.727 z = -2.337 p = 0.019	0.940 z = 3.569 p < 0.001	1.070 z = 4.104 p < 0.001
White	1.975 z = 6.778 p < 0.001	0.727 z = 2.337 p = 0.019	–	1.667 z = 5.646 p < 0.001	1.798 z = 6.135 p < 0.001
Yellow	0.308 z = 1.286 p = 0.198	-0.940 z = -3.569 p < 0.001	-1.667 z = -5.646 p < 0.001	–	0.131 z = 0.541 p = 0.589
Red	0.178 z = 0.749 p = 0.454	-1.070 z = -4.104 p < 0.001	-1.798 z = -6.135 p < 0.001	0.131 z = 0.541 p = 0.589	–

3.1.2. Catching success

In total during the experiment, 57% of the traps were successful in catching at least one male, with 170 instances of one or more caught males and 129 instances of zero caught males. Traps in the blue and white light treatments had significantly lower catching success than traps in the yellow, red and control treatments (Fig. 8, Table 3). Catching success did not differ significantly between the yellow and red light treatments and the control (Fig. 8, Table 3) or between the blue and white light treatments (Fig. 8, Table 3). Thus, results from the binary analysis were otherwise in line with the results form the analysis conducted using the number of males, except that the difference between the blue and white light treatments was no longer significant.

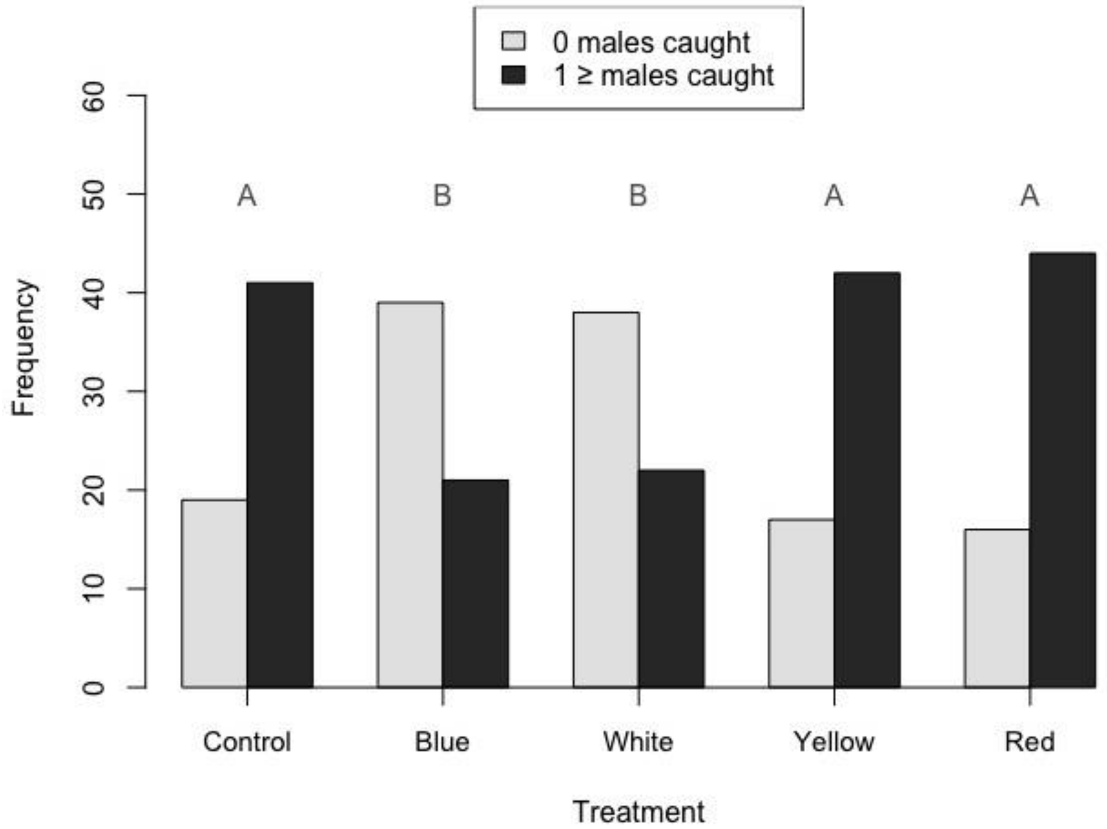

Figure 8. Catching success of traps in the different light treatments. Black bars show the number of traps that successfully caught at least one male in each treatment, whereas light grey bars signify traps that failed to catch any males. Treatments with a different letter (A or B) were significantly different from each other (logistic regression). N = 60 in all treatments except the yellow-light treatment, where N = 59.

Table 3. Estimates, z-values and p-values of pairwise comparisons of catching success between the different light treatments using logistic regression. Comparisons are done against the treatments listed in the left side column. Significant p-values are underlined.

TREATMENT	Control	Blue	White	Yellow	Red
Control	–	-1.388 z = -3.581 <u>p < 0.001</u>	-1.316 z = -3.411 <u>p < 0.001</u>	0.1353 z = 0.339 p = 0.735	0.2425 z = 0.339 p = 0.547
Blue	1.388 z = 3.581 <u>p < 0.001</u>	–	0.073 z = 0.190 p = 0.849	1.524 z = 3.859 <u>p < 0.001</u>	1.631 z = 4.096 <u>p < 0.001</u>
White	1.316 z = 3.411 <u>p < 0.001</u>	-0.073 z = -0.190 p = 0.849	–	1.451 z = 3.693 <u>p < 0.001</u>	1.558 z = 3.932 <u>p < 0.001</u>

Yellow	-0.135 z = -1.524 p = 0.735	-1.524 z = -3.859 p < 0.001	-1.451 z = -3.693 p < 0.001	–	0.107 z = 0.262 p = 0.794
Red	-0.2425 z = -0.602 p = 0.547	-1.631 z = -4.096 p < 0.001	-1.558 z = -3.932 p < 0.001	-0.107 z = -0.262 p = 0.794	–

3.1.3. The effect of light intensity

In addition to spectra, the intensity of the artificial lights might have affected the male attraction success of illuminated traps, as the lights used were not completely uniform in intensity between treatments due to the color filters used affecting the light output, despite efforts taken to mitigate this (see Table 1). Because the intensity of each light color was measured only once and not separately for every observation, it could not be included as a factor in the statistical analyses. However, comparing the numbers of males caught in each treatment and their respective light intensities shows no clear relationship between artificial light intensity and male catch size independent from artificial light color (Fig. 9).

The highest numbers of males were found in the control treatment with no artificial light at all, whereas the second highest numbers were in the red light treatment, which had the highest light intensity (Fig. 9). Controversially, the yellow light treatment, which had the next largest catch sizes and no significant difference in catch size from the red and control treatments, had the lowest intensity light (Fig. 9, Table 2). The white light treatment, which had the smallest catch sizes, had an intermediate light intensity between the yellow and blue light treatments (Fig. 9). Thus, the differences in male attraction success between treatments cannot be attributed to artificial light intensity alone, and the color of the light must play a part.

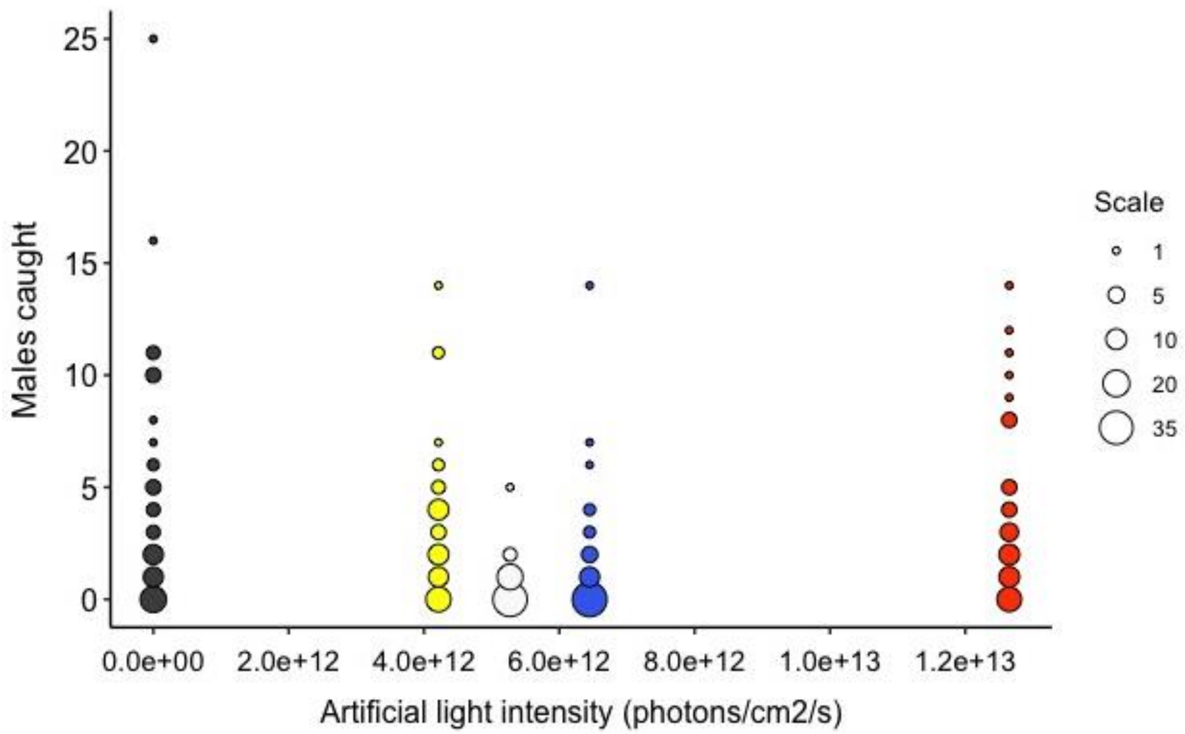

Figure 9. Male catch sizes plotted against artificial light intensity in the different treatments, measured as photons/cm^2/s. Point color corresponds to light color, and point size indicates number of observations; the larger the point, the more traps there were with a given number of males. Light intensity refers to the “extra light” from the artificial light source, with the measurements taken in an otherwise completely dark room.

3.2. Laboratory choice experiment

Males in the yellow light treatment showed significant preference for the unilluminated control female over the illuminated female (Fig. 10). In the red light treatments, however, males chose the illuminated female or the illuminated area with no female more often than the control female, although due to the low number of replicates these differences in preference were not statistically significant (Fig. 10).

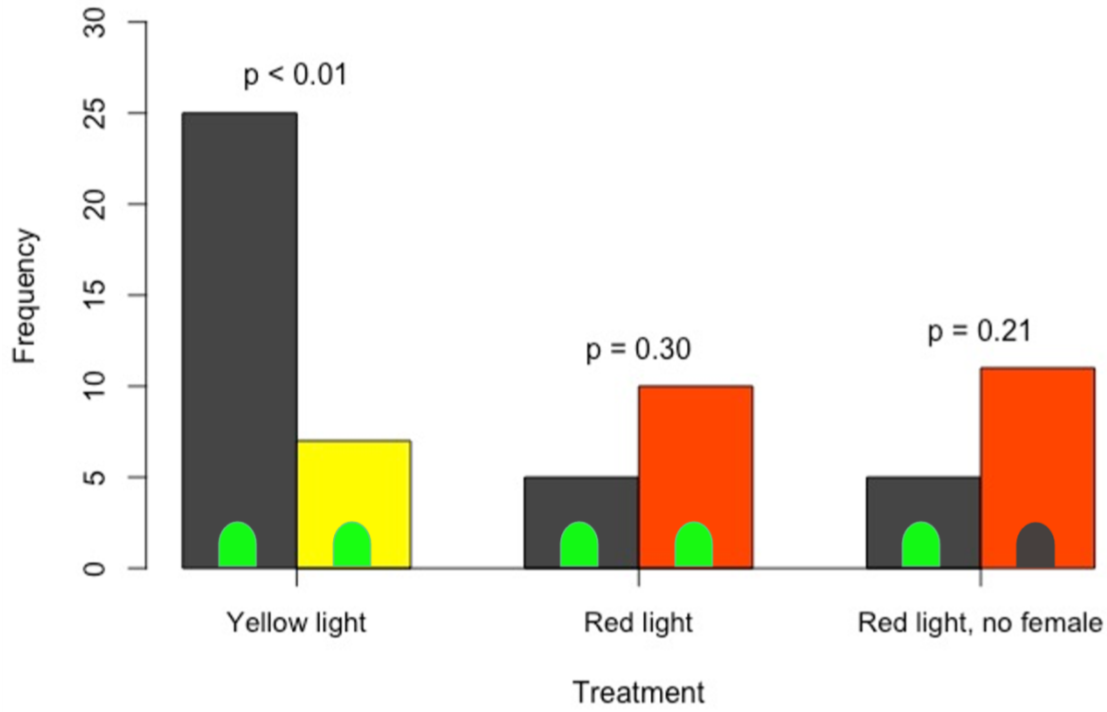

Figure 10. Male choice for a dummy female with different artificial light set-ups. Dark grey (left side) bars show the number of males that chose the unilluminated control female in each treatment. Colored (right side, yellow or red) bars show the number of males that chose the artificial light illuminated alternative. In the yellow light treatment, this was a lit dummy female under yellow light, in the red light treatment a lit dummy female under red light, and in the "red light, no female" treatment the red light illuminated area with the dummy female switched off. P-values for preference within each treatment are given above the bars (two-sided exact binomial test).

4. Discussion

4.1. Artificial light interference with mate attraction

The results show that the effects of artificial light on mate attraction in the common glow-worm depend on the spectrum of light. In natural conditions in the field, dummy females exposed to relatively short wavelengths of artificial light (blue light with a peak at 452 nm and white light with a peak at 449 nm) suffered decreased mate attraction success compared to dummy females exposed to longer wavelengths of artificial light (yellow light with a peak at 575 nm and red light with a peak at 625 nm). Furthermore, the mate attraction success of dummy females under yellow and red artificial light did not differ from the mate attraction success of unilluminated control dummy females.

The results for white light (and blue light, which had a very similar, only narrower, spectrum) were in line with previous studies, in which white artificial light was found to hinder the ability of female glow-worms to attract males (e.g., Bird & Parker 2014, Elgert et al. 2020a, Stewart et al. 2020). The finding that yellow and red artificial light had no apparent effect on mate attraction success, however, was somewhat surprising. Due to previous findings of lowered mate attraction success even under sodium lamps, I had hypothesized that mate attraction success would be lowered in all artificial light treatments compared to the control, with the exception that red light might not have an effect if male glow-worms are unable to perceive it, and that the negative effect would be stronger in the short wavelength treatments. This hypothesis was correct in part of the decreased mate attraction success in the white and blue light treatments, but not in part of the yellow light treatment, which was not found to have an effect. Previously, Ineichen and Rüttimann (2012) had found yellow-tinted artificial light from high-pressure sodium streetlights to prevent mate attraction in the glow-worm, although this might be because the light intensity of the streetlights was much higher than the intensity of the artificial lights used in this experiment. Furthermore, Van den Broeck et al. (2021b) found that female glow-worms remained unmated longer when exposed to light from low-pressure sodium streetlights, even when light intensity was low.

To further inspect the unexpectedly high mate attraction success of dummy females under yellow light in the field experiment, I conducted laboratory trials to see how the light affected male choice between two dummy females. I found that males preferred the unilluminated control female over the female under yellow light, but not unequivocally. Furthermore, I observed males showing interest towards the artificial light source itself, on several cases attempting to climb or fly towards the light source rather than approaching either of the dummy females. I assumed this might be because the spectrum of the yellow light included a portion of green similar to the glow of a female (yellow light peak at 575 nm, female light spectrum 550-570 nm (Schwalb 1961, De Cock 2004). Thus, males might have been attracted to the artificial light because it resembled female glow.

In order to see whether the males would also show interest towards red light, which did not include a green component, I conducted more trials using red light instead of yellow. Instead of showing less attraction, the males seemed more interested in the red light, choosing the illuminated dummy female in more trials than the unilluminated dummy female and continuing to attempt to approach the light source. The males even continued to head towards the light source rather than the unilluminated dummy female when the dummy female under the red light was turned off. Due to time constraints limiting the number of trials that could be performed and prioritization of the testing of different experimental set-ups over replicates of the same set-up, the sample sizes for the red-light treatments were low. Thus, the differences in preference between the unilluminated control female and the red-illuminated female or area were not statistically significant. However, the results show rather clearly that there was no preference toward the unilluminated female, unlike in the yellow light treatment, as males chose it only in 31-33% of the cases. Furthermore, the results indicate a possible male preference towards the red light illuminated female and/or area, although further study is needed to confirm the effect. There are also some cases in previous literature that indicate possible male attraction towards red light. Booth et al. (2004) found that adding a blue component to a female mimicking stimulus reduced its attractiveness to male glow-worms, whereas adding a red component did not. However, their study design only tested change in attractiveness in one direction, and thus left unclear whether the addition of a red component actually *increased* the attractiveness of the female mimicking stimulus. Additionally, Schwalb (1961) observed some glow-worm males making approaches towards red lights.

The apparently equal mate attraction success of dummy females under yellow and red artificial light and dummy females not exposed to artificial light in the field experiment could have several explanations. It might be due to male glow-worms not being able to perceive longer wavelength artificial light and thus the light not interfering with the visibility of female signaling. In another lampyrid species, the firefly *Aquatica ficta*, male signaling behavior has been found to be altered by exposure to short and mid wavelength artificial light, but not by exposure to long wavelength (≥ 597 nm) artificial light, implying visual insensitivity to yellow to red light (Owens et al. 2018). However, this appears not to be the case for the glow-worm. In the laboratory trials yellow light was shown to decrease female attractiveness, and while the evidence for an effect of red light was not conclusive, it suggested an increase in attractiveness. Furthermore, males were observed to approach both the yellow and red light sources as if attracted to them. Thus, the males appeared to be able to see the light.

Another explanation for the apparent lack of difference in mate attraction success between the long wavelength treatments and the control is that especially yellow and possibly also red artificial light did suppress female signal visibility, but to such a low degree that it did not have a discernible effect. There is indication that male glow-worms are not able to accurately judge differences in brightness between females that are far apart from each other (Borshagovski et al. 2019). Thus, since the dummy females used here were alone under the artificial lights and on average 50 m away from each other, small reductions in their apparent brightness might not have affected their attractiveness to males. Furthermore, the dummy female LED-lights were somewhat brighter than an average real glow-worm female (A.-M. Borshagovski 2017-2018, unpublished data), so even with a slight reduction in their apparent brightness they could have still appeared “bright enough” for males. Whether or not yellow and red artificial light cause any reductions to female signal visibility could be tested in a future experiment by adding a competitor of equal brightness for direct comparison. One dummy female could be placed within the cone of light and another a short distance away outside the cone of light, similarly to Elgert et al. (2020a) but using artificial light of varying spectra instead of only white light.

A third potential explanation for the high number of males caught in the long wavelength treatments is that long wavelength (yellow to red) artificial light in itself attracts male glow-worms. Positive phototaxis (attraction) in response to artificial lights is common in insects, with many moths, beetles, flies, and aquatic insects showing attraction especially to short wavelength (blue and UV) light (Park & Lee 2017, Owens & Lewis 2018). Attraction to long wavelength light is rarer, but not unheard of, with for example some pest insects being attracted to red light, and nymphs of aquatic insects showing preference for mid wavelength (green and yellow) light (Park & Lee 2017, Kühne et al. 2021). Furthermore, fireflies of the genus *Diaphanes* have been found to be attracted to traps with a red LED-light (Pacheco et al. 2016). In the field experiment, long wavelength light attracting male glow-worms could mean that the high male attraction success of dummy females in the yellow and red light treatments was due to males being lured to the trap site by the artificial light, and possibly only noticing the dummy female when already close. This could also compensate for any reduction in the apparent brightness of the dummy females caused by the artificial light, especially for the yellow light treatment.

4.2. Artificial light effects on glow-worms

If male glow-worms are attracted to artificial light, light pollution could form evolutionary traps (Schlaepfer et al. 2002) for glow-worms in two ways. Artificially illuminated areas may act as equal-preference ecological traps (Robertson & Hutto 2006) for female glow-worms if the females are unable to differentiate between illuminated and unilluminated areas when choosing their display sites. Previous studies have indeed found female glow-worms glowing in illuminated areas near streetlights, where they also suffer decreased mate attraction success and remain unmated for longer (Ineichen & Rüttimann 2012, Van den Broeck et al. 2021b). Furthermore, female glow-worms have also been shown to react to artificial light maladaptively by not moving away when exposed to it (Elgert et al. 2020a). Delays in mating caused by artificial light exposure are likely to be costly for the females due to the short adult lifespans of glow-worms and the loss of fecundity with prolonged time spent unmated (Hopkins et al. 2021). The males, in turn, may experience an evolutionary trap through attraction to long wavelength artificial light, even if it does not interfere with female signal visibility as much as short wavelength artificial light does. Maladaptive attraction to artificial lights through positive phototaxis is well documented in other nocturnal insects, most notably moths, but most often in response to short wavelength or polarized light (Owens & Lewis 2018). Lampyrids generally appear not to be attracted to short wavelength light (Buck 1937, Schwalb 1961, Lall & Worthy 2000, Booth et al. 2004), but could suffer similar detrimental fitness outcomes from attraction to long wavelength light, including overheating and exhaustion from approaching the lights, or simply missing out on breeding opportunities by chasing artificial lights instead of females.

Attraction to long wavelength artificial lights by glow-worm males could be due to inability of the males to differentiate between long wavelength artificial lights and glowing females. The specifics of glow-worm color vision are not clear, but according to Booth et al. (2004) it appears to be based on chromatic opponency with spectral tuning from a yellow filter pigment. A behavioral experiment by Booth et al. (2004) indicates that the response of male glow-worms to female signaling is mediated by an antagonistic relationship between photoreceptors sensitive to short (< 500 nm) and long (> 500 nm) wavelengths. Thus, short wavelength lights peaking under 500 nm (such as my blue, 452 nm, and white, 449 nm, lights) would be distinct from the green light of females (550-570 nm) and thus not attractive to males, whereas longer wavelength lights peaking over 500 nm (such as my yellow, 575 nm, and red, 625 nm, lights) could to the male glow-worm eye resemble the glow of females.

Artificial light at night could thus have detrimental consequences for glow-worm populations by interfering with their reproduction in several ways. Blueish-white light, as from many modern LED-lights, can refrain female glow-worms from glowing (Elgert et al. 2020a) or reduce their attractiveness to males (Bird & Parker 2014, Stewart et al. 2020, Van den Broeck et al. 2021a, this study). Amber artificial light, as from sodium lamps, can also reduce the mate attraction success of glow-worm females, as observed by Ineichen & Rüttimann (2012) and Van den Broeck et al. (2021b) for females glowing under streetlights, and the laboratory part of this study where males were found to prefer the unilluminated dummy female over the dummy female under yellow light. Additionally, preliminary results from the laboratory part of this study indicate that long wavelength artificial lights (yellow and red) might attract male glow-worms through positive phototaxis and lure them away from females. However, further study is needed to confirm the relationship between male glow-worms and long wavelength artificial lights, and the potential for an evolutionary trap.

4.3. Implications for mitigation

Spectral tuning of artificial lights has been suggested as a mitigation measure for reducing the harmful impacts nighttime illumination on ecosystems, with amber light often presented as a less ecologically severe alternative cool white light. The results from the field experiment support this notion, as the male attraction success of dummy females under yellow artificial lights was not significantly reduced unlike that of dummy females under blue and white lights, indicating a lesser impact of yellow artificial light on glow-worm reproduction. However, recommending amber artificial lighting instead of blueish light on areas with glow-worms might still not be sustainable, as I observed potential attraction of male glow-worms towards long wavelength artificial lights, which in itself might have fitness consequences. Similarly, Owens and Lewis (2021) found for the firefly *Photinus obscurellus* that all tested colors of artificial light (cool white, warm white, blue, amber and red) suppressed the courting activity of pairs, with bright amber light having the greatest impact. This suggests that spectral tuning, at least alone, might not be an effective mitigation measure. In addition to the possible futility of finding a non-detrimental spectrum of light for a single species, such as the glow-worm, the needs of other species in the ecosystem need to be taken into account as well. Different species tend to have different light sensitivities, and thus a universally suitable solution would be difficult to find. Alternative or additional solutions for reducing the ecological impacts of lighting can include reducing light intensity, limiting direct glare through the shielding of lights, and decreasing the duration of lighting through motion detection or part-night lighting (Longcore & Rich 2016). For glow-worms and fireflies, dimming of lights, reducing their duration (Elgert et al. 2021), and switching off of unnecessary lighting could be particularly effective solutions.

In general, this study adds to the knowledge about the ecological effects of light pollution, in particular for the role of light spectrum. The study shows that different artificial light spectra can have different ecological effects, and these effects may be context dependent, and have different consequences for males and females. It also provides a potential example of positive phototaxis towards long wavelength light in insects, when most studies on insect attraction to light are on species attracted to short wavelength or polarized light (Owens & Lewis 2018).

5. Conclusions

In the field experiment, I found that long wavelength (yellow and red) artificial light reduced mate attraction success in the common glow-worm less than short wavelength (blue and white) artificial light. If this is due to long wavelength artificial light decreasing female signal visibility only to a low degree or not at all, this finding could be used to mitigate the negative effects of light pollution on glow-worm reproduction, by favoring yellow colored artificial lighting over blueish white lighting on areas with glow-worm populations. However, if male glow-worms are attracted to yellow/red light, this might not be without problems. Long wavelength artificial lights could form evolutionary traps for male glow-worms, by attracting them to areas where there might not be any females. In that case, the safest option for glow-worm reproduction would be simply to reduce the amount of artificial light at night around glow-worm habitats.

In conclusion, artificial light wavelength appears to be an important factor in determining the effects of ecological light pollution on glow-worms, with potentially important implications for glow-worm conservation. Furthermore, these results add to the general knowledge about the ecological effects of light pollution.

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