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# Behavioral responses of bioluminescent fireflies to artificial light at night

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Bioluminescent insects have been the subject of scientific interest and popular wonder for millennia. But in the 21st century, the fireflies, click beetles, and cave glow-worms that brighten our nights are threatened by an unprecedented competitor: anthropogenic light pollution. Artificial lights can obscure the light-based signals on which these and other bioluminescent organisms rely to court mates, deter predators, and attract prey. In the following review we summarize a recent influx of research into the behavioral consequences of artificial light at night for firefly beetles (Coleoptera: Lampyridae), which we organize into four distinct courtship signaling systems. We conclude by highlighting several opportunities for further research to advance this emerging field and by offering a set of up-to-date lighting recommendations that can help land managers and other stakeholders balance public safety and ecological sustainability.

## KEYWORDS

Lampyridae, bioluminescence, firefly, light pollution, artificial light at night (ALAN)

## Introduction

Advances in lighting technology have rapidly increased the scale and intensity of anthropogenic light pollution over the past century. Recent estimates suggest that at least 22.5% of the habitable land surface of the earth currently experiences artificially bright night skies (Falchi et al., 2016), and that night skies have become 49% brighter on average within the last 25 years (Sánchez de Miguel et al., 2021). Artificial light sources responsible include streetlights, car headlights, security lights, facade lighting, stadium lighting, illuminated advertisements, and sources associated with agriculture and industry, e.g., greenhouse lighting or uncurtained office windows (Luginbuhl et al., 2009). Atmospheric scattering of upwelling light produces skyglow, a bright haze visible many kilometers beyond its source that further contributes to light pollution (Kyba et al., 2015; Figures 1A–E).

Unprecedented increases in night sky brightness threaten all taxa that have evolved under predictable cycles of light and dark (Gaston et al., 2017). However, nocturnal insects may be especially vulnerable to the encroachment of artificial light at night (ALAN) into their habitats due to their high visual sensitivity (Warrant, 2017), small body size relative to artificial light sources, and tendency toward positive phototaxis or “flight-to-light” behavior (Owens and Lewis, 2018; Owens et al., 2020). Certain charismatic nocturnal insect taxa capable of bioluminescent communication, fireflies the most successful and species among them (Oba and Schultz, 2014), are likely to be both particularly at risk and particularly able to inspire public interest in dark sky conservation.

Worldwide, over 2200 species of firefly and glow-worm beetles (family Lampyridae, hereafter referred to collectively as fireflies), are currently described (Martin et al., 2019). All firefly species bioluminesce in their larval stage, an adaptation which presumably originated to warn predators of their unpalatable chemical defenses (Branham and Wenzel, 2003; Powell et al., 2022; but note Kok et al., 2019). Most species subsequently co-opted this ability to produce both aposematic signals and sexual advertisements during their brief adult stage (Leavell et al., 2018). Firefly adults typically restrict their courtship activity to a characteristic crepuscular or nocturnal temporal niche, with flight periods lasting from only 20 min up to several hours. Certain species in the genus *Photuris* have further adapted their signals into foraging lures (Lloyd, 2017).

All types of bioluminescent signal are susceptible to environmental masking (Johnsen et al., 2004). Natural light from the sun or moon can be a predictable obstacle to visibility (Gunn and Gunn, 2012; see also Branham and Faust, 2019), but artificial light from local sources is not only significantly brighter but also spatially, temporally, and spectrally novel. Consequently, ALAN likely acts as a strong selective pressure (Hopkins et al., 2018) that has rapidly intensified in recent years following the development of increasingly efficient and broad-spectrum lighting technologies such as LEDs (Elvidge et al., 2010). If artificial light masks bioluminescent signals, increases in predation rates and decreases in mate success could cause firefly populations to rapidly decline.

In this review, we update an earlier synthesis (Owens and Lewis, 2018) to summarize a flurry of recent studies examining the influence of ALAN on the bioluminescent behaviors of fireflies. Throughout we discuss relevant risk factors that are likely to make certain species especially vulnerable to artificial light. We conclude by pointing out persistent gaps in our understanding of firefly conservation behavior, highlighting several future research directions that we believe will advance this emerging field, and offering a set of informed guidelines to help conservationists develop and maintain “firefly friendly” light environments for at-risk species. The studies reviewed below (Table 1) employed artificial lights with widely varying intensities as well as different temporal, spatial, and spectral

distributions; to simplify comparisons, where possible we report intensities in lux, an incomplete but relatively accessible measure of the brightness of broad-spectrum light as viewed by humans.

## Firefly visual systems

To understand the effects of ALAN on fireflies, it is crucial to first understand how they perceive light. Fireflies are red-green colorblind (Figure 2; Buck, 1937; Booth et al., 2004; Owens et al., 2018). The common ancestor of all beetles lacked a blue photoreceptor, presumably sacrificing spectral sensitivity to increase total sensitivity (Sharkey et al., 2017). Fireflies appear to have maintained this inherited configuration, with only one unique copy each of UV-sensitive (UVS) and long-wavelength-sensitive (LWS) photoreceptors detected in all species investigated to date (Oba and Kainuma, 2009; Sander and Hall, 2015). Firefly LWS photoreceptors can be tuned to absorb conspecific bioluminescence through the addition of overlying filter pigments (Cronin et al., 2000). Neural comparisons of input from LWS and UVS photoreceptors may permit limited color discrimination in the UV-blue-green range (e.g., Booth et al., 2004).

The bioluminescence emission spectrum and corresponding long-wavelength spectral sensitivity of a given species are usually characteristic of its particular temporal or photic niche. Nocturnal fireflies tend to produce green bioluminescence and to be broadly sensitive to long wavelengths (Figure 2A). In contrast, the compound eyes of crepuscular fireflies often contain red or pink filter pigments that screen out the blue-green ambient light of twilight, increasing the visibility of their signals against surrounding foliage (Cronin et al., 2000; Lall et al., 2009); many of these species produce yellow bioluminescence to maximize visibility within this visual system (Figure 2B; Lall et al., 1980b). Notably some nocturnal fireflies with green bioluminescence, including *Photuris versicolor* (Cronin et al., 2000) and *Lampyris noctiluca* (Booth et al., 2004) have yellow filter pigments in the frontal-dorsal regions of their compound eyes, which have been posited to screen out downwelling skylight.

In contrast to the large and complex compound eyes of adults, most firefly larvae possess only a single pair of bilateral stemmata (Murphy and Moiseff, 2019). Despite structural differences, however, the simple eyes of *Photuris* larvae are functionally similar to the compound eyes of *Photuris* adults: they are most sensitive to light in the blue-to-green region of the visible light spectrum and appear capable of discriminating colors in this region as well (Murphy and Moiseff, 2019). *Photuris* larvae move away from artificial light even after their optic nerve has been severed, suggesting that an alternative sensory pathway transmits information on ambient light intensity to the brain (Murphy and Moiseff, 2020). Intrinsically

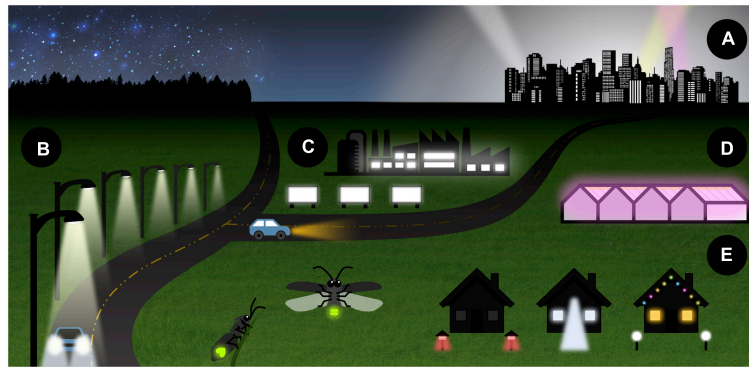


FIGURE 1

Artificial light at night (ALAN) emanates from diverse sources that vary widely in intensity as well as temporal, spatial, and spectral distribution. Major sources of ALAN include (A) diffuse skyglow, sometimes visible at a great distance from urban centers, (B) artificial lights used in transportation such as streetlights and car headlights, (C) commercial lighting, including billboards and the lit windows of commercial buildings, (D) agricultural lighting, including grow lights used in greenhouses, and (E) private lighting such as security lights, decorative lights, and lit windows.

photosensitive areas of the brain, previously documented in *Luciola lateralis* and *Luciola cruciata* adults (Hariyama, 2000), may be responsible.

## Firefly courtship signaling systems

Fireflies employ diverse visual and chemical signals as sexual advertisements (Ohba, 2004; Lloyd, 2008; da Silveira and Mermudes, 2014), but most species can be categorized into one of four primary signaling systems [Figure 3; adapted from Lewis (2009)]. The impact of artificial light is likely to be contingent upon these different courtship behaviors, briefly described below.

Dark fireflies (Figure 3A) are species with diurnal adults that do not employ bioluminescent courtship signals. Instead, females are known or presumed to use pheromones to attract flying males, which tend to have elongated and elaborated antennae but limited vision (da Silveira and Mermudes, 2014; Stanger-Hall et al., 2018). Male attraction to female pheromones has been documented in *Lucidota atra* (Lloyd, 1972), *Lucidina biplagiata* (Ohba, 2004), and *Phosphaenus hemipterus* (De Cock and Matthysen, 2005).

Glow-worm fireflies or glow-worms (Figure 3B) are sexually dimorphic species with brachypterous or apterous females that are incapable of flight, and which initiate courtship by emitting continuous glows while perched near the ground. In some species such as *Pyrocoelia rufa* (Ohba, 2004) females attract males with pheromones in addition to continuous glows. The European glow-worm *L. noctiluca* is widespread throughout Europe and the UK, where glow-worm fireflies predominate (De Cock, 2009). Glow-worm males are fully winged and search for female glow signals, and possibly pheromones, from the air. In some species such as the blue ghost *Phausis reticulata*

(De Cock et al., 2014) and the tracker ghost *Amydetes fastigiata* (Vaz et al., 2021) males also emit prolonged glows. Due to the presumably limited dispersal ability of flightless females, glow-worm fireflies may be highly vulnerable to habitat degradation and fragmentation resulting from ALAN.

Roving flashing fireflies (Figure 3C) are species where both sexes signal using discrete bursts of light. Females of these species are often sedentary, though usually fully winged and capable of flight. Flying males advertise by repeating a species-specific flash pattern at regular intervals, and receptive females answer with response flashes (Ohba, 2004; Lewis and Cratsley, 2008). This flash exchange – known as a courtship dialog – continues until the male locates and mounts the female, and is characteristic of many firefly genera including *Luciola*, *Aquatica*, *Pyroctomena*, and *Photinus* (Stanger-Hall and Lloyd, 2015). Females in the genus *Photuris* (Souto et al., 2019) are specialist predators of other flashing fireflies, luring patrolling males by mimicking the response flashes of conspecific females (Lloyd, 1980), hawking them from the air (Lloyd and Wing, 1983), and stealing them from spider webs (Faust, 2012). In a few species, such as *Photinus carolinus*, *Photinus knulli*, and *Photuris frontalis* in the United States (Sarfati et al., 2021, 2022), *Photinus palaciosi* in Mexico, and *Luciola* sp. in eastern Europe (Baldaccini et al., 1969), flying males synchronize their courtship advertisements when they reach sufficient densities.

Stationary synchronous fireflies (Figure 3D) have in recent decades become popular tourist attractions due to the visual spectacle of their courtship displays (Cheng et al., 2021; Lewis et al., 2021). Males of these species form conspicuous leks, congregating *en masse* each evening within particular visually prominent display trees (Cratsley et al., 2012; Prasertkul, 2018; Jaikla et al., 2020b). Stationary males perch on leaves and collectively signal by flashing together in tight synchrony (Cratsley et al., 2012; Prasertkul, 2018; Jaikla et al., 2020b).

**TABLE 1** Conclusively documented behavioral and developmental effects of artificial light on fireflies. Where appropriate, the intensity of each artificial light treatment has been provided in lux.

Group	Species	Behavioral response	Light treatment	Reference
Glow-worms	<i>Lampyris noctiluca</i> (nocturnal)	Males in the field less likely to approach artificially illuminated imitation females	≤0.35 lux	Stewart et al. (2020)
			7 lux	Elgert et al. (2020)
			≤0.025 lux	Van den Broeck et al. (2021b)
		Females in the field glow over more evenings under artificial illumination	0.1–8.5 lux existing streetlights (low-pressure sodium)	Van den Broeck et al. (2021a)
		Females in the laboratory glow for fewer minutes under artificial illumination	15–20 lux	Elgert et al. (2021b)
			2.5 lux (incandescent)	Dreisig (1978)
	Females in the laboratory never glow under artificial illumination	10 lux (incandescent)	Dreisig (1978)	
Roving Flashing Fireflies	<i>Aquatica ficta</i>	Males in the laboratory emit more conspicuous alarm flashes less often under artificial illumination	N/A Short/mid-wavelength monochromatic LEDs	Owens et al. (2018)
	<i>Photinus pyralis</i> (crepuscular)	Equal male courtship flash activity observed near artificial lights in the field but tethered females respond less often	300 lux	Firebaugh and Haynes (2016)
		Males in the field emit fewer courtship flashes under artificial illumination	175 lux	Firebaugh and Haynes (2019)
		Marked females in the field move independently and mate successfully under artificial illumination	> 20 lux existing floodlights (white LED)	Owens and Lewis (2022)
	<i>Photinus marginellus</i> (crepuscular)	Marked females in the field move independently and mate successfully under artificial illumination	> 20 lux existing floodlights (white LED)	Owens and Lewis (2022)
		Less male courtship flash activity observed near artificial lights in the field	1.2 lux (mercury vapor)	Costin and Boulton (2016)
	<i>Photinus greeni</i> (crepuscular)	Males in the field less likely to approach artificially illuminated imitation females	5 lux	Owens and Lewis (2022)
	<i>Photinus obscurellus</i> (semi-nocturnal)	Males in the laboratory emit more conspicuous courtship flashes less often under artificial illumination, while females nearly entirely cease responding	Amber: 24–240 lux monochromatic LEDs	Owens and Lewis (2021b)
		Pairs in the laboratory mate under dim but not bright artificial illumination	Dim: 3 lux, Bright: 30 lux	Owens and Lewis (2022)
		Females in the field less likely to mate successfully under artificial illumination	5 lux	Owens and Lewis (2022)
<i>Photinus carolinus</i> (nocturnal)	Less male courtship flash activity observed near artificial lights in the field	Amber: 150 lux monochromatic LEDs	Owens et al. (2022)	

(Continued)

TABLE 1 (Continued)

Group	Species	Behavioral response	Light treatment	Reference
	<i>Photuris</i> sp.	Less courtship/foraging flash activity observed near artificial lights in the field	1.2 lux (mercury vapor)	Costin and Boulton (2016)
	<i>Photinus</i> sp1 (nocturnal)	Fewer flashing males observed along artificially illuminated transects	0.5–4.5 lux existing floodlights (metal halide)	Hagen et al. (2015)
	<i>Photuris versicolor</i> (nocturnal)	Less courtship/foraging flash activity observed near artificial lights in the field	300 lux	Firebaugh and Haynes (2016)
	<i>Sclerotia aquatilis</i>	Pairs in the laboratory eventually mate successfully under artificial illumination	0.05–0.3 lux (fluorescent)	Thancharoen (2007)
Stationary synchronous fireflies	<i>Pteroptyx valida</i>	Males in the field repeatedly congregate (lek) within artificially illuminated display trees	7–14 lux existing streetlights (fluorescent)	Prasertkul (2018)
	<i>Pteroptyx malacca</i>	Males in the laboratory flash less often, and with less synchrony, in response to camera flashes	N/A	Thancharoen and Masoh (2019)
Larvae	<i>Aquatia ficta</i>	Aquatic larvae in the laboratory show high mortality following chronic exposure to artificial illumination	<0.01 lux	Chen et al. (2021)
	<i>Lampyris noctiluca</i>	Larvae in the field less likely to glow under moonlight and/or urban skyglow	N/A	De Cock (2004)
	<i>Lamprigera</i> sp.	Larvae in the field less likely to forage under artificial illumination, more likely to move away or appear immobilized	3–4.5 lux existing streetlights (white LED)	Wanjiru Mbugua et al. (2020)
	<i>Phosphaenus hemipterus</i>	Larvae in the field less likely to glow under moonlight and/or urban skyglow	N/A	De Cock (2004)
	<i>Photinus obscurellus</i>	Larvae in the laboratory unaffected by chronic exposure to artificial illumination	50 lux	Owens and Lewis (2021a)
	<i>Photuris</i> sp.	Larvae in the laboratory gain weight more quickly during chronic exposure to artificial illumination	50 lux	Owens and Lewis (2021a)
		Larvae in the laboratory less likely to forage near artificial lights, more likely to move away horizontally or vertically	800 lux	Owens and Lewis (2021a)
		Larvae in the laboratory reduce surface activity under artificial illumination	915 lux	Murphy and Moiseff (2020)

Because lux is a measurement of the brightness of downwelling light as perceived by humans, it is strongly skewed by the position of the lux meter sensor with respect to the target light source as well as differences in the spectral distribution of said source. We note the bulb type employed (where available) when it differs from the current experimental standard, broad-spectrum white LED.

Flying and flashing females orient toward display trees from surrounding areas. Once females reach the lek, complex courtship interactions precede mating (Case, 1980). Example include southeast Asian mangrove species *Pteroptyx tener*,

*Pteroptyx malacca* (Jusoh et al., 2018), and *Pygoluciola qingyu* (Fu and Ballantyne, 2008).

In the following section we review what is currently known about how ALAN impacts adult courtship in each of these

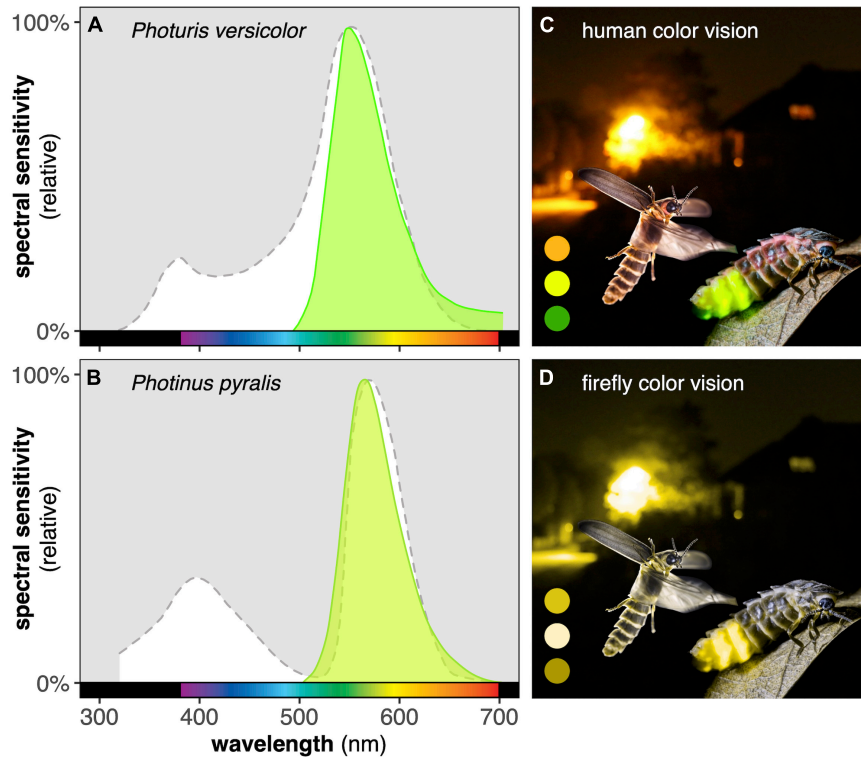


FIGURE 2

Firefly eyes have been optimized to absorb conspecific signals. The spectral sensitivities of nocturnal *Photuris versicolor* (A) and crepuscular *Photinus pyralis* (B) fireflies both peak near the peak wavelength of conspecific bioluminescence (emission spectra shown in green). Fireflies only possess one LWS photoreceptor and are therefore fully red-green colorblind. This means that an image containing a range of green, yellow, and orange regions, as viewed by most humans (C), will appear nearly monochromatic to fireflies (D), with orange and green regions indistinguishable from dim yellow regions. Spectral sensitivities of both species and spectral distribution of *P. versicolor* bioluminescence modified from Lall et al. (1980a) and Lall (1981); spectral distribution of *P. pyralis* bioluminescence modified from Hall et al. (2016). Image credits: background by MVDB, stationary female glow-worm by Robert Canis (robertcanis.com), flying male glow-worm by Hubert Polacek; protanopia color vision simulation from pilestone.com.

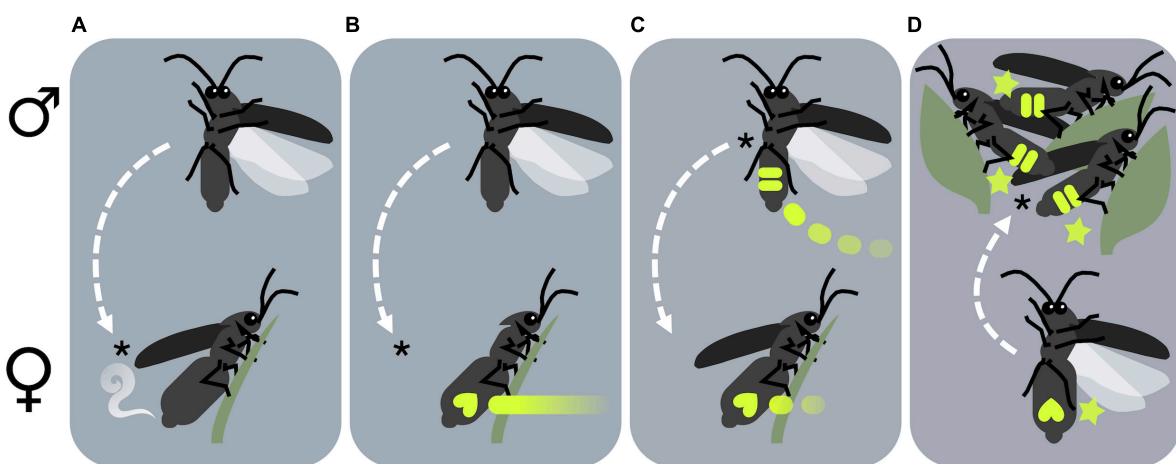


FIGURE 3

Fireflies may be grouped according to their courtship behavior into one of four signaling systems: either (A) dark, (B) glow-worm, (C) roving flashing, or (D) stationary synchronous fireflies (see main text for explanations of each signaling system). Each panel depicts males (above) and females (below), with asterisks (\*) denoting the primary signaler (the sex which initiates courtship), and dashed arrows indicating the direction of movement toward the mating location.

distinct signaling systems, then consider how ALAN impacts adult survivorship and larval development.

## Effects of artificial light at night on firefly behavior

### Courtship

#### Dark fireflies

Dark firefly adults do not rely on light signals for courtship (Figure 3A). The impact of artificial light on courtship and mating success in these species is therefore likely to depend upon how novel external light cues interact with the internal timekeeping mechanisms (“clocks”) that regulate daily and seasonal rhythms of activity in most terrestrial taxa (Gaston et al., 2017), and whether this results in temporal disorientation (*sensu* Owens and Lewis, 2018). All fireflies, including species with non-bioluminescent adults, pupate and eclose at certain times of year, and partake in behaviors such as courtship, mating, and oviposition at certain times of day. Artificial light exposure late in the day or summer may prolong daily and seasonal activity, delaying dormancy, while artificial light exposure early in the day or spring may advance activity. Artificial light rich in blue wavelengths may be especially disorienting, as these wavelengths have been shown to most strongly suppress production of melatonin in *Drosophila* and other taxa (Cashmore et al., 1999).

#### Glow-worm fireflies

Because patrolling male glow-worms are attracted to continuous glows (Figure 3B), they may confuse continuously operating artificial lights for large receptive females and thereby fall into a potent evolutionary trap (Haynes and Robertson, 2021). Glow-worm flight-to-light behavior has not been documented on a large scale (but see Bek, 2015; Kivelä, 2022). However, small points of artificial light (e.g., from LEDs) have been effectively used to trap males both as a part of surveys (Pacheco et al., 2016) and studies of glow-worm courtship (De Cock et al., 2014). Bespoke “imitation females” have been used to elucidate several aspects of glow-worm physiology and behavior (e.g., Booth et al., 2004).

The European glow-worm *L. noctiluca* enjoys a wide distribution (De Cock, 2009), and has served as a model organism for the majority of studies investigating the impact of ALAN on the courtship and mate success of bioluminescent fireflies (Table 1). Stewart et al. (2020), Elgert et al. (2021a), and Van den Broeck et al. (2021b) all found that when imitation female glow signals were illuminated by broad-spectrum white LEDs, they attracted fewer *L. noctiluca* males compared to unilluminated controls (see also Ineichen and Rüttimann, 2012; Bird and Parker, 2014; Kivelä, 2022), and that this difference was magnified under brighter illumination. ALAN spectra, intensity,

and directionality have become a focus of recent research as they might be adjusted to minimize detrimental effects. Elgert et al. (2020) found that 7 lux of downwelling ALAN, which is dimmer than the light cast by most streetlights, significantly decreased the attractiveness of imitation females to males. Stewart et al. (2020) found effects of horizontally-directed ALAN up to 40 m away from the source, where it measured approximately 0.35 lux. Using a similar experimental setup with upwelling ALAN, Van den Broeck et al. (2021b) saw significantly decreased attractiveness of imitation females under only 0.025 lux of ALAN, similar in intensity to moonlight (Kyba et al., 2017). The authors also compared the impact of illumination by cool vs. warm white LEDs, which emit different ratios of blue to longer wavelengths, and found that both treatments interfered equally with the ability of males to locate imitation females.

Limiting the duration of artificial light could be another way to minimize detrimental effects. Van den Broeck et al. (2021a) observed the effects of long-term exposure to ALAN on the mate success of live females in the field by repeatedly checking whether or not they were glowing (*L. noctiluca* females cease glowing once they have mated; Tyler, 2002). While females in dark sites (< 0.1 lux) glowed for only a single evening, females in areas lit by low-pressure sodium street lights (0.1–8.5 lux) glowed for a median of six and as many as 24 evenings, indicating that these artificially illuminated females experienced significantly decreased mate success. However, in a recent laboratory experiment Elgert et al. (2021b) observed that females were significantly more likely to cease glowing when artificially illuminated: on average, females went dark after only 26 min of continuous ALAN exposure. This behavioral difference could be explained by the brighter (15–20 lux) and more direct artificial light used in the lab study, or by the relatively short timescale. In an early laboratory experiment, Dreisig (1978) found that 2.5 lux of artificial light reduced the duration of glow activity from an average of 139 min to only 51 min and that females never began to glow under 10 lux of artificial light. Between 0.001 and 1.0 lux the duration of glow activity was similar to that under natural conditions. The suppressive effect of ALAN on the production of glow signals by female glow-worms may therefore be weaker in the field, where artificial illumination is comparatively dim and indirect, and may also abate over multiple evenings.

Both abbreviated and prolonged glowing periods due to ALAN could be associated with fitness costs. *L. noctiluca* females that never glow are significantly less likely to attract nearby males (De Cock et al., 2014), while those that glow over multiple evenings likely do so only because they remain unmated (Tyler, 2002). Even if these females do eventually mate, delays are energetically costly: glow-worms are capital breeders that rarely feed as adults (Wing, 1989; Tyler, 2002), and the energy they require for self-maintenance and bioluminescence depletes over time (Baudry et al., 2021). Some of this energy comes from metabolized eggs (Wing, 1989), steeply reducing fecundity (Horne et al., 2017; Hopkins et al., 2021). Prolonged

glowing periods could also increase predation risk, although few predators are able or willing to overcome glow-worm chemical defenses (see section “Predator-prey interactions” below; De Cock and Matthysen, 2001; Lewis et al., 2011). Small females may be especially vulnerable to artificial light, both because their glows tend to be dimmer (Borshagovski et al., 2020), and therefore less visible under artificial illumination, and because they have fewer energy reserves with which to produce them. This may explain why smaller females cease glowing earlier under ALAN than do their larger counterparts (Elgert et al., 2021b; Hopkins et al., 2021).

### Roving flashing fireflies

Fireflies that exchange precisely timed, discrete flashes as part of courtship (Figure 3C) seem unlikely to mistake continuously glowing artificial light sources for conspecifics. However, like other bioluminescent taxa, these species are nevertheless vulnerable to masking effects of artificial light.

Several recent studies have examined the impact of ALAN on courtship signaling by North American flashing fireflies, primarily in the genera *Photinus* and *Photuris* (Table 1). Under moderately dim artificial light, a mixed species assemblage reduced their courtship flash activity (number of flash patterns per minute) to 50% of the baseline rate (1.2 lux; Costin and Boulton, 2016). Males of the common crepuscular species *Photinus pyralis* flashed at 75% of their baseline rate when placed directly beneath a bright artificial light source (175 lux; Firebaugh and Haynes, 2019), while nocturnal *Photuris versicolor* fireflies flashed at 30% of baseline within 10 m of a similar source (300 lux; Firebaugh and Haynes, 2016). In the laboratory, males of the semi-nocturnal species *Photinus obscurellus* flashed at approximately 50% of baseline under dim and bright artificial light (24 or 240 lux; Owens and Lewis, 2021b; see also Owens and Lewis, 2022). The number of semi-nocturnal *Photinus sp1* males observed flashing in a transect 60 m from a bright floodlight was 13% of baseline (4 lux; Hagen et al., 2015). Similarly, at a popular firefly ecotourism site, males of the fully nocturnal, synchronous species *P. carolinus* flashed at only 4% of baseline within 5 m of an artificial light source (150 lux, broad-spectrum amber; Owens et al., 2022). Reductions in male courtship flash activity are frequently assumed to correspond to reductions in mate success, but a recent report suggests the strength of this relationship also varies by species (Owens and Lewis, 2022).

How ALAN impacts female courtship flash activity has been less well studied, perhaps because in flashing fireflies, females are typically more cryptic. In most species, however, female behavior determines mate success: the likelihood of any male successfully locating and mating with a female depends on how often she answers his advertisement flashes (Demary et al., 2005; Owens and Lewis, 2022). Recent studies on two *Photinus* species suggest that females are even more sensitive than males to downwelling ALAN (Firebaugh and Haynes, 2016; Owens and

Lewis, 2021b). In *P. pyralis*, white light (175 lux) suppressed female response rates to around 50% of baseline (Firebaugh and Haynes, 2016, 2019). In *P. obscurellus*, female response rates declined to only 10% of baseline under white light (24 or 240 lux), and 50% of baseline under dim red light (Owens and Lewis, 2021b). Females of these species perch near the ground and search the sky for male advertisements, and may therefore be more likely to look directly into an artificial light source than are patrolling males searching the ground for females. Whether subsequent light-adaptation of their compound eyes prevents females from perceiving male flashes entirely or reduces male attractiveness by making their courtship flashes appear dimmer remains unknown. Regardless, reductions in female response flash activity are once again assumed to correspond to reductions in mate success.

Direct investigations into the impact of ALAN on mate success in flashing fireflies have had surprisingly mixed results. In the field, males of the crepuscular species *Photinus greeni* almost never approached imitation females that were directly illuminated when there were unilluminated competitors nearby (5 lux; Owens and Lewis, 2022). However, an early study by Thancharoen (2007) found that pairs of crepuscular *Sclerotia aquatilis* fireflies enclosed together in the laboratory (theoretically obviating the effects of sexual competition and/or impaired mate location) mated successfully under very dim light (0.05–0.3 lux), although courtship and mounting behaviors were prolonged. *P. obscurellus* pairs enclosed together in the laboratory mated successfully under dim light (3 lux) but not bright light (30 lux; Owens and Lewis, 2022). Dim light (5 lux) was relatively more disruptive to the mate success of *P. obscurellus* females permitted to move freely in the field, yet even bright light (>20 lux) had no detectable impact on the mate success of females of the crepuscular species *P. pyralis* and *Photinus marginellus* (Owens and Lewis, 2022).

Some roving flashing fireflies appear therefore capable of behaviorally adapting to ALAN. *P. obscurellus* males in the laboratory plastically increased the intensity, duration, and density (number of flashes per flash pattern) of their advertisement flashes in response to increases in ambient light levels, although these behavioral adaptations were unable to rescue baseline female response rates (Owens and Lewis, 2021b; see also Owens and Lewis, 2022). Other species, especially those active near sunset, may be even more capable of competing with visual noise (but note Borshagovski et al., 2020) or may be able to rely on redundant, as yet undescribed pheromone cues when engaging in courtship and mating activity in a less informative visual environment.

### Stationary synchronous fireflies

Among the most visually impressive of all animal courtships are the communal displays (Figure 3D) created by various lekking fireflies that range from East India through Thailand, Malaysia and Indonesia across to the Philippines



and Papua New Guinea (Ballantyne and Lambkin, 2013; Jusoh et al., 2018; Jaikla et al., 2020a). Such fireflies include several *Pteroptyx* species, in which thousands of males gather in visually prominent display trees along tidal rivers and flash synchronously to create a collective courtship signal that attracts flying females from surrounding areas (Wong and Yeap, 2012; Jusoh et al., 2018; Jaikla et al., 2020a). These congregating fireflies are star attractions in a booming ecotourism sector throughout this region (Lewis et al., 2021), yet surprisingly little is known about how ALAN impacts their behavior or population persistence.

In addition to the disappearance of their mangrove forest habitat, Wong and Yeap (2012) mention bright artificial lights associated with shrimp farms and tourism infrastructure as possible threats to *Pteroptyx* fireflies in Malaysia. However, Prasertkul (2018) recorded large congregations of *Pteroptyx valida* and *P. malaccae* that remained year-round in close proximity to artificial illumination from fluorescent streetlights (3–14 lux) and house lights (0.5–5 lux) in an urban park near Bangkok, Thailand. It thus appears, at least in this urban setting, that light pollution does not prevent *Pteroptyx* males from congregating. It remains unknown whether artificial light might impact mate attraction in congregating fireflies, for example by disrupting male flash synchrony or decreasing female recruitment into congregations. Even after females arrive within *Pteroptyx* display trees, the sexes continue to communicate using flash signals (Case, 1980). In apparent competitive interactions, males flash while aiming their lanterns directly toward nearby males. Before attempting copulation, males also flash while curling their lanterns directly in front of the eyes of the focal female. Additional work is needed to determine whether ALAN affects these close-range sexual interactions.

When poorly managed, tourism exposes local firefly populations to artificial light in numerous ways: distant semi-permanent sources associated with infrastructure (e.g., signage, buildings, and roads) and close-range, transient flash photography. During field observations of *Pteroptyx* spp., Lloyd (1973) reported that males were readily attracted to flashes from a small incandescent penlight, including some males that approached from up to 75 feet away. Thancharoen and Masoh (2019) studied small aggregations of *P. malaccae* brought into the laboratory to examine how tourist photography might impact courtship and oviposition. Flash illumination from smartphones and digital cameras, as well as red autofocus lights, temporarily reduced male flash activity, although most males eventually resumed flashing and successfully mounted females. Males also exhibited decreased synchrony following all types of camera illumination, suggesting that unregulated tourist photography could impede their ability to synchronize in the field. Based on these findings, recently published guidelines for sustainable firefly tourism recommend limiting flashlight

and phone use and prohibiting flash photography (Lewis et al., 2021).

## Predator-prey interactions

Many, but not all, fireflies have protective chemical defenses (Eisner et al., 1997; Tyler et al., 2008; Fu et al., 2009; Berger et al., 2021) that prevent attack by most predators, especially vertebrates (Day, 2011). For firefly adults, bioluminescence is a main component of a multimodal aposematic signal that is also thought to include reflectance-based red, yellow, and black warning coloration (Stevens and Ruxton, 2012), wing beat frequencies (Leavell et al., 2018), and ultrasonic clicks (Krivoruchko et al., 2021). Firefly larvae employ bioluminescence exclusively as an aposematic signal, in combination with warning coloration (De Cock and Matthysen, 2001), and likely have done so for close to 150 million years (Martin et al., 2017; Powell et al., 2022). By interfering with the detection of these reflectance- and emission-based visual signals of unpalatability, ALAN has the potential to heighten predation on firefly adults and larvae (Briolat et al., 2021).

Owens et al. (2018) exposed male *Aquatica ficta* fireflies to artificial illumination of varying spectra and intensity while recording the aposematic alarm flashes they produced in response to the constraints of the experimental apparatus. Alarmed *A. ficta* males responded to ALAN much as did advertising *P. obscurellus* males in a later study (Owens and Lewis, 2021b): their flashes became more conspicuous (brighter and longer) under short- to mid-wavelength artificial light, but were produced at only 45% of the baseline rate. Similarly, an early field study found that *L. noctiluca* and *P. hemipterus* glow-worm larvae glowed less often under bright night skies, especially when passing clouds diffused moonlight and artificial light from nearby developments into their usually dark habitats (De Cock, 2004).

For roving flashing fireflies in the genus *Photuris*, bioluminescence functions in their roles as both predator and prey (Souto et al., 2019). Firebaugh and Haynes (2019) attempted to document interactions between female *P. versicolor* predators and male *P. pyralis* prey within artificially illuminated field enclosures (175 lux). ALAN reduced the flash activity of both species, but no predation was observed in either lit or unlit field enclosures; hence the influence of ALAN on these particular predator-prey interactions remains unclear (Lewis and Owens, 2019).

## Development

The effects of ALAN on earlier firefly life stages are relatively unexplored (Table 1). Owens and Lewis (2021a) conducted laboratory experiments to investigate how ALAN affects the

development of immature *Photuris* sp. and *P. obscurellus* fireflies. Long-term exposure to artificial light at night (50 lux) did not impact overall survivorship or the duration of egg, larval, and pupal stages in either species, both of which spend the majority of their larval lifespan underground. It did however, accelerate weight gain of *Photuris* larvae, perhaps by prolonging perceived daylength – assessed before or during nightly foraging bouts on the soil surface – and thus delaying diapause (Gaston et al., 2017). Rearing aquatic *A. ficta* larvae under very dim ALAN for 2 weeks resulted in high mortality both immediately following and several months after exposure (Chen et al., 2021). Subsequent gene expression profiling of these larvae suggested that ALAN may perturb hormone regulation and suppress reproductive development.

Three recent studies report on larval movements in response to ALAN. Wanjiru Mbugua et al. (2020) found that *Lamprigera* sp. larvae foraging in an urban park could often be found near paved trails, but avoided areas illuminated by streetlights ( $\geq 3$  lux); the few larvae found directly beneath lit streetlights tended to be immobile. Similarly, *Photuris* larvae exposed in the laboratory to point sources of ALAN (800 lux) at the start of their nightly surface foraging period moved toward darker areas, but a significant number burrowed beneath the surface instead of dispersing across it (Owens and Lewis, 2021a). Murphy and Moiseff (2020) also found that uniform ALAN ( $\sim 915$  lux) reduced surface movements of *Photuris* larvae. Such behavioral responses may arise because sufficiently bright ALAN appears to prolong daylength, and nocturnal larvae are inactive during the “day.” By immobilizing larvae, ALAN could increase their chances of being trampled in heavily trafficked areas (an already frequent occurrence: Lehtonen et al., 2021) and impede their ability to disperse into darker habitats where they might enjoy greater reproductive success as adults.

In contrast to most species, the later larval instars of *L. noctiluca* glow-worms (Tyler, 2002; Tyler, 2013) and related species (De Cock and Matthysen, 2001) regularly exhibit diurnal activity. While preparing to pupate, these “walkabout” larvae can often be found crawling over bare soil, rocks, or pavement in broad daylight (e.g., Lehtonen et al., 2021), presumably searching for pupation sites and, among females, associated display sites (Tyler, 2013). If so, individuals may not detect ALAN until they reach their relatively philopatric adult stage, which would explain why adult females can so often be found signaling unsuccessfully from brightly lit display sites (Ineichen and Rüttimann, 2012; Van den Broeck et al., 2021a). In fact, late-instar females that actively search for open habitat (Lehtonen et al., 2021) may use environmental light as a cue for habitat quality, in which case ALAN sources operating before dusk or after dawn could act as ecological traps (*sensu* Robertson et al., 2017).

Further research should reveal which, if any, particular aspects of artificial light environments (spatial, temporal, spectral, etc.) most affect fireflies of all life stages.

## Future directions

### Visual ecology

Because the firefly visual system is highly optimized, what a species perceives can reveal a great deal about how they might respond to artificial light. Unfortunately, little is known about the vision of most species. Electrorretinography and photoreceptor gene sequencing efforts have both thus far primarily revealed the spectral sensitivities of North American (Lall et al., 2009; Sander and Hall, 2015) and Asian (Eguchi et al., 1984) roving flashing fireflies (but see Booth et al., 2004). Data on changes in overall sensitivity due to light-adaptation of the compound eye are also urgently needed to understand the mechanisms underlying the impact of artificial light on courtship and mate success (but see Lall, 1993; Oba and Kainuma, 2009; Smith, 2011). For example, it remains unknown whether glow-worm males and roving flashing firefly females fail to respond to artificially illuminated conspecifics because they are blind to their courtship signals, because their courtship signals appear less bright against the background, or because ALAN transitions fireflies from a mode of nocturnal courtship behavior to one of diurnal resting behavior through temporal disorientation.

### Movement ecology

Fireflies that are negatively impacted by artificial light may be able to persist by sheltering in shaded refuges or dispersing to darker areas of the landscape. For example, species that typically occupy open habitats such as lawns, meadows, or grasslands may aggregate along forest edges or in forest clearings where their signals are more likely to be detected. Whether light-polluted populations are capable of fully transitioning to new habitat types remains unknown, as are the associated fitness costs: even if adults are relatively flexible in their habitat requirements their juvenile stages may not be. Field studies of firefly movement under artificial light are rare and almost exclusively involve single generations of largely subterranean larvae (Wanjiru Mbugua et al., 2020; Owens and Lewis, 2021a; see also Kakehashi et al., 2014) or species that are relatively resilient to ALAN (Firebaugh and Haynes, 2016; Owens and Lewis, 2022; but see Gardiner and Didham, 2021). The primary dispersing life stage (larvae, adult males or females) is also unknown for nearly every species (but see Kaufmann, 1965), despite how crucial this information is for conservation planning (Schultz et al., 2019).

In the absence of long-term survey data (see below), genetic differentiation can reflect the movement of firefly populations not just on evolutionary timescales (Suzuki et al., 2004; Lower et al., 2018; Kim et al., 2021) but also the approximately 20–200 years timescales most relevant to artificial light (e.g., Dayton and Szczys, 2021). Population genetic studies could

reveal whether different species have moved toward or away from intensely light-polluted habitats over time, and whether particular sources have resulted in population sinks or barriers to gene flow, e.g., if lines of regularly spaced streetlights along roads intensify habitat fragmentation. Comparative field surveys and behavioral studies could help confirm and elaborate upon these results. For example, female *L. noctiluca* glow-worms are significantly less abundant near artificial lights (Gardiner and Didham, 2021) but marked individuals rarely leave artificially illuminated display sites either in the field or the laboratory (Elgert et al., 2020; Van den Broeck et al., 2021a), meaning that the current distribution may be symptomatic of a population sink.

Nocturnal insects such as moths, mayflies, and gnats can be maladaptively attracted to artificial lights (Haynes and Robertson, 2021). While male glow-worms have repeatedly been shown to approach artificial lights that are sufficiently dim and long-wavelength so as to resemble female conspecifics (Schwalb, 1961; Booth et al., 2004; Bek, 2015; Pacheco et al., 2016), fireflies are not commonly thought to be attracted to the broad-spectrum artificial lights used for public safety, unless they somehow simulate conspecific courtship signals (i.e., flash patterns). Surprisingly, however, one recent study captured significant numbers of *P. pyralis* and *Photuris* fireflies at non-flashing broad-spectrum light traps (Firebaugh and Haynes, 2019). Because species that are attracted to or simply not repelled by ALAN could be at significantly greater risk of courtship disruption and subsequent population decline, broader understanding of the phototactic tendencies of fireflies should be a research priority.

## Evolutionary adaptation

Few studies have investigated whether fireflies may be evolving physiologically or behaviorally in response to artificial light, a novel selection pressure (Hopkins et al., 2018). Several possibilities merit further investigation.

The amplification of intensity-based sexual selection in light-polluted habitats may result in firefly populations that emit more intense bioluminescent courtship signals, possibly at negligible metabolic cost (Woods et al., 2007). At higher latitudes, *L. noctiluca* females possess larger light organs that emit brighter glows, presumably to attract males during the relatively short and bright summer nights (Borshagovski et al., 2020; compare to Owens et al., 2018). Simulated conspecific courtship advertisements of greater intensity also garner more frequent responses from *P. pyralis* females (Vencl and Carlson, 1998) and attract more *L. noctiluca* males, both in darkness (Hopkins et al., 2015) and under artificial light (Elgert et al., 2021a). Evolutionary adaptations that increase the conspicuousness of bioluminescent signals in order to preserve lines of visual communication may be augmented *via*

the addition of more filter pigments in the compound eye that further narrow long-wavelength sensitivity to the peak wavelength of conspecific bioluminescence.

Alternatively, firefly populations may shift away from a primarily visual communication system toward greater reliance on chemical signals. Pheromones are broadly used as sexual signals by diurnal dark fireflies (Stanger-Hall et al., 2018), and also contribute to the multimodal courtship signals of some nocturnal glow-worms (Ohba, 2004); their use by other firefly species has yet to be fully investigated. Chemical signals should be relatively unaffected by ALAN and therefore may more reliably attract conspecifics within severely light-polluted habitats. Comparisons of multiple urban and rural populations of the same firefly species (e.g., Santangelo et al., 2022) can disentangle the conflicting possibilities described above to reveal whether artificial light promotes or inhibits bioluminescent signaling behavior. If consistent differences are observed, common garden experiments will be able to reveal whether these differences are the result of phenotypic plasticity or rapid evolution. Artificial selection on species that can be reared in the laboratory could then help elucidate the timescales on which such differences are likely to arise and quantify their benefits for reproductive fitness.

A third, related possibility is that some firefly species are already relatively resilient to artificial light due to favorable life history traits (e.g., flightedness, lack of habitat specificity, diurnal or crepuscular temporal niche, use of multimodal courtship signals, asynchronicity, etc.), and are gradually replacing less resilient species within severely light-polluted habitats (see Khattar et al., 2022). For example, *P. pyralis*, the most widespread roving flashing firefly in North America, has a crepuscular courtship period and appears to be relatively unaffected by artificial light (Firebaugh and Haynes, 2016; Owens and Lewis, 2022); *P. pyralis* and other crepuscular species may even be able to capitalize on resultant expansions in their temporal or photic niche, while fully nocturnal species are left at a disadvantage. Although it can be difficult to track the abundances of individual firefly species within a community due to the skill required for species identification (e.g., Lloyd, 2017), long-term expert surveys may be able to document changes in species composition over time and by doing so help predict the future for firefly populations on an increasingly light-polluted planet.

## Conservation recommendations

Clearly much remains to be done. Although long-term survey data are sparse, both anecdotal reports and expert opinion suggest certain firefly populations have recently undergone population declines (Jusoh and Hashim, 2012;

Khoo et al., 2016; Atkins et al., 2017; Faust, 2017; Lloyd, 2017; Gardiner and Didham, 2020; Lewis et al., 2020; Fallon et al., 2021; see also Chatragadda, 2020). A survey of international firefly experts ranked ALAN among the top three threats to fireflies in nearly every geographic region (Lewis et al., 2020). Even in the absence of evidence demonstrating that ALAN is a direct causal factor in firefly declines (but see Cornelisse et al., 2019), the myriad negative impacts of ALAN reviewed here suggest the urgent need for conservation action, especially as the extent and intensity of artificial light continues to grow (Vaz et al., 2021). Many straightforward measures have already been proposed to address the general catastrophe of insect declines (Harvey et al., 2020), and fireflies can act as flagship species to galvanize these efforts. We already know enough to recommend several high priority, no-regret conservation actions for keeping their magic alive, including:

- Prevent habitat degradation by removing or limiting ALAN within protected areas and other locations that support at-risk firefly species.
- Launch education and outreach programs to promote locally appropriate firefly-friendly lighting guidelines (see below).
- Establish standardized monitoring programs to track long-term population trends for fireflies occurring along an ALAN gradient.

Targeted community science monitoring programs (e.g., the UK Glow-worm Survey, Observatoire des vers luisants et lucioles, Night Lights of Kuala Selangor Nature Park, Mass Audubon Firefly Watch, etc.) can be of immense value in identifying firefly populations on the decline. These programs should be continued, expanded, and where possible unified into a single standardized platform that supports species identification (by trained observers or machine-learning algorithms, e.g., Goh et al., 2022). The responses of fireflies to ALAN are highly species-specific, and measures of general firefly activity without accompanying species information can be compromised by changes in species composition. Similarly, firefly surveys should aim to count individuals instead of flashes or glow signals, due to the known effects of ALAN on courtship signaling behavior.

The studies we have reviewed here also provide the basis for more specific lighting recommendations. The simplest and most effective conservation measure is to switch off any lights situated in and around known firefly and glow-worm habitats during mating seasons. On low-traffic roadways, motion sensors that switch off streetlights when vehicles are absent can offer an efficient conservation solution. Where removing artificial lights is not possible for safety reasons, proper shielding should be installed on streetlights to limit light spillage into firefly and glow-worm habitat. Given that extremely low levels of

artificial light reduce mating success of *L. noctiluca* glow-worms (Van den Broeck et al., 2021b), simply dimming streetlights may not suffice to mitigate ALAN impact as it does for some other taxa. Gardiner and Didham (2021) recommend a minimum distance of 100 m between artificial light and glow-worm habitat. Vaz et al. (2021) point out the importance of establishing new protected areas within the darkest places where at-risk fireflies are found, as well as reducing ALAN within existing protected areas. Unfortunately, evidence suggests that no spectrum of artificial light is universally “firefly friendly” (Owens et al., 2018, 2022; Owens and Lewis, 2021b). However, red light is preferable to other colors as it is much less visible to insects generally (van der Kooi et al., 2020); green, yellow, and amber light should be avoided because they are likely to be especially disruptive due to their spectral overlap with firefly bioluminescence.

## Author contributions

AO: conceptualization, writing – original draft, review and editing, and visualization. MV: writing – original draft, review and editing, and visualization. RD: writing – original draft, review and editing, and supervision. SL: conceptualization, writing – original draft, review and editing, and supervision. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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