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Artificial lighting impairs mate attraction in a nocturnal capital breeder

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Artificial lighting at night (ALAN) is increasingly recognised as having negative effects on many organisms, though the exact mechanisms remain unclear. Glow worms are likely susceptible to ALAN because females use bioluminescence to signal to attract males. We quantified the impact of ALAN by comparing the efficacy of traps that mimicked females to attract males in the presence or absence of a white artificial light source (ALS). Illuminated traps attracted fewer males than did traps in the dark. Illuminated traps closer to the ALS attracted fewer males than those further away, whereas traps in the dark attracted similar numbers of males up to 40m from the ALS. Thus, ALAN impedes females' ability to attract males, the effect increasing with light intensity. Consequently, ALAN potentially affects glow worms' fecundity and long-term population survival. More broadly, this study emphasises the potentially severe deleterious effects of ALAN upon nocturnal insect populations.

***Keywords*: Artificial lighting at night (ALAN), visual ecology, transect, sexual selection, mate attraction, mate choice**

INTRODUCTION

Evidence is accumulating that insect populations have declined by as much as 80% over recent decades across parts of Europe (Seibold *et al.*, 2019), although there is considerable variation across studies and taxa. Severe insect declines would threaten the stability and functioning of ecosystems and ultimately affect the ecosystem services that beneficial insects provide, such as crop pollination or reducing herbivory through predation. The causes of these declines remain largely unknown and several factors have been implicated including artificial lighting at night (ALAN) (Grubisic *et al.*, 2018; Owens *et al.*, 2019), which is increasingly recognised as having negative effects on many organisms, from humans to invertebrates (Davies *et al.*, 2013; Gaston *et al.*, 2015; Hölker *et al.*, 2010; Longcore & Rich, 2004;

Royal Commission on Environmental Pollution, 2009). ALAN can disrupt animal communication (Longcore & Rich, 2004), navigation (Salmon *et al*., 1995; Ogden, 1996), reproduction (Kempenaers *et al*., 2010; Longcore, 2010; Rand *et al*., 1997), and ecological interactions (Sanders *et al*., 2018) but how it does so remains a major open question (Owens *et al*., 2019; Gaston *et al*., 2013,2015).

The European glow worm (*Lampyris noctiluca* L.) is an iconic insect species that engenders particular public appeal and support. Glow worms are beetles in the family Lampyridae (fireflies) and share with them a number of critical vulnerabilities (Reed *et al*., 2019): dietary specialisation on snails, a tendency to occur in small isolated populations and limited powers of dispersal confined to one sex. Larvae and adult females are flightless, leaving winged adult males as the main life history stage in which individuals disperse, although little is known about the frequency and distance over which this occurs. This makes glow worms especially susceptible to population isolation resulting from habitat fragmentation. Several studies have indicated recent population and range declines in glow worms (Tyler, 2002; Scagell, 2018; Gardiner, 2007; Gardiner & Tyler, 2002; Bird & Parker, 2014, Ineichen & Rüttimann, 2012, Gardiner & Didham, 2020), but the causes are largely unknown and likely to be multifactorial.

Glow worms are likely to be particularly susceptible to ALAN because of their dependence on nocturnal reproductive behaviour and an unusual sexual signalling system in which glowing females use bioluminescence to transmit an honest fertility signal to males; a brighter glow indicates a larger female and therefore greater potential fecundity (Hopkins *et al*., 2015). Females are capital breeders (Tyler, 2002; Jönsson, 1997) using energy stores accumulated prior to pupation to fuel breeding (Tyler, 2002; Gardiner & Didham, 2020). Male glow worms detect the females' glow using their large compound eyes and fly towards them (Tyler, 2002). Anything that reduces the ability of males to detect glowing females, including ALAN, ultimately reduces the reproductive potential of the population. Likewise, any barriers to successful male dispersal, including ALAN, would further exacerbate the problems of population isolation caused by the inability of females to disperse between habitat fragments.

MATERIALS AND METHODS

Site and Animals

Experiments took place in an area of grazed chalk grassland within the Mount Caburn National Nature Reserve, East Sussex, UK (50°51'31.8"N 0°03'10.8"E). This site is known to have a substantial glow worm population (Booth *et al*., 2004).

Traps

We constructed bespoke traps in which a single green (550nm) LED was mounted above a funnel trap with a funnel 8cm in diameter at the top tapering to 2cm at the bottom (Booth *et al*., 2004). The LED was held on 1mm wire facing upward above the centre of the funnel in line with the upper edge of the trap. Each LED was fed with a 25mA current powered by three 1.5V batteries through a transistor (ACY19 Germanium PNP) to ensure a constant light emission intensity. Traps were placed upright on the ground so that the LED was approximately 18cm above the soil surface. The narrow spectrum emission of the 550nm LED (Supplemental Figure 1a) closely resembled the narrow spectrum emission of the female glow worm (Supplemental Figure 1b). Male glow worms attracted to the LED typically fell through the funnel into the collection vessel below where they were temporarily retained. We observed no adverse effects on the subsequent behaviour of the male glow worms caught in these traps.

Lighting

To simulate typical LED street lights, we used a Solaris Megastar™ SLA24A/h lamp (Nightsearcher Ltd, Farlington, U.K.) mounted facing horizontally at 2.75m above the ground on a metal tripod and powered by a 12V battery. The emission spectrum of this artificial light source (ALS) (Supplemental Figure 1c) resembled the emission spectrum of a typical LED street light (Elvidge *et al*., 2010; Rowse *et al*., 2016). Illuminance emitted by the ALS, measured by a light meter (Handyman TEK1336, Newhaven, U.K.), decayed with distance from the lamp to below the level of detection at 55m (Supplemental Figure 2).

Transect

Two transects were established along level ground running due east and due west from a single ALS, so that it could be shone directly along either transect. Single traps were positioned at 5m intervals along each transect. Throughout 2016 and 2017, these transects spanned 50m in each direction from the ALS (20 traps). Throughout 2018 and 2019 additional traps were added to span up to 55m from the ALS (22 traps).

Procedure

Experiments occurred between 21:00 and 23:00, during June and July 2016-2019, at temperatures >17^{o}C and wind speeds <4 on the Beaufort scale. The first part of the experiment ran for ~40 minutes with the ALS shining along one transect (selected at random), leaving the opposite transect in darkness. This was repeated ~15 minutes later but with the lamp facing in the opposite direction. At the end of each run, male glow worms inside each trap were counted and released. Trap LEDs were not turned on until the ALS was on, and were turned off before the ALS was turned off. When experiments were run on consecutive nights, the direction in which the lamp shone in the first run was reversed.

Statistical analysis

All statistical analyses were conducted in R v3.5.1 (R Core Team, 2018). The numbers of males in traps were analysed using Poisson family generalised linear mixed effects models (GLMM) from the "lme4" package (Bates *et al*., 2015), allowing count data as a response and trial nested within year as a random effect. For some models, traps were binned into pairs based upon distance from the ALS to ensure model convergence. A maximal model was fitted initially (Supplemental Table 1), and non-significant terms were removed step-wise until only significant terms remained. Significant model terms were assessed using Wald Chi-square tests (Type II ANOVA) from the "Car" package (Fox & Weisberg, 2019). Model selection was further verified by comparing AIC scores, with only the lowest scoring model selected. Post-hoc comparisons of levels within significant model terms were conducted with the `glht` function within the "multcomp" package (Hothorn *et al.*, 2008). The p-values were adjusted to account for multiple comparisons.

RESULTS & DISCUSSION

The numbers of males attracted to each trap along either 50m transect differed depending on the distance of the trap from the ALS: the further away, the greater the number of male glow worms that were attracted to the trap (X^2=299.90, Z=10, p<0.001; Figure 1a). The number of males attracted to the most distant trap was greater than in adjacent traps in both the illuminated and dark transects (Figure 1a). This may be due to the reduction in light intensity from the ALS allowing greater numbers of males to locate the traps or may be a consequence of males stopping at the first trap they encounter. To distinguish between these possibilities, we reduced or extended the transect length by a single trap. Turning off the 50m trap significantly increased the numbers of males captured by the 45m trap in both the illuminated and dark transects in comparison to when the 50m trap was turned on (Z=3.88, d.f.=1, p<0.001; Figure 1b). Likewise, the addition of a 55m trap to both transects caused a significant reduction in the numbers of males captured by the 50m trap (Z=4.52, d.f.=1, p<0.001; Figure 1c). These results are compatible with the terminal traps in each transect recruiting males from a larger area without competition from the neighbouring trap, coupled with these males stopping at the first trap they encounter, rather than a direct effect of reduced light intensity from the central light source.

We excluded the most distant traps (45-55m) to avoid the marked increase in the number of males attracted to the final trap of the transect affecting subsequent analysis. We binned pairs of trap from the remaining region from 5 to 40m, comparing the illuminated and dark transects. Combined, traps in the dark transect attracted significantly more males than did traps in the illuminated transect (X^2=78.92, d.f.=3, p<0.001; Figure 2). Moreover, comparison of the number of males caught by traps in the dark transect with those at equivalent distances from the ALS in the illuminated transect revealed that dark traps attracted significantly more males (Z>3.15, d.f.=20, p<0.03; Figure 2). Thus, illumination from the ALS reduced the number of males captured by traps.

Illuminated traps at 5-10m captured similar numbers of males to traps at 15-20m from the ALS (Z=2.35, d.f.=20, p=0.24), as did traps at 25-30m compared with 35-40m from the ALS (Z=0.83, d.f.=20, p=0.99). However, male catch was significantly higher in illuminated traps at 25-30m and 35-40m than in traps at 5-10m and 15-20m on the same transect (Z>6.79, d.f.=20, p<0.001) demonstrating that the effect of ALAN on male capture diminished with distance from the central light source. In contrast, within the dark transect there was no difference in the number of males captured by traps, irrespective of their distance from the ALS up to 40m (Z<1.85, d.f.=20, p>0.55). The impact of direct illumination was so great that dark traps within 20m of the central light source had a greater catch than did illuminated traps 25-40m away (Z>3.63, d.f.=20, p<0.03). Indeed, dark traps caught significantly more males than illuminated traps at all distances (Z>3.15, d.f.=20, p<0.03). This increased ability of traps in the dark transect to attract males in comparison with traps at an equivalent distance in the illuminated transect extended to 55m from the ALS (Z=4.22, d.f.=1, p>0.001).

Artificial lighting at night (ALAN) reduced the ability of traps containing a 550nm LED that mimicked female glow worms (Booth *et al*., 2004) to attract males. The number of males attracted was reduced by ~95% within 10m of the artificial light source (ALS), and though the impact of ALAN diminishes with distance, it remains severe; traps within 5-20m attracted 85% fewer males than those 25-40m away. Indeed, direct illumination reduces the ability to attract males even 55m from the ALS. Traps in the dark always attracted a greater number of males than directly illuminated traps and attracted similar numbers of males irrespective of their distance from the ALS. Thus, direct illumination by ALAN would severely reduce the ability of female glow worms to attract males over long distances, affecting reproduction and, consequently, long-term population survival.

The reduction in the ability of females to attract males may be a consequence of the mechanisms underpinning visual attraction in male European glow worms (Booth *et al*., 2004). Male glow worms are attracted to the ~550nm narrow band emission of a female (Supplemental Figure 1A) and to LEDs that closely mimic this (Supplemental Figure 1B) but combining this signal with short wavelength light ~485nm substantially reduces attraction (Booth *et al*., 2004). Therefore, the prominent short wavelength peak at ~450nm in the ALS emission spectrum (Supplemental Figure 1C) may also reduce male attraction. Additional mechanisms may also play a role in reducing the attractiveness of the female signal. For example, the luminance produced by the ALS illumination and the foliage surrounding a female may reduce the contrast of the female signal. Light adaptation of *L. noctiluca* photoreceptors may also play an important role but, to our knowledge, it has not been described. Photoreceptors of *Photinus* fireflies show saturating responses to light flashes over just two log units of intensity suggesting that they have a limited ability to encode high light intensities (Cronin *et al*., 2000). Consequently, the increased absorption of photons by male photoreceptors exposed to ALAN may cause light adaptation (Laughlin, 1989), reducing sensitivity to the female signal.

Peripheral traps in both transects attracted unexpectedly large numbers of males, which is consistent with males being attracted to and stopping at the first trap they encounter. The linear structure of our transects may have exaggerated this effect because males flying along the transect must encounter one trap first. More typically, females are spread throughout a landscape, though several may be glowing within close proximity. Although males have previously been shown to prefer brighter females (Hopkins *et al*., 2015), this may be influenced by the order in which females are encountered, reducing the advantage of being larger and glowing more strongly.

Directly illuminated females may need to glow for longer to attract males or, in the worst cases, may be unable to attract one at all. Unmated females have been recorded glowing for many weeks to attract males (Tyler, 2002). However, prolonged glowing consumes energy potentially diverting it from the production of eggs, which develop fully only after mating (Tyler, 2002; Hopkins *et al*., 2015), reducing fecundity when mating occurs (Gardiner & Tyler, 2002). It could also increase predation risk thereby reducing survival, though their toxicity means female glow worms have few predators (Tyler, 2002). Smaller females producing a dimmer glow (Hopkins *et al*., 2015) and possessing lower energy reserves to sustain glowing may be affected disproportionately. ALAN may also cause males to spend more time engaged in search flights, depleting their energy reserves and impeding their ability to find a mate. Moreover, ALAN may prevent males from expressing their preference for mating with brighter females (Hopkins *et al*., 2015; Booth *et al*., 2004), which are also the most fecund. Thus, by reducing successful mating, interfering with mate preferences, and depleting energy reserves, ALAN is likely to reduce the number of glow worms in subsequent generations and have a major impact upon their populations.

Although street lighting has been widespread in the UK since the 1930s, there has been recent, widespread replacement of narrow spectrum orange low-pressure sodium lamps and high-pressure sodium lamps by broad spectrum ‘white’ LED lighting (Royal Commission on Environmental Pollution, 2009; De Almeida *et al*., 2014; Pawson *et al*., 2014; Rowse *et al*., 2016). Low-pressure sodium lamps have a narrow spectral emission dominated by the D-lines near 589nm (Kirchhoff & Bunsen, 1860), whereas typical ‘white’ LED street lights have a broad spectrum with a short wavelength peak near 450nm and a broad, long wavelength peak spanning ~490-690nm (Elvidge *et al*., 2010; Rowse *et al*., 2016). The spectral sensitivity of *L. noctiluca* photoreceptors is unknown but those of *Photinus* fireflies have narrow spectral sensitivities, which suggests that the emission spectrum of low-pressure sodium lights may interfere less with female glow worm signals than broad spectrum LED street lights, though this remains untested. The similarity between the emission spectra of typical ‘white’ LED street lights and the ALS employed in this study (Supplemental Figure 1C) suggests that the impact of direct illumination on male glow worms’ ability to find females demonstrated by our experiments is representative of the impact of direct street lighting. Whether European glow worm populations are so severely affected as our results suggest depends upon their proximity to direct street lighting. Our results suggest that females can attract males even when signalling close to LED street lighting provided they are not directly illuminated, due to the rapid attenuation of illumination with distance from the ALS (Supplemental Figure 2).

Light pollution is now widespread, one recent study suggesting that 80% of the Earth’s skies are affected in this way (Kyba *et al*., 2017). In Europe, where *L. noctiluca* is found, 99% of skies are light polluted (Kyba *et al*., 2017). LED street lighting has made light pollution increasingly intrusive in the natural environment, extending its impact to a wider range of species (Royal Commission on Environmental Pollution, 2009; Gaston *et al*., 2015). Indeed, light pollution is present across much of the known range of glow worms in England and Wales (R. Scagell and J.P.W. Scharlemann, pers. comm.), though how much of this is direct illumination and how much is indirect is unknown. Consequently, the presence of ALAN throughout their range may have substantial effects upon glow worm populations, though this may be less severe than the worst possible case predicted by our experiments if it does not involve direct illumination. Simple measures such as screening of glow worm sites from ALAN or the use of baffles on luminaires to reduce stray light could improve sustainability of glow worm populations by ensuring direct illumination is restricted to those areas where it is needed, such as roads and pedestrian footpaths. ALAN may also affect other aspects of glow worm life history such as gene exchange between separate populations; whether illuminated areas act as barriers to male dispersal is unknown but would repay further study.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization and methodology: A.J.A.S., J.E.N.; Data acquisition: A.J.A.S., J.E.N.; Statistical analysis: C.D.P.; Writing: J.E.N., A.J.A.S., C.D.P.; Visualisation: C.D.P., J.E.N.; Project administration and funding acquisition: J.E.N., A.J.A.S.

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Data availability

The data are available in the supplementary information.

Figure legends

Figure 1. Artificial lighting at night (ALAN) reduces male glow worm attraction to traps. A. The number of males attracted to each trap in the 50m transects. B. The number of males attracted to the 45m trap in the transects when the 50m trap is on or off. C. The mean (± SD) number of males attracted to the 50m trap in the transects when the 55m trap is absent or present. Each bar shows the mean (± SD) number of males. Numbers from the illuminated transect are shown in yellow, whilst numbers from the dark transect are shown in blue.

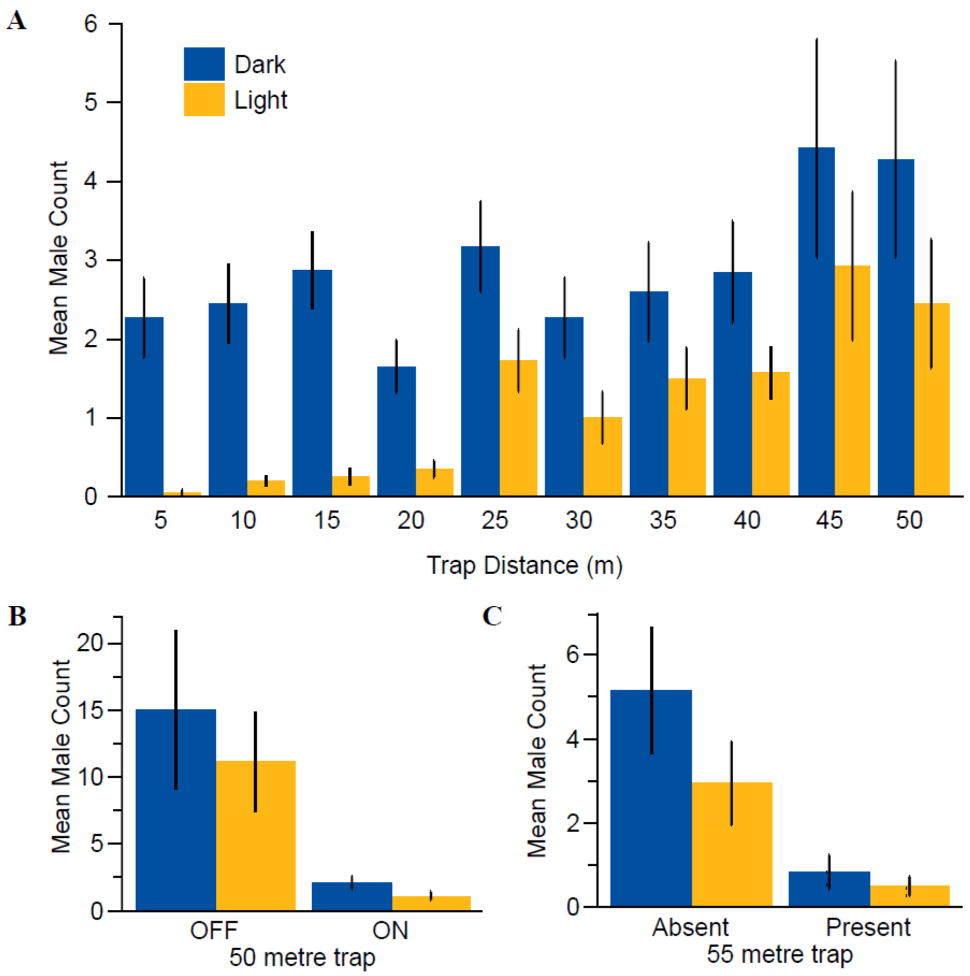

Figure 2. Proximity to an artificial light source reduces trap efficacy. The mean (± SD) number of males attracted to binned pairs of traps in the illuminated or dark transects.