© 2020. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2020) 223, jeb229146. doi:10.1242/jeb.229146

SHORT COMMUNICATION

# Artificial lighting impairs mate attraction in a nocturnal capital breeder

Alan J. A. Stewart[1], Craig D. Perl[1,2] and Jeremy E. Niven[1,*]

## ABSTRACT

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 40 m 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.

**KEY WORDS: 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 and Rich, 2004; Royal Commission on Environmental Pollution, 2009). ALAN can disrupt animal communication (Longcore and 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 and Tyler, 2002; Bird and Parker, 2014; Ineichen and Rüttimann, 2012; Gardiner and 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 and 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 (550 nm) LED was mounted above a funnel trap with a funnel 8 cm in diameter at the top tapering to 2 cm at the bottom (Booth et al., 2004). The LED was held on 1 mm wire facing upward above the centre of the funnel in line with the upper edge of the trap. Each LED was fed with a 25 mA current powered by three 1.5 V 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 18 cm above the soil surface. The narrow spectrum emission of the 550 nm LED (Fig. S1A) closely resembled the narrow spectrum emission of the female glow worm (Fig. S1B). Male glow worms attracted to the LED typically fell

[1]School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG, UK. [2]Department of Zoology: Functional Morphology, Stockholm University, Svante Arrhenius väg 18b, 106 91 Stockholm, Sweden.

*Author for correspondence (j.e.niven@sussex.ac.uk)

A.J.A.S., 0000-0001-7878-8879; J.E.N., 0000-0001-7786-5254

Received 15 May 2020; Accepted 8 July 2020

Journal of Experimental Biology

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, UK) mounted facing horizontally at 2.75 m above the ground on a metal tripod and powered by a 12 V battery. The emission spectrum of this artificial light source (ALS) (Fig. S1C) 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, UK), decayed with distance from the lamp to below the level of detection at 55 m (Fig. S2).

### 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 5 m intervals along each transect. Throughout 2016 and 2017, these transects spanned 50 m in each direction from the ALS (20 traps). Throughout 2018 and 2019, additional traps were added to span up to 55 m from the ALS (22 traps).

### Procedure

Experiments occurred between 21:00 h and 23:00 h, during June and July 2016–2019, at temperatures >17°C and wind speeds <4 on the Beaufort scale. The first part of the experiment ran for ∼40 min with the ALS shining along one transect (selected at random), leaving the opposite transect in darkness. This was repeated ∼15 min 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 (http://www.R-project.org/). The number of males in the traps was analysed using Poisson family generalised linear mixed effects models (GLMM) from the 'lme4' package (Bates et al., 2015), with 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 (Table S1), 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 and 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 AND DISCUSSION

The number of males attracted to each trap along either 50 m 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 ($\chi^2$=299.90, $Z$=10, $P$<0.001; Fig. 1A; Table S2). The number of males attracted to the most distant trap was greater than in adjacent traps in both the illuminated and dark

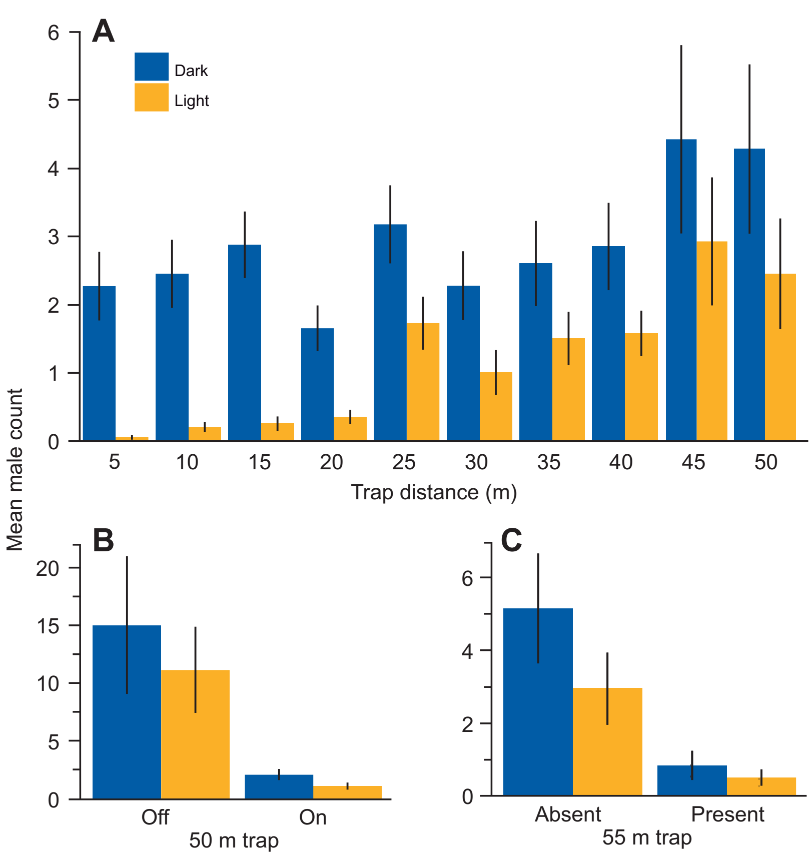


**Fig. 1. Artificial lighting at night (ALAN) reduces male glow worm attraction to traps.** (A) The number of males attracted to each trap in the 50 m transects. (B) The number of males attracted to the 45 m trap in the transects when the 50 m trap was on or off. (C) The number of males attracted to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

transects (Fig. 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 50 m trap significantly increased the number of males captured by the 45 m trap in both the illuminated and dark transects in comparison to when the 50 m trap was turned on ($Z$=3.88, d.f.=1, $P$<0.001; Fig. 1B). Likewise, the addition of a 55 m trap to both transects caused a significant reduction in the number of males captured by the 50 m trap ($Z$=4.52, d.f.=1, $P$<0.001; Fig. 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 (45–55 m) to avoid the marked increase in the number of males attracted to the final trap of the transect affecting subsequent analysis. We binned data from pairs of traps from the remaining region from 5 to 40 m, comparing the illuminated and dark transects. Combined, traps in the dark transect attracted significantly more males than did traps in the illuminated transect ($\chi^2$=78.92, d.f.=3, $P$<0.001; Fig. 2). Moreover, comparison of the number of males caught by traps in the dark transect with that 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; Fig. 2). Thus, illumination from the ALS reduced the number of males captured by traps.

Illuminated traps at 5–10 m captured similar numbers of males to traps at 15–20 m from the ALS ($Z$=2.35, d.f.=20, $P$=0.24), as did traps at 25–30 m compared with those at 35–40 m from the ALS ($Z$=0.83, d.f.=20, $P$=0.99). However, male catch was significantly higher in illuminated traps at 25–30 m and 35–40 m than in traps at 5–10 m and 15–20 m 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 40 m ($Z$<1.85, d.f.=20, $P$>0.55). The impact of direct illumination was so great that dark traps within 20 m of the central light source had a greater catch than did illuminated traps 25–40 m 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 55 m from the ALS ($Z$=4.22, d.f.=1, $P$>0.001).

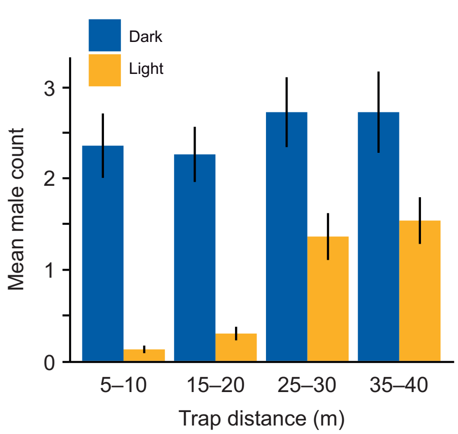


**Fig. 2. Proximity to an artificial light source reduces trap efficacy.** The mean (±s.d.) number of males attracted to binned pairs of traps in the illuminated or dark transects.

ALAN reduced the ability of traps containing a 550 nm LED that mimicked female glow worms (Booth et al., 2004) to attract males. The number of males attracted was reduced by ∼95% within 10 m of the ALS, and though the impact of ALAN diminished with distance, it remained severe; traps within 5–20 m attracted 85% fewer males than those 25–40 m away. Indeed, direct illumination reduced the ability to attract males even 55 m 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 ∼550 nm narrow band emission of a female (Fig. S1A) and to LEDs that closely mimic this (Fig. S1B) but combining this signal with short wavelength light of ∼485 nm substantially reduces attraction (Booth et al., 2004). Therefore, the prominent short wavelength peak at ∼450 nm in the ALS emission spectrum (Fig. S1C) 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 and 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 and Bader, 2014; Rowse et al., 2016). Low-pressure sodium lamps have a narrow spectral emission dominated by the D-lines near 589 nm (Kirchhoff and Bunsen, 1860), whereas typical 'white' LED street lights have a broad spectrum with a short wavelength peak near 450 nm and a broad, long wavelength peak spanning ∼490–690 nm (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 (Fig. S1C) 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 as severely affected as our results suggest depends upon their proximity to direct street lighting. Furthermore, our findings indicate that females can attract males even when signalling close to LED street lighting, provided they are not directly illuminated, because of the rapid attenuation of illumination with distance from the ALS (Fig. S2).

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, personal communication), 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 the 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.

**Acknowledgements**
We thank Jörn Scharlemann, Wiebke Schuett and Tom Stewart for help with experiments, and Chris Wade for the loan of the light source. We also thank Noora Nevala and Tom Baden for the use of their spectrophotometer.

**Competing interests**
The authors declare no competing or financial interests.

**Author contributions**
Conceptualization: A.J.A.S., J.E.N.; Methodology: A.J.A.S., J.E.N.; Formal analysis: C.D.P.; Investigation: A.J.A.S., J.E.N.; Data curation: A.J.A.S.; Writing - original draft: A.J.A.S., J.E.N.; Writing - review & editing: A.J.A.S., C.D.P., J.E.N.; Visualization: C.D.P., J.E.N.; Supervision: A.J.A.S., J.E.N.; Project administration: A.J.A.S., J.E.N.; Funding acquisition: A.J.A.S., J.E.N.

**Funding**
This work was supported by the University of Sussex Research Development Fund (RDF8-005 to A.J.A.S. and J.E.N.) and a UKRI Biotechnology and Biological Sciences Research Council project grant (BB/S018093/1 to J.E.N. and A.J.A.S).

**Supplementary information**
Supplementary information available online at
https://jeb.biologists.org/lookup/doi/10.1242/jeb.229146.supplemental

**References**
**Bates, D., Mächler, M., Bolker, B. and Walker, S.** (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-48. doi:10.18637/jss.v067.i01
**Bird, S. and Parker, J.** (2014). Low levels of light pollution may block the ability of male glow-worms (*Lampyris noctiluca* L.) to locate females. *J. Insect. Cons.* **18**, 737. doi: 10.1007/s10841-014-9664-2
**Booth, D., Stewart, A. J. A. and Osorio, D.** (2004). Colour vision in the glow-worm *Lampyris noctiluca* (L.) (Coleoptera: Lampyridae): evidence for a green-blue chromatic mechanism. *J. Exp. Biol* **207**, 2373-2378. doi:10.1242/jeb.01044
**Cronin, T. W., Järvilehto, M., Weckström, M. and Lall, , A. B.** (2000). Tuning of photoreceptor spectral sensitivity in fireflies (Coleoptera: Lampyridae). *J. Comp. Physiol. A* **186**, 1-12. doi:10.1007/s003590050001
**Davies, T. W., Bennie, J., Inger, R., Hempel Ibarra, N. and Gaston, K. J.** (2013). Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Glob. Change Biol.* **19**, 1417-1423. doi:10.1111/gcb.12166
**De Almeida, A., Santos, B., Paolo, B. and Quicheron, M.** (2014). Solid state lighting review—potential and challenges in Europe. *Renew. Sust. Energ. Rev.* **34**, 30-48. doi:10.1016/j.rser.2014.02.029
**Elvidge, C. D., Keith, D. M., Tuttle, B. T. and Baugh, K. E.** (2010). Spectral identification of lighting type and character. *Sensors* **10**, 3961-3988. doi:10.3390/s100403961
**Fox, J. and Weisberg, S.** (2019). *An R Companion to Applied Regression*, 3rd edn. Thousand Oaks, CA: Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/
**Gardiner, T.** (2007). Short-term changes (2001-2005) in Glow-worm *Lampyris noctiluca* L. (Coleoptera: Lampyridae) abundance in Essex. *Brit. J. Entomol. Nat. Hist.* **20**, 1-7.
**Gardiner, T. and Didham, R. K.** (2020). Glowing, glowing, gone? Monitoring long-term trends in glow-worm numbers in south-east England. *Insect Conserv. Diver.* **13**, 162-174. doi: 10.1111/icad.12407
**Gardiner, T. and Tyler, J.** (2002). Are glow-worms disappearing? *Brit. Wild* **13**, 313-319.
**Gaston, K. J., Bennie, J., Davies, T. W. and Hopkins, J.** (2013). The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev. Camb. Philos. Soc.* **88**, 912-927. doi: 10.1111/brv.12036
**Gaston, K. J., Visser, M. E. and Hölker, F.** (2015). The biological impacts of artificial light at night: the research challenge. *Phil. Trans. R. Soc. B* **370**, 20140133. doi:10.1098/rstb.2014.0133
**Grubisic, M., van Grunsven, R. H. A., Kyba, C. C. M., Manfrin, A. and Hölker, F.** (2018). Insect declines and agroecosystems: does light pollution matter? *Ann. App. Biol.* **173**, 180. doi:10.1111/aab.12440
**Hölker, F., Wolter, C., Perkin, E. K. and Tockner, K.** (2010). Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681-682. doi:10.1016/j.tree.2010.09.007
**Hopkins, J., Baudry, G., Candolin, U. and Kaitala, A.** (2015). I'm sexy and I glow it: female ornamentation in a nocturnal capital breeder. *Biol. Lett* **11**, 20150599. doi:10.1098/rsbl.2015.0599
**Hothorn, T., Bretz, F. and Westfall, P.** (2008). Simultaneous Inference in General Parametric Models. *Biom. J.* **50**, 346-363. doi:10.1002/bimj.200810425
**Ineichen, S. and Rüttimann, B.** (2012). Impact of artificial light on the distribution of the common European glow-worm, *Lampyris noctiluca* (Coleoptera: Lampyridae). *Lampyrid* **2**, 31-36.
**Jönsson, K. I.** (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57-66. doi:10.2307/ 3545800
**Kempenaers, B., Borgström, P., Loës, P., Schlicht, E. and Valcu, M.** (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr. Biol* **20**, 1735-1739. doi: 10.1016/j.cub.2010.08.028
**Kirchhoff and Bunsen** (1860). Chemical analysis by spectrum-observations. *Philos. Mag.* **20**, 89-109. doi:10.1080/14786446008642913
**Kyba, C. C. M., Kuester, T., de Miguel, A. S., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C. D., Gaston, K. J. and Guanter, L.** (2017). Artificially lit

surface of Earth at night increasing in radiance and extent. *Sci. Adv.* **3**, e1701528. doi:10.1126/sciadv.1701528
**Laughlin, S. B.** (1989). The role of sensory adaptation in the retina. *J. Exp. Biol* **146**, 39-62.
**Longcore, T.** (2010). Sensory ecology: night lights alter reproductive behavior of blue tits. *Curr. Biol* **20**, R893-R895. doi.org/10.1016/j.cub.2010.09.011
**Longcore, T. and Rich, C.** (2004). Ecological light pollution. *Frontiers Ecol. Env* **2**, 191-198. doi:10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2
**Ogden, L. J. E.** (1996). *Collision Course: The Hazards of Lighted Structures and Windows to Migrating Birds*. Toronto, Canada: WWF Canada & Fatal Light Awareness Program.
**Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K. and Seymoure, B.** (2019). Light pollution is a driver of insect declines. *Biol. Conserv.* **15**, e0229476. doi:10.2139/ssrn.3378835
**Pawson, S. M. and Bader, M. K.-F.** (2014). LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecol. Appl* **24**, 1561-1568. doi:10.1890/14-0468.1
**Rand, A. S., Bridarolli, M. E., Dries, L. and Ryan, M. J.** (1997). Light levels influence female choice in túngara frogs: predation risk assessment? *Copeia* **2**, 447-450. doi:10.2307/1447770
**Reed, J. M., Nguyen, A., Owens, A. C. S. & Lewis, S. M**. (2019). Linking the seven forms of rarity to extinction threats and risk factors: an assessment of North American fireflies. *Biodivers. Conserv*. doi.org/10.1007/s10531-019-01869-7
**Rowse, E. G., Harris, S. and Jones, G.** (2016). The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. *PLoS ONE* **11**, e0150884. doi: 10.1371/journal.pone.0150884
**Royal Commission on Environmental Pollution** (2009). *Artificial Light in the Environment*. London, UK: The Stationary Office.
**Salmon, M., Tolbert, M. G., Painter, D. P., Goff, M. and Reiners, R.** (1995). Behavior of loggerhead sea turtles on an urban beach. II. Hatching orientation. *J. Herpetol* **29**, 568-576. doi:10.2307/1564740
**Sanders, D., Kehoe, R., Cruse, D., van Veen, F. J. F. and Gaston, K. J.** (2018). Low levels of artificial light at night strengthen top-down control in insect food web. *Curr. Biol* **28**, 2474-2478. doi:10.1016/j.cub.2018.05.078
**Scagell, R.** (2018). UK Glow worm Survey. www.glowworms.org.uk.
**Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., et al.** (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* **574**, 671-674. doi:10.1038/s41586-019-1684-3
**Tyler, J.** (2002). *The Glow-Worm*. Kent, UK: Lakeside Printing Ltd.