Multiple night-time LED lighting strategies impact grassland invertebrate assemblages

Running head: LED lighting impacts grassland invertebrates

Thomas W. Davies, Jonathan Bennie, Dave Cruse, Dan Blumgart, Richard Inger and Kevin J. Gaston.

Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK.

Corresponding authors: Thomas Davies; Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK; Thomas.Davies@exeter.ac.uk

Jonathan Bennie; Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9FE, UK; J.J.Bennie@exeter.ac.uk

Key Words: Artificial light at night, Light Emitting Diodes, LED, light pollution, grassland, invertebrates, spiders, beetles.

Primary Research Article

Abstract

White Light Emitting Diodes (LEDs) are rapidly replacing conventional outdoor lighting technologies around the world. Despite rising concerns over their impact on the environment and human health, the flexibility of LEDs has been advocated as a means of mitigating the ecological impacts of globally widespread outdoor night-time lighting through spectral manipulation, dimming and switching lights off during periods of low demand. We conducted a three year field experiment in which each of these lighting strategies was simulated in a previously artificial light naïve grassland ecosystem. White LEDs both increased the total abundance and changed the assemblage composition of adult spiders and beetles. Dimming LEDs by 50% or manipulating their spectra to reduce ecologically damaging wavelengths partially reduced the number of commoner species affected from seven to four. A combination of dimming by 50% and switching lights off between midnight and 04:00 am showed the most promise for reducing the ecological costs of LEDs, but the abundances of two otherwise common species were still affected. The environmental consequences of using alternative lighting technologies are increasingly well established. These results suggest that while management strategies using LEDs can be an effective means of reducing the number of taxa affected, averting the ecological impacts of night-time lighting may ultimately require avoiding its use altogether.

Introduction

White Light Emitting Diodes (LEDs) have come to revolutionise the way we illuminate the night. Their improved energy efficiency over alternative electric lighting makes LEDs highly attractive for cutting costs and reducing the world's CO_2 emissions (Schubert & Kim, 2005, Pimputkar *et al.*, 2009, although see Kyba *et al*. 2014). Such are the potential cost savings that LEDs have risen from a 9% share in the global lighting market in 2011 to 45% in 2014, and are forecast to reach 69% by 2020 (Zissis & Bertoldi, 2014). Their compact design and low heat loss has led to LEDs becoming near ubiquitous in all aspects of human life from interior, exterior and decorative lighting to desktop, handheld and wearable displays. Yet while LEDs have been hailed for improving energy efficiency and combating global climate change, the dramatic pace of this revolution has raised numerous concerns among environmental scientists and human health experts (Falchi *et al.*, 2011, Davies *et al.*, 2014, Haim & Zubidat, 2015). From a health perspective, the prominent peak of blue wavelength light emitted by commonly used white LEDs occurs at the most effective frequency for suppressing melatonin production (West *et al.*, 2011, Haim & Zubidat, 2015), and has been linked to sleep disorders, obesity and the progression of some cancers (Cajochen *et al.*, 2011, Falchi *et al.*, 2011, Haim & Portnov, 2013, Chang *et al.*, 2015, Keshet-Sitton *et al.*, 2015). Ecologically, a variety of biological processes are known to be sensitive both to the short wavelength peak and broad range of wavelengths emitted by white LEDs, including circadian rhythms (de Jong *et al.*, 2016), organism navigation (van Langevelde *et al.*, 2011, Båtnes *et al.*, 2013, Rivas *et al.*, 2015), reproduction (Gorbunov & Falkowski, 2002), and colour guided behaviours (Davies *et al.*, 2013, Gaston *et al.*, 2012). Consequently, outdoor LED lighting is likely disrupting the balance of species interactions (Davies *et al.*, 2013) and creating unprecedented niche overlaps between nocturnal and diurnal species (Macgregor *et al.*, 2014).

The counter narrative to these concerns has been that the numerous documented ecological impacts of night-time lighting can be mitigated by capitalising on the flexibility offered by LEDs while simultaneously benefiting from their cost saving and CO_2 cutting credentials (Schubert & Kim, 2005, Gaston *et al.*, 2012, Gaston, 2013). A number of management strategies have been proposed to minimize the impacts of artificial light on the environment which LEDs make feasible, including manipulating spectra to avoid ecologically damaging wavelengths, dimming, and switching lights off during periods of low demand (Gaston *et al.*, 2012). These strategies have been widely adopted to cut local government expenditure in the fallout from the 2008 financial crisis, but with no investigation of whether they mitigate the ecological impacts of using either LEDs or night-time artificial light more generally.

Using a manipulative three year field experiment in which night-time lighting was introduced into a previously artificial light naïve grassland ecosystem, we determined the impact of white LED lighting on the structure and composition of adult spider (Aranaea) and beetle (Coleoptera) assemblages, and investigated the utility of alternative LED management strategies for mitigating these effects. We define our assemblages following the convention of Fauth *et al*. (1996) as '*phylogenetically related groups within a community*' where a community is considered '*as a collection of species occurring in the same place at the same time*'.

Methods

Overview

Twenty-four 16m^2 plots (n=6 per treatment) were illuminated at night (in addition to six unlit control plots) with cool white LED lighting equivalent to that experienced at ground level under LED street lighting (High Intensity White, HIW; 29.6 ± 1.2 SE lux), LED street lighting that is dimmed by 50% (Dimmed White, DW; 14.6 ± 0.3 SE lux), LED street lighting that is both dimmed and timed to switch off between midnight and 04:00am (Dimmed White Timer, DWT; 14.4 ± 0.8 lux), and amber LED lighting (AMB; 18.2 ± 1.3 lux) with a spectral peak at 588nm (approximating that of low pressure sodium street lighting widely used during the mid to late 20th century). Lights were switched on in April 2012 and maintained thereafter. Mobile invertebrates were collected from underneath the lights for three days and three nights in May, July and September (total annual sampling effort of nine days and nights) of each year using 8cm diameter pitfall traps.

Experimental setup

The thirty 16m^2 artificially lit and control plots (n=6 per treatment) were established across 0.12km^2 of previously grazed temperate grassland (Figure S1) in the UK (lat: 50.035159; long: -5.206489). Each light consisted of a down facing panel of either 24 cool white (HIW), 12 cool white (DW) or 72 amber (AMB) LEDs (spectra given in Bennie *et al*. (2015)) mounted 1m above ground level on a wooden frame. The dimmed part night lighting treatment (DWT) was created using a timer which switched additional dimmed white lighting rigs off between 00:00am and 04:00am GMT. Unlit control plots contained only the wooden frame. LEDs were mounted inside boxed housings which directed the light across a 16m^2 treatment area and prevented light spill into neighbouring plots. Each replicate was 5m apart in a randomly allocated grid pattern. All LEDs were powered via thirteen 12V 125Ah batteries trickle charged with 100W solar panels, and automatically switched on at dusk (70 lux) and off at dawn (110 lux). Lights were switched on in April 2012, maintained all year round for the duration of the study and the light levels recorded bimonthly each fieldwork season using a photo/radiometer (HD2102.2, Delta Ohm, Caselle di Selvazzano, Italy). The vegetation was cut back and removed in October and March of each year to simulate the impact of hay meadow management on the system.

Sampling

Pitfall trapping was conducted for three days and three nights per month during May, July and September of each year. Diurnal and nocturnal species were caught and enumerated separately, so that inferences could be drawn regarding whether differences in abundance were primarily driven by impacts on organism movement at night, or reflected compositional effects that occurred irrespective of the time of day. Nocturnal and diurnal assemblages were trapped separately by placing two pitfall traps within each plot, and swapping a lid between them at dawn and dusk on each sampling day. Trap contents were rinsed through a 500µm mesh sieve to isolate mobile macrofauna and preserved in 90% Industrial Methylated Spirit or Ethanol pending analysis in the laboratory. Adult spiders (Araneae) and beetles (Coleoptera) were identified to the lowest practicable resolution (species level wherever possible) using a range of identification guides (Joy, 1932, Roberts, 1993, Luff, 2007, Lott, 2009, Lott & Anderson, 2011) and enumerated. Herbivores were not included in the analysis because their abundances are not well represented by pitfall traps (rather than, say, suction sampling), which are the most appropriate method for sampling large mobile ground dwelling invertebrates that are known to be affected by street lighting (Davies *et al*. 2012).

Statistics

The impact of light treatment (Treatment) and time of day (Time: day or night) on the total abundance and composition of spider and beetle assemblages was compared relative to the controls in each year separately. Poisson generalised linear mixed effects models were performed on total abundance data using the R package lme4 (Bates *et al.*, 2015), while assemblage composition was analysed using permutational Multivariate Analysis of Variance (perMANOVA) in the R package vegan (Oksanen *et al.*, 2015).

For total abundance, four nested models (~Treatment; ~Treatment + Time; ~Treatment:Time; and a null intercept only) were first fitted to the data with plot included as a random effect to control for repeated measures taken from the same plots at different times of day (day and night). The most parsimonious of these (that with the lowest value of Akaike's Information Criterion, AIC) was then selected and the significance of the model terms tested using likelihood ratio tests (Table 1). Pairwise contrasts between light treatments and controls (supporting information Table S1), and high intensity white lighting (HIW) and alternative lighting treatments (supporting information Table S2) were extracted for the most parsimonious models using the R package lsmeans (Lenth, 2015).

The impact of light treatment and time of day (Treatment:Time) on the composition of spider and beetle assemblages was assessed using perMANOVA performed on zero adjusted Bray-Curtis (Clarke *et al.*, 2006) dissimilarity matrices calculated from log($x+1$) transformed species abundance data. Pairwise contrasts between light treatments and controls (supporting information Table S1), and high intensity white (HIW) and alternative light treatments (supporting information Table S2) were extracted by performing independent tests for each Treatment:Time combination where these two terms significantly interacted with each other, and each Treatment level when they did not.

The impact of the light treatments on the abundance of each taxon was assessed in each year. Individual taxa display differing patterns of rarity and dispersion, hence we followed the approach outlined by Zuur *et al*. (2009) to identify the most parsimonious model to fit in each case. Poisson, negative binomial, zero adjusted Poisson and zero adjusted negative binomial generalized linear models were fitted in each species abundance ~ Treatment analysis using the R package gamlss (Rigby & Stasinopoulos, 2005), and the most parsimonious model selected using AIC. The selected model was used to assess the impact of light treatment on the abundance of that species via a likelihood ratio test comparing the full model

(~Treatment) with a null intercept only model (supporting information Table S3). Abundance data collected during the day and the night were pooled in order to maximise the number of species with sufficient occurrence across replicates (occurring in n>=10 replicates) for tests to be reliably performed in each year. Pairwise contrasts (supporting information Table S4) between treatments and controls were extracted from the full model, except in cases where a taxon was not present in any control plot, but was present within treatment plots. In these instances pairwise contrasts were extracted from a no intercept model so that abundances under each light treatment were compared to 0.

We did not correct values of α for the high volume (320) of tests performed in the study as it allows the number taxa sampled and the species richness of the community, the number of years sampled and number of treatments compared to have undue influence on the results. Indeed the application of corrections for false discovery rate in ecological field studies is disputed (Moran 2003), and the number of tests performed in this case is sufficiently high that correcting for false discoveries would likely inflate our Type II error rate.

Results

During the 27 day sampling effort, we collected 5,180 individuals that were later identified into 136 taxa representing 8 families of spider and 14 families of beetle. 92.6% of taxa representing 72% of individuals were identified to species level, 5.9% of taxa representing 26% of individuals to genus and 2.2% of taxa representing 2% of individuals to family or subfamily.

LED impacts on assemblage structure and composition

The total abundance and composition of the spider assemblage was significantly affected by the introduction of the night-time LED lighting treatments within the first year (Table 1, Fig. 1, results of pairwise contrasts with controls and HIW are given in Tables S1 & S2 respectively). The total abundance of spiders was significantly higher under the amber, high intensity white and dimmed white LEDs compared to controls during both the day and the night (Fig. 1b, Table S1) in 2012, indicating that individuals attracted to lit habitats at night did not re-disperse during the day. Switching dimmed white LEDs off between 00:00 and 04:00 (DWT) avoided these impacts during the day (Fig. 1b, Table S1) and reduced them compared to all night high intensity white LED lighting (HIW) at night (Table S2). As the total abundance of spiders declined across all treatments throughout the study, pairwise differences between the controls and light treatments progressively disappeared (Fig. 1b, Table S1), first at night and then during the day. By the end of September 2013, spider abundance was significantly higher under all of the light treatments during the day, but only the amber (AMB) and high intensity white (HIW) LEDs had an impact at night (Fig. 1b, Table S1). A combination of dimming high intensity white LEDs and switching them off between 00:00 and 04:00 (DWT) reduced impacts on spider abundance during the day and the night in 2013, while amber (AMB) and dimmed white LEDs (DW) reduced these impacts at night only (Table S2). No impact of the lights on spider abundance was observed during 2014 (Table 1). These changes in spider abundance were reflected in tests of assemblage composition, which was significantly dissimilar between all lighting strategies and the controls both during the day and night in 2012; the amber (AMB), high intensity white (HIW) and dimmed white (DW) LEDs were significantly dissimilar from the controls during both the day and the night in 2013; and only amber (AMB) LEDs had an impact at night during 2014 (Table S1).

Beetles displayed the inverse response to spiders over time. Significant differences in total abundance between light treatments and controls were not observed until 2014 (Table S1; Fig. 1c,d). High intensity white (HIW) and dimmed white (DW) LED treatments significantly increased the abundance of beetles compared to controls during 2014 (Table S1; Fig. 1c,d), an effect that was consistent between the day and the night (Table 1). These impacts were ameliorated by a combination of dimming and switching LEDs off between 00:00 and 04:00 (DWT) which avoided the observed impacts of other white lighting strategies during both the day and night (Table S1, Table S2). Compositional effects were not observed until 2014 when the assemblages collected from under the high intensity white (HIW) and dimmed white (DW) LED treatments were significantly dissimilar from controls (Table S1), reflecting the results for total abundance.

Comparing lighting strategies

We evaluated the ecological impact of each lighting strategy by comparing the total number of taxa whose abundances were significantly affected by each light treatment in any year of the study as derived using generalised linear models (see Methods). Abundance data collected during the day and the night were pooled for this analysis in order to maximise the number of species with sufficient occurrence across replicates (n>=10) for tests to be reliably performed in each year. Of the twenty four commonly occurring taxa for which tests could be reliably performed, the abundances of eight (33%) including five spider (Lycosidae: *Trochosa ruricola;* Tetragnathidae: *Pachygnatha degeeri*; Linyphiidae: *Dicymbium nigrum*, *Centromerita bicolor*, and *Oedothorax spp*, *retuses* and *fuscus* combined) and three beetle taxa (Carabidae: *Pterostichus niger*; Pselaphidae: *Rybaxis longicornis*; Ptiliidae: *Acrotrichis spp.*) were significantly higher under at least one of the light treatments (Fig. 2; Treatment effects are given Table S3; pairwise contrasts with controls are given in Table S4) in one or more years of the study, although pairwise differences between treatments and controls could not be established for *C. bicolor* due to low numbers (Fig. 2c, Table S4).

The number of taxa affected by each of the lighting strategies over the three year study and in each separate year is summarised in Fig. 3a,b. All night illumination with high intensity white (HIW) LEDs had the most taxonomically widespread impact, significantly affecting the abundance of seven (three beetle and four spider) taxa throughout the study (Fig. 3a). None of the alternative lighting strategies fully mitigated for these effects. Changing the irradiance spectrum of LED lighting to amber light (AMB) comparative to that of low pressure sodium lamps, and dimming the illuminance of high intensity white LEDs by 50% (DW) reduced the number of taxa affected to four. Amber (AMB) LEDs did not mitigate the impact of high intensity white (HIW) LEDs on any affected spider species, but successfully avoided impacts on beetles (Fig. 3b). A combination of dimming high intensity white LEDs by 50% and switching them off between 00:00 and 04:00 AM GMT (DWT) showed the most promise for mitigating their impact, but still significantly increased the abundances of two species compared to controls, one of which (*T. ruricola*) is an apex predator in grassland invertebrate communities.

Abundances of spiders attracted to artificial light at night dramatically declined throughout the study (Fig. 2a-e) until effects were no longer detectable in 2014 (Fig. 3b), while those of beetles attracted to artificial light at night increased until 2014 (Fig. 2f-h) when differences between treatments and controls were first observed. It was not possible to establish whether these temporal trends were caused by the artificial light treatments due to low replication in time (n=3 years) and the potential for them to be driven by site level effects. Compositional changes over time were instead consistent with those expected in UK invertebrate communities following a switch from intensive grazing to management by cutting (Bell *et al.*, 2001), although we cannot rule out the possible influence of inter-annual variability in climate. Inconsistencies in the years where treatment effects on taxon abundance were observed (in Fig. 2) likely result from higher site level species abundances increasing the detectability of aggregations in artificially lit plots.

Discussion

While a handful of studies have so far evaluated the utility of manipulating the spectra, intensity or timing of artificial lights to reduce their ecological impacts (Pawson & Bader, 2014, Azam *et al.*, 2015, De Jong *et al.*, 2015, Rivas *et al.*, 2015), none have provided a direct comparison of these approaches. This study demonstrates for the first time the impacts that modern LED lighting can have on the structure and composition of ground dwelling invertebrate assemblages. We find that changing the spectra of or dimming white LEDs holds limited potential for mitigating these effects, while a combination of dimming and switching lights off during periods of low demand has more potential, but does not completely avert ecological impacts. Our results also provide the first experimental evidence to back up observations that artificial light from street lighting can change the composition of ground dwelling invertebrate communities causing predatory species to aggregate in brightly lit areas (Davies *et al.*, 2012), and extend the range of technologies known to cause such effects from high pressure sodium to LED and likely low pressure sodium also (given the close approximation of the spectral peak of amber LEDs to this technology).

While the rapid expansion of LED lighting is a recent phenomenon, a variety of ecological impacts have already been documented, including increasing the attraction of aerial invertebrates to light sources (Pawson & Bader, 2014); inhibiting predator avoidance behaviours (Wakefield *et al.*, 2015) and reproduction in moths (van Geffen *et al.*, 2015); changing patterns of foraging by bats (Stone *et al.*, 2012); disrupting daily vertical migration patterns in emergent fauna of marine benthic ecosystems (Navarro-Barranco & Hughes, 2015), and altering recruitment to and consequently the composition of marine sessile invertebrate communities (Davies *et al.*, 2015). We find that cool white LED lighting at illuminances of at least 14 lux or above changes the composition of grassland spider and beetle assemblages. White LEDs affected the distribution of different taxonomic groups as the system responded to the cessation of grazing, suggesting that LED lighting can impact a range of species which typically occur under contrasting management regimes (for example grazed agricultural systems adjacent to street lights, as well as non-grazed roadside verges). We conclude that increasingly popular LED street lights are likely having profound impacts on ground-dwelling invertebrates within grassland ecosystems such as roadside verges, which provide important refuges and corridors for dispersal in heavily modified landscapes (Eversham & Telfer, 1994). Taking into account the recently demonstrated impact of white LEDs on artificially assembled grassland invertebrate food webs (Bennie *et al.*, 2015), the potential for this rapidly expanding lighting technology to elicit cascading impacts of artificial light throughout the wider ecosystem by aggregating apex predators such as *T. ruricola* and *P. niger* in brightly lit areas is clear.

The focus for limiting the ecological impacts of white LEDs has so far been on manipulating their spectra to avoid emitting wavelengths which disproportionately affect the environment (Brüning *et al.*, 2016, Longcore *et al.*, 2015, Pawson & Bader, 2014, Rivas *et al.*, 2015). In the current study amber LEDs, which completely avoided blue-green wavelengths known to attract Lepidoptera (van Langevelde *et al.*, 2011), did not mitigate the effects of white LEDs on grassland spiders, while beetles were less sensitive to amber compared to white LEDs. Spectral manipulation has also shown taxonomically inconsistent potential for reducing the attractiveness of lights to aerial invertebrates (Longcore *et al.*, 2015, Pawson & Bader, 2014). We suggest that while appealing in theory, it is unlikely that spectral manipulation can be used to avert all of the ecological impacts of night-time lighting in practice, as different species behaviours are evolutionarily adapted to utilise contrasting wavelengths of light (Davies *et al*. 2013). Indeed, the close approximation of our amber LEDs to the irradiance spectrum of low pressure sodium lamps suggests that street lighting likely had widespread impacts on the composition of grassland spider assemblages in regions where it was used throughout the 20th century.

A combination of dimming white LEDs to 14 lux and switching them off between 00:00am and 04:00am showed most promise for minimising their potential to cause ecological damage but did not completely avoid any impacts. To our knowledge, this is the first assessment of the utility of part night lighting for mitigating the impacts of outdoor lighting on invertebrates, and evidence of its benefits for other artificial light sensitive taxa is limited. Simulations have revealed that this strategy holds limited potential for reducing the impacts of night-time lighting on photophobic bats (Day *et al.*, 2015), and field studies indicate inconsistent benefits between different species (Azam *et al.*, 2015). Hence while we find evidence that a combination of dimming and switching lights off during periods of low demand best reduces the environmental costs of using white LEDs, it is clear that averting any ecological impacts of LEDs ultimately requires limiting their use and indeed that of night-time lighting more broadly. Further, our study may underestimate the impact of LED mitigation strategies on ground dwelling invertebrates, since in real world scenarios the different lighting approaches are unlikely to be deployed in combination, as they are in our experimental setup.

Forecasts suggest that LED lighting will account for 69% of the global lighting market by 2020 (Zissis & Bertoldi, 2014), and the limited number of studies so far conducted indicate that this transition will likely have environmental ramifications. Here we have shown, the influence that LED lighting has on invertebrate assemblages by aggregating predatory species into brightly lit areas, a finding which suggests this technology could have widespread impacts on ecosystems through trophic cascades. Management strategies using LEDs do hold the potential to partially mitigate these impacts, but we conclude they are unlikely to avert the current and future ecological effects of night-time lighting.

Acknowledgements

The research leading to this paper has received funding from the European Research Council (ERC) under the EU's Seventh Framework Program (FP7/2007–2013)/ ERC grant agreement No 268504 to KJG.

References

Azam C, Kerbiriou C, Vernet A *et al.* (2015) Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? Global Change Biology*,* **21**, 4333-4341.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software*,* **67**, 1-48.

Båtnes AS, Miljeteig C, Berge J, Greenacre M, Johnsen G (2013) Quantifying the light sensitivity of *Calanus* spp. during the polar night: potential for orchestrated migrations conducted by ambient light from the sun, moon, or aurora borealis? Polar Biology*,* **38**, 51-65.

Bell JR, Wheater CP, Cullen W (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. Journal of Zoology*,* **255**, 377-387.

Bennie J, Davies TW, Cruse D, Inger R, Gaston KJ (2015) Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. Philosophical Transactions of the Royal Society B*,* **370**, 20140131.

Brüning A, Hölker F, Franke S, Kleiner W, Kloas W (2016) Impact of different colours of artificial light at night on melatonin rhythm and gene expression of gonadotropins in European perch. Science of the Total Environment*,* **543, Part A**, 214-222.

Cajochen C, Frey S, Anders D *et al.* (2011) Evening exposure to a light-emitting diodes (LED)-backlit computer screen affects circadian physiology and cognitive performance. Journal of Applied Physiology*,* **110**, 1432-1438.

Chang A-M, Aeschbach D, Duffy JF, Czeisler CA (2015) Evening use of light-emitting eReaders negatively affects sleep, circadian timing, and next-morning alertness. Proceedings of the National Academy of Sciences, U.S.A., **112**, 1232-1237.

Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis

coefficient for denuded assemblages. Journal of Experimental Marine Biology and Ecology, **330**, 55-80.
Davies TW, Bennie J, Gaston KJ (2012) Street lighting changes the composition of invertebrate communities. Biology Letters, **8**, 764-767.
Davies TW, Bennie J, Inger R, De Ibarra NH, Gaston KJ (2013) Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? Global Change Biology, **19**, 1417-1423.
Davies TW, Coleman M, Griffith KM, Jenkins SR (2015) Night-time lighting alters the composition of marine epifaunal communities. Biology Letters, **11**, 20150080.
Davies TW, Duffy JP, Bennie J, Gaston KJ (2014) The nature, extent, and ecological implications of marine light pollution. Frontiers in Ecology and the Environment, **12**, 347-355.
Day J, Baker J, Schofield H, Mathews F, Gaston KJ (2015) Part-night lighting: implications for bat conservation. Animal Conservation, **18**, 512-516.
De Jong M, Jeninga L, Ouyang JQ, Van Oers K, Spoelstra K, Visser ME (2016) Dose-dependent responses of avian daily rhythms to artificial light at night. Physiology & Behavior, **155**, 172-179.
De Jong M, Ouyang JQ, Da Silva A, Van Grunsven RH, Kempenaers B, Visser ME, Spoelstra K (2015) Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. Philosophical Transactions of the Royal Society B, **370**, 20140128.
Eversham BC, Telfer MG (1994) Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? Biodiversity & Conservation, **3**, 538-545.
Falchi F, Cinzano P, Elvidge CD, Keith DM, Haim A (2011) Limiting the impact of light pollution on human health, environment and stellar visibility. Journal of Environmental Management, **92**, 2714-2722.
Fauth, JE, Bernardo, J, Camara, M, Resetarits, WJ, Van Buskirk, J & McCollum, SA (1996) Simplifying the jargon of community ecology: A conceptual approach. *The American Naturalist,* **147,** 282-286.
Gaston KJ (2013) Sustainability: A green light for efficiency. Nature, **497**, 560-561.
Gaston KJ, Davies TW, Bennie J, Hopkins J (2012) Reducing the ecological consequences of night-time light pollution: options and developments. Journal of Applied Ecology, **49**, 1256-1266.
Gorbunov MY, Falkowski PG (2002) Photoreceptors in the cnidarian hosts allow symbiotic corals to sense blue moonlight. Limnology and Oceanography, **47**, 309-315.
Haim A, Portnov BA (2013) *Light Pollution as a New Risk Factor for Human Breast and Prostate Cancers,* New York, Springer.
Haim A, Zubidat AE (2015) LED light between Nobel Prize and cancer risk factor. Chronobiology International, **32**, 725-727.
Joy N.H. (1932) *A practical handbook to British Beetles*. Riverside Press, Endinburgh.
Keshet-Sitton A, Or-Chen K, Yitzhak S, Tzabary I, Haim A (2015) Can avoiding light at night reduce the risk of breast cancer? Integrative Cancer Therapies, **15**, 145-152.
Kyba, C, Hänel, A & Hölker, F (2014) Redefining efficiency for outdoor lighting. *Energy & Environmental Science,* **7,** 1806-1809.
Lenth R (2015) lsmeans: Least-Squares Means. R package version 2.21-1.
Longcore T, Aldern HL, Eggers JF *et al.* (2015) Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. Philosophical Transactions of the Royal Society of London B, **370**, 20140125.
Lott D.A. (2009) *The Staphylinidae (rove beetles) of Britain and Ireland Part 5: Scaphidiinae, Piestinae, Oxytelinae*. Field Studies Council, Shrewsbury, 100pp.

Lott D.A. & Anderson R. (2011) *The staphylinidae (rove beetles) of Britain and Ireland Parts 7 & 8: Oxyporinae, Steninae, Euaesthetinae, Pseodopsinae, Paederinae, Stapylininae*. Field Studies Council, Shrewsbury, 340pp.

Luff M.L. (2007) *The Carabidae (ground beetles) of Britain and Ireland*. Field Studies Council, Shrewsbury, 247pp.

Macgregor CJ, Pocock MJO, Fox R, Evans DM (2014) Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. Ecological Entomology, **40**, 187-198.

Moran, M.D. (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos,* **100,** 403-405.

Navarro-Barranco C, Hughes LE (2015) Effects of light pollution on the emergent fauna of shallow marine ecosystems: Amphipods as a case study. Marine Pollution Bulletin, **94**, 235-240.

Oksanen J, Guillaume B, Kindt R *et al.* (2015) vegan: Community Ecology Package. R package version 2.3-1.

Pawson SM, Bader MKF (2014) LED lighting increases the ecological impact of light pollution irrespective of color temperature. Ecological Applications, **24**, 1561-1568.

Pimputkar S, Speck JS, Denbaars SP, Nakamura S (2009) Prospects for LED lighting. Nature Photonics, **3**, 180-182.

Rigby RA, Stasinopoulos DM (2005) Generalized additive models for location, scale and shape. Applied Statistics, **54**, 507-554.

Rivas ML, Santidrián Tomillo P, Diéguez Uribeondo J, Marco A (2015) Leatherback hatchling sea-finding in response to artificial lighting: Interaction between wavelength and moonlight. Journal of Experimental Marine Biology and Ecology, **463**, 143-149.

Roberts M.J. (1993) *The Spiders of Great Britian and Ireland Parts 1 & 2*. Harley Books, Colchester.

Schubert EF, Kim JK (2005) Solid-state light sources getting smart. Science, **308**, 1274-1278.

Stone EL, Jones G, Harris S (2012) Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. Global Change Biology, **18**, 2458-2465.

Van Geffen KG, Van Eck E, De Boer RA, Van Grunsven RHA, Salis L, Berendse F, Veenendaal EM (2015) Artificial light at night inhibits mating in a Geometrid moth. Insect Conservation and Diversity, **8**, 282-287.

Van Langevelde F, Ettema JA, Donners M, Wallisdevries MF, Groenendijk D (2011) Effect of spectral composition of artificial light on the attraction of moths. Biological Conservation, **144**, 2274-2281.

Wakefield A, Stone EL, Jones G, Harris S (2015) Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls. Royal Society Open Science, **2**, 150291.

West KE, Jablonski MR, Warfield B *et al.* (2011) Blue light from light-emitting diodes elicits a dose-dependent suppression of melatonin in humans. Journal of Applied Physiology, **110**, 619-626.

Zissis G, Bertoldi P (2014) 2014 Update on the status of the LED market. European Commission Report EU 27000 EN. pp Page.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*, Spinger Verlag.

Supporting information captions

Table S1. Pairwise contrasts between light treatments and controls for models with significant Treatment or Treatment*Time effects in Table 1.

Table S2. Pairwise contrasts between High Intensity White and other LED lighting strategies for models with significant Treatment or Treatment*Time effects in Table 1.

Table S3. The impact of light treatments on the abundances of spider and beetle taxa in a temperate grassland ecosystem.

Table S4. Pairwise contrasts of the difference in abundance between light treatments and controls for species with significant light treatment effects in Table S3.

Table 1. The impact of alternative LED lighting scenarios on the structure and composition of nocturnal and diurnal spider and beetle assemblages in a temperate grassland. For total abundance (*n*), the value of Akaike's Information Criterion (AIC) is presented for models of increasing complexity including a null intercept only (NULL), first order effects of light treatment and time, and a Treatment:Time interaction. Results are presented for those models with the lowest AIC value, with those which are significant at the 95% confidence level underlined. Pairwise comparisons between light treatments and controls were extracted from models with the lowest value of AIC, presented in supporting information Table S1, and illustrated in Figure 1.

			Null	Light treatment			+ Time of day			+ Treatment*Time		
Group	**Response**	**Year**	**AIC**	F,χ^2	***P***	**AIC**	F,χ^2	***P***	**AIC**	F,χ^2	***P***	**AIC**
Spiders	*n*	2012[*]	486	25.52	<0.001	469	0.04	0.842	471	16.16	0.003	463
		2013[*]	432	22.61	<0.001	417	0.01	0.911	419	11.87	0.018	416
		2014[*]	588	1.44	0.837	594	129.96	<0.001	466	20.70	<0.001	454
	Comp	2012[†]	-	3.37	0.002	-	47.77	0.001	-	1.28	0.21	-
		2013[†]	-	2.55	0.002	-	21.12	0.001	-	0.81	0.731	-
		2014[†]	-	0.94	0.562	-	27.03	0.001	-	2.08	0.016	-
Beetles	*n*	2012[*]	380	1.97	0.741	386	81.50	<0.001	306	-	-	309
		2013[*]	285	-	-	288	-	-	289	-	-	291
		2014[*]	413	11.57	0.021	410	104.96	<0.001	307	-	-	308
		2012[†]	-	0.85	0.709	-	12.61	0.001	-	1.28	0.128	-
	Comp	2013[†]	-	1.04	0.394	-	2.65	0.006	-	0.88	0.721	-
		2014[†]	-	1.55	0.030	-	13.29	0.001	-	1.07	0.341	-

[*]Poisson GLMM performed on univariate abundance (*n*) data.
[†]perMANOVA performed on Bray Curtis dissimilarity matrices calculated from log(x+1) transformed multivariate assemblage composition data.
n total abundance
Comp Composition

Figure 1. The impact of alternative LED lighting strategies on the abundance of temperate grassland spiders (Araneae) and beetles (Coleoptera). A and B: Total number of individual spiders and beetles caught in each year respectively. Bar heights and error bars denote means ± 95% confidence intervals. Stars denote differences with the controls that were significant with 95% (*), 99% (**) and 99.9% or greater (***) confidence. Results from these pairwise comparisons are presented in supporting information Table S1. Legend in A applies to all panels; CON = Control, AMB = Amber (18.2 ± 1.3 lux), HIW= High Intensity White (29.6 ± 1.2 SE lux), DW = Dimmed White (14.6 ± 0.3 SE lux), DWT = Dimmed White Timer (14.4 ± 0.8 lux) switched off between 00:00 and 04:00AM GMT.

Figure 2. The impact of alternative LED lighting strategies on the abundance of light sensitive spider (Araneae) and beetle (Coleoptera) taxa from 2012 to 2014. A-E: Abundances of spider taxa; F-H: Abundances of beetle taxa. Bar heights and error bars denote means ± 95% confidence intervals. Stars denote differences with the controls which were significant with 95% (*), 99% (**) and 99.9% or greater (***) confidence. Results from these pairwise comparisons are presented in Table S4. Legend is the same as for Figure 1. Note that *Oedothorax spp* consists of two species *retuses* and *fuscus*. Significant treatment effects were observed for *C. bicolor* (supporting information Table S3), but pairwise contrasts were not significantly different from controls (supporting information Table S4), likely due to difficulty in detecting differences in species with low overall abundance.

Figure 3. Pervasiveness of the impact that alternative LED lighting strategies have on the abundance of spider (Araneae) and beetle (Coleoptera) taxa in a temperate grassland ecosystem. A & B: Bar heights represent the number of grassland beetle and

spider taxa whose abundance was significantly affected by alternative LED lighting strategies over three years (A), and in separate years (B). Note that in all taxa abundances were significantly higher relative to the controls when performing pairwise comparisons (Fig. 2). The number of spider and beetle taxa affected by each treatment in each year is denoted in B by the number of spiders and beetles within bars. The number of taxa affected in B are compared to changes in the total abundance (*n*) of spiders (solid line) and beetles (broken line) throughout the study with axis for each presented on the right side of the plot.

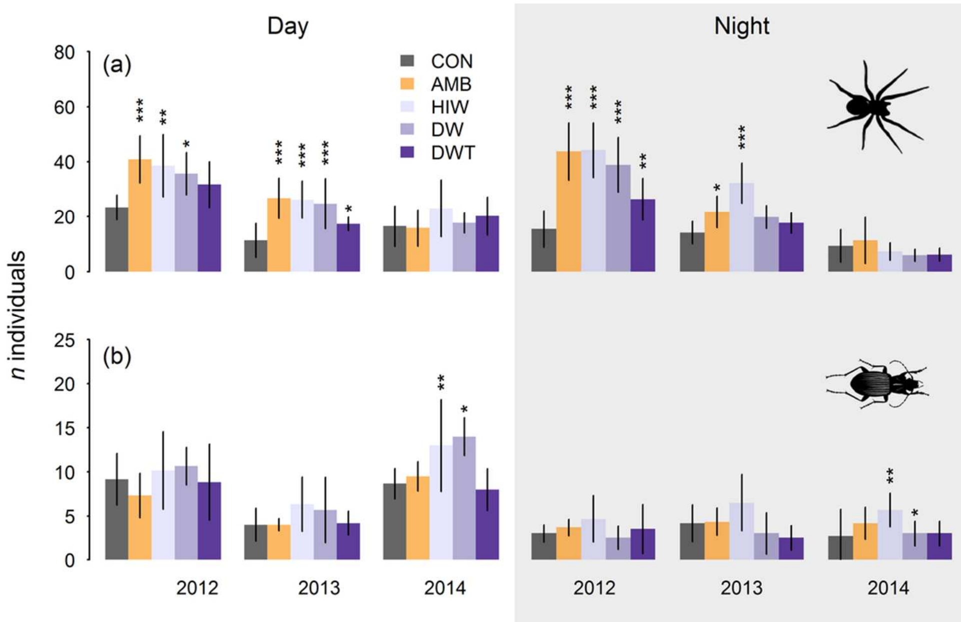

Figure 1. The impact of alternative LED lighting strategies on the abundance of temperate grassland spiders (Araneae) and beetles (Coleoptera). A and B: Total number of individual spiders and beetles caught in each year respectively. Bar heights and error bars denote means ± 95% confidence intervals. Stars denote differences with the controls that were significant with 95% (*), 99% (**) and 99.9% or greater (***) confidence. Results from these pairwise comparisons are presented in supporting information Table S1. Legend in A applies to all panels; CON = Control, AMB = Amber (18.2 ± 1.3 lux), HIW= High Intensity White (29.6 ± 1.2 SE lux), DW = Dimmed White (14.6 ± 0.3 SE lux), DWT = Dimmed White Timer (14.4 ± 0.8 lux) switched off between 00:00 and 04:00AM GMT.

Fig. 1

99x62mm (300 x 300 DPI)

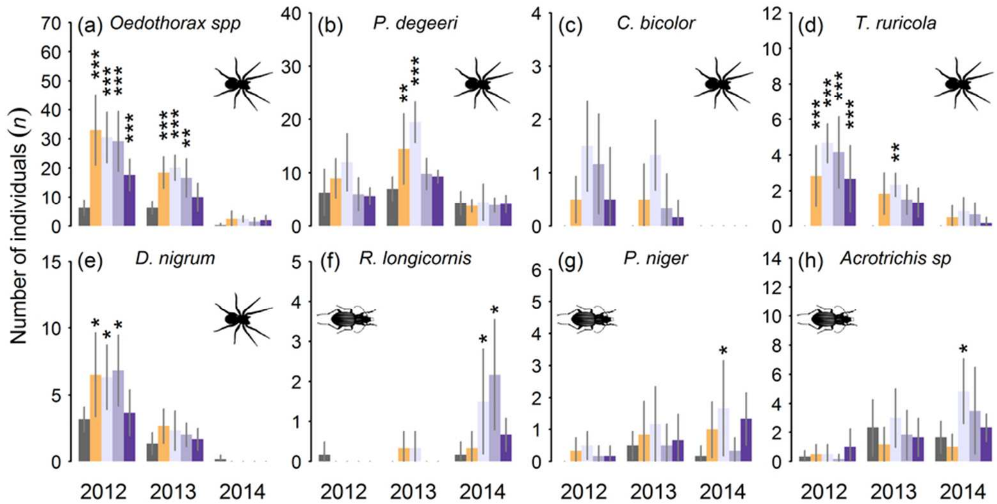

Figure 2. The impact of alternative LED lighting strategies on the abundance of light sensitive spider (Araneae) and beetle (Coleoptera) taxa from 2012 to 2014. A-E: Abundances of spider taxa; F-H: Abundances of beetle taxa. Bar heights and error bars denote means ± 95% confidence intervals. Stars denote differences with the controls which were significant with 95% (*), 99% (**) and 99.9% or greater (***) confidence. Results from these pairwise comparisons are presented in Table S4. Legend is the same as for Figure 1. Note that Oedothorax spp consists of two species retuses and fuscus. Significant treatment effects were observed for C. bicolor (supporting information Table S3), but pairwise contrasts were not significantly different from controls (supporting information Table S4), likely due to difficulty in detecting differences in species with low overall abundance.
Fig. 2
84x45mm (300 x 300 DPI)

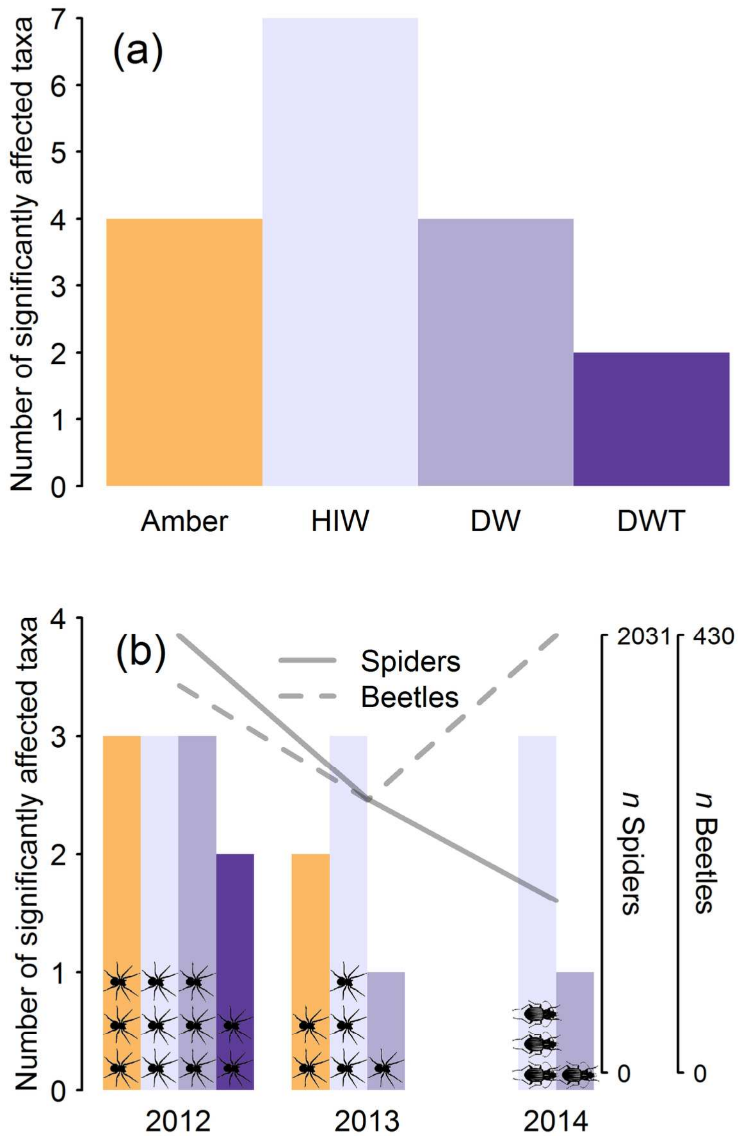

Figure 3. Pervasiveness of the impact that alternative LED lighting strategies have on the abundance of spider (Araneae) and beetle (Coleoptera) taxa in a temperate grassland ecosystem. A & B: Bar heights represent the number of grassland beetle and spider taxa whose abundance was significantly affected by alternative LED lighting strategies over three years (A), and in separate years (B). Note that in all taxa abundances were significantly higher relative to the controls when performing pairwise comparisons (Fig. 2). The number of spider and beetle taxa affected by each treatment in each year is denoted in B by the number of spiders and beetles within bars. The number of taxa affected in B are compared to changes in the total abundance (n) of spiders (solid line) and beetles (broken line) throughout the study with axis for each presented on the right side of the plot.
Fig. 3
119x192mm (300 x 300 DPI)