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DR JONATHAN JAMES BENNIE (Orcid ID : 0000-0003-4394-2041)

DR THOMAS WYNTER DAVIES (Orcid ID : 0000-0002-4673-9893)

PROFESSOR KEVIN J GASTON (Orcid ID : 0000-0002-7235-7928)

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Artificial Light at Night Causes Top-down and Bottom-up Trophic Effects on Invertebrate Populations

Running title: Trophic Effects of Artificial Light

Jonathan Bennie[1,3], Thomas W Davies[1,2,4], David Cruse[1,5], Richard Inger[1,6] and Kevin J. Gaston[1,7]

[1]Environment and Sustainability Institute, University of Exeter, Cornwall Campus, Penryn, Cornwall

UK TR10 9FE

[2]School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey UK LL59 5AB

[3] email: j.j.bennie@exeter.ac.uk

[4] email: thomas.davies@bangor.ac.uk

[5] email: d.cruse@exeter.ac.uk

[6] email: richinger@gmail.com

[7] email: k.j.gaston@exeter.ac.uk

Corresponding authors: Jonathan Bennie, Thomas Davies or Kevin Gaston (joint corresponding authors), Environment and Sustainability Institute, University of Exeter, Cornwall Campus, Penryn, Cornwall UK TR10 9FE, j.j.bennie@exeter.ac.uk, +44 1326 259476

Abstract

1. Globally, many ecosystems are exposed to artificial light at night. Nighttime lighting has direct biological impacts on species at all trophic levels. However, the effects of artificial light on biotic interactions remain, for the most part, to be determined.

2. We exposed experimental mesocosms containing combinations of grassland plants and invertebrate herbivores and predators to illumination at night over a three-year period to simulate conditions under different common forms of street lighting.

3. We demonstrate both top-down (predation controlled) and bottom-up (resource controlled) impacts of artificial light at night in grassland communities. The impacts on invertebrate herbivore abundance were wavelength dependent and mediated via other trophic levels.

4. White LED lighting decreased the abundance of a generalist herbivore mollusc by 55% in the presence of a visual predator, but not in its absence, while monochromatic amber light (with a peak wavelength similar to low pressure sodium lighting) decreased abundance of a specialist herbivore

aphid (by 17%) by reducing the cover and flower abundance of its main food plant in the system. Artificial white light also significantly increased the food plant's foliar carbon to nitrogen ratio.

5. We conclude that exposure to artificial light at night can trigger ecological effects spanning trophic levels, and that the nature of such impacts depends on the wavelengths emitted by the lighting technology employed.

6. *Policy implications*. Our results confirm that artificial light at night, at illuminance levels similar to roadside vegetation, can have population effects mediated by both top-down and bottom-up effects on ecosystems. Given the increasing ubiquity of light pollution at night, these impacts may be widespread in the environment. These results underline the importance of minimising ecosystem disruption by reducing light pollution in natural and semi-natural ecosystems.

Keywords

Light pollution, Photopollution, Grasslands, Trophic levels, Aphids, Molluscs, artificial light, street lights

INTRODUCTION

Throughout evolutionary time, most terrestrial ecosystems have been exposed to regular daily cycles of sunlight and darkness. Common adaptations to light cycles include endogenous circadian rhythms (McClung 2001; Panda *et al.*, 2002), photoperiodic detection of the seasons (Provencio 2010), partitioning of activity throughout the diel, lunar and annual cycles (Bennie *et al.*, 2014), or adaptation to nocturnal or diurnal activity through specialised sensory systems (Greiner 2006). Light acts as a signal and as a resource, providing energy for photosynthesis, and as a limiting factor for the partitioning of time (Kronfeld-Schor and Dayan 2003). Adaptive responses to the spectral composition of natural light are also widespread, for example in the use of red/far red ratios in

shade detection in plants (Franklin and Whitelam 2005), and in the detection of water depth due to the attenuation of different wavelengths of light in corals (Mundy and Babcock 1998).

Exposure to artificial light at night has increasingly encroached on the natural environment (Bennie *et al.*, 2015a; Gaston *et al.*, 2015). Lighting not only affects ecosystems in the vicinity of human activity, but illuminated transport networks fragment landscapes, isolating dark patches of habitat (Threlfall *et al.*, 2013), and diffuse light or "skyglow" extends the area exposed to low levels of artificial light for tens to hundreds of kilometres around towns and cities (Kyba *et al.*, 2011; Kyba and Hölker 2013). A wide range of ecological effects of artificial light have been recorded (Gaston *et al*., 2013). They have the potential to alter population dynamics (Gaston and Bennie 2014), restructure ecological communities (Davies *et al.,* 2012, 2015; Spoelstra *et al.,* 2015; Manfrin *et al.,* 2017), alter species interactions (Macgregor *et al.,* 2014), and change the provision of ecosystem functions and services (Lewanzik and Voigt 2014; Meyer and Sullivan 2013). An estimated 23% of the land mass experiences nighttime sky brightness at a level that is considered light-polluted (Falchi *et al.*, 2016) with light pollution growing globally at a rate of around 2% a year (Kyba *et al.,* 2017).

Despite the evidence of profound ecological impacts across different taxonomic groups, and growing evidence that restructuring of ecological communities under artificial light may be widespread, the effect of artificial nighttime light on biotic interactions remains poorly understood. Such effects could be "top down", in which direct effects on predators or foragers have secondary effects on lower trophic levels, or "bottom up", in which direct effects of artificial light on primary producers impact populations at higher trophic levels (Bennie *et al.*, 2015b). Top-down and bottom-up effects may restructure food webs (Rzanny *et al.*, 2013) and anthropogenic pressures may impact both kinds of interactions simultaneously (Van der Putten *et al.*, 2013). Indeed, for drivers of global environmental change such as CO_2 enrichment, nitrogen deposition, climate change, biotic invasions and land use, species interactions frequently mediate the response of ecosystems (Tylianakis et al., 2008). Disentangling direct effects, top-down and bottom-up biotic interactions is therefore critical

to understanding, and mitigating, the ecosystem-level effects of artificial light at night. In order to disentangle these effects, there is a need for controlled, replicated field experiments in tractable systems.

We present data from an experimental grassland system designed to elucidate top-down and bottom-up effects of artificial light at night. The experiment compared control treatments which experienced natural darkness at night with experimental treatments simulating both low-pressure sodium and white LED street lighting. We monitored the populations of herbivores, and the cover and flowering of plants, to investigate the response of these simple ecosystems to nighttime illumination, and assess whether effects bridge up or down trophic levels. We specifically looked for three forms of response: (i) top down effects, in which we would expect to detect a response to artificial light in herbivores and/or plants in the presence of predators but not in their absence, indicating that the response to light is mediated by predation rate; (ii) bottom-up effects, in which we expect to detect a response to artificial light in herbivores in both the presence and absence of predators, and a corresponding response in plants in the presence and absence of herbivores, indicating that the latter response is mediated by resource availability; and (iii) non-trophic or indeterminate effects, in which we would detect a response in one trophic level only. Here we report combined results for three years of data from the experiment (2013 to 2015), providing evidence for both bottom-up effects of artificial light on a specialist herbivore, mediated by direct effects of artificial light on its food plant, and top-down effects on a generalist herbivore, mediated by direct effects of artificial light on predation rate.

MATERIALS AND METHODS

Experimental design

We established 54 experimental grassland 'mesocosms' outdoors in July 2012 (see supplementary figure S1; Bennie *et al.* 2015b) in a 35 m x 35 m field enclosure at the University of Exeter's Penryn Campus (50°10' N, 5°7' W, altitude 106m). Each mesocosm consisted of a 1 m long, 0.5 m wide and 0.2 m deep trough, lined with woven plastic textile for drainage and filled with coarse builder's sand, and mounted on a wooden platform 0.75 m above the ground. In each mesocosm, 72 individual grassland plants were planted, representing four individuals of each of 18 common grassland species grown in spring from seed gathered locally from wild plants in 2011. These were selected to be representative of species common in roadside verges in the local area and comprised six grasses (*Anthoxanthum odoratum, Agrostis tenuis, Holcus lanatus, Cynosurus cristatus, Dactylis glomerata* and *Festuca ovina*), four legumes (*Lotus corniculatus, Lotus pedunculatus, Trifolium dubium* and *Trifolium pratense*), and eight non-leguminous forbs (*Leucanthemum vulgare, Achillea millefolium, Leontodon saxatilis, Hypochaeris radicata, Prunella vulgaris, Centaurea nigra, Ranunculus acris* and *Plantago lanceolata*). Seeds were sown in sand in seed trays in a polytunnel during February 2012 and seedlings were transplanted first into modular trays and then planted in a randomized grid pattern 5 cm apart within the central section of each mesocosm in July 2012. A standard nutrient solution was applied during July 2012 to establish initial plant growth. Each mesocosm was enclosed by a wooden frame 1 m tall and lined with fine anti-thrip mesh to isolate the plant and invertebrate community. A zip in the mesh provided access for maintenance and measurements. All mesocosms were treated with a biodegradable insecticide (pyrethrin) and molluscicide (ferric phosphate pellets) following initial planting to prevent the accidental introduction of invertebrates with sand or seedlings.

Three levels of trophic complexity were established in the mesocosms. Eighteen mesocosms contained plants only, 18 (bitrophic treatments) contained both plants and herbivores, and 18 (tritrophic treatments) contained plants, herbivores and predators. The plants-only treatment mesocosms were treated at regular intervals with insecticide and molluscicide to prevent the unintentional establishment of invertebrate populations. Both the bitrophic and tritrophic treatments received phased introductions of 20 individuals each of the pea aphid *Acyrthosiphon pisum* and 30 individuals of the grey field slug *Deroceras reticulatum* from May to June 2013. Populations of *A. pisum* persisted throughout the experiment, peaking during summer each year and overwintering as both eggs and adults; populations of *D. reticulatum* persisted until autumn/winter 2014 when numbers declined drastically in all mesocosms and showed no sign of recovery with most searches showing zero monthly counts. A further 30 individuals were introduced from June to September 2015. To avoid any confounding effects of this reintroduction, only data on this species prior to the decline, up to September 2014, are analysed here. *A. pisum* is a specialist feeder on legumes, and individuals were gathered from wild populations feeding on the leguminous forb *Lotus pedunculatus*. *D. reticulatum* is a generalist omnivore, feeding predominantly on the foliage of a wide range of plant species. The tritrophic treatments also received introductions of four adult individuals (one male, three females) of the predatory ground beetle *Pterostichus melanarius* in August 2013, July 2014 and three individuals (one male, two females) in August 2015, and nine unsexed adult individuals of the ladybird *Adalia bipunctata* in May 2013, 10 adults in May 2014, and 10 individuals (5 adult and 5 final instar larvae) in May 2015. *A. bipunctata* is a specialist predator of aphids; *P. melanarius* is a generalist predator that will feed on the most available prey, including both slugs and aphids (Pollet and Desender 1987). We found no reference in the literature to *P. melanarius* feeding on *A. bipunctata* or other ladybird adults or larvae, but this possibility cannot be ruled out. Individuals of *A. pisum, D. reticulatum* and *P. melanarius* were collected from wild populations in grassland in the vicinity of the experimental site; *A. bipunctata* were obtained from a commercial horticultural supplier (Green Gardener, Stokesby, U.K.).

Two light treatments (white and amber) and unlit controls were allocated to mesocosms in a cross-factorial design with trophic level, with six replicates of each light and trophic treatment combination randomly distributed within a grid pattern (supplementary figure S2). The light treatments each consisted of a strip of light-emitting diodes (LEDs) mounted on a wooden bar across the top of the mesocosm and facing downwards. The 'white' treatment consisted of 'cool white' LEDs, with a spectrum similar to those in commercial LED street lighting systems (see supplementary figure S3). The 'amber' treatment consisted of a virtually monochromatic LED strip with a single narrow peak in the orange portion of the spectrum, around 588 nm, to simulate the peak emittance of monochromatic low-pressure sodium (LPS) lighting at 589.3 nm.

The LED strips were cut to a length so that both lighting treatments provided an illuminance of approximately 10 lx at the unshaded sand surface and 15 lx at 20 cm height. These illuminance levels are within the range of those typical of roadside vegetation under street lights (Bennie *et al.* 2016). Light treatments were powered by 12 V, 125 Ah vehicle batteries and triggered by light-detecting photocells mounted on top of the frame, to switch on at sunset (when ambient light levels fell below 70 lx) and off at sunrise (above 110 lx). Unlit controls reproduced the mounting bar and structure of the lit treatments but had no light source. Nighttime light levels measured within the control mesocosms were comparable to background levels in an adjacent unlit area of the campus, typically around 0.1 lx at full moon and 0.01 lx at new moon. Illuminance measurements were taken with a photoradiometer calibrated to a CIE curve (HD2102.2, Delta Ohm, Caselle di Selvazzano, Italy).

Vegetation sampling

Plant cover for each species was measured in July of each year using a 30 cm long point-quadrat frame (Sutherland 2000) with seven pins at 5cm spacing. The frame was placed along five transects at 10cm spacing across the central section of the mesocosm, to form a 30 x 40 cm grid of 35 pin

drops (pin diameter 5 mm) covering the central planted area of the mesocosm. The number of pin drops that made contact with each species was recorded.

The abundance of flowers of *Lotus pedunculatus,* the dominant leguminous forb, was analysed due to the importance of the flowers as a seasonal food source for the aphid *A. pisum* in the system. The abundance of flowers was recorded in each of the 54 mesocosms every two weeks from April to September of each year. The number of mature, but not yet senescent, inflorescences were counted on each occasion. In order to estimate the total resource available to the aphid across the season, we pooled all data from surveys during June, July and August of each year and analysed the total number of flowers.

In June 2015, leaf samples were collected from *L. pedunculatus* to measure the carbon to nitrogen (C/N) ratio of the leaves of this species. Leaves from the tips of four growing shoots of the species were collected, where possible from four separate plants, before being freeze-dried, combined into a single sample per mesocosm and homogenised. Dry samples were analysed immediately in a SerCon Callisto CF_IRMS 20-22 Mass Spectrometer. Total carbon and nitrogen contents were measured and the C/N ratio calculated.

Invertebrate sampling

The abundance of *A. pisum* was assessed every two weeks from April to September in each year, by a single observer using a three-minute timed count in each mesocosm. During the three minutes, the vegetation was thoroughly and systematically searched by hand and all aphids observed were counted.

The abundance of *D. reticulatum* was assessed by a monthly 5 minute timed count by multiple observers by torchlight in the evening at least 30 minutes after sunset, when the species was active. Treatment lights were switched off before sunset on the nights of surveys to avoid the confounding

effects of light on activity, or differences in detection rates under different light conditions. During counting, recorded individuals of *D. reticulatum* were temporarily removed from the mesocosm to avoid multiple counts of the same individual. For both herbivore species, the duration of timed searches was chosen to maximise information from a reasonable sampling effort. The search times were imposed as early trials showed that the rate of discovery of new individuals decreased rapidly when the duration of searches were extended further. A fixed-duration survey standardised search effort, limited the time during which the mesocosm was open, and in the case of *A. pisum*, avoided the risk of accidentally double-counting individuals.

Due to the complexity of the vegetation, and the difficulty of searching the substrate without damaging the plants, it was not possible to assess predator abundance systematically within this system after their introduction. However, individuals of both predator species were observed in the majority of tritrophic treatments throughout the summer months, so we conclude that populations persisted throughout the breeding season. Fresh adult *P. melanarius* were observed in spring 2014, suggesting that breeding of this species took place (supplementary table S1). No larvae of either species were observed, and there was no evidence that *A. bipunctata* successfully bred or overwintered within the mesocosms.

Data analyses

Vegetation cover data were analysed using a generalised linear mixed model with a binomial error structure, fitted using penalised maximum likelihood estimation with the gamlss package (Rigby and Stasinopoulos 2005) in R v 3.0.1 (R Core Team 2013). Each functional group (grasses, legumes and non-leguminous forbs) was analysed separately, with year (*YEAR*, coded as a categorical variable), light treatment (*LIGHT*; coded as control, amber or white), the presence of herbivores (*HERB*; coded as presence/absence), and the presence of predators (*PRED*, coded as presence/absence) as

predictor variables, as well as the interaction terms *YEAR:LIGHT*, *YEAR:HERB YEAR:PRED, YEAR:LIGHT:HERB* and *YEAR:LIGHT:PRED.* Mesocosm identity (*PLOT*) was included as a random variable (with random intercept and slope with respect to *YEAR*), to allow for repeated measures of the same mesocosm in different years. A full list of cover values for each species is presented in the supplementary material (table S2).

Flowering data for *Lotus pedunculatus* were analysed using a generalised linear mixed model with a negative binomial error structure, fitted using penalised maximum likelihood estimation in the gamlss package. Since the availability of inflorescences over the whole season was of interest, the total number of mature inflorescences for June, July and August of each year was aggregated into annual totals, and modelled as above with *YEAR* (coded as a categorical variable), interactions with year and light treatment (*YEAR:LIGHT*), the presence of herbivores (*YEAR:HERB*), and the presence of predators (*YEAR:PRED*), and three-way interactions (*YEAR:HERB:LIGHT* and *YEAR:PRED:LIGHT*) as fixed factors and mesocosm identity (*PLOT*) as a random factor, to control for repeated measures.

Since measurements of *L. pedunculatus* foliar C/N ratios were available for just one year (2015), these were analysed for effects of light using a generalised linear model in which C/N ratio was modelled with light treatment, presence of herbivores and presence of predators, and their interactions as fixed factors (*LIGHT, HERB, PRED, LIGHT:HERB and LIGHT:PRED*).

In all analyses of vegetation, flowering and C/N ratios the full model was tested for statistical significance against a null model (effect of year and random term only) using a chi-square test (Pinheiro and Bates 2009); interaction terms were replaced by simple terms for the treatment, or dropped altogether, if the resulting model had a lower AIC value. The appropriateness of the choice of link function was confirmed by visual assessment of quantile (Q-Q) plots of the model residuals and predicted values.

Aphid and slug counts were analysed using a generalised linear mixed model with a zero-inflated negative binomial error structure fitted using the gamlss package. In these analyses, monthly, rather than annual counts were modelled as a function of *DATE* (as a categorical variable with a unique value for each monthly time point), *LIGHT* (control, amber or white), and *PRED* (presence or absence of predators), as well as interactions between *DATE, LIGHT* and *PRED*, as fixed factors, and with mesocosm identity (*PLOT*) as a random factor. Interaction terms between *DATE* and other fixed factors were dropped from the model if they did not decrease AIC values, but interactions between *LIGHT* and *PRED* were retained, in order to test whether effects of the light treatment were mediated by the presence or absence of predators. Normality of the residuals was confirmed by visual assessment of quantile (Q-Q) plots of the model residuals and predicted values.

RESULTS

Effects of light, herbivory and predation on vegetation cover

The most parsimonious model for the cover of grasses did not include any effects of light or trophic level, but showed significant differences between years (R^2 = 0.75, p < 0.001). The most parsimonious model for leguminous forbs (R^2 = 0.71) included effects of year, light and trophic treatments, as well as two-way interactions between year and both light treatment and trophic treatments. There was a 27% decrease in cover in the presence of herbivores only (effect of herbivores significant at p < 0.001), but only a 14% decrease when both herbivores and predators were present (effect of predators significant at p = 0.016) across all years. In 2015, there was a 19% decrease in legume cover under amber lights and 12% decrease in under white lights (significant at p = 0.032 and p = 0.040 respectively). For non-leguminous forbs, the most parsimonious model included effects of year, light and trophic treatments, but no interaction terms. There was a 16% increase in cover in the presence of herbivores only (effect of herbivores significant at p < 0.001) and

a 10% increase in cover in the presence of herbivores and predators (effect of predators significant at p = 0.017). No significant effects of light treatment were detected on the cover of grasses or non-leguminous forbs. No interactions between light and herbivory or predation were found to be significant. The models selected are shown in supplementary table S3, and terms and properties of the most parsimonious model are shown in supplementary table S4.

Effects of light, herbivory and predation on flowering and C/N ratios of *L. pedunculatus*

There were significant effects of both artificial light and herbivory on the number of inflorescences produced by *L. pedunculatus* (Figure 1b). Under both amber and white nighttime light, this species produced significantly fewer flower heads in all years (49% fewer at p < 0.001 and 29% fewer at p = 0.0176 respectively); there were also significantly fewer inflorescences observed in the presence of herbivores (45% fewer at p < 0.001). The model had an R^2 value of 0.39. No significant effects of the presence of predators on inflorescence count were found, nor were there significant interactions between trophic treatment and light treatment. Model selection and terms and properties of the model are shown in supplementary tables S5 and S6.

There was a significant effect of artificial white light on C/N ratios in *L. pedunculatus* leaves in 2015 (P=0.0045); C/N ratios were decreased by 29.5% on average compared to controls. Model selection and terms and properties of the model are shown in supplementary tables S7 and S8.

Effects of light and predators on *A. pisum* abundance

The most parsimonious model for *A. pisum* abundance did not include interaction terms between date and light treatment or date and predation. Across all years, the abundance of *A. pisum* was 17% lower under the amber nighttime light treatment (Figure 2a, p = 0.002). No significant effects of white light, predation or interactions were found. The alternative model forms and terms and

properties of the most parsimonious model are shown in supplementary tables S9 and S10; monthly counts are shown in supplementary figure S4.

Effects of light and predators on *D. reticulatum* abundance

The abundance of *D. reticulatum* was significantly decreased (by 55%) under the combination of white nighttime light and predation (Figure 2b; p = 0.026); the negative effect of predation alone was not significant at the 95% confidence level (P = 0.13), nor was any significant effect of white light detected in the absence of predators. Again, including interaction effects for individual months of data did not improve the parsimony of the model as judged by AIC values. The alternative model forms and terms and properties of the most parsimonious model are shown in supplementary tables S11 and S12; monthly counts are shown in supplementary figure S5.

DISCUSSION

There is an increasing awareness of ecological light pollution as an important environmental issue, and recognition both of the extent to which natural and semi-natural ecosystems are exposed to anthropogenic light at night (Bennie *et al.* 2015a, Gaston *et al.*, 2015) and of the value of habitats that have now come to be frequently illuminated, such as roadside verges and hedgerows (Hovd and Skogen 2005; Cousins 2006; Hanley and Wilkins 2015), domestic gardens (Davies *et al.*, 2009; Goddard *et al.*, 2010) and urban ecosystems (Angold *et al.*, 2006; Gaston *et al.*, 2013; Stott *et al.*, 2015) for biodiversity conservation and the maintenance of ecosystem services.

This study demonstrates that continuous artificial light at night equivalent to that recorded in roadside vegetation under street lighting, can cause population-level effects on plants and invertebrates, that these effects can be mediated by both top-down and bottom-up processes, and that the nature of these effects depends on the lighting technology employed.

Exposure to white LED light significantly reduced numbers of the generalist herbivore *D. reticulatum* in the presence of predators, but not in their absence (Figure 2b). We conclude that predation rates by *P. melanarius* were higher under the white nighttime light, driving a top-down effect on *D. reticulatum* abundance. *P. melanarius* is a nocturnal predator that locates its prey by sight and olfactory cues, and broad spectrum light may therefore aid its prey location and/or increase its activity; Allema *et al*. (2012) found variation in activity levels in this species under different wavelengths of light, with both males and females spending less time moving under high-pressure sodium lighting than under red LEDs. While the spectra of these lights are not comparable with the present study, it is clear that activity patterns in this species are sensitive to different wavelengths of artificial light.

Pitfall trap catches of some predatory invertebrates including carabid beetles are known to be higher under street lights in road verges (Davies *et al.*, 2012), although Manfrin *et al.,* (2017) found reduced trap rates of carabid species under high-pressure sodium lighting. Other predator species aggregate around artificial light, utilising it to hunt at night, including reptiles (Garber 1978), bats (Blake *et al.*, 1994), birds (Negro *et al.*, 2000), spiders (Frank 2009) and fish (Becker *et al.*, 2012), but determining the impact of increased predation rates on prey populations is challenging. Our results show that light at night can decrease prey species abundance through increasing predator density, activity, or efficiency, highlighting the potential for far reaching impacts on predator-prey dynamics.

Exposure to amber light significantly decreased the abundance of the specialist herbivore *A. pisum* both in the presence and absence of predators (Figure 2a). We have previously shown that *A. pisum* populations declined more rapidly in amber light treatments in late summer than they did in dark or white-lit treatments (Bennie *et al.,* 2015b); the results of the present study show that the pattern was maintained over three years and is likely driven by resource availability. We base this conclusion on the significant effect of artificial light on leguminous plants in this system, regardless of whether herbivores were present or absent. Three measures of legume resource availability and

quality for aphids were reduced under artificial light treatments. Total legume cover was reduced under amber and white light by 2015, the final year of this study. Inflorescence abundance of *L. pedunculatus* was reduced under both amber and white light. The C/N ratio of the main food plant of *A. pisum*, inversely related to forage quality (Bezemer and Jones 1998), was significantly higher under white lights when measured in 2015.

While there is evidence that photoperiod may have a direct effect on aphid reproduction (Erlykova 2003), Sanders *et al.* (2015) found that white LED nighttime lighting reduced abundance of two aphid species, including *A. pisum* established on an experimental monoculture of beans *Vicia faba*, associated with a decrease in biomass of their food resource. In the current study there is strong evidence that artificial light decreased the abundance of food for this species. Artificial light had a detectable effect on the composition of plant species within the mesocosms, decreasing the cover of legumes compared to other functional types in the third year of the study, and decreasing the number of flowers of the most abundant legume *L. pedunculatus* in all three years. The more pronounced effect of the amber, rather than white, treatment is consistent with previous observations (Cathey and Campbell 1975) that incandescent and sodium light sources are more effective in producing vegetative and flowering responses in plants than other sources (Briggs 2006; Bennie 2016).

There has been a global shift away from gas-discharge lamps, including sodium lights, towards solid state LED lighting, with the aim of decreased energy consumption, although it has been argued that efficiency gains lead to a compensatory increase in lighting use, offsetting energy savings (Kyba *et al.,* 2017). In principle, LED technology could allow greater flexibility in the wavelengths of light emitted; however in practice the vast majority of outdoor "white" LED lighting currently installed is based on blue LEDs with a yellow phosphor coating producing a blue-rich white light. This shift towards exposure to short-wavelength light has caused concern for human health (West *et al.,* 2011) and ecological systems (Davies *et al.,* 2017). Known ecological responses to light at night vary in

their sensitivity to different wavelengths, although many responses appear to be more sensitive to "blue" light (Longcore *et al.,* 2018). Our results suggest that the response of an ecosystem to changes in the intensity and spectra of artificial light in the environment may be complex and mediated through multiple physiological pathways and trophic levels.

The implications of such findings for planning ecologically sensitive outdoor lighting are important. While much is still unknown about the ecological consequences of artificial light at night, we propose three principles for lighting design based on the evidence to date. First, the precautionary step of avoiding any illumination around natural and semi-natural ecosystems should be taken. Particular care should be taken around the habitats of species for which there is strong evidence of direct harmful effects of artificial light, but the ecosystem-level impacts are likely to be far wider than the small group of species for which the direct effects of light are well known. Second, where illuminating the environment is deemed necessary due to overriding concerns of public amenity or safety, lighting should be limited to the time, intensity and place at which it is required (Gaston *et al.,* 2012). Here, the flexibility of solid state lighting technology in terms of enhanced directionality, dimming and rapid "warm up" times probably offers untapped potential, as do "smart" lighting technologies that can respond to changing local pedestrian or traffic activity levels. Third, the ecological impacts of artificial light may be reduced by controlling the emission spectra and/or lighting technology employed in different situations, but there may not be a single most "environmentally sensitive" lighting technology. Our results suggest that great care should be taken to consider both the physiological and ecological pathways through which the impacts of artificial light are realised. Plants, and hence specialist herbivores, are likely to be susceptible to higher wavelength light, particularly the red/far red ratio (Cathey and Campbell 1975; Briggs 2006; Bennie et al., 2016), while many physiological pathways such as cryptochrome and melatonin, and behaviours such as insect phototaxis are most sensitive to lower-wavelength blue light (Longcore *et al.,* 2018). Species that are able to utilise artificial light for vision, are likely to respond to broad wavelength "white" light. While ecological light pollution is a global phenomena, the range of

impacts, and the most effective mitigation strategies, may vary with the species composition and structure of the local ecosystem. In each case, an assessment not only of the responses of individual species within an ecosystem but also how these impacts may cascade through trophic levels is critical if we are to manage and mitigate the ecological impacts of artificial light at night.

AUTHORS' CONTRIBUTIONS

KG conceived the idea for this study and secured funding, KG, JB, TD and DC designed the experiment. DC, JB and TD built and maintained the experiment and collected data. JB, TD and RI analysed the data, JB wrote the initial manuscript and all authors contributed to subsequent revisions. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository doi:10.5061/dryad.8217n76 (Bennie et al., 2018).

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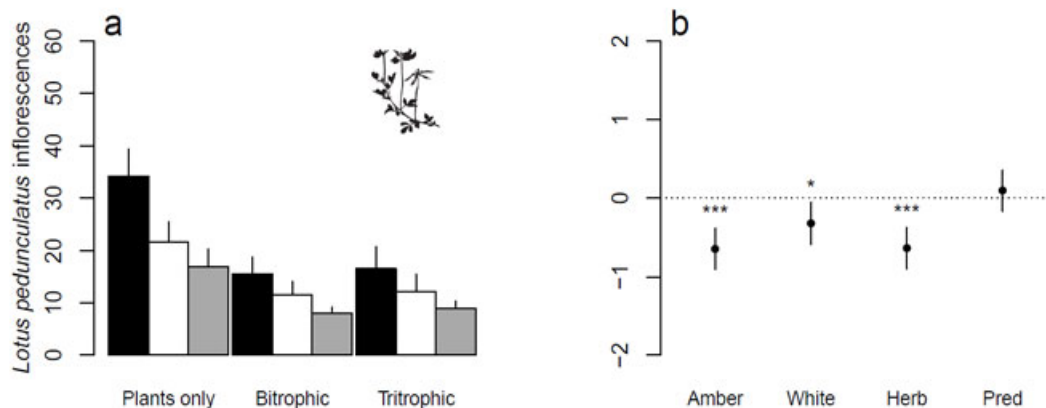
Fig. 1 Counts of *Lotus pedunculatus* inflorescences in mesocosms. (a) mean annual numbers of flower heads recorded over all bi-weekly counts during summer (from June to August) during 2013 to 2015. Black bars are unlit, white bars represent the white light treatment and dark grey Amber treatment. Vertical lines represent standard deviations, *n*=6 in each case. (b) Effect sizes of artificial

light treatments (Amber and White) and the presence of herbivores (Herb) and predators (Pred) on

L. pedunculatus flower counts 2013-2015. Points indicate parameter estimates, associated lines indicate 95% confidence intervals, and stars indicate effects significantly differing from zero (* $P<0.05$, ** $P<0.01$, *** $P< 0.001$)
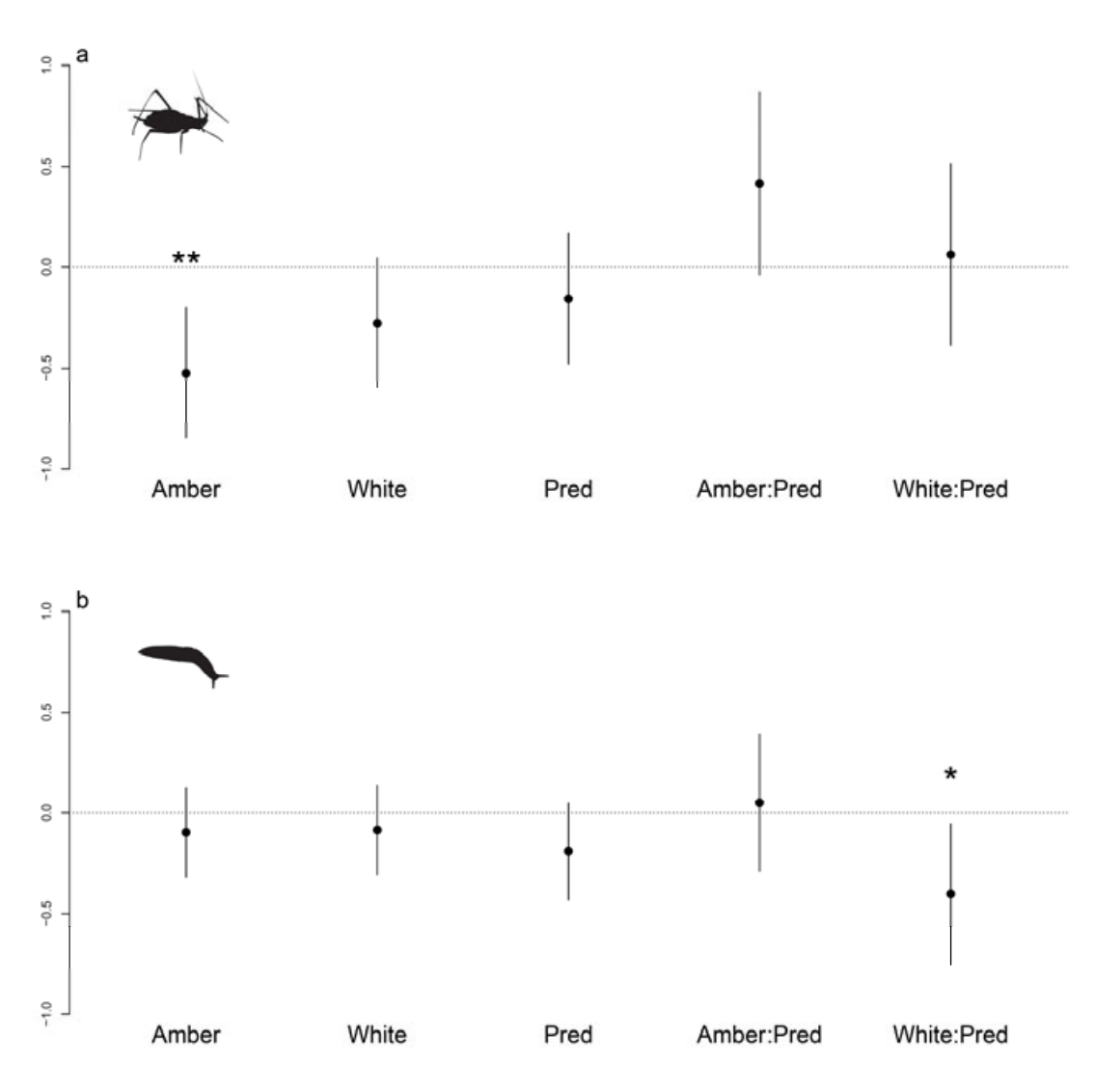
Fig. 2 Effect sizes of artificial light treatments (Amber and White) and the presence of predators (Pred) on (a) *Acyrthosiphon pisum* and (b) *Deroceras reticulatum* abundance.. Points indicate parameter estimates, associated lines indicate 95% confidence intervals, and stars indicate estimates significantly differing from zero (* $P<0.05$, ** $P<0.01$, *** $P< 0.001$).