Insect Science

Insect Science (2019) 26, 770–776, DOI 10.1111/1744-7917.12574

ORIGINAL ARTICLE

Direct and indirect effects of light pollution on the performance of an herbivorous insect

Kylee Grenis and Shannon M. Murphy

Department of Biological Sciences, University of Denver, Denver, Colorado, USA

Abstract Light pollution is a global disturbance with resounding impacts on a wide variety of organisms, but our understanding of these impacts is restricted to relatively few higher vertebrate species. We tested the direct effects of light pollution on herbivore performance as well as indirect effects mediated by host plant quality. We found that artificial light from streetlights alters plant toughness. Additionally, we found evidence of both direct and indirect effects of light pollution on the performance of an herbivorous insect, which indicates that streetlights can have cascading impacts on multiple trophic levels. Our novel findings suggest that light pollution can alter plant–insect interactions and thus may have important community-wide consequences.

Key words anthropogenic disturbance; continuous photoperiod; light pollution; Lepidoptera

Introduction

More than half of the world's population lives in urban or suburban areas (McIntyre *et al.*, 2001) and the associated development has caused nearly 20% of the Earth's night skies to be affected by anthropogenic light (Cinzano *et al.*, 2001; Kyba *et al.*, 2011). Humans light the night to increase nighttime activity, promote safety, and deter criminal behavior (Painter, 1996), but frequent exposure to long periods of uninterrupted light has negative impacts not only on humans, but also on adjacent natural communities (Longcore & Rich, 2004). Some species, for example, require the dark to forage successfully (Rotics *et al.*, 2011) while others use naturally occurring light, like the moon, as a cue for key behaviors like finding appropriate habitat or orientation during flight (Frank, 1988; Tuxbury & Salmon, 2005; Kriska *et al.*, 2009). Although light pollution is relatively well-studied for some vertebrates, such as bats, birds, turtles, and humans (Rydell, 1992, 2006; Rich & Longcore, 2006; Navara & Nelson, 2007; Jung & Kalko, 2010; Kempenaers *et al.*, 2010; Santos *et al.*, 2010; Falchi *et al.*, 2011; Bedrosian & Nelson, 2013; Davies *et al.*, 2013; Gaston *et al.*, 2013; Kamrowski *et al.*, 2014; Da Silva *et al.*, 2015; Hale *et al.*, 2015 and references therein), the impacts of artificial lighting have been explored for few invertebrate systems (Rich & Longcore, 2006; but see Davies *et al.*, 2012, 2013; Bennie *et al.*, 2015) and not at all for plant communities that are surrounded by urban areas (Neil & Wu, 2006). Furthermore, most studies of light pollution focus on individual species and lack a community perspective (Gaston *et al.*, 2015). Recently there have been several calls in the literature for studies that investigate how the effects of light pollution vary among species, especially plants and nonvertebrate animals for which we know relatively little, and associated effects on populations, communities, ecosystems, species interactions and ecosystem services (Hölker *et al.*, 2010a,b; Gaston *et al.*, 2013; Lyytimäki, 2013; Macgregor *et al.*, 2014; Gaston *et al.*, 2015). If light pollution has significant effects on individual species, it follows that it may have important implications for trophic dynamics by altering species interactions.

Plants exposed to light pollution at night may perform differently than conspecifics under ambient conditions

Correspondence: Kylee Grenis, Department of Biological Sciences University of Denver 2190 E. Iliff Ave, Denver, Colorado 80210, USA. Tel: +1 303 871 7571; fax: +1 303 871 3471; email: kgrenis@gmail.com

because day-length and photoperiod are important signals for plants. Under natural conditions, many plants are cued by day-length to germinate, grow, reproduce, and senesce (Raven *et al.*, 1986) and for some sensitive species, any disturbance in lighting regime may prevent individuals from progressing into different life stages (Raven *et al.*, 1986; Neil & Wu, 2006). For instance, one study done in urban systems found that trees planted near street lights delay or stop leaf abscission compared to individuals not near artificial lights (Matzke, 1936) and another study found that a leguminous plant produced fewer flower heads when exposed to artificial lights (Bennie *et al.*, 2015). Yet most of the literature on how continuous photoperiods affect plants only considers agricultural and horticultural systems (Harvey, 1922; Briggs, 2006; Neil & Wu, 2006) and rarely focus on species in the natural environment. It is unknown if light pollution from streetlights changes plant traits in natural communities that are important to herbivores. Notably, whether consumers are directly or indirectly affected by artificial night lighting has never been tested.

In this study, we test the hypothesis that light pollution affects herbivore performance. We tested whether herbivore growth and survival are directly affected by exposure of the herbivore to artificial night light during development. Additionally, we examined whether herbivore growth and survival are indirectly affected by the development of their host plant under artificial night light.

Materials and methods

Study system

The Denver-Metro area has many Open Space programs devoted to preserving and restoring native ecosystems along the Eastern Foothills of the Colorado Rocky Mountains. Open Spaces generally consist of patches of mixed grass prairie with a number of both native and invasive species of forbs and grasses; trees and other woody vegetation are limited to small riparian drainages (Nufio *et al.*, 2010; Hinners *et al.*, 2012). These patches are "islands" of prairie habitat in an otherwise residentially developed landscape, but they maintain a diverse community of insects including bees, butterflies, grasshoppers, and moths (Nufio *et al.*, 2010; Hinners *et al.*, 2012; Robinson *et al.*, 2012). We collected the plants and insects for our experiment from eight prairie sites between 5 and 15 ha in size with 2–5 high-pressure sodium streetlights along at least one edge of the site (Table S1).

Plant performance

To determine whether streetlights affect plant traits in the field, we focused on smooth brome (*Bromus inermis* Leyss.) as it was the only species found reliably at all eight field sites. Within each of the eight field sites (Table S1), we haphazardly selected five streetlit locations (7 – 12 lux) and five unilluminated (0 lux) along the site edge for plant collection; the unilluminated edge locations were paired with streetlit locations (mean = 37 m apart) so that the two treatments were interspersed along site edges and not clumped. We confirmed that each edge site was illuminated and unilluminated at night in a previous experiment (Grenis *et al.*, 2015). At each location (streetlit or unilluminated), we collected five culms of grass from within a ~5 m radius of the streetlight or five culms of grass from the unilluminated edge for a total ~400 culms collected (8 sites × 2 treatments [lit vs. unilluminated] × 5 locations/treatment × 5 culms/location). In the laboratory, we washed the plants, pooled them by location and then measured leaf toughness, aboveground dry biomass and C : N ratio. We measured plant toughness of the first green blade of grass per culm using the cup-string method detailed in Hendricks *et al.* (2011); this method tests toughness using the amount of sand required to pull a safety pin through a blade of grass. After we measured leaf toughness, we placed aboveground tissues in a drying oven at 60 °C for 3 d to measure dry tissue biomass. To measure treatment effects on C : N ratio, we ground the aboveground biomass in a mixer mill (Retsch MM400) and sent processed samples to the Cornell Stable Isotope Laboratory for nutrient analysis.

Herbivore performance

In late June of 2014, we collected early instar *Apamea sordens* Guenée larvae from our field sites (Table S1) using sweep nets under streetlights and along unilluminated edges. *Apamea sordens* are climbing cutworms and feed on both smooth brome seed heads and leaves. We identified the larvae using COI (cytochrome oxidase I) sequences isolated using LepF1 and LepR1 primers; we sent samples to Eurofins Scientific for sequencing and matched sequences to *A. sordens* using BLAST and BOLD. This species has a high rate of barcode consistency across wide geographic areas (Zahiri *et al.*, 2014).

We brought the larvae back to the laboratory and kept each larva in an individual 0.5 L deli container. We designed a complete factorial experiment to test both the direct and plant-mediated indirect effects of streetlights on larval fitness. To test the indirect effects of streetlights on larval fitness mediated by host plant effects, we reared larvae on smooth brome that corresponded to the plants where we had collected the larvae from the field: plants collected from under streetlights in the field or plants collected from along the unilluminated edge. We continued to feed larvae the host plant species on which we found them because we were not interested in looking at host-switching effects in this experiment. We fed each larva its corresponding host plant species ad libitum once per week by replacing the old plant material in each deli container with freshly collected plant material. To test the direct effects of artificial lighting on larval fitness, we placed half of the larvae feeding on each type of host plant (streetlit or unilluminated) into the greenhouse under high-pressure sodium lamps that illuminated them from 21:00 until 06:00, mirroring average streetlight duration during the summer, and we placed the other half of the larvae from each host plant treatment into control (ambient) conditions with normal day-night cycles (4 plant/lighting treatments ~20 larvae/treatment = 82 larvae total). The streetlight treatment in the greenhouse used the same type of light, high-pressure sodium, as the streetlights in the field, which are highly conserved across spectral composition (Elvidge *et al.*, 2010). During feedings, we monitored survival and removed any frass. Additionally, we measured body mass of ten randomly selected larvae from each treatment at the beginning of the experiment and every following week for 10 weeks to estimate growth rates and accumulated body mass. At the end of the summer, we measured final body mass of all larvae.

Statistical analyses

To determine whether streetlights affect smooth brome plants in the field, we used a two-way ANOVA with *patch location* (streetlight edge or unilluminated edge), *field site*, and the *patch location* × *field site* interaction as independent variables. We kept field site as a fixed effect because of our small number of field sites (Warton & Hui, 2011). We used aboveground biomass, toughness, and C : N ratio as the dependent variables.

We analyzed data from the larval performance study using Kaplan–Meier survival curves for each of the four plant/lighting treatment combinations. We also used two-way repeated measures ANOVAs with *light treatment*, *host plant*, and the *light treatment* × *host plant* interaction as the independent variables with growth rate and mass of the 40 weekly monitored larvae as continuous dependent variables. These data violated the assumption of sphericity (growth rate: $\chi^2 = 93.11$, df = 35, $P < 0.0001$, mass: $\chi^2 = 178.6$, df = 44, $P < 0.0001$) so we used a repeated measures MANOVA with a Greenhouse–Geisser degrees of freedom correction for these analyses (growth rate: $\varepsilon = 0.50$, mass: $\varepsilon = 0.27$). To determine at which time points treatments differed, we used two-way ANOVAs at each time point with a Bonferroni correction. Additionally, to evaluate performance of larvae at the end of the experiment, we used a two-way ANOVA with *light treatment*, *host plant*, and the *light treatment* × *host plant* interaction as independent variables and final body mass as the continuous dependent variable. We used JMP v 11 for all analyses (SAS Institute Inc., Cary, NC, USA).

Results

Plant performance

For the smooth brome plants we collected from the field, there were no differences in aboveground biomass and C : N ratio for plants collected from under streetlights or the unilluminated edge (aboveground: $F_{1,21} = 0.7$, $P = 0.4$; C : N ratio: $F_{1,20} = 0.9$, $P = 0.3$; Figs. 1A, B). However, plants in the field did differ in toughness; plants growing under streetlights were tougher than those growing along unilluminated edges ($F_{1,21} = 4.89$, $P = 0.04$; Fig. 1C). Site was not significant in any of these analyses.

Herbivore performance

All larvae in the four treatments of our full factorial experiment started out at similar sizes based on body length ($F_{3,144} = 0.96$, $P = 0.4$). Larval survival did not differ among the four treatments for either host plant or light treatment (Log-Rank $\chi^2 = 1.88$, df = 3, $P = 0.6$).

For larval body mass, we found a marginally significant three-way interaction between light treatment (streetlights vs. unilluminated in greenhouse), host plant treatment (plants collected under streetlights vs. unilluminated in field) and time ($F_{2.43,58.29} = 2.74$, $P = 0.06$). After week 2, the larvae in the unilluminated conditions gained more mass than larvae in the streetlight treatment and continued to have greater body mass for the duration of the experiment (*time* × *treatment*: $F_{2.43,58.29} = 15.37$, $P < 0.0001$; Fig. 2). At week 8 in the experiment, larvae feeding on unilluminated host plants had gained more mass than larvae feeding on streetlight host plants, but only in the unilluminated treatment (Fig. 2). However, the final mass of all larvae did not show any host plant effects; larvae growing under streetlights were smaller than their conspecifics growing under unilluminated conditions regardless of whether they were reared on host plants collected from streetlight or unilluminated habitats ($F_{1,67} = 47.62$, $P < 0.0001$; Fig. 3).

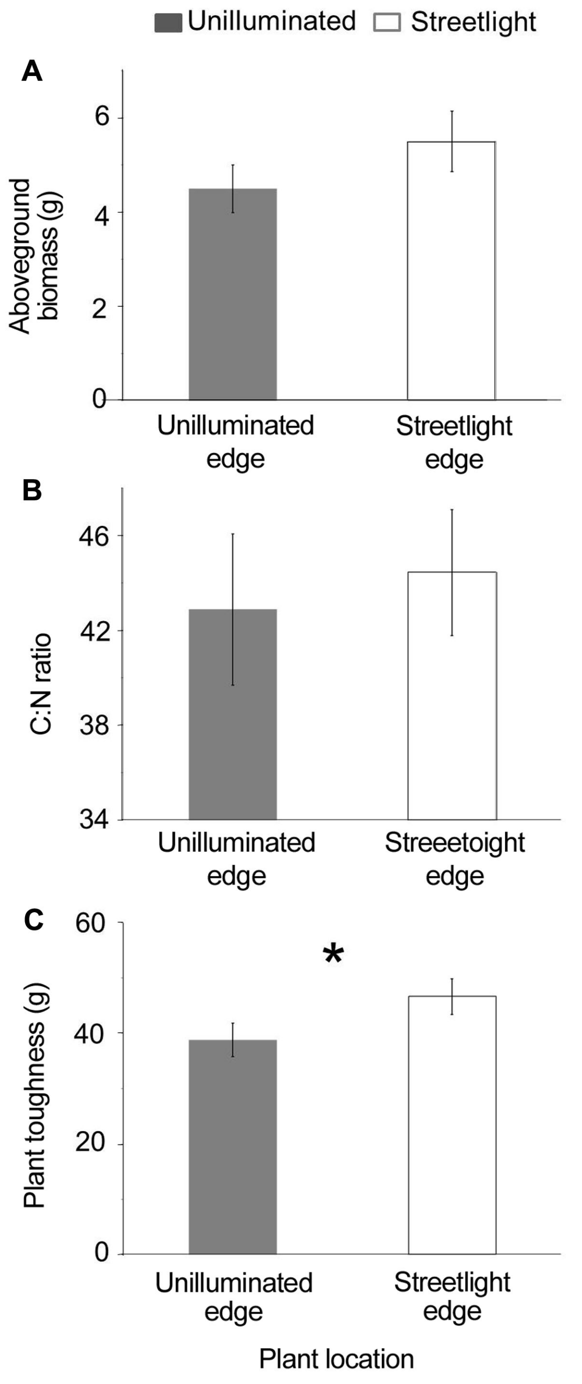

Fig. 1 Effects of streetlight exposure on (A) above-ground dry biomass, (B) C : N ratio, and (C) plant toughness of smooth brome collected in the field. White bars indicate plants collected under streetlights and gray bars represent plants collected from unilluminated edges. Bars show the mean of each measure ± 1 SE. Asterisks indicate significant differences between treatments ($P < 0.05$).

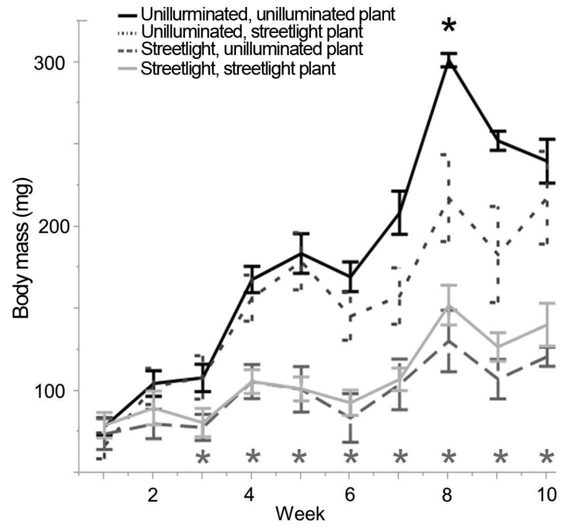

Fig. 2 Effects of both streetlight exposure and host plant treatment on larval mass accumulation. The lines show the mean mass at each time point ± 1 SE in each of the four combinations of herbivore light treatment (unilluminated or streetlight) and host plant treatment (unilluminated or streetlight). The gray asterisks show time points when larval mass differed significantly between unilluminated and streetlight conditions and the black asterisk indicates the time point when larval mass differed significantly by host plant treatment (unilluminated and streetlight) in the unilluminated condition ($P < 0.05$).

Discussion

We found that streetlights affect larval performance both directly and indirectly via induced changes in host plant quality. We found that larvae reared under streetlights weighed 43% less than larvae reared under unilluminated conditions; light pollution thus has a direct negative effect on larval fitness. Body mass is an accepted proxy for lifetime fitness in many Lepidoptera (Schoonhoven *et al.*, 2005; Price *et al.*, 2011). Because the direct effect of light pollution on larval mass was so strong, this could have serious impacts for larvae developing under streetlights. First, larvae with low body mass translate into adults with fewer resources for finding mates and producing offspring (Loewy *et al.*, 2013). Second, larvae with less mass may need to spend more development time as larvae before pupating (Schoonhoven *et al.*, 2005; Price *et al.*, 2011); however, our study is limited because we did not measure growth rate between instars, only between weeks which limits the evidence for slow growth/high mortality hypothesis. The larval stage has the highest amount of mortality and exposes larvae to predators for a longer period of time (Varley & Gradwell, 1960; Clancy & Price, 1987). It is worth noting that although light pollution does

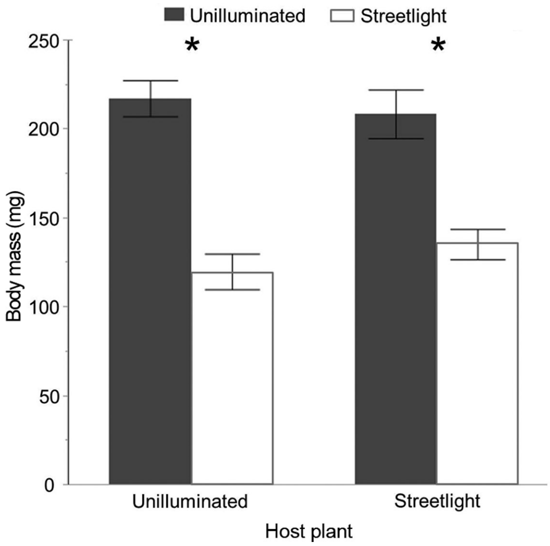

Fig. 3 Mean larval body mass (± 1 SE) for larvae reared 10 weeks in unilluminated or streetlight conditions and on host plants collected under unilluminated or streetlight conditions. The gray bars indicate larvae reared in unilluminated conditions and the white bars represent larvae reared in the streetlight treatment. Asterisks indicate significant differences between light environment treatments ($P < 0.05$).

not directly increase predation rate on larvae in our system (Grenis *et al.*, 2015), streetlights may indirectly increase mortality from predators by increasing larval development time and therefore increasing their exposure time to predators. Thus, light pollution can have detrimental fitness impacts on both larvae developing under streetlights and for those adults that lay eggs near streetlights.

We also found that streetlights can affect larval performance indirectly, via effects on host plant. Larvae reared under unilluminated conditions and fed host plants that we collected from under streetlights can have significantly lower body mass than larvae consuming plants from unilluminated conditions. Our results show that streetlights indirectly decreased larval fitness via changes in host plant quality as plants collected from under streetlights in the field were tougher than those not under streetlights. Additionally, these plant changes appear to vary in importance during different points in larval development. Notably, we only found host-plant-mediated differences in fitness in the unilluminated treatment, perhaps because the direct, negative effect of streetlights was so large, but larvae in the field would not encounter similar conditions as streetlight plants exist only under streetlights. Although it is possible that the variation in toughness is due to a streetlight characteristic other than night lighting (e.g., soil compaction during streetlight installation), we have evidence from controlled greenhouse experiments that nighttime light pollution alters a number of plant traits (aboveground biomass, C : N ratio, toughness) for a variety of plant species (Grenis & Murphy, unpublished data). Smooth brome is an invasive species in Colorado and since plants growing under streetlights are tougher than those along the unilluminated edge, they are likely more resistant to insect herbivores, which may affect invasion dynamics in streetlit conditions but needs further exploration. For example, future studies should test additional plant species in the field to determine whether other plant species respond similarly to streetlights as smooth brome and whether differences in herbivore consumption have fitness effects on the plants themselves.

In summary, streetlights have both direct and indirect impacts on herbivores; larvae are smaller when reared under streetlights (direct), and streetlights change plant traits that lead to reduced larval growth (indirect). Our results provide evidence that the impacts of ecological light pollution in the environment have the potential to alter plant–herbivore interactions. While our study presents an important first step, these interactions should be investigated in the field as well to determine to what extent light pollution can alter natural communities and species interactions.

Acknowledgments

We would like to thank the City and County of Broomfield, the City of Lakewood, the City of Louisville, and the South Suburban Parks and Recreation District for use of field sites. We are grateful for the lab and field help of M. Berge, G. Connor, C. Hallagan, and C. Harris, B. Babar, E. Barnes, G. Connor, S. DeSilva, C. Hallagan, S. Gosnell, S. Kraft, M. Mayeda, S. Neuder, G. Sommerville, and S. Winsett. We thank B. Horowitz, M. Vidal, and T. Quinn for help with barcoding *Apamea sordens*. We would also like to thank C. Nufio, the University of Denver's Organismal Biology Group, and an anonymous reviewer for helpful comments on previous drafts.

Disclosure

The authors have no conflict of interest to declare.

References

Bedrosian, T.A. and Nelson, R.J. (2013) Influence of the modern light environment on mood. *Molecular psychiatry*. *Nature Publishing Group*, 18, 751–757.

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

Briggs, W.R. (2006) Physiology of plant responses to artificial lighting. *Ecological Consequences of Artificial Night Lighting* (eds. C. Rich & T. Longcore), 1st edn, pp. 389–411. Island Press, Washington,

Cinzano, P., Falchi, F. and Elvidge, C.D. (2001) The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, 328, 689–707.

Clancy, K.M. and Price, P.W. (1987) Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. *Ecology*, 68, 733–737.

Davies, T.W., Bennie, J. and Gaston, K.J. (2012) Street lighting changes the composition of invertebrate communities. *Biology Letters*, 144, 2274–2276.

Davies, T.W., Bennie, J., Inger, R., de Ibarra, N.H. and Gaston, K.J. (2013) Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Global Change Biology*, 19, 1417–1423.

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.

Falchi, F., Cinzano, P., Elvidge, C.D., Keith, D.M. and Haim, A. (2011) Limiting the impact of light pollution on human health, environment and stellar visibility. *Journal of Environmental Management*, 92, 2714–2722.

Frank, K.D. (1988) Impact of outdoor lighting on moths: an assessment. *Journal of the Lepidopterists' Society*, 42, 63–93.

Gaston, K.J., Bennie, J., Davies, T.W. and Hopkins, J. (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biological Reviews*, 88, 912–927.

Gaston, K.J., Visser, M.E. and Hölker, F. (2015) The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 370, https://doi.org/10.1098/rstb.2014.0133.

Grenis, K., Tjossem, B. and Murphy, S.M. (2015) Predation of larval Lepidoptera in habitat fragments varies spatially and temporally but is not affected by light pollution. *Journal of Insect Conservation*, 19, 559–566.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G. and Sadler, J.P. (2015) The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Global Change Biology*, 21, 2467–2478.

Harvey, R.B. (1922) Growth of plants in artificial light. *Botanical Gazette*, 74, 447–451.

Hendricks, L.G., Mossop, H.E. and Kicklighter, C.E. (2011) Palatability and Chemical Defense of Phragmites australis to the Marsh Periwinkle Snail Littoraria irrorata. *Journal of Chemical Ecology*, 37, 838–845.

Hinners, S.J., Kearns, C.A. and Wessman, C.A. (2012) Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. *Ecological Applications*, 22, 1923–1935.

Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D. *et al*. (2010a) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecology and Society*, 15, 13.

Hölker, F., Wolter, C., Perkin, E.K. and Tockner, K. (2010b) Light pollution as a biodiversity threat. *Trends in Ecology and Evolution*, 25, 681–682.

Jung, K. and Kalko, E.K.V. (2010) Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *Journal of Mammalogy*, 91, 144–153.

Kamrowski, R.L., Limpus, C., Jones, R., Anderson, S. and Hamann, M. (2014) Temporal changes in artificial light exposure of marine turtle nesting areas. *Global Change Biology*, 20, 2437–2449.

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. *Current Biology*, 20, 1735–1739.

Kriska, G., Bernáth, B., Farkas, R. and Horváth, G. (2009) Degrees of polarization of reflected light eliciting polarotaxis in dragonflies (Odonata), mayflies (Ephemeroptera) and tabanid flies (Tabanidae). *Journal of Insect Physiology*, 55, 1167–1173.

Kyba, C.M., Ruhtz, T., Fischer, J. and Hölker, F. (2011) Cloud coverage acts as an amplifier for ecological light pollution in urban ecosystems. *PLoS ONE*, 6, e17307.

Loewy, K.J., Flansburg, A.L., Grenis, K., Kjeldgaard, M.K., McCarty, J., Montesano, L. *et al*. (2013) Life history traits and rearing techniques for fall webworms (*Hyphantria cunea* Drury) in Colorado. *Journal of the Lepidopterists' Society*, 67, 196–205.

Longcore, T. and Rich, C. (2004) Ecological light pollution. *Frontiers in Ecology and the Environment*, 2, 191–198.

Lyytimäki, J. (2013) Nature's nocturnal services: Light pollution as a non-recognised challenge for ecosystem services research and management. *Ecosystem Services*, 3, 44–48.

Macgregor, C.J., Pocock, M.J.O., Fox, R. and Evans, D.M. (2014) Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology*, 40, 187–198.

Matzke, E.B. (1936) The effect of street lights in delaying leaf-fall in certain trees. *American Journal of Botany*, 23, 446–452.

McIntyre, N.E., Rango, J., Fagan, W.F. and Faeth, S.H. (2001) Ground arthropod community structure in a heterogeneous urban environment. *Landscape and Urban Planning*, 52, 257–274.

Navara, K.J. and Nelson, R.J. (2007) The dark side of light at night: physiological, epidemiological, and ecological consequences. *Journal of Pineal Research*, 43, 215–224.

Neil, K. and Wu, J. (2006) Effects of urbanization on plant flowering phenology: a review. *Urban Ecosystems*, 9, 243–257.

Nufio, C.R., McClenahan, J.L. and Bowers, M.D. (2010) Grasshopper response to reductions in habitat area as mediated by subfamily classification and life history traits. *Journal of Insect Conservation*, 15, 409–419.

Painter, K. (1996) The influence of street lighting improvements on crime, fear and pedestrian street use, after dark. *Landscape and Urban Planning*, 35(2–3), 193–201.

Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. and Kaplan, I. (2011) *Insect Ecology: Behavior, Populations, and Communities* (ed. P.W. Price). Cambridge University Press, New York.

Raven, P.H., Evert, R.F. and Eichhorn, S.E. (1986) *Biology of Plants* (eds. S. Anderson & G. Hefta), 4th edn. Worth Publishers, Inc, New York.

Rich, C. and Longcore, T. (2006) *Ecological Consequences of Artificial Night Lighting* (eds. C. Rich & T. Longcore). Island Press, Washington, DC.

Robinson, N., Armstead, S. and Bowers, M.D. (2012) Butterfly community ecology: the influences of habitat type, weather patterns, and dominant species in a temperate ecosystem. *Entomologia Experimentalis et Applicata*, 145, 50–61.

Rotics, S., Dayan, T. and Kronfeld-Schor, N. (2011) Effect of artificial night lighting on temporally partitioned spiny mice. *Journal of Mammalogy*, 92, 159–168.

Rydell, J. (1992) Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, 6, 744–750.

Rydell, J. (2006) Bats and their insect prey at streetlights. *Ecological Consequences of Artificial Night Lighting* (eds. C. Rich & T. Longcore), pp. 43–60. Island Press, Washington, DC.

Santos, C.D., Miranda, A.C., Granadeiro, J.P., Lourenço, P.M., Saraiva, S. and Palmeirim, J.M. (2010) Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecologica*, 36, 166–172.

Schoonhoven, L.M., van Loon, J.J.A. and Dicke, M. (2005) *Insect–Plant Biology*, 2nd edn. Oxford University Press, Oxford.

Da Silva, A., Valcu, M. and Kempenaers, B. (2015) Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 370(1667), pii: 20140126.

Tuxbury, S.M. and Salmon, M. (2005) Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation*, 121, 311–316.

Varley, A.G.C. and Gradwell, G.R. (1960) Key factors in population studies. *Journal of Animal Ecology*, 29, 399–401.

Warton, D.I. and Hui, F.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92, 3–10.

Zahiri, R., Lafontaine, J.D., Schmidt, B.C., DeWaard, J.R., Zakharov, E.V. and Hebert, P.D.N. (2014) A transcontinental challenge—a test of DNA barcode performance for 1,541 species of Canadian Noctuoidea (Lepidoptera). *PLoS ONE*, 9(3), e92797.

Manuscript received June 16, 2017
Final version received December 18, 2017
Accepted January 26, 2018

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Field site name, area, location, and number of streetlights along the edge of the site.