Report

Current Biology

Low Levels of Artificial Light at Night Strengthen Top-Down Control in Insect Food Web

Highlights

- Artificial light at night, at varying intensities, is globally widespread
- Intensity of artificial light determines the community response in an insect food web
- Impacts of artificial light on interactions between species may be very common

Authors

Dirk Sanders, Rachel Kehoe, Dave Cruse, F.J. Frank van Veen, Kevin J. Gaston

Correspondence

d.sanders@exeter.ac.uk

In Brief

Sanders et al. demonstrate how different intensities of artificial light at night change interactions in experimental insect food webs between aphids and parasitoid wasps as their natural enemies. Major food web parameters such as parasitism rate, aphid abundance, and plant biomass were correlated with light intensity, highlighting that outcomes for ecological communities depend very much on the intensity of this widespread human impact.

Sanders et al., 2018, Current Biology *28*, 2474–2478
August 6, 2018
https://doi.org/10.1016/j.cub.2018.05.078

CellPress

Current Biology
Report

Low Levels of Artificial Light at Night Strengthen Top-Down Control in Insect Food Web

Dirk Sanders,[1,3,*] Rachel Kehoe,[2] Dave Cruse,[1] F.J. Frank van Veen,[2] and Kevin J. Gaston[1]
[1]Environment and Sustainability Institute, University of Exeter, Penryn, Penryn, Cornwall TR10 9FE, UK
[2]Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, Penryn, Cornwall TR10 9FE, UK
[3]Lead Contact
*Correspondence: d.sanders@exeter.ac.uk
https://doi.org/10.1016/j.cub.2018.05.078

SUMMARY

Artificial light has transformed the nighttime environment of large areas of the earth, with 88% of Europe and almost 50% of the United States experiencing light-polluted night skies [1]. The consequences for ecosystems range from exposure to high light intensities in the vicinity of direct light sources to the very widespread but lower lighting levels further away [2]. While it is known that species exhibit a range of physiological and behavioral responses to artificial nighttime lighting [e.g., 3–5], there is a need to gain a mechanistic understanding of whole ecological community impacts [6, 7], especially to different light intensities. Using a mesocosm field experiment with insect communities, we determined the impact of intensities of artificial light ranging from 0.1 to 100 lux on different trophic levels and interactions between species. Strikingly, we found the strongest impact at low levels of artificial lighting (0.1 to 5 lux), which led to a 1.8 times overall reduction in aphid densities. Mechanistically, artificial light at night increased the efficiency of parasitoid wasps in attacking aphids, with twice the parasitism rate under low light levels compared to unlit controls. However, at higher light levels, parasitoid wasps spent longer away from the aphid host plants, diminishing this increased efficiency. Therefore, aphids reached higher densities under increased light intensity as compared to low levels of lighting, where they were limited by higher parasitoid efficiency. Our study highlights the importance of different intensities of artificial light in driving the strength of species interactions and ecosystem functions.

RESULTS AND DISCUSSION

We assembled replicate plant-aphid-parasitoid communities (see food web in Figure 1F) in 48 mesocosms in the field and exposed them to different intensities of artificial light, ranging from 0.1 to 100 lux, at night for 10 aphid generations. To understand the mechanisms behind the impacts of artificial light, we complemented the field experiment with small-scale experiments under more controlled conditions.

In the field experiment, we found that low levels of artificial light at night (0.1 to 5 lux), representing severe skyglow or direct light effects away from the immediate vicinity of typical streetlight sources, had a strong impact on insect communities. The overall abundance of all three aphid species (*Megoura viciae*, *Acyrthosiphon pisum*, *Aphis fabae*) feeding on bean plants was reduced by 45.5% under low lighting levels in comparison to the control treatment with natural light levels (Figure 1; treatments 0.1 lux [$t = -3.87$, $p = 0.0005$], 1 lux [$t = -2.57$, $p = 0.0147$], and 5 lux [$t = -2.75$, $p = 0.0095$], df = 7,35), while the higher levels of lighting (more typical of the immediate vicinity of streetlights and more intense forms of lighting, such as those used in sports stadia and around industrial installations) did not affect their densities ($p > 0.1$). The marked impact of low-level lighting on aphid numbers was driven by a 56.2% decline of the most abundant aphid species (*M. viciae*) in 0.1, 1, and 5 lux treatments when compared to the control (Figure 1; treatments 0.1 lux [$t = -2.97$, $p = 0.0053$], 1 lux [$t = -1.95$, $p = 0.0587$], and 5 lux [$t = -3.11$, $p = 0.0037$], df = 7,35). The aphid *A. pisum* responded to light treatments with a similar trend to that of *M. viciae*, though this pattern was not statistically significant compared to the control (overall treatment effect, $\chi^2 = 5.90$, df = 7, $p = 0.5511$). The aphid *A. fabae* had a less predictable response to the treatments, with a negative effect at 10 lux as compared to the control (Figure 1; df = 7,35, $t = -2.26$, $p = 0.0304$) and a trend to higher densities in the 5- and 100-lux treatments. The grain aphid *Sitobion avenae*, feeding on barley plants, did not respond to the treatments (overall treatment effect, $\chi^2 = 2.10$, df = 7, $p = 0.9541$).

While we found a strong overall decline in aphid densities under low levels of light compared to control conditions without light, aphid abundance increased from treatments with low lighting to medium and high lighting levels, showing that the negative impact on aphids was alleviated under higher-intensity light treatments. Increasing light intensity (including all light treatments from 0.1 to 100 lux) had a positive effect on overall bean aphid numbers (Figure 1; df = 1,35, $t = 2.65$, $p = 0.0119$, with the model explaining 40% [conditional R^2] and the fixed effect explaining 10% [marginal R^2] of the variation).

To explain the responses of the aphids, it is necessary to look at the impact of the artificial light treatments on their resource (the plants), as well as on their top-down control through parasitoids. To test for the impact of light intensity (0, 0.1, 5, 20, and 100 lux) on bean plant biomass, we conducted an additional

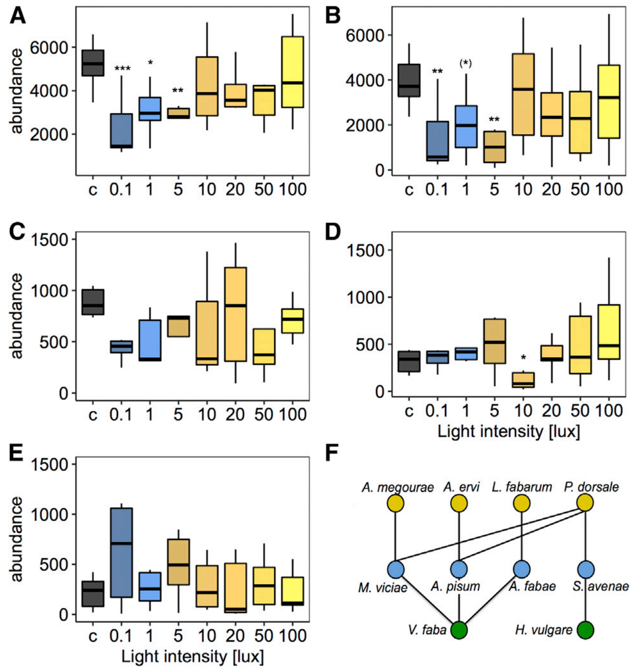

Figure 1. Aphid Densities in the Field Experiment

(A–E) Boxplots presenting the median and the lower and upper quartiles, 25% and 75%, of cumulative aphid densities for (A) all three aphids on *Vicia faba*, (B) *M. viciae*, (C) *A. pisum*, (D) *A. fabae*, and (E) *S. avenae* in mesocosms without light treatments (c, control) and in different treatments with increased light intensities at night (0.1, 1, 5, 10, 20, 50, and 100 lux). Each treatment was replicated six times. Statistical significance levels for comparison to the control treatment: (*) p = 0.05, *p < 0.05, **p < 0.01, ***p < 0.001.

(F) Food web structure of the experimental insect communities, with two plant species—broad bean (*V. faba*) and barley (*Hordeum vulgare*)—and with three aphid species on beans—*A. fabae*, *A. pisum*, and *M. viciae*. Each of the aphid species was attacked by a specialist parasitoid, these being *L. fabarum*, *A. ervi*, and *A. megourae*, respectively. The grain aphid *S. avenae* fed on barley. The generalist parasitoid *Praon dorsale* attacked the aphids *S. avenae*, *A. pisum*, and *M. viciae*.

See Figure S1 for population dynamics.

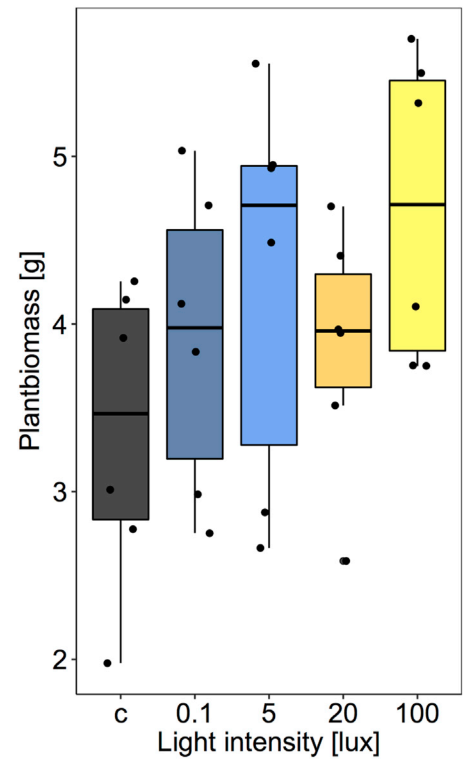

Figure 2. Plant Biomass in Greenhouse Experiment without Aphids

V. faba plant biomass in control (black) and light treatments (0.1, 5, 20, and 100 lux). Presented are the median and the lower and upper quartiles, 25% and 75% (based on six replicates).

See Figure S2 for plant biomass in the field experiment.

experiment under controlled environmental conditions in a greenhouse in the absence of aphids on plants. This revealed a positive correlation between light intensity and plant biomass (Figure 2; df = 1,23, t = 2.23, p = 0.0357). We found a similar trend in the plant biomass data from the field experiment—where aphids were also present—but only in the 20-lux treatment with significantly higher plant biomass than in the control (Figure S2; overall treatment effect: χ^2 = 16.56, df = 7, p = 0.0205). The biomass of barley showed no response in the field experiment (Figure S2; overall treatment effect: χ^2 = 12.70, df = 7, p = 0.080). In sum, artificial light at night, at least at higher levels, has the potential to increase plant biomass, most likely through an increased photosynthesis rate of plants, leading to a positive bottom-up effect [8, 9], but this effect is variable between species.

The parasitism rate of *Aphidius megourae* attacking the aphid *M. viciae* in the field experiment increased from 5% in the unlit control treatments to 10% in low-light treatments (Figure 3B; z = 2.910, p = 0.0036). The parasitism rate of neither of the other host-specific parasitoids, *Aphidius ervi* and *Lysiphlebus fabarum*, responded significantly to light treatments, but that of the latter showed a similar trend to *A. megourae* (Figures 3C and 3D). A 2-fold increase in parasitism rate is a strong response, especially over multiple generations, and can explain the observed effects of low lighting treatments on aphid numbers. We found a strong decline in the overall parasitism rate (including all parasitoid species) from a low to high level of nighttime lighting (Figure 3A; linear regression between light intensity and parasitism rate, z = −2.656, p = 0.0079).

The strong dependence of the strength of host-parasitoid interactions on artificial light intensities in a field experiment under natural conditions is an important result and worthy of further examination. We first compared the functional response of *A. megourae* under control conditions to medium light levels (20 lux). The relationship between host density and the number of successful attacks by *A. megourae* can be described by a type 2 functional response (Figure 4A). The fitted curve for the light treatment showed that parasitoid attacks saturated at a much higher level than in the control, demonstrating that the parasitoids can attack more aphids in the 20-lux light treatment—almost doubling attack rate under high-host-density situations (Figure 4A). To test whether this effect could explain the increased parasitism rate in the field experiment under low-level lighting, we then compared the number of successful attacks by *A. megourae* in control conditions to low-intensity (1 lux) and medium-intensity (20 lux) treatments (Figure 4B). This revealed

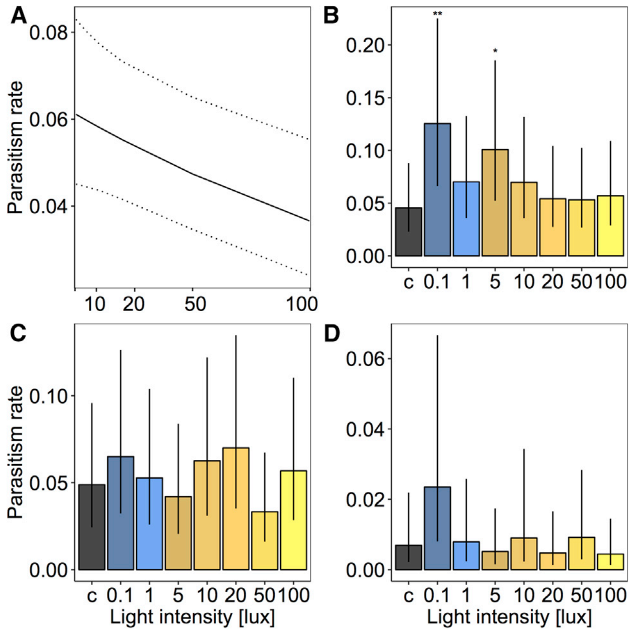

Figure 3. Parasitism Rate in the Field Experiment

(A) Mean and 95% confidence interval (CI) for overall parasitism rate (all species) in relation to light intensity (0.1–100 lux).

(B–D) Mean and 95% CI showing the parasitism rate for each of the parasitoid species (B) *A. megourae*, (C) *A. ervi*, and (D) *L. fabarum* in control communities without artificial light at night (C) and communities exposed to different light intensities (0.1, 1, 5, 10, 20, 50, and 100 lux) at night (n = 6 for each treatment). The parasitism rate for the generalist parasitoid *P. dorsale* is not shown due to the low number of *Praon* aphid mummies detected in the experiment (see Figure S1H). Statistical significance level for comparison to the control treatment: *$p < 0.05$, **$p < 0.01$.

that the number of attacks increased significantly in the 1-lux treatment ($t = 3.17$, $p = 0.0053$, df = 2,18) and marginally not significantly under 20 lux ($t = 2.07$, $p = 0.0536$, df = 2,18). These results indicate that the activity of these parasitoids is strongly influenced by photoperiod [10]. We then showed that this is indeed the case for the parasitoid *A. megourae*, with the vast majority of parasitoid attacks happening during the day in a 12:12 day:night regime that included no artificial light at night. Parasitism rate was 18% during daylight, dropping to 2.5% during dark hours (Figure S3; $z = 7.294$, $p < 0.0001$); this species responds more strongly to photoperiod than has previously been shown for the parasitoid *A. ervi* [11], explaining the stronger response to artificial light in the field experiment. Artificial light at night thus extends the time budget of day-active parasitoids and increases their ability to control aphid populations even at very low intensities of artificial light. This usage of the so-called "nighttime niche" appears to be more widespread, with evidence from increased predation rates in ladybirds [12] and changed feeding habits of lizards [13] and birds [14]. However, the overall decline in parasitism rate with increasing light levels suggests that this niche is strongly dependent on light intensity, as the parasitoids are more efficient under low-level lighting. We therefore tested for the behavioral response of *A. megourae* parasitoids to different light intensities in a setting with a mesocosm that contained a plant with 100 aphids. We found a strong negative linear relationship between the proportion of female parasitoids that stayed on the plant and light intensity (Figure 4C, $t = -4.51$, $p < 0.001$, df = 1,13). Therefore, at higher light levels, the majority of parasitoids leave the plants with aphids, explaining why the parasitism rate is so strongly dependent on the level of light and the parasitoids most efficient at low light levels.

Overall, despite a potential bottom-up effect through increased plant biomass providing more resources for aphids under higher light intensities, we show that the interaction between the aphids and parasitoids is the critical driver for the observed responses in the field experiment. Higher aphid densities were strongly associated with lower parasitism rates under control and high-light treatments. Our experiment demonstrates that different intensities of artificial light at night change species interactions and food web dynamics in insect communities. As species interactions are an important building block of ecological communities, this can have far-reaching consequences for community stability and ecosystem functions. As demonstrated for other environmental stressors, some species respond, while others remain unaffected. In our communities, the most abundant species responded, thereby driving the whole community response, and because species are interconnected in food webs, even single-species responses can drive whole-community changes [15].

Host-parasitoid interactions are some of the most common food web interactions in terrestrial ecosystems [16], both natural and agricultural. The mechanisms demonstrated in our experimental communities therefore have major implications for ecosystems exposed to artificial light at night.

The "broad-spectrum" white lights used are typical of those being installed widely across the world for streetlighting and other outdoor purposes, particularly as the economic benefits associated with light-emitting diode (LED) technologies are exploited [17]; our findings may not be relevant to spectra more commonly associated with older lighting types, such as narrow-spectrum low-pressure sodium lamps. The surprisingly strong community response to low-level artificial light is of major concern, because such light intensities are very widespread and becoming more so with the continued spread in the extent of artificial lighting at 2% per annum [18].

Our study further demonstrates that it is important to consider that the impacts of artificial light at night are strongly light-intensity dependent and, within a community context, not necessarily possible to predict from single-species responses. Prediction of the community response requires knowledge of major pathways, such as the balance between bottom-up and top-down effects. Species interactions are central to understanding the impact of artificial light at night on ecological communities and any resultant effects on ecosystem functions and stability.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS

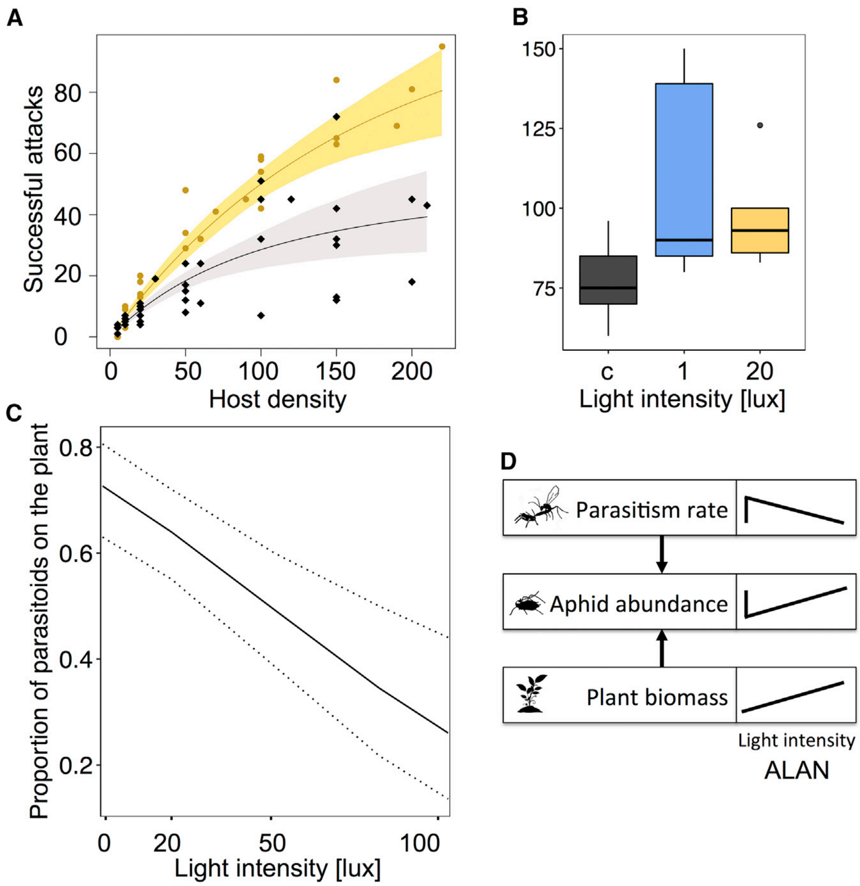

Figure 4. Parasitoid Functional Response and Behavior

(A) Functional response with a fitted type 2 curve and 95% CI for the parasitoid *A. megourae* attacking its host *M. viciae* under control (no light: black diamonds) and 20 lux at night (medium light intensity: yellow circles).

(B) Number of successful attacks in control and 1- and 20-lux treatment (n = 10, 8, and 6, respectively) showing the median and the lower and upper quartiles, 25% and 75%, for host density 140–180.

(C) Proportion of *A. megourae* parasitoids staying in a plant with aphids under different light intensities (measured for 0, 1, 5, 20, and 100 lux).

(D) Overview of the responses of different trophic levels to increasing ALAN intensities.

See Figure S3 for attack rate during day and night.

- METHOD DETAILS
  - Field experiment
  - Plant biomass without aphids
  - Parasitoid functional response and attack rate
  - Parasitoid activity
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Field experiment
  - Plant biomass without aphids
  - Parasitoid functional response
  - Parasitoid attack rate during light and dark period
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and can be found with this article online at https://doi.org/10.1016/j.cub.2018.05.078.

ACKNOWLEDGMENTS

The research leading to this paper was funded from NERC grant NE/N001672/1. We thank two anonymous reviewers and E. Frago for their very constructive comments. H. Akester, S. Bekker, S. Edwards, and M. Hordley helped with the field experiment.

AUTHOR CONTRIBUTIONS

K.J.G. and F.J.F.v.V. conceived the project. K.J.G., F.J.F.v.V., and D.S. designed the experiments. D.S., R.K., and D.C. carried out the experiments. D.S. analyzed the data and wrote the first draft of the manuscript. All authors contributed to the manuscript. K.J.G. and F.J.F.v.V. acquired the funding for the work.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: August 8, 2017
Revised: April 20, 2018
Accepted: May 24, 2018
Published: July 26, 2018

REFERENCES

1. Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B.A., Rybnikova, N.A., and Furgoni, R. (2016). The new world atlas of artificial night sky brightness. Sci. Adv. *2*, e1600377.
2. 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. Philos. Trans. R. Soc. Lond. B Biol. Sci. *370*, 20140131.
3. Gaston, K.J., Bennie, J., Davies, T.W., and Hopkins, J. (2013). The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol. Rev. Camb. Philos. Soc. *88*, 912–927. https://doi.org/10.1111/brv.12036.
4. Miller, M.W. (2006). Apparent effects of light pollution on singing behavior of American robins. Condor *108*, 130–139.
5. Stone, E.L., Jones, G., and Harris, S. (2009). Street lighting disturbs commuting bats. Curr. Biol. *19*, 1123–1127.

6. Gaston, K.J., Davies, T.W., Bennie, J., and Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: options and developments. J. Appl. Ecol. *49*, 1256–1266.
7. Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., and Fontaine, C. (2017). Artificial light at night as a new threat to pollination. Nature *548*, 206–209.
8. Bennie, J., Duffy, J.P., Davies, T.W., Correa-Cano, M.E., and Gaston, K.J. (2015). Global trends in exposure to light pollution in natural terrestrial ecosystems. Remote Sens. *7*, 2715–2730.
9. Bennie, J., Davies, T.W., Cruse, D., and Gaston, K.J. (2016). Ecological effects of artificial light at night on wild plants. J. Ecol. *104*, 611–620.
10. Godfray, H.C.J. (1994). Parasitoids: behavioral and evolutionary ecology (Princeton University Press).
11. He, X.Z., Wang, Q., and Teulon, D.A.J. (2004). Emergence, sexual maturation and oviposition of *Aphidius ervi* (Hymenoptera: Aphidiidae). NZ Plant Prot. *57*, 214–220.
12. Miller, C.R., Barton, B.T., Zhu, L., Radeloff, V.C., Oliver, K.M., Harmon, J.P., and Ives, A.R. (2017). Combined effects of night warming and light pollution on predator-prey interactions. Proc. Biol. Sci. *284*, 20171195.
13. Zozaya, S.M., Alford, R.A., and Schwarzkopf, L. (2015). Invasive house geckos are more willing to use artificial lights than are native geckos. Austral Ecol. *40*, 982–987.
14. Stracey, C.M., Wynn, B., and Robinson, S.K. (2014). Light pollution allows the northern mockingbird (*Mimus polyglottos*) to feed nestlings after dark. Wilson J. Ornithol. *126*, 366–369.
15. Sanders, D., and Gaston, K.J. (2018). How ecological communities respond to artificial light at night. J. Exp. Zool. A. Ecol. Integr. Physiol. Published online April 14, 2018. https://doi.org/10.1002/jez.2157.
16. Hassell, M.P. (2000). Host–parasitoid population dynamics. J. Anim. Ecol. *69*, 543–566.
17. Pust, P., Schmidt, P.J., and Schnick, W. (2015). A revolution in lighting. Nat. Mater. *14*, 454–458.
18. Kyba, C.C.M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C.D., Gaston, K.J., and Guanter, L. (2017). Artificially lit surface of Earth at night increasing in radiance and extent. Sci. Adv. *3*, e1701528.
19. R Development Core Team (2016). R: A language and environment for statistical computing (Vienna, Austria: R Foundation for Statistical Computing).
20. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team. (2016). nlme: Linear and Nonlinear Mixed Effects Models (R Foundation for Statistical Computing).
21. Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. J. Stat. Softw. *67*, 1–48.
22. Fox, J. (2003). Effect displays in R for generalised linear models. J. Stat. Softw. *8*, 1–27.
23. Pritchard, D. (2017). frair: Tools for Functional Response Analysis (R Foundation for Statistical Computing).
24. Kyba, C.C., Tong, K.P., Bennie, J., Birriel, I., Birriel, J.J., Cool, A., Danielsen, A., Davies, T.W., Outer, P.N., Edwards, W., et al. (2015). Worldwide variations in artificial skyglow. Sci. Rep. *5*, 8409.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Raw data	This paper	NERC Environmental Information Data Centre. https://catalogue.ceh.ac.uk/id/d30168d3-6cbb-4d75-b73c-276e6083a1fe
Experimental Models: Organisms/Strains		
Vicia faba, var the Sutton	Kings Seeds, UK.	N/A
Hordeum vulgare	Kings Seeds, UK.	N/A
Megoura viciae	Stock cultures, Penryn, UK	(Buckton)
Acyrthosiphon pisum	University of Oxford, UK	(Harris)
Aphis fabae	Silwood Park, Berkshire, UK	(Scopoli)
Sitobion avenae	Stock cultures, Penryn, UK	(Fabricius)
Aphidius megourae	Stock cultures, Penryn, UK	(Stary)
Aphidius ervi	Koppert, Netherlands	(Haliday)
Lysiphlebus fabarum	Stock cultures, Penryn, UK	(Marshall)
Praon dorsale	Stock cultures, Penryn, UK	(Haliday)
Software and Algorithms		
R version 3.3.2	[19]	https://cran.r-project.org/bin/windows/base/old/3.3.2/
Package nlme	[20]	https://cran.r-project.org/web/packages/nlme/nlme.pdf
Package lme4	[21]	https://cran.r-project.org/web/packages/lme4/index.html
Package effects	[22]	https://cran.r-project.org/web/packages/effects/index.html
Package frair	[23]	ftp://cran.r-project.org/pub/R/web/packages/frair/frair.pdf
Other		
36 W ‘Daylight White 5050 SMD LEDs’ (cold white 5000 – 7000 Kelvin, see Figure S5 for spectrum)	Ledcenter.uk, London,	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for reagents and resources should be directed to and will be fulfilled by the Lead Contact, Dirk Sanders (d.sanders@exeter.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The replicate experimental plant-insect communities (see Figure 1F) consisted of two plant species: broad bean (*Vicia faba*, L., var. the Sutton) and barley (*Hordeum vulgare* L.), with bean plants as a resource for three aphid species: (1) the black bean aphid *Aphis fabae* (Scopoli), (2) the pea aphid *Acyrthosiphon pisum* (Harris), and (3) the vetch aphid *Megoura viciae* (Buckton). Each of the aphid species was attacked by a specialist parasitoid, these being *Lysiphlebus fabarum* (Marshall), *Aphidius ervi* (Haliday), and *Aphidius megourae* (Stary), respectively. Barley plants were a resource for the grain aphid *Sitobion avenae* (Fabricius). These separate communities were linked by the generalist parasitoid *Praon dorsale* (Haliday), which attacked the aphids *S. avenae*, *A. pisum*, and *M. viciae*. Bean and barley seeds were bought from Kings Seeds, UK. Parasitoids were collected in the field (*L. fabarum* and *A. megourae, P. dorsale*) and received from Koppert, Netherlands (*A. ervi*). Aphids were from existing laboratory cultures *A. fabae* (Silwood Park, Berkshire, U.K), *A. pisum* (University of Oxford, UK) and *M. viciae* found on *Lathyrus pratensis* plants (Penryn, UK). Prior to the experiments, parasitoid and aphid cultures were kept in a controlled environment room at 20°C, with a 16:8-h light:dark cycle.

METHOD DETAILS

Field experiment

Experimental communities were established in 47.5 × 47.5 × 47.5 cm Bug Dorm mesocosms (BugDorm-44545F Insect Rearing Cage, Megaview Science, Taiwan), which were secured with a wooden frame and raised slightly above the surrounding vegetation, ensuring that all mesocosms were at a similar height. Mesocosms were located 1.5 m apart, and the vegetation around them was mown fortnightly. The experiment was conducted in a contained field site at the University of Exeter, Cornwall.

Light level treatments covered a range of light intensities; low light treatments (0.1, 1 and 5 lux) replicating city skyglow levels and levels away from the immediate vicinity of streetlights, medium light treatments (10 and 20 lux) replicating levels in the immediate vicinity of streetlights, and high light level treatments (50 and 100 lux) replicating more extreme lighting, for example stadium or festival lighting. Each of the artificial light level treatments (0.1, 1, 5, 10, 20, 50 and 100 lux), and an unlit control were replicated 6 times and arranged in a randomized block design. Lighting was located at the top of each mesocosm, and consisted of 36 W 'Daylight White 5050 SMD LEDs' (Ledcenter.uk, London, cold white 5000 – 7000 Kelvin, see Figure S4 for spectrum).

The lighting levels were manipulated using a resistor to ensure the correct lux for each treatment. Artificial lights were turned on only at night, by use of a dusk-dawn sensor, switching on at 70 lux and off at 110 lux. Wooden barriers between the cages prevented spillover of light to neighboring mesocosms and mesocosms further away. Light levels were measured with a lux meter (Delta OHM HD2102- 39 -V2.3 with Illuminance probe LP 471 PHOT/SICRAM module measurement range starting at 0.01 lux with a resolution of 0.01 lux) in every mesocosm to confirm the light levels per treatment. We compared treatment effects against a control treatment without additional light but exposed to the varying influence of moonlight and very low levels of skyglow as there were no direct light sources in the vicinity of the field site. This means the control is not a entirely dark control but a natural nighttime light (as would be experienced in the absence of streetlights) to which each treatment added the artificial light at a certain intensity. Field experiments are important because they indeed include the natural variation as experienced by natural communities but under more controlled conditions. The field site does experience low levels of artificial light at night through skyglow (as would be the case throughout much of Europe [1]), but readings from a Sky Quality Meter regularly reach values of 21 $mag_{SQM}/arcsec^2$ (lower levels occur, as would be expected, under moonlight and clouds), which compares favorably with what has been assumed to be a natural radiance of 21.6 $mag_{SQM}/arcsec^2$ [24]; note that higher values of these units mean less illuminance.

The experiment was set up on 29th July 2016, with 3 pots of broad beans and 1 with barley plants placed in each mesocosm and then a week later completed to a total of 6 pots of broad beans and 2 pots of barley per mesocosm. Five individuals of each aphid species were placed on the appropriate plant species and left for 2 weeks to grow in numbers. At weeks 2 and 3, two mated female parasitoids of each species were released into each mesocosm. Each week, the two oldest plant pots from each tray were replaced with 2-week-old plants, while leaving the plant matter and all insects in the mesocosm. This replicates the natural behavior of aphid colonies, which typically show cycles of dispersal to fresh host plants.

From week 1 until the termination of the experiment after 9 weeks, all species on half of the plants were counted on a weekly basis. If no individuals of a particular species were found in a particular replicate, the entire mesocosm was checked to confirm presence or absence.

Plant biomass without aphids

We used 5 different light treatments to test for the effect of artificial light on plant biomass, in the absence of aphids: an unlit control, 0.1, 5, 20, and 100 lux. Each of the light treatments was replicated 6 times and arranged in a randomized block design. For each replicate a single 2 week old bean plant was placed in a 47.5 × 47.5 × 47.5 cm Bug Dorm cage, in a greenhouse with a 16: 8 hours light: dark period. The experiment ran for 3 weeks, at which point the plants were washed clean of soil, the aboveground and belowground parts separated, and dried at 50°C for 48 hours. They were then weighed to within 0.001 g.

Parasitoid functional response and attack rate

Third instar *M. viciae* aphid individuals were set onto 2 week old plants at densities varying from 5 to 200, with each plant placed in a 47.5 × 47.5 × 47.5 cm Bug Dorm cage, in the contained field site at the University of Exeter, Cornwall. One female *A. megourae* parasitoid was placed in each cage for a 24-hour period, after which point it was removed. Aphids were then left for 2 weeks before all mummies were counted. We used two treatments: unlit controls and artificial light at night at 20 lux. This experiment ran at the same time as the large field experiment.

We compared parasitoid attack rate between control (no light), 1 lux and 20 lux treatment. 1 female *A. megourae* parasitoid was released on a plant with 150 *M. viciae* aphids, and left for 24 h. This was done in a controlled Temperature room at 20°C and 16: 8 hours light: dark period. Each treatment was replicated 6 times, and parasitoid mummies were counted after 2 weeks.

Parasitoid activity

To test for the behavioral response of parasitoids to different light intensities, 100 3rd instar *M. viciae* aphids were placed on a 3 week old broad bean (*V. faba* plant) and allowed to settle in a climate chamber with a 16:8 light: dark cycle for 24 hours. This infested plant was then placed in a cage in complete darkness. Different light treatments were then applied over the top of the cage, these being 0 (control) 1, 5, 20, and 100 lux, measureable at the height of the plant (in exactly the same setting as for the field experiment). 20 mated female A. *megourae* parasitoids were then released into the cage, and were left for one hour. After one hour the locations of the parasitoids (on the or away from plant) were noted. Preliminary tests using the artificial light treatments along with red lights showed that there was a period of 20 s for counting before the parasitoids changed their location or activity after the counting light was put on.

To test for parasitoid attack rate during day and night, single broad bean plants were infected with 60 3rd star *M. viciae* aphids per plant, and placed in a 20 × 20 × 40 cm cage constructed of untreated wood and thrip netting. These aphids were left to settle for

1 day before being placed in incubators (Percival Model 1-30 vl) set to 18°C with a 12:12 day night cycle and 75% humidity. A single, mated female *A. megourae* parasitoid was placed in each cage, and left for 12 hours in either dark or light settings. After 12 hours the parasitoid was removed and placed in another cage, again with 60 3rd instar aphids and left for a further 12 hours at the opposite light treatment. After the removal of the parasitoid, each cage was placed in a controlled temperature room at 18 degrees and a 16:8 day night cycle for mummies to develop. After 2 weeks the number of mummies per cage was counted.

QUANTIFICATION AND STATISTICAL ANALYSIS

All data were analyzed using the open source software R 3.3.2 [19].

Field experiment

The impact of light treatments on plant biomass and aphid populations in the field experiment was analyzed with linear mixed effects models using the function lme from the package nlme [20]. We included treatment (with 8 levels) as a fixed factor, while block was included as a random factor. As response variables we used aphid cumulative numbers (for each of the species the sum of aphids counted per single mesocosm) and plant dry weight (separated for bean and barley plants). We also tested for a linear response of overall aphid numbers to increasing light intensity (0.1 to 100 lux).

Parasitism rate was analyzed using generalized linear mixed models assuming a binomial error distribution and using the logit link function. The response variable was the bivariate variable containing 'cumulative parasitoid mummies of aphid species i' and 'cumulative abundance of alive aphids for species i', where 'i' can be the cumulative abundance or mummy number of *A. fabae*, *M. viciae*, or *A. pisum*. The parasitism rate of the generalist parasitoid *P. dorsale* was not analyzed due to the low sample size. Block was included as a random factor, and to account for over-dispersion, an additional observation-level random factor was added. For this analysis we used the function glmer from the package lme4 [21]. To obtain 95% credible intervals for the model predictions, we used the R-package "effects" [22]. We also tested for a correlation between overall parasitism rate in the community (including all parasitoid species) and light intensity (0.1 to 100 lux).

Plant biomass without aphids

The impact of light treatments on plant biomass in the absence of aphids was analyzed with linear mixed effects models using the function lme from the package nlme [20]. We included light intensity (0, 0.1, 5, 20, 100 lux) as a continuous explanatory variable, while block was included as a random factor. As response variable we used plant dry weight per single mesocosm.

Parasitoid functional response

The functional response curve for the parasitoid *A. megourae* attacking aphids under unlit control conditions and the treatment with artificial light at night (20 lux) were fitted using the function frair_fit and confidence intervals were estimated with frair_boot from the frair package [23].

Parasitoid attack rate during light and dark period

Parasitoid behavior under different light intensities (0, 1, 5, 20, 100 lux) and parasitism rate in dark and light periods were analyzed using generalized linear models assuming a quasi-binomial error distribution. The response was the bivariate variable containing 'parasitoids on the plant' and 'and parasitoids away from the plant' in the first and'*A. megourae* parasitoid mummies' and 'abundance of alive *M. viciae* aphids' for the latter analysis, which was analyzed with treatment (12 h light or 12 h dark period) as explanatory. To obtain 95% credible intervals for the model predictions we used the R-package "effects" [22].

DATA AND SOFTWARE AVAILABILITY

All data used in this study have been deposited at the NERC Environmental Information Data Centre under the link https://catalogue.ceh.ac.uk/id/d30168d3-6cbb-4d75-b73c-276e6083a1fe.