BIOLOGY LETTERS

rsbl.royalsocietypublishing.org

Research

Cite this article: Altermatt F, Ebert D. 2016 Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biol. Lett.* **12**: 20160111. http://dx.doi.org/10.1098/rsbl.2016.0111

Received: 10 February 2016
Accepted: 15 March 2016

Subject Areas:
evolution, ecology, behaviour, environmental science

Keywords:
Lepidoptera, *Yponomeuta*, environmental change, adaptation, natural selection

Author for correspondence:
Florian Altermatt
e-mail: florian.altermatt@eawag.ch

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2016.0111 or via http://rsbl.royalsocietypublishing.org.

THE ROYAL SOCIETY PUBLISHING

Global change biology

Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution

Florian Altermatt[1,2,3] and Dieter Ebert[3]

[1]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland
[2]Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Überlandstrasse 133, 8600 Dübendorf, Switzerland
[3]Department of Environmental Sciences, Zoology, University of Basel, Vesalgasse 1, 4051 Basel, Switzerland

FA, 0000-0002-4831-6958

The globally increasing light pollution is a well-recognized threat to ecosystems, with negative effects on human, animal and plant wellbeing. The most well-known and widely documented consequence of light pollution is the generally fatal attraction of nocturnal insects to artificial light sources. However, the evolutionary consequences are unknown. Here we report that moth populations from urban areas with high, globally relevant levels of light pollution over several decades show a significantly reduced flight-to-light behaviour compared with populations of the same species from pristine dark-sky habitats. Using a common garden setting, we reared moths from 10 different populations from early-instar larvae and experimentally compared their flight-to-light behaviour under standardized conditions. Moths from urban populations had a significant reduction in the flight-to-light behaviour compared with pristine populations. The reduced attraction to light sources of 'city moths' may directly increase these individuals' survival and reproduction. We anticipate that it comes with a reduced mobility, which negatively affects foraging as well as colonization ability. As nocturnal insects are of eminent significance as pollinators and the primary food source of many vertebrates, an evolutionary change of the flight-to-light behaviour thereby potentially cascades across species interaction networks.

1. Background

Anthropogenic light pollution is recognized as a global environmental change negatively affecting humans [1], animals [2,3] and microbes [4]. The negative effects are well-known and even captured in the Shakespearian saying 'Thus hath the candle singed the moth', referring to someone tempted by something that eventually will lead to his downfall. As a global phenomenon [5,6], light pollution is a by-product of urbanization [6] and interferes with the natural day–night cycle, resulting in changed phenologies of organisms in the polluted habitat [7]. An even more direct effect of light pollution is the widely observed attraction of organisms ranging from migrating birds to insects to the light sources, which can result in increased mortality through direct burning or increased exposure to predators [8,9]. Furthermore, attraction to light may lure organisms out of their native habitat and interfere with normal feeding behaviour, mating and reproduction [3]. The negative effects of light pollution on community composition [4,10], population dynamics and organisms' Darwinian fitness [11] have been globally documented, and mortality at artificial light sources can be 40- to 100-fold higher than in dark-sky populations [3,8].

Surprisingly, however, little is known about the potential evolutionary consequences. Existing data show that there is a high variability among species and

Table 1. Localities of the 10 studied populations from France (F) or Switzerland (CH). Light-pollution estimates are from taken from DataRadiance (see Methods). These light-pollution values were measures in 2012, and we use them as a proxy for the last decade.

site/country	latitude/longitude	population	light pollution (10^{-9} Watt cm^{-2} × sr)	no. of tested individuals
Blochmont/F	47°26′16″ N 7°14′10″ E	dark-sky	0.25–0.4	53
Kleinlützel/CH	47°25′55″ N 7°22′57″ E	dark-sky	0.4–1	93
Kiffis/F	47°26′18″ N 7°17′59″ E	dark-sky	0.4–1	89
Doucier/F	46°39′40″ N 5°41′21″ E	dark-sky	0.4–1	66
Lutterbach/F	47°46′12″ N 7°3′36″ E	dark-sky	1–3	19
Allschwil/CH	47°32′52″ N 7°32′80″ E	light-polluted	20–40	144
Reinach/CH	47°31′50″ N 7°36′25″ E	light-polluted	20–40	170
Hegenheim/F	47°33′43″ N 7°31′14″ E	light-polluted	>40	75
Basel Kannenfeld/CH	47°33′59″ N 7°34′19″ E	light-polluted	>40	129
Basel Spalentor/CH	47°33′28″ N 7°34′53″ E	light-polluted	>40	210

sexes to be attracted by light [12,13], and anecdotal evidence from naturalists even indicates within-species variation [14]. Given the detrimental effect of the flight-to-light behaviour in polluted areas it has been postulated that natural selection should favour individuals with a lower propensity of being attracted by light [7,12].

Organisms' phenotypic and genetic responses to anthropogenic environmental changes are well-known, such as the classic example of industrial melanism of the peppered moth. However, possible selective responses to light pollution have not yet been documented, even though artificial night lighting has strongly increased over the last decades [3], has a pronounced geographical variation [6], and is having increasingly negative effects on many species [3], creating the necessary conditions for directional selection and adaptation to a novel anthropogenic stressor. Here, we report an experimental quantification of a reduced flight-to-light behaviour of small ermine moths from populations occurring in areas with high light pollution compared with populations with low pollution.

2. Methods

(a) Study organism and study sites

We used the small ermine moth (*Yponomeuta cagnagella*), which is widely distributed across Europe. Its larvae feed strictly on European spindle (*Euonymus europaeus*) [15]. Larvae live in loose silk-webs, forming gregarious full-sib groups on their host plants. In order to test for an effect of multi-generational exposure to artificial light pollution on flight-to-light behaviour, we collected larvae of the small ermine moths in areas with low-to-medium levels of light pollution (less than 3×10^{-9} W sr^{-1} cm^{-2}; subsequently called dark-sky populations; table 1) and in areas which have been exposed to strong light pollution for several decades (current light pollution 20 to more than 40×10^{-9} W sr^{-1} cm^{-2}; subsequently called light-polluted populations, data from http://www.lightpollutionmap.info) [6]. The latter populations were always sampled in the immediate vicinity of streetlights in urban parks or along streets (maximum distance to light source 20–50 m).

(b) Laboratory conditions

We collected second-instar larvae, such that organisms were independently sampled with respect to the subsequent experimental test method, in 10 independent populations from locations in northwestern Switzerland and in eastern France in spring 2007 (table 1). These populations were not connected by suitable habitat and represented independent units. At each location, larvae from multiple full-sib family clutches were collected. Some of these populations had been used in a previous analysis on sex-specific flight-to-light behaviour [12]. Larvae were reared in the laboratory under standardized, common garden conditions in 500 ml plastic boxes at 80% relative humidity and a daily light–dark cycle of L16 : D8 h, including 1 h dusk and dawn phases. The temperature were 23°C during the light phase, and 19°C during the dark phase. Food was provided ad libitum.

(c) Flight-to-light experiment

We experimentally tested the flight-to-light behaviour of small ermine moths in an indoor flight cage, measuring 5.7 × 2.5 m at the bottom, 5.7 × 1.8 m at the top and of 3 m height (see electronic supplementary material, figure S1). In this cage, moths can be attracted from every position, as the effective range of the light traps used is about 3–5 m [13]. Temperature and humidity in the flight cage were held constant at 20–22°C and 60–80% relative humidity, respectively.

A standard Heath trap equipped with a fluorescent tube (Philips, Eindhoven, The Netherlands, TL 6 W/05; see electronic supplementary material, figure S2) was placed at the long-end side of the flight cage. Previous to the experiment, adult moths were individually marked and kept at L16 : D8 cycle such that they adapted physiologically to the day-to-night change. For the flight-to-light experiment, we used individuals 2–3 days post-eclosion before they were sexually mature. We thereby pooled individuals from different families and populations of origin. Moths were released at the opposite end to the lamp, and the tests started at the onset of dusk. The species flies generally at night and is not only crepuscular. We recorded the number and identity of all moths captured by the light trap and all moths not attracted after 8 h.

(d) Analysis

We used a generalized linear mixed effect model to test for a difference in flight-to-light behaviour of moths originating from light-polluted areas versus dark-sky areas. As response variable, we used the odds ratio of individuals attracted versus individuals not attracted, and a model with a binomial error distribution. Light pollution, sex and their interaction were included as fixed effects in the model, whereas populations and family nested

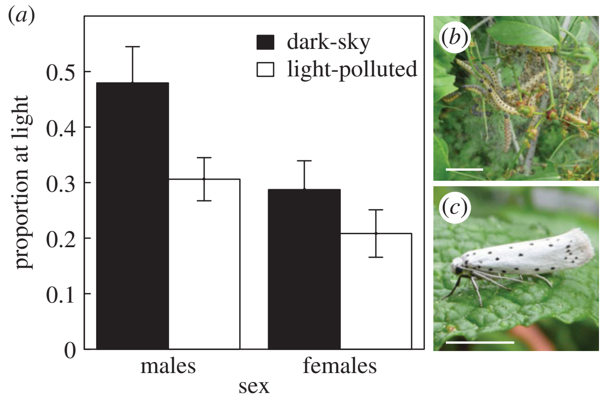

Figure 1. Flight-to-light behaviour of small ermine moths from dark-sky and light-polluted populations. (*a*) Proportion (mean ± s.e. across all populations) of small ermine moths attracted by artificial light under controlled experimental conditions. Overall, moths from populations which have been experiencing extensive light pollution are significantly less attracted to the light than moths from populations without light pollution (dark sky; $p = 0.036$). (*b*) Larvae of the small ermine moth (*Yponomeuta cagnagella*) on its host plant European spindle (*Euonymus europaeus*). (*c*) Adult small ermine moth. Scale bars, 5 mm. (Online version in colour.)

within populations were included as random effects. Analyses were done in R v. 3.0.1 [16].

3. Results

We tested the flight-to-light behaviour of 1048 adult moths (table 1). Individuals from the populations experiencing high light pollution had a significantly lower propensity to fly to light (Z-value $= -2.1$, $p = 0.036$; figure 1) than individuals from the populations from dark-sky areas. Overall, the mean reduction in flight-to-light behaviour was 30% (36% reduction for males and 28% reduction for females). Furthermore, females were overall significantly less attracted by light ((Z-value $= 4.3$, $p < 0.001$, see also [12])). There was no significant interaction between population of origin and sex on the flight-to-light behaviour, and the interaction term was removed from the model. The sex ratio within populations did not deviate from 1 : 1 (mean ± s.e. of females relative to males was 1.04 ± 0.11, $p > 0.8$).

4. Discussion

We experimentally showed that small ermine moths from populations exposed for many generations to high levels of light pollution common to urban and suburban areas have a significantly reduced propensity to fly to light compared with moths from dark-sky populations. As moths and other insects attracted to artificial light are experiencing high levels of mortality and reduced fitness [2,8,9], we interpret this as evidence for an adaptive response following Darwinian fitness selection caused by human induced change in environmental conditions. We cannot completely exclude that some of the observed effect was due to developmental differences based on the site of origin affecting adult behaviour or other selective agents associated with urbanization. However, as we collected the larvae at a very early stage (second instar) and raised them in a common garden, we think this is less likely than a common selective difference with respect to light pollution linked to urbanization.

The implications of our finding are important and manifold. First, a reduced flight-to-light behaviour may release natural populations from some of the negative consequences of artificial light pollution [2]. Specifically, there may be less direct mortality [8,14] and lower predation risk [9,10]. Second, the lower propensity for flight-to-light in city populations suggests that the original function of this behaviour is in fact not essential for survival in urban landscapes. This might be because the adaptive value of this behaviour is generally weaker than the benefits of reducing this behaviour in light-polluted environments. Alternatively, in illuminated urban environments, the need to exhibit flight-to-light behaviour might be reduced. Third, a difference in the flight-to-light propensity between rural and urban populations may bias biodiversity surveys based on commonly used light traps [13], in particular if populations of different species respond differently to changes in light condition.

Consistent with many other species, males are the more mobile sex in small ermine moths, and are thus also more often attracted to light [12]. Of note, males from light-polluted habitats exhibited an almost identical flight-to-light behaviour to females from dark-sky habitats (figure 1*a*). The reduced flight-to-light propensity, however, may come with a cost. Explanations for the reduced flight behaviour of moths originating from light-polluted populations include that these moths have a behaviourally or physiologically reduced perception or reaction to the light [14]. For example, size of the eyes, light receptors in the eyes or information processing of perceived light might be altered. Alternatively, the reduced flight-to-light response may be caused by a decrease in overall mobility. Such a change could have far-reaching consequences, as a reduced mobility is known to negatively interact with habitat fragmentation and dispersal, to reduce flower visiting rates and pollination or take the moths out of the sky, and thus reduce prey availability for the nocturnal insectivores, such as bats or spiders.

Given the recent recognition of the pollution effects acting on individuals to ecosystems, there have been calls to reduce light pollution and street light intensity [3]. While this is commendable, our demonstration of a presumably adaptive change in flight-to-light behaviour in populations having been exposed to long-term light pollution suggests that the effects of light pollution on natural populations may not necessarily vanish immediately when the lights are turned off, and that light pollution has already resulted in systematic changes in organisms' behaviour. This advocates for preventing light pollution, event at low levels, from spreading to areas that are so far unaffected, in order both to reduce the direct negative effects of light pollution as well as to prevent long-term evolutionary changes.

Data accessibility. Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.v1885.

Authors' contributions. F.A. and D.E. developed the ideas, F.A. conducted the experiments, analysed the data and wrote a first draft of the manuscript. D.E. contributed substantially to interpretation and revisions of the manuscript. Both authors gave final approval for publication and agree to be held accountable for the content herein.

Competing interests. We declare we have no competing interests.

Funding. F.A. and D.E. are supported by the Swiss National Science Foundation (grants nos PP00P3_150698, 3100AD-116029 and 31003A_146462). There are no competing interests.

Acknowledgements. We thank A. Baumeyer, J. Hottinger, V. Mislin and E. Städler for technical advice, C. Little and three anonymous colleagues for comments and O. Petchey for discussions.

References

1. Falchi F, Cinzano P, Elvidge CD, Keith DM, Haim A. 2011 Limiting the impact of light pollution on human health, environment and stellar visibility. *J. Environ. Manage.* **92**, 2714–2722. (doi:10.1016/j.jenvman.2011.06.029)
2. Hölker F, Wolter C, Perkin EK, Tockner K. 2010 Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681–682. (doi:10.1016/j.tree.2010.09.007)
3. Longcore T, Rich C. 2004 Ecological light pollution. *Front. Ecol. Environ.* **2**, 191–198. (doi:10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2)
4. Hölker F, Wurzbacher C, Weißenborn C, Monaghan MT, Holzhauer SIJ, Premke K. 2015 Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. *Phil. Trans. R. Soc. B* **370**, 20140130. (doi:10.1098/rstb.2014.0130)
5. Bennie J, Duffy JP, Davies TW, Correa-Cano ME, Gaston KJ. 2015 Global trends in exposure to light pollution in natural terrestrial ecosystems. *Remote Sens.* **7**, 2715–2730. (doi:10.3390/rs70302715)
6. Cinzano P, Falchi F, Elvidge CD. 2001 The first world atlas of the artificial night sky brightness. *Mon. Not. Royal Astron. Soc.* **328**, 689–707. (doi:10.1046/j.1365-8711.2001.04882.x)
7. Gaston KJ, Bennie J, Davies TW, Hopkins J. 2013 The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev.* **88**, 912–927. (doi:10.1111/brv.12036)
8. Jones J, Francis CM. 2003 The effects of light characteristics on avian mortality at lighthouses. *J. Avian Biol.* **34**, 328–333. (doi:10.1111/j.0908-8857.2003.03183.x)
9. Warren AD. 1990 Predation of five species of Noctuidae at ultraviolet light by the Western Yellowjacket (Hymenoptera: Vespidae). *J. Lepidopterists' Soc.* **44**, 32.
10. Davies TW, Bennie J, Gaston KJ. 2012 Street lighting changes the composition of invertebrate communities. *Biol. Lett.* **8**, 764–767. (doi:10.1098/rsbl.2012.0216)
11. Gaston KJ, Gaston S, Bennie J, Hopkins J. 2014 Benefits and costs of artificial nighttime lighting of the environment. *Environ. Rev.* **23**, 14–23. (doi:10.1139/er-2014-0041)
12. Altermatt F, Baumeyer A, Ebert D. 2009 Experimental evidence for male biased flight-to-light behavior in two moth species. *Entomol. Exp. Appl.* **130**, 289. (doi:10.1111/j.1570-7458.2008.00817.x)
13. Baker RR, Sadovy Y. 1978 The distance and nature of the light-trap response of moths. *Nature* **276**, 818–821. (doi:10.1038/276818a0)
14. Frank KD. 1988 Impact of outdoor lighting on moths: an assessment. *J. Lepidopterists' Soc.* **42**, 63–93.
15. Menken SB, Herrebout WM, Wiebes JT. 1992 Small ermine moths (*Yponomeuta*): their host relations and evolution. *Annu. Rev. Entomol.* **37**, 41–66. (doi:10.1146/annurev.en.37.010192.000353)
16. R Development Core Team. 2013 *R: A language and environment for statistical computing. Version 3.0.1*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.