

# Declines in moth populations stress the need for conserving dark nights

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## Abstract

Given the global continuous rise, artificial light at night is often considered a driving force behind moth population declines. Although negative effects on individuals have been shown, there is no evidence for effects on population sizes to date. Therefore, we compared population trends of Dutch macromoth fauna over the period 1985–2015 between moth species that differ in phototaxis and adult circadian rhythm. We found that moth species that show positive phototaxis or are nocturnally active have stronger negative population trends than species that are not attracted to light or are diurnal species. Our results indicate that artificial light at night is an important factor in explaining declines in moth populations in regions with high artificial night sky brightness. Our study supports efforts to reduce the impacts of artificial light at night by promoting lamps that do not attract insects and reduce overall levels of illumination in rural areas to reverse declines of moth populations.

## KEYWORDS

artificial light at night, ecological traits, ecology of the night, Lepidoptera, light pollution, phototaxis

## 1 | INTRODUCTION

Artificial light at night strongly alters the environment of nocturnally active species (Gaston, Bennie, Davies, & Hopkins, 2013; Rich & Longcore, 2006). Moths (Lepidoptera) represent a large, diverse, geographically widespread and largely nocturnal species group and are generally strongly attracted to artificial light (i.e. they exhibit phototaxis) (Macgregor, Evans, Fox, & Pocock, 2017; Van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011). Due to phototaxis, artificial light is considered to be one of the driving forces behind observed moth population declines in regions with high artificial night sky

brightness (Bennie, Davies, Duffy, Inger, & Gaston, 2014), such as the UK (Conrad, Warren, Fox, Parsons, & Woiwod, 2006; Fox, 2013) and the Netherlands (Groenendijk & Ellis, 2011). Although negative effects on individuals have been shown, such as reduced foraging and reproduction as well as increased mortality (Altermatt, Baumeyer, & Ebert, 2009; Van Geffen et al., 2015; Van Langevelde, Van Grunsven, Veenendaal, & Fijen, 2017), evidence for negative effects of artificial light at night on moth population sizes is still lacking (Fox, 2013; Gaston & Bennie, 2014; Spoelstra et al., 2015).

Understanding the possible causes for population declines of moths is important, as species from this group are thought to play

important functional roles in food webs, as bulk food for birds and bats, as herbivores and as pollinators (Macgregor, Pocock, Fox, & Evans, 2015; Rich & Longcore, 2006). Moth population declines may therefore have consequences for ecosystem functioning. Moreover, due to their sensitivity to changes, in combination with their high population densities and high species richness, moths can be indicators for environmental assessments (Rákósy & Schmitt, 2011) as well as for insect biodiversity trends (Fox, 2013). Given the continuous rise in global levels of artificial night lighting, at an average annual increase of 6% (0%–20% per year from 1950 to 2008 depending on geographic region, Hölker et al., 2010), we face the challenge to determine whether moth population trends are affected by artificial light at night.

We compared population trends in Dutch macromoth fauna (defined as the species belonging to the families covered in Waring and Townsend (2015)) over the period 1985–2015 between species that differ in two ecological traits that are directly related to light: phototaxis and adult circadian rhythm. We expected that species that are nocturnally active will show stronger population declines than species that are diurnally active. Likewise, we expected a similar contrast between species that exhibit positive phototaxis and those that do not. Because various ecological traits have previously been linked to moth distribution decrease (e.g. Fox et al., 2014; Mattila, Kaitala, Komonen, Kotiaho, & Päivinen, 2006; Mattila, Kotiaho, Kaitala, & Komonen, 2008), we first examined the relevance of the two light-related traits in comparison with a range of other relevant traits.

## 2 | MATERIALS AND METHODS

We used the database Noctua, which covers faunistic information of all Lepidoptera groups that have occurred in the Netherlands from about 1800 till the present. At the moment of this study, the database contained more than 3.5 million records for macromoths. Sources include publications, unpublished records and notebooks, and information provided either directly by citizens or through data collection websites, in particular [www.waarneming.nl](http://www.waarneming.nl). All records were checked in a validation procedure (see Groenendijk & Ellis, 2011 for more information). In the Noctua database, the majority of the used sampling method is unknown (on average 71%). For the records with known sampling methods, 91% were derived from light traps, 2.4% used sugar traps, 6.2% were based on sight without any attractant, and 0.1% used other methods, such as pheromone traps. There was no significant trend over time in the relative proportion of these sampling methods.

For each species, we calculated the abundance for the whole of the Netherlands per year by obtaining the sum of the log-transformed number of individuals divided by the number of collection events for each species. A collection event is defined as an event where a person observes one or more moth species on a particular date within one-kilometre square (see [www.vlinderstichting.nl/vlinders/overzicht-vlinders](http://www.vlinderstichting.nl/vlinders/overzicht-vlinders)). In this way, the intensity of recording effort is

factored out. Migratory species were left out of the calculations, as for nonresident species, population fluctuations are mostly determined elsewhere. We limited the data to the period from 1985 onwards to accomplish sufficient data quality and coverage.

From the c. 800 macromoth species that occur in the Netherlands (Waring & Townsend, 2015), we calculated the population trend for 481 species over the period 1985–2015. For each species, we fitted a linear regression line through the abundance data over the years. The slope of this regression was used as a measure for the population trend of each moth species (cf. Groenendijk & Ellis, 2011). We only included species in the analysis that were observed in at least 10 years during this period and where >5% of the variation was explained by the regression. Outliers were excluded ( $Z$ -value  $< -3$  and  $> 3$ ). Although the number of collection events may be different between regions and over the years, we believe that these differences will not have a big impact on the population trends as (1) we corrected for the number of collection events per year per species, and (2) it would only happen if the fraction of moth species active during the night or the fraction phototactic moth species differ between the regions, which we do not expect.

The ecological traits of the moth species in our study were derived from the literature, the moth collection of Naturalis Biodiversity Center, and based on the pooled expert knowledge (M.F. WallisDeVries, M.E. Huigens, W.N. Ellis, R. de Vos, unpublished data of Dutch Butterfly Conservation, Working group Lepidoptera Faunistics and Naturalis Biodiversity Center). We compared the relevance of the two traits related to light, phototaxis and adult circadian rhythm, to nine other ecological traits (see Table 1 for further explanation): (1) voltinism—univoltine species may be at a disadvantage in the face of climate change as the ability to adapt evolutionary to a changing environment may be facilitated by increased voltinism (Altermatt, 2010); (2) length of flight period—moth species with shorter flight periods may have declined more in distribution (Mattila et al., 2006, 2008); (3) host plant specificity—monophagous and oligophagous moth species may not be able to track climate change (Braschler & Hill, 2007); (4) soil fertility conditions of the host plant—moth species with host plants found on soils with low nitrogen values may show negative population trends (Fox et al., 2014; Pöyry et al., 2017); (5) habitat structure—moth species found in open habitats may have negative population trends (Öckinger, Hammarstedt, Nilsson, & Smith, 2006); (6) drinking nectar—population declines of butterfly species could be linked to a substantial decline in overall flower abundance and specific nectar plants (Dicks et al., 2015; WallisDeVries, Van Swaay, & Plate, 2012); (7) forewing length (proxy for body size)—moth species with larger body size are thought to decline at higher rates than smaller species (Mattila, Kaitala, Komonen, Päivinen, & Kotiaho, 2011; Mattila et al., 2006, 2008); (8) overwintering phase—moth species overwintering as egg may have negative population trends (Conrad, Woiwod, Parsons, Fox, & Warren, 2004; Groenendijk & Ellis, 2011); and (9) (occasionally) found in urban areas such as gardens, city parks, road and railway verges—moth species

**TABLE 1** Ecological traits of 481 moth species for which we have data on population trends from 1985 to 2015 in the Netherlands. For the qualitative (categorical) variables, the different classes per traits are given, whereas the range is given for the quantitative variables

Ecological trait	Explanation	Sources
Phototaxis	(1) Attracted to light, (2) occasionally attracted to light and (3) not attracted to light	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Adult circadian rhythm	(1) Diurnally active, (2) nocturnally active and (3) active during both day and night	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Voltinism	(1) 1 generation per year, (2) >1 generation per year	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Length of flight period	Continuous (2–18 weeks)	<a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a> , Pöyry et al. (2017)
Host plant specificity	(1) Monophagous (1 genus), (2) oligophagous (1 family), (3) polyphagous (>1 family)	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Soil fertility conditions of host plant (nitrogen)	Ellenberg <i>N</i> -values (continuous 1–8)	Pöyry et al. (2017)
Habitat structure	(1) Preferring open habitat, (2) preferring closed habitat and (3) generalist	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Forewing length	Continuous (8–48 mm)	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>
Nectar drinking	(1) No, (2) Yes	Waring and Townsend (2015), Ebert (2005) & proboscis assessments collection Naturalis Biodiversity Center
Overwintering phase <sup>a</sup>	(1) Egg, (2) caterpillar and (3) pupa	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a> , Ebert (2005), <a href="http://www.lepidoptera.se">www.lepidoptera.se</a>
Occurring (occasionally) in urban areas	(1) Yes, (2) No	Waring and Townsend (2015), <a href="http://www.vlinderstichting.nl/vlinders/overzicht-vlinders">www.vlinderstichting.nl/vlinders/overzicht-vlinders</a>

<sup>a</sup>Species that overwinter as adults were excluded ( $N = 8$ ).

in urban areas are thought to decrease in population size due to, among others, habitat deterioration, fragmentation and chemical pollution (Bates et al., 2014). To show the relevance of the two traits related to light in explaining the variation in these traits among the moth species, we used a rotated PCA for both quantitative and qualitative data (functions PCAmix and PCARot) of the package “PCAmixdata” (Chavent, Kuentz-Simonet, Labenne, & Saracco, 2014) in R (version 3.4.1, R Core Team, 2017), as eight of the eleven traits were categorical variables (Table 1).

To check for differences in collection method or effort between groups of moth species that could possibly explain our findings, we determined the number of collection events per group (Supplementary Material 1 from the online Supporting Information). Overall there was an increase in collection events over time. We tested the differences in this increase between the groups of moth species using a general linear model (GLM, function *lm*) in R. We found a significant increase in collection events over time (GLM: Year  $F_{1,58} = 1046.7$ ,  $p < .001$ ), with more collection events for the nocturnally active species than the diurnally active species (circadian rhythm  $F_{1,58} = 4.3$ ,  $p = .043$ ), but no difference in slope between these two groups (year  $\times$  circadian rhythm  $F_{1,58} = 3.7$ ,  $p = .061$ ). This analysis shows that increase in collection events over time does not significantly differ between the nocturnally and diurnally active species. We also found an increase in collection events over time for the groups of moth species that are attracted and not attracted to light (GLM: Year

$F_{1,58} = 712.3$ ,  $p < .001$ ), with more collection events for the species attracted to light (phototaxis  $F_{1,58} = 20.0$ ,  $p < .001$ ). The increase in the number of collection events for the group of species that are not attracted was steeper than for the species attracted to light (year  $\times$  phototaxis  $F_{1,58} = 18.8$ ,  $p < .001$ ). This suggests that if we find the expected larger decline in moth species attracted to light, this cannot be explained by a decrease in catching method or effort over time for the species attracted to light.

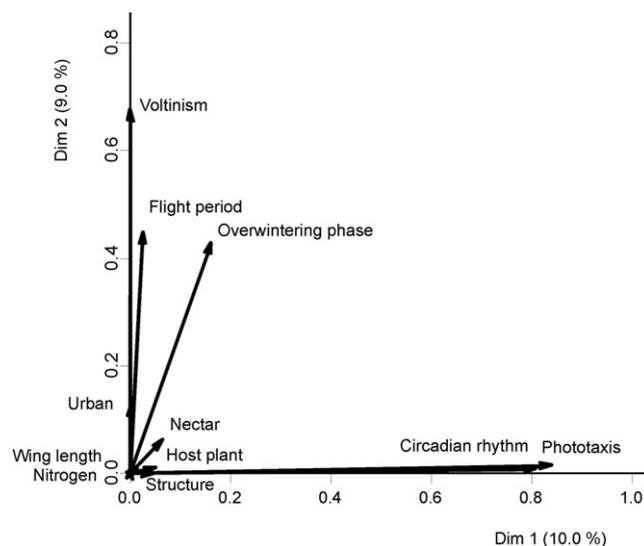
To account for potentially confounding effects of phylogenetic relatedness among the moth species, we used an ultrametric tree that included our 481 species (Essens, Van Langevelde, Vos, Van Swaay, & WallisDeVries, 2017; Mutanen et al., 2016, Supplementary Material 2) and included the phylogenetic correlation matrix implied by this tree in the linear model using generalized least squares (GLS) of the “nlme” package in R (Pinheiro et al., 2016) to test whether there were differences in population trends between the groups of moths in relation to (1) phototaxis (attracted, occasionally attracted and not attracted to light) or (2) adult circadian rhythm (active as adult during the day, night or both day and night). The GLS was followed by the Tukey–Kramer post hoc test (using the “multcomp” package in R, Hothorn, Bretz, & Westfall, 2008). We used the option *corPagel* in the GLS to estimate Pagel's  $\lambda$ , which indicates the strength of the phylogenetic signal in the dependent variable (Symonds & Blomberg, 2014). Depending on the lowest AIC score, we used either the restricted

maximum likelihood (REML) or maximum likelihood (ML) for the GLS.

### 3 | RESULTS

The traits related to light, phototaxis and adult circadian rhythm, explain most variation in the PCA of eleven ecological traits of 481 moth species, as these traits are highly correlated with the first axis (and phototaxis and adult circadian rhythm are highly correlated, Figure 1, Table 2). The second axis is highly correlated with voltinism, length of the flight period and overwintering phase. These three ecological traits may be related to the sensitivity of moth species to climate change (Altermatt, 2010; Groenendijk & Ellis, 2011; Mattila et al., 2006, 2008). The first axis of the PCA was correlated with the population trends (Pearson's product-moment  $r = .16$ ,  $t = 3.38$ ,  $df = 457$ ,  $p < .001$ ), whereas the second axis did not correlate with the population trends ( $r = -.04$ ,  $t = -0.82$ ,  $df = 457$ ,  $p = .41$ ). The results of the PCA show that differences in population trends due to phototaxis and adult circadian rhythm cannot be explained by the other traits as these are independent (orthogonal) to these two light-related traits.

We found that population trends contrasted between moth species that differ in the degree to which they exhibit phototaxis (GLS:  $F_{2,453} = 5.00$ ,  $p = .006$ ,  $\lambda = -0.080$ ), where moth species attracted to light had stronger negative population trends than species not attracted to light (Figure 2a). Moth species that are occasionally attracted to light did not differ from the other two groups. The



**FIGURE 1** Squared loadings of the first and second axes (Dim 1 and Dim 2) of the rotated PCA of the ecological traits of 481 moth species (see Table 1 for explanation of the variables, and Table 2 for the correlation coefficients of the variables with the two axes). The titles of the axes give the percentage of explained variation of the traits (between brackets). The PCA is performed based on three numerical variables and eight categorical variables

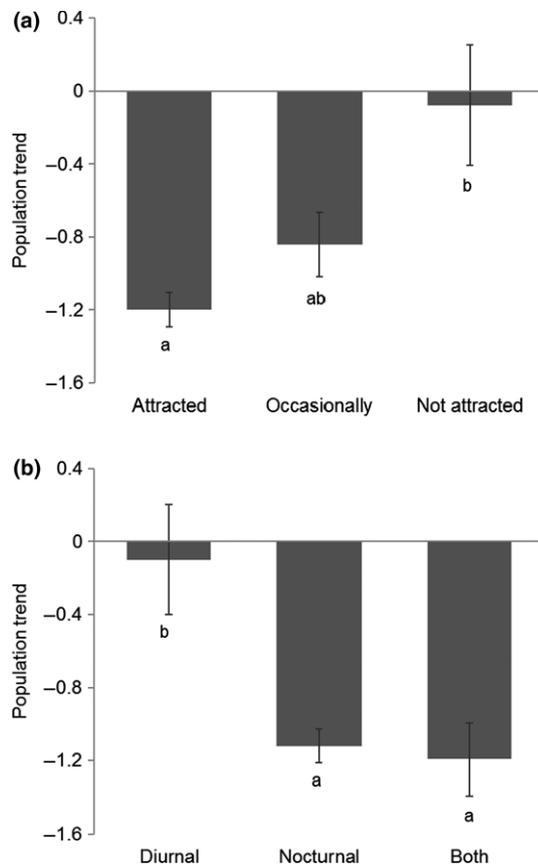
**TABLE 2** Correlation coefficients for the ecological traits of the moth species with the first two axes (Dim 1 and Dim 2) of the PCA, and the eigenvalue and percentage explained variation of these two axes (see Table 1 for explanation of the variables and Figure 1 for the graph). Correlation coefficients were calculated as the square root of the squared loadings after rotation provided by “PCARot” of the R package “PCAmixdata” (Chavent et al., 2014)

Ecological trait	Dim 1	Dim 2
Soil fertility conditions of host plant (nitrogen)	0.00	0.14
Length of flight period	0.14	0.67
Forewing length	0.14	0.14
Host plant specificity	0.22	0.10
Voltinism	0.00	0.82
Phototaxis	0.91	0.10
Adult circadian rhythm	0.89	0.10
Habitat structure	0.22	0.00
Overwintering phase	0.40	0.65
Nectar drinking	0.24	0.24
Urban area	0.00	0.36
Eigenvalue	2.0	1.8
% Explained variation	10.0	9.0

phylogenetic signal parameter  $\lambda$  was very weak, but its 95% confidence intervals excluded 0 (between  $-0.082$  and  $-0.078$ , probably due to the large sample size). Negative values for Pagel's  $\lambda$  mean that closely related species have negatively correlated traits. We also found differences between moth species that differ in adult circadian rhythm (GLS:  $F_{2,470} = 3.192$ ,  $p = .042$ ,  $\lambda = 0.021$ ), where nocturnal moth species and species that are active during both day and night had stronger negative population trends than diurnal species (Figure 2b). The 95% confidence interval of  $\lambda$  included 0 (between  $-0.080$  and  $0.122$ ). For all models, the ML method of estimation had the lowest AIC. The same analysis per family (for which  $N > 20$ ) is reported in Supplementary Material 3.

### 4 | DISCUSSION

Our study for the first time indicates artificial lighting as a driver of rapid moth population declines in extensively illuminated countries such as the Netherlands. During the years for which we had data on moth abundances, there was a net increase in the percentage of land area in the Netherlands with an increase in brightness of night-time light between 1995 and 2000 and between 2005 and 2010 (Bennie et al., 2014), which may be due to the increase in urban area (e.g. 31% increase from 1981 to 2008, <http://www.clo.nl/>) and the total length of the roads (e.g. 7% increase from 2001 to 2017, <http://stat.line.cbs.nl/Statweb/>). This trend suggests that the area affected and the intensity of artificial light at night may have increased over the period covered by our study. We found that species that have positive phototaxis or are nocturnally active show strong population



**FIGURE 2** Mean population trends ( $\pm$ SEM) for moth species that differ in (a) phototaxis and (b) adult circadian rhythm. Letters indicate significant differences between the groups (see text for statistics). The sample sizes ( $N$ ) per group are (a) attracted (384), occasionally attracted (54) and not attracted (20), and (b) diurnal (23), nocturnal (370) and both (82). In our data, 82% of 384 moth species that are attracted to light and 85% of 54 moth species that are occasionally attracted to light are nocturnally active as adult, whereas 84% of the 20 moth species that are not attracted to light are diurnally active

declines. Although other possible explanations for population declines, such as habitat loss, fragmentation, industrial pollution, agrochemical pollution and climate change (Fox, 2013; Mattila et al., 2006), may very well contribute to this decline, the differences between groups of moth species that differ in ecological traits related to light strongly suggest that artificial light at night is an important cause of decline. This conclusion is supported by our PCA results that show that patterns in population trends between groups of moths differing in phototaxis or adult circadian rhythm cannot be explained by nine other traits that have previously been suggested to relate to the decline in moths (voltinism, length of flight period, host plant specificity, soil fertility conditions of the host plant, body size, nectar drinking, habitat structure, overwintering phase, occurring in urban areas) (Altermatt, 2010; Bates et al., 2014; Braschler & Hill, 2007; Fox et al., 2014; Groenendijk & Ellis, 2011; Mattila et al., 2006, 2008; Öckinger et al., 2006).

Previous studies have failed to separate the negative effects of artificial light from other factors associated with urbanization, such

as habitat deterioration and fragmentation. For example, Bates et al. (2014) showed a negative association between urbanization and the abundance and species richness of moths in gardens, but they could not disentangle the effects of artificial light at night in urban environments from the highly correlated effects of urbanization. Our study shows that there was no correlation between the moth species that (occasionally) occur in urban areas and the ones that are either attracted to light or are active during the night, suggesting that the moth declines are more likely due to light pollution than just occurring in urban areas.

The high number of phototactic species that are more likely to be recorded in large numbers in light traps could give more power to detect changes (increases as well as decreases) for these species. However, as we used the slope of the population trend of each species without considering the significance of its value, this should not be biased by variation in abundance between species. We therefore do not consider this statistical argument as an alternative explanation for our findings.

Many studies have found attraction of moths to lamps (e.g. Somers-Yeates, Hodgson, McGregor, Spalding, & French-Constant, 2013; Van Langevelde et al., 2011). As the influence of single lamps is limited to at most a few tens of metres (Baker & Sadovy, 1978; Degen et al., 2016) and artificial night lighting is mainly used in urban areas and alongside infrastructure, it is not *prima facie* obvious that effects on population trends would be found (Spoelstra et al., 2015), as large parts of rural areas are not directly illuminated. Hence, we would expect to find limited effects of artificial light at night on population trends when sampled over a large area. Our results suggest that the effects of artificial lighting extend far beyond the directly illuminated areas, as we found strong population declines in moth species that are nocturnally active and/or have positive phototaxis. There may be indirect, additive effects to the light emitted by lamps, creating unfavourable conditions for moths in a much larger area, namely (1) background illumination induced by the accumulation of artificial lighting, such as sky glow (Davies, Bennie, Inger, Ibarra, & Gaston, 2013), or (2) rows of street lamps that can act as barriers limiting the exchange of individuals between dark areas (Degen et al., 2016). Moreover, not only moths can be affected by the direct and indirect effects of light, but also their host plants, for example the impact of light on flower head density, which cascades on to pollinators and herbivores (Bennie, Davies, Cruse, Inger, & Gaston, 2015). Alternatively, some moth species can display sustained flight activity and cover considerable distances (Betzholtz & Franzén, 2011; Jones, Lim, Bell, Hill, & Chapman, 2016) facing a high probability that they end up within the attraction range of scattered lamps, explaining the effect of lamps at a larger scale than is directly illuminated.

Moth species are likely to adapt to light conditions that have been present already for many decades, as natural selection should favour individuals with a low propensity of being attracted by light (Furlong, Wright, & Dossdall, 2011; Gaston et al., 2013). Indeed, this adaptation was observed for the small ermine moth (*Yponomeuta cagnagella*): individuals from populations in urban areas show

reduced flight-to-light behaviour compared to individuals from dark-sky populations (Altermatt & Ebert, 2016). Although this result was obtained for only a single moth species, the observed adaptation suggests that artificial light can indeed be a strong selective force because of reduced fitness, which supports our findings that artificial lighting negatively affects population trends. If many species have such capacity to adapt to artificial lighting, we would expect declines in abundance to have been mitigated to some extent. On the other hand, reduced flight-to-light behaviour can also lead to lower catching probabilities of light traps used to monitor changes in number of moths, which may result in lower observed population densities over time. The potential for adaptation requires analysis of population trends over a long period of time, as in our study, together with experiments to test what ecological and life-history traits allow for adaptation to artificial lighting. However, when populations continue to decline, adaptive capacity may also decrease due to lowered genetic diversity (Vanden Broeck et al., 2017).

The negative population trends of moth species that are nocturnally active or have positive phototaxis agree with findings at the level of individuals, where moths show reduced foraging, pollen transport, dispersal and reproduction when subjected to artificial light compared to dark conditions (Altermatt et al., 2009; Macgregor et al., 2017; Van Geffen et al., 2015; Van Langevelde et al., 2017). In experiments on individual behaviour, the effects of lamps that differ in spectral composition can be tested (e.g. Van Geffen et al., 2015; Van Langevelde et al., 2017), which was not possible in our study. Given that our data were collected at a large temporal and spatial scale, we can only assume that the majority of street lights that were and are still present in the study area are traditional high-intensity discharge lamps, often a mix including narrow-spectrum low-pressure sodium (LPS) lighting and broad-spectrum light sources such as high-pressure sodium (HPS) lighting. These lamps are known to attract many moths (Davies et al., 2013; Plummer, Hale, O'Callaghan, Sadler, & Siriwardena, 2016; Rich & Longcore, 2006; Somers-Yeates et al., 2013; Van Langevelde et al., 2011). Our study adds weight to existing calls to reduce the impacts of artificial night lighting and mitigation using lamps that are less attractive to insects, that is lighting rich in long wavelengths, lower intensity or shorter duration of use (Gaston et al., 2012). The changes in lamp types should not only reduce the attractiveness of the lamps for nocturnal organisms, but also reduce the level of background illumination using lights that are better shielded so that large parts of rural areas are (more) dark. The negative effects on nocturnal organisms are then limited to the close proximity of light sources, and darkness will be restored over the greater part of rural areas in order to reverse the decline in moth populations.

## ACKNOWLEDGEMENTS

We are grateful to all citizen observers who have added their moth records to the *Noctua* database, making this study possible.

## CONFLICT OF INTEREST

We declare we have no competing interests.

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## REFERENCES

- Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society of London B*, 277, 1281–1287. <https://doi.org/10.1098/rspb.2009.1910>
- Altermatt, F., Baumeier, A., & Ebert, D. (2009). Experimental evidence for male biased flight-to-light behavior in two moth species. *Entomologia Experimentalis et Applicata*, 130, 259–265. <https://doi.org/10.1111/j.1570-7458.2008.00817.x>
- Altermatt, F., & Ebert, D. (2016). Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biology Letters*, 12, 20160111. <https://doi.org/10.1098/rsbl.2016.0111>
- Baker, R. B., & Sadovy, Y. (1978). The distance and nature of light-trap response of moth. *Nature*, 276, 818–821. <https://doi.org/10.1038/276818a0>
- Bates, A. J., Sadler, J. P., Grundy, D., Lowe, N., Davis, G., Baker, D., ... Young, H. (2014). Garden and landscape-scale correlates of moths of differing conservation status: Significant effects of urbanization and habitat diversity. *PLoS ONE*, 9, e86925. <https://doi.org/10.1371/journal.pone.0086925>
- Bennie, J., Davies, T. W., Cruse, D., Inger, R., & 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 B*, 370, 20140131. <https://doi.org/10.1098/rstb.2014.0131>
- Bennie, J., Davies, T. W., Duffy, J. P., Inger, R., & Gaston, K. J. (2014). Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Scientific Reports*, 4, 3789.
- Betzholtz, P. E., & Franzén, M. (2011). Mobility is related to species traits in noctuid moths. *Ecological Entomology*, 36, 369–376. <https://doi.org/10.1111/j.1365-2311.2011.01281.x>
- Braschler, B., & Hill, J. K. (2007). Role of larval host plants in the climate-driven range expansion of the butterfly *Polygonia c-album*. *Journal of Animal Ecology*, 76, 415–423. <https://doi.org/10.1111/j.1365-2656.2007.01217.x>
- Chavent, M., Kuentz-Simonet, V., Labenne, A., & Saracco, J. (2014). *Multivariate analysis of mixed data: The PCAmixdata R package*.
- Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. (2006). Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132, 279–291. <https://doi.org/10.1016/j.biocon.2006.04.020>
- Conrad, K. F., Woiwod, I. P., Parsons, M., Fox, R., & Warren, M. S. (2004). Long-term population trends in widespread British moths. *Journal of Insect Conservation*, 8, 119–136. <https://doi.org/10.1007/s10841-004-1332-5>
- Davies, T. W., Bennie, J., Inger, R., Ibarra, N. H., & Gaston, K. J. (2013). Artificial light pollution: Are shifting spectral signatures changing the balance of species interactions? *Global Change Biology*, 19, 1417–1423. <https://doi.org/10.1111/gcb.12166>
- Degen, T., Mitesser, O., Perkin, E. K., Weiß, N. S., Oehlert, M., Mattig, E., & Hölker, F. (2016). Street lighting: Sex-independent impacts on moth movement. *Journal of Animal Ecology*, 85, 1352–1360. <https://doi.org/10.1111/1365-2656.12540>
- Dicks, L. V., Baude, M., Roberts, S. P. M., Phillips, J., Green, M., & Carvell, C. (2015). How much flower-rich habitat is enough for wild

- pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, 40, 22–35. <https://doi.org/10.1111/een.12226>
- Ebert, G. (2005). *Die Schmetterlinge Baden-Württembergs*. Stuttgart, Germany: Eugen Ulmer KG.
- Essens, T., Van Langevelde, F., Vos, R. A., Van Swaay, C. A. M., & WallisDeVries, M. F. (2017). Ecological determinants of butterfly vulnerability across the European continent. *Journal of Insect Conservation*, 21, 439–450. <https://doi.org/10.1007/s10841-017-9972-4>
- Fox, R. (2013). The decline of moths in Great Britain: A review of possible causes. *Insect Conservation and Diversity*, 6, 5–19. <https://doi.org/10.1111/j.1752-4598.2012.00186.x>
- Fox, R., Oliver, T. H., Harrower, C., Parsons, M. S., Thomas, C. D., & Roy, D. B. (2014). Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *Journal of Applied Ecology*, 51, 949–957. <https://doi.org/10.1111/1365-2664.12256>
- Furlong, M. J., Wright, D. J., & Dodsall, L. M. (2011). Diamondback moth ecology and management: Problems, progress, and prospects. *Annual Review of Entomology*, 58, 517–541.
- Gaston, K. J., & Bennie, J. (2014). Demographic effects of artificial nighttime lighting on animal populations. *Environmental Reviews*, 22, 323–330. <https://doi.org/10.1139/er-2014-0005>
- Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews*, 88, 912–927. <https://doi.org/10.1111/brv.12036>
- Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: Options and developments. *Journal of Applied Ecology*, 49, 1256–1266. <https://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Groenendijk, D., & Ellis, W. N. (2011). The state of the Dutch larger moth fauna. *Journal of Insect Conservation*, 15, 95–101. <https://doi.org/10.1007/s10841-010-9326-y>
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., ... Tockner, K. (2010). The dark side of light: A transdisciplinary research agenda for light pollution policy. *Ecology and Society*, 15, 13. <https://doi.org/10.5751/ES-03685-150413>
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363. [https://doi.org/10.1002/\(ISSN\)1521-4036](https://doi.org/10.1002/(ISSN)1521-4036)
- Jones, H. B., Lim, K. S., Bell, J. R., Hill, J. K., & Chapman, J. W. (2016). Quantifying interspecific variation in dispersal ability of noctuid moths using an advanced tethered flight technique. *Ecology and Evolution*, 6, 181–190. <https://doi.org/10.1002/ece3.1861>
- Macgregor, C. J., Evans, D. M., Fox, R., & Pocock, M. J. (2017). The dark side of street lighting: Impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology*, 23, 697–707. <https://doi.org/10.1111/gcb.13371>
- Macgregor, C. J., Pocock, M. J. O., Fox, R., & Evans, D. M. (2015). Pollination by nocturnal Lepidoptera, and the effects of light pollution: A review. *Ecological Entomology*, 40, 187–198. <https://doi.org/10.1111/een.12174>
- Mattila, N., Kaitala, V., Komonen, A., Kotiaho, J. S., & Päivinen, J. (2006). Ecological determinants of distribution decline and risk of extinction in moths. *Conservation Biology*, 20, 1161–1168. <https://doi.org/10.1111/j.1523-1739.2006.00404.x>
- Mattila, N., Kaitala, V., Komonen, A., Päivinen, J., & Kotiaho, J. S. (2011). Ecological correlates of distribution change and range shift in butterflies. *Insect Conservation and Diversity*, 4, 239–246. <https://doi.org/10.1111/j.1752-4598.2011.00141.x>
- Mattila, N., Kotiaho, J. S., Kaitala, V., & Komonen, A. (2008). The use of ecological traits in extinction risk assessments: A case study on geometrid moths. *Biological Conservation*, 141, 2322–2328. <https://doi.org/10.1016/j.biocon.2008.06.024>
- Mutanen, M., Kivelä, S. M., Vos, R. A., Doorenweerd, C., Ratnasingham, S., Hausmann, A., ... Godfray, H. C. J. (2016). Species-level para- and polyphyly in DNA barcode gene trees: Strong operational bias in European Lepidoptera. *Systematic Biology*, 65, 1024–1040. <https://doi.org/10.1093/sysbio/syw044>
- Öckinger, E., Hammarstedt, O., Nilsson, S. G., & Smith, H. G. (2006). The relationship between local extinctions of grassland butterflies and increased soil nitrogen levels. *Biological Conservation*, 128, 564–573. <https://doi.org/10.1016/j.biocon.2005.10.024>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., & Van Willigen, B. (2016). *Package 'nlme'*. *Linear and nonlinear mixed effects models*.
- Plummer, K. E., Hale, J. D., O'Callaghan, M. J., Sadler, J. P., & Siriwardena, G. M. (2016). Investigating the impact of street lighting changes on garden moth communities. *Journal of Urban Ecology*, 2, 1–10.
- Pöyry, J., Carvalheiro, L. G., Heikkinen, R. K., Kühn, I., Kuussaari, M., Schweiger, O., ... Franzén, M. (2017). The effects of soil eutrophication propagate to higher trophic levels. *Global Ecology and Biogeography*, 26, 18–30. <https://doi.org/10.1111/geb.12521>
- R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rákósy, L., & Schmitt, T. (2011). Are butterflies and moths suitable ecological indicator systems for restoration measures of semi-natural calcareous grassland habitats? *Ecological Indicators*, 11, 1040–1045. <https://doi.org/10.1016/j.ecolind.2010.10.010>
- Rich, C., & Longcore, T. (Eds.) (2006). *Ecological consequences of artificial night lighting*. Washington, DC: Island Press.
- Somers-Yeates, R., Hodgson, D., McGregor, P. K., Spalding, A., & French-Constant, R. H. (2013). Shedding light on moths: Shorter wavelengths attract noctuids more than geometrids. *Biology Letters*, 9, 20130376. <https://doi.org/10.1098/rsbl.2013.0376>
- Spoelstra, K., Van Grunsven, R. H. A., Donners, M., Gienapp, P., Huigens, M. E., Slaterus, R., ... Veenendaal, E. (2015). Experimental illumination of natural habitat—an experimental set-up to assess the direct and indirect ecological consequences of artificial light of different spectral composition. *Philosophical Transactions of the Royal Society B*, 370, 20140129. <https://doi.org/10.1098/rstb.2014.0129>
- Symonds, M. R. E., & Blomberg, S. P. (2014). A primer on phylogenetic generalised least squares (PGLS). In L. Z. Garamszegi (Ed.), *Modern phylogenetic comparative methods and their application in evolutionary biology: Concepts and practice* (pp. 105–130). Berlin, Germany: Springer-Verlag.
- Van Geffen, K. G., Van Eck, E., De Boer, R. A., Van Grunsven, R. H. A., Salis, L., Berendse, F., & Veenendaal, E. M. (2015). Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity*, 8, 282–287. <https://doi.org/10.1111/icad.12116>
- Van Langevelde, F., Ettema, J., Donners, M., WallisDeVries, M. F., & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144, 2274–2281. <https://doi.org/10.1016/j.biocon.2011.06.004>
- Van Langevelde, F., Van Grunsven, R. H., Veenendaal, E. M., & Fijen, T. P. (2017). Artificial night lighting inhibits feeding in moths. *Biology Letters*, 13, 20160874. <https://doi.org/10.1098/rsbl.2016.0874>
- Vanden Broeck, A., Maes, D., Kelager, A., Wynhoff, I., WallisDeVries, M. F., Nash, D. R., ... Mergeay, J. (2017). Gene flow and effective population sizes of the butterfly *Maculinea alcon* in a highly fragmented, anthropogenic landscape. *Biological Conservation*, 209, 89–97. <https://doi.org/10.1016/j.biocon.2017.02.001>

- WallisDeVries, M. F., Van Swaay, C. A., & Plate, C. L. (2012). Changes in nectar supply: A possible cause of widespread butterfly decline. *Current Zoology*, *58*, 384–391. <https://doi.org/10.1093/czoolo/58.3.384>
- Waring, P., & Townsend, M. (2015). *Nachtvinders: De nieuwe veldgids voor Nederland en België*. Utrecht/Antwerpen: Kosmos Uitgevers.

**How to cite this article:** van Langevelde F, Braamburg-Annegarn M, Huigens ME, et al. Declines in moth populations stress the need for conserving dark nights. *Glob Change Biol.* 2018;24:925–932. <https://doi.org/10.1111/gcb.14008>

## SUPPORTING INFORMATION

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