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Lack of local adaptation of feeding and calling behaviours by *Yponomeuta cagnagellus* moths in response to artificial light at night

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Abstract

1. Artificial light at night (ALAN) is one of the suggested drivers of the global decline in insects, including moths.
2. ALAN strongly affects moth physiology and behaviour, but it remains unknown whether ALAN is a selective pressure that drives adaptation and evolution in moths.
3. We assess whether feeding and calling behaviours of *Yponomeuta cagnagellus* moths are locally adapted to ALAN. Collected from locations that were either illuminated or dark at night-time for several decades, moths were exposed to different light intensities in a laboratory experiment.
4. Male moths, but not female moths, fed less frequently in bright light than in dark or dim conditions. Female calling was less frequent in dimly or brightly lit conditions than in the dark treatment. Individuals from illuminated source populations showed increased feeding behaviour by males and marginally decreased calling behaviour by females.
5. Our study suggests that ALAN affects the phenotypical calling behaviour by females and feeding behaviour by male moths of *Y. cagnagellus* but has not resulted in adaptation. Long-term ALAN conditions also affected feeding and marginally affected calling frequency. Reduced calling in lit conditions, perhaps driven by a reduced need for such behaviour because of an increase in visual cues or through the proximity of individuals in lit conditions, may result in long-term adaptation.
6. Studies into more moth species are required to determine the extent to which a lack of adaptation to ALAN may contribute to current global declines in moth populations.

KEYWORDS

adaptation, insect decline, light pollution, moths

INTRODUCTION

Recent studies have indicated annual declines in insect abundance in terrestrial ecosystems around the world, albeit with much

variation across taxonomic groups and geographical regions (see Wagner et al., 2021, for a recent review). Among the generally declining groups are moths, and light pollution [artificial light at night (ALAN)] has been posed as one of the drivers of their

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decline (Boyes et al., 2021; Owens et al., 2019; Van Grunsven et al., 2020; Van Langevelde et al., 2018). Moths are important pollinators (Macgregor & Scott-Brown, 2020), support predatory and parasitoid insect populations and are food for many vertebrates. Given the ongoing decline in moth abundance, and the possible role of ALAN therein, it is crucial to understand the potential for moth populations to adapt to ALAN.

Moths are known to be attracted by light sources, for example, streetlights (Degen et al., 2016), and the effect may differ between lamps with different light spectra (Van Langevelde et al., 2011). ALAN can alter moths' feeding behaviour (Van Langevelde et al., 2017). Moreover, it can reduce the production of sex pheromones and change their chemical composition (Van Geffen et al., 2015), alter flight-to-light behaviour (Altermatt et al., 2009) and alter sex ratios (Altermatt & Ebert, 2016). ALAN may also distort temporal differences in mating activity between species, which can break down temporal barriers that would otherwise prevent inter-specific mating (Hopkins et al., 2018).

After stability of the natural daily dark–light rhythms over evolutionary time scales (Gaston et al., 2014), the propensity of ALAN is changing the night-time environment at an unprecedented rate around the world (Falchi et al., 2016). Given these changes, ALAN may constitute an emerging selective pressure, which can introduce adaptation and evolutionary changes in species (Desouhant et al., 2019; Hopkins et al., 2018; Swaddle et al., 2015). While ALAN-driven changes in moth physiology and behaviour appear strong (Boyes et al., 2021), there are surprisingly few investigations of evolutionary changes and local adaptation in response to ALAN. One of the few studies that assess the adaptation of moth behavioural responses to ALAN found that populations from urban areas with high levels of light pollution over several decades showed a significant reduction in flight-to-light behaviour compared to populations of the same species from pristine dark-sky habitats (Altermatt & Ebert, 2016). This adaptive response may reduce mortality risk through reductions in direct mortality and predation in illuminated populations compared to dark populations (Altermatt & Ebert, 2016). Moths display both feeding and calling behaviour (the latter refers to the release of pheromones by females, advertising sexual receptiveness) during dark periods (Allison & Cardé, 2016; Hendrikse, 1979) and these behaviours are, at least in some species, reduced by ALAN (Van Geffen et al., 2015; Van Geffen et al., 2015; Van Langevelde et al., 2017). Therefore, ALAN could be a selective pressure that locally favours, over generations, moths with increased frequency of feeding and calling behaviour under illuminated conditions. Rather than depending on darkness, the ability to feed or call during illuminated nights would give them a selective advantage. This may result in local adaptation, which occurs when differential pressures of natural selection cause a local population (e.g., a population of moths in an area with high-intensity ALAN) to evolve heritable traits that provide an advantage in its local environmental conditions, regardless of the consequences of these traits for fitness in other habitats (Kawecki & Ebert, 2004).

In this study, we assess whether local adaptation has occurred in the feeding and calling behaviour of *Yponomeuta cagnagellus* moths in response to ALAN. We exposed individuals from populations from

either illuminated or dark locations to different levels of light intensity in a laboratory experiment. We expected that individuals originating from dark populations show more darkness dependent behaviour compared to individuals from illuminated populations. While a decrease in feeding and calling activity under illumination treatments would indicate a direct phenotypical response to ALAN, adaptation to ALAN would be evidenced when individuals from lit source locations show higher activity in illumination treatments (a decreased sensitivity to ALAN) than individuals from dark source locations.

METHODS

Species collection

This study used adults of the spindle ermine moth (*Y. cagnagellus*, Hubner, 1813 – Lepidoptera: Yponomeutidae) to assess whether adaptation of calling and feeding behaviour occurred in response to our light treatments. Using this species provides three advantages for this study. Firstly, this species has shown adaptation of its flight-to-light response to ALAN (Altermatt & Ebert, 2016) and since it feeds and shows calling behaviour in periods of darkness (Allison & Cardé, 2016; Hendrikse, 1979), it is possible that these behaviours may also be selected for by ALAN conditions. Secondly, mark-recapture details show that 'most males and females do not disperse farther than some 10 meters' from their release site (Menken et al., 1992). Such dispersal limitation can result in genetic isolation of populations and therefore create opportunity for local adaptation. High site fidelity, however, does not preclude episodic long-distance dispersal and gene flow in this species (Menken et al., 1992), which would reduce the rate of adaptation (Lehmann et al., 2017; Slatkin, 1987). Nevertheless, if selection is sufficiently strong, local adaptation is possible even in dispersive insects with substantial gene flow (Komatsu & Akimoto, 1995; Mopper et al., 2000; Stiling & Rossi, 1998). Lastly, larvae of our study species are relatively easy to find, because they create conspicuous web-like structures on their obligatory host plant (*Euonymus europaeus*) (Menken et al., 1992).

Approximately, 100 larvae were collected from populations at each of 13 coastal locations in the Netherlands, with six populations being located within 10 m of at least one street light (further referred to as a 'lit locations', and the other locations being 'dark locations'). Locations were selected where the streetlight had been situated in the same place for at least one decade, allowing for the possibility of local adaptation to the light environment, particularly given the low dispersal range and the short generation time (1 year) of this species. Given the longevity of the host plants, the long-term presence of the moth species in the region, and the moth's high site fidelity, we assume that the populations have been present at these locations for a long time. Locations were at least 1.1 km apart. To determine the distance to the nearest street light in the dark locations in the field, we used detailed digital local topography maps (Basisregistratie Grootschalige Topografie, available on pdok.nl) and the Near Tool in ArcGIS 10.0. The average distance from dark locations to the nearest street light was 305 m (range 62–561 m).

Until the start of the experiment, the collected larvae (and later moths) were kept in a controlled climate room that was warm (26°C) and lit (24.2 lux) between 10:00 and 19:00 h. Collected larvae were kept in one box per population, and individual chrysalises were removed and each kept in a 250-ml transparent container capped with white insect mesh until the start of the experiment. Each day, containers were checked and the day of hatching was noted. Healthy adults hatched from the larvae of 10 of the 13 original populations, representing four lit locations and six dark locations (Figure 1).

Experimental design and behaviour observations

To test adaptation of feeding and calling behaviour to ALAN, we exposed adult *Y. cagnagellus*, grown from larvae collected from dark and lit source locations to different light intensities in a laboratory experiment, repeated over eight nights, with a design loosely based on the study by Van Langevelde et al. (2017). The experimental setup consisted of a wall with 21 compartments of 20 x 20 x 20 cm; compartments were only open to the front. A light was fitted at the top of each compartment, lit at one of the three allocated intensities (resulting in seven compartments each with dark, dim, and bright light

treatment). Light intensity was measured at ground level in the compartments, as this is the level where it would be received by the moths the majority of the time. The bright light treatment consisted of white light (Philips CorePro LEDcapsuleLV 0.9-10 W G4 827) at high intensity (18.15 lux, typical intensity found at shrub/tree level directly below a streetlight). For the dim treatment, the same lights were dimmed to the low intensity by placing white plastic diffusers over the lamps (4.84 lux, typical of ground level below a streetlight, Da Silva et al., 2015). Light levels in the dark control were 0.03 lux.

Twelve hours prior to each of the eight experimental nights, we randomly selected up to 21 male and 21 female moths that hatched 6–10 (average 7) days prior. This age coincides with the peak in calling behaviour by adult females (Allison & Cardé, 2016). New individuals were used in every experimental night. Each night, moths were randomly assigned to a compartment such that each compartment received a male and a female placed in their 250-ml containers with insect gauze. Exact numbers of moths used each night depended on the number of available adult moths of the right age. In total, 230 individuals were used, including 115 males and 115 females, with between 8 and 16 individuals of each sex per location (mean 11.5 per sex per location).

Moths were starved from 12 h prior to 30 min prior to the start of the experiment, after which they received a 2:8 sugar-water-soaked cotton bud inside their container. The side of the container facing the other container in the same compartment was taped off with black, non-transparent tape. Individual moths, therefore, had no visual cues to detect the other moth in their compartment, but the white insect gauze top allowed potential pheromone communication. At the start of the experiment at 21:00, the lights were turned on in the compartments with the dim and bright light treatments. Every 8 min until 23:30, we observed the behaviour of the moths in each compartment in a fixed order, resulting in 20 observations per moth over the course of the night. At each observation time, we noted the presence (yes/no) of feeding behaviour for both sexes, and the presence (yes/no) of calling behaviour: when the female moth releases pheromones, she has a specific position where she exposes her pheromone glands by ventrally bending and extending her abdomen (Weissling & Knight, 1996). A Sony DCR-SR85 infrared-sensitive camera was used to observe moth behaviour in the dark control treatment (Van Langevelde et al., 2017).

Statistical analyses

All analyses were performed in R (v.3.5) (R Core Team, 2018). We used generalised linear mixed models using model builder in the *glmmTMB* package v.1.0.1 (Brooke et al., 2017) to test the differences in behaviour between the light treatments. The response variable was the relative frequency of behaviour (proportion of times that feeding or calling behaviour was present out of the 20 observations, akin to success rate), which was modelled with a beta-binomial distribution with logit link function. The beta-binomial distribution allows for different relative frequencies of behaviour between individuals and

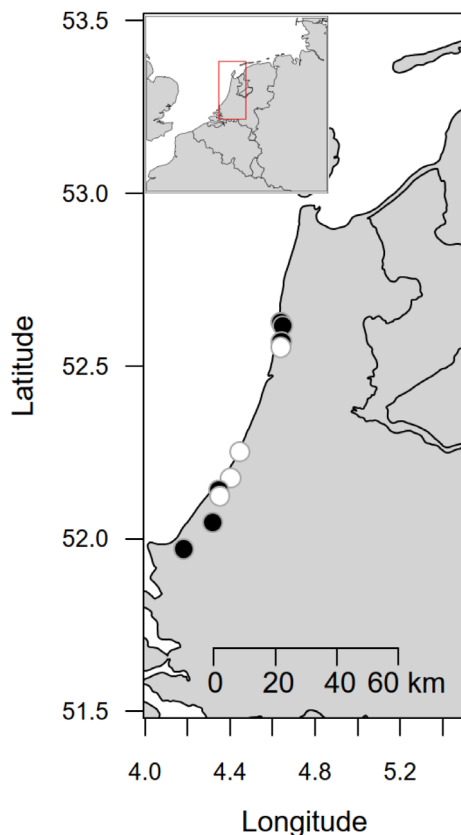


FIGURE 1 Location of the 10 source populations of *Yponomeuta cagnagellus* moths in The Netherlands (insert) used in the experiment. Black and white symbols indicate dark and lit source locations, respectively. The minimum distance between sampling locations was 1.1 km

captures overdispersion. Behaviour in response to ALAN may be sex-dependent (Altermatt et al., 2009; Van Geffen et al., 2014), and our preliminary analyses showed this to be the case for feeding behaviour in this study, so we separately ran the models for male and female feeding behaviour. Calling behaviour is only displayed by females, so these models were only run for females. The models included the following fixed factors: ALAN light at source location (dark or lit), experimental light treatment (dark, dim or bright intensity), and their two-way interaction.

Since individuals of a population may also have other behavioural differences unrelated to the effect of ALAN, we included population as a random intercept. As experimental conditions may have differed between nights and possibly affected the results, we also included experimental night as a random intercept.

We recognised that time allocation could play a role in the behaviour of female moths: when a female is performing calling behaviour, she cannot simultaneously show feeding behaviour (and vice versa). We therefore assessed whether this was the case by including the frequency of feeding activity as a fixed effect in the models of female calling behaviour, and vice versa. When a female moth is performing calling behaviour, sex pheromones are emitted to attract males (Van Geffen et al., 2015), and this may distract the males from feeding. For the full model of feeding behaviour of male moths, we therefore included, as a fixed effect, the relative frequency of calling behaviour by the female in the same compartment. In all cases, these behavioural variables as explanatory variables were not significant. The final models described below therefore include only the experimental treatments (ALAN at the source location, experimental light treatment) and their two-way interaction.

We ran the same above-mentioned models for the prevalence of feeding and calling behaviour (binary response whether any feeding or calling event occurred during the 20 observation times), using a binomial response model with a logit link. As the results are qualitatively similar to the models for the frequency of behaviour, they are not reported here, but provided in Table S1 and Figure S1.

None of the 17 moths from dark source populations assessed under bright light conditions displayed any feeding activity. While (beta)binomial models deal well with zeroes (and ones) in data, when all observations in a treatment combination are zero, confidence intervals cannot be accurately computed. Prior to running the frequency model, we therefore added a very small non-zero value to all feeding frequencies for all males (Figure 2). Errors were not able to be accurately estimated for the binomial model of male feeding prevalence (see Figure S1).

Residual diagnostics, including tests for dispersion, outliers and heterogeneity of variance were run using the *DHARMA* package v 0.4.4 (Hartig, 2021). Based on this, for male feeding frequency alone, we included light treatment, light at source location, and experimental night in the dispersion formula to account for heterogeneity of variance between treatments. Differences between the levels of significant treatments were tested using a Tukey–Kramer post hoc test adjusted for multiple tests ($\alpha = 0.05$), model summaries were created using type II analysis of deviance in the *car* package v. 3.0-11

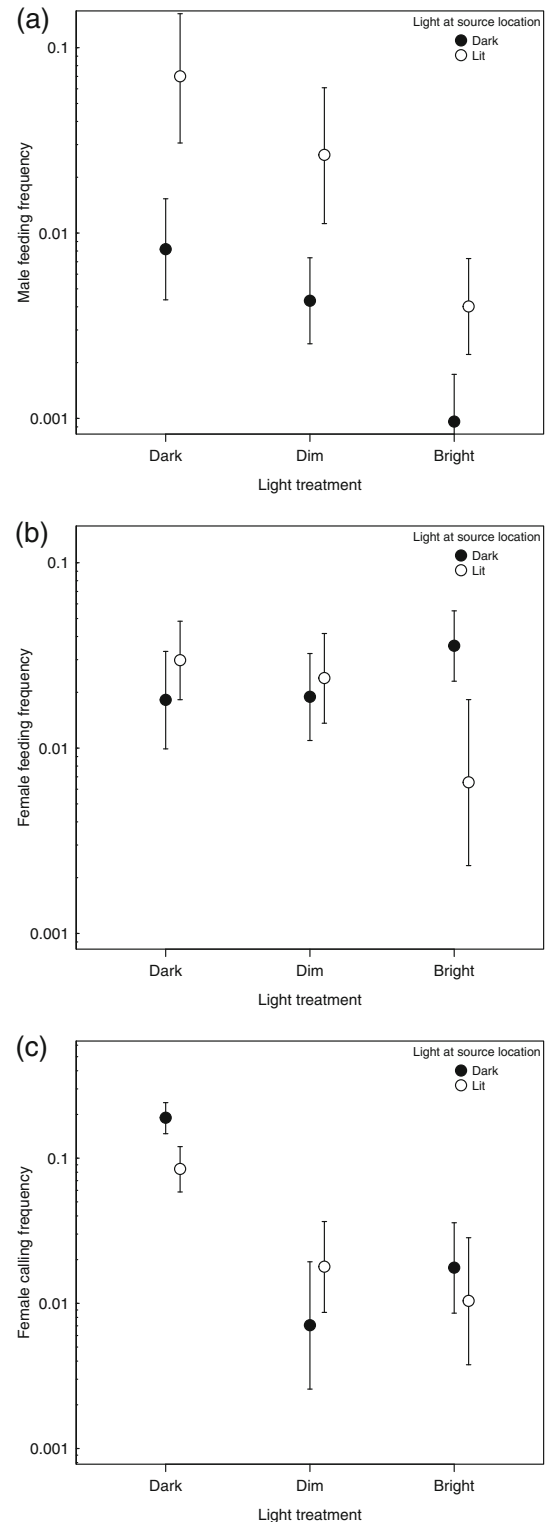


FIGURE 2 Modelled effect of light treatment light at location on feeding (a,b) and calling (c) frequency of *Yponomeuta cagnagellus* moths (males (a), females (b,c)). Shown are estimated marginal means (± 1 SE) presented on a log-scale. The frequency is calculated as the proportion of 20 events in which behaviour was observed. In (a), to allow accurate model performance when all observations in a treatment combination are zero (males from dark locations exposed to bright light treatment), a small non-zero value was added to all male feeding frequencies (see [Methods](#) section)

(Fox & Weisberg, 2019) and plots were created using model output summarised by the *emmeans* package (v.1.5.2-1) (Lenth, 2020).

RESULTS

There was evidence that male feeding behaviour was affected by light treatment (Table 1, Figure 2a). Males were more likely to feed in the dark treatment and dim treatments (mean 0.02 and 0.01, respectively) than in the bright (mean 0.002) treatment ($p < 0.001$, $p = 0.006$, respectively). Feeding behaviour of male moths was also affected by light at source location. Male moths from lit source locations fed more frequently than those from dark locations (mean 0.02 vs. 0.003, $p = 0.005$). None of the male moths from dark locations exposed to the bright light treatment ($n = 17$) showed any feeding behaviour (see also Methods section and Figure S1).

In contrast, there was no evidence that the feeding behaviour by female moths was affected by light environment at the source location, the light treatment imposed, or by their interaction (Table 1, Figure 2b).

Nevertheless, female calling behaviour was associated with light treatment ($p < 0.0001$). Calling frequency in the dark control treatment was much higher than that of moths in the dim or bright treatments ($p < 0.002$, dark mean 0.13 vs. dim and bright c. 0.01, Figure 2c). There was some evidence of increased calling behaviour in populations from dark locations than lit locations ($p = 0.10$), although this difference (mean 0.03 vs. 0.025, Figure 2c) was much smaller than the magnitude difference caused by the experimental treatment. There was no evidence of an interaction between Location and Treatment. Overall, female moths in dark treatment conditions displayed more calling behaviour than those in illuminated treatments.

TABLE 1 Summary glmmTMB model outputs assessing the effect of light at location (lit/unlit), light treatment (dark/dim/bright) and their interaction on the intensity of feeding and calling behaviour by *Yponomeuta cagnagellus* moths ($n = 115$)

	Chi. sq	d.f.	<i>p</i>
Feeding frequency male			
Light at location	9.605	1	0.002
Light treatment	29.942	2	<0.0001
Light at location × Light treatment	0.833	2	0.66
Feeding frequency female			
Light at location	<0.001	1	0.98
Light treatment	0.274	2	0.87
Light at location × Light treatment	3.094	2	0.21
Calling frequency female			
Light at location	2.638	1	0.10
Light treatment	24.775	2	<0.0001
Light at location × Light treatment	2.0253	2	0.36

Bold *p*-values indicate $p \leq 0.05$, and bold and italics values indicate $0.1 \leq p < 0.05$

DISCUSSION

Light pollution has been coined as a driver of the decline of moth populations, which is observed in many places in the world (Van Langevelde et al., 2018), suggesting that ALAN may be a selection pressure for moths, which may ultimately lead to the local adaptation of populations to their light environment (Altermatt & Ebert, 2016). In our study, we tested whether feeding and calling behaviour by *Y. cagnagellus* moths was adapted to ALAN by assessing whether these behaviours differed between populations from long-term illuminated and dark locations in response to different light treatments. A difference in the sensitivity to ALAN by individuals from populations with a long-term exposure to ALAN compared with dark controls would be a clear indication of adaptation to ALAN. We found that individuals from illuminated and dark locations were equally affected by the light treatments. Hence, the feeding and calling behaviour of *Y. cagnagellus* moths that have been exposed to artificial light have not adapted to ALAN; however, we did find phenotypical behavioural responses to light treatment and differences in behaviour between moths from illuminated and dark source populations.

Our experimental light treatment resulted in less frequent feeding by male moths. A previous study also found an inhibition of feeding under ALAN of different colours when assessing different moth species (Van Langevelde et al., 2017). Here, feeding frequency by males of *Y. cagnagellus* strongly reduced with increasing light treatment, to the extent that very little to no feeding by males was observed under the bright light treatment. When feeding intensity is negatively affected under ALAN, as appears may be the case for male moths in this study, and if this is sustained, this may have negative fitness (e.g., fecundity) implications (Boyes et al., 2021; Van Langevelde et al., 2017). However, the sustained character of these phenotypical responses remains to be determined (see the following).

The frequency of female feeding, in contrast to that of males, was neither associated with the light treatment nor the light environment at the source location. Sex bias in the flight-to-light response has been reported in the same species as in our study, disproportionately affecting this response in males (Altermatt & Ebert, 2016). However, with regard to feeding under ALAN, Van Langevelde et al. (2017) did not find significant differences in response between the sexes. However, the different species they assessed were not closely related to the species studied here, nor were the moths assessed while sexually active. We also noted a lower feeding frequency by females than males. Our experiment was dominated by sexually active females (58% of females across the dark treatment showed at least some calling behaviour, see Figure S1). It may be that for sexually active female moths, calling has a higher priority than feeding, while some sustained food intake, relatively unaffected by external conditions, may be required to not unduly affect pheromone production, secretion and reproduction rates (Foster & Johnson, 2010; Wenninger & Landolt, 2011).

Female moths in the dark control showed more calling behaviour than those in the lit treatments (Figure 2c). This is consistent with long-standing observations that moths primarily produce

pheromones (Van Geffen, Groot, et al., 2015) and perform calling behaviour during darkness (Hendrikse, 1979). Finding similarly low levels of calling under dimly and brightly lit conditions suggests that calling behaviour is already reduced at low levels of ALAN. However, the mechanism behind this change in behaviour remains to be determined. One possible driver is a reduced need for calling due to an increased use of visual cues. Conspicuous patterns of wings can also function as mate recognition signals (Jiggins et al., 2001), and the white and spotted wings of *Y. cagnagellus* may render visual cues to be used over olfactory cues when illuminated. It also makes sense that calling in lit conditions may make females more vulnerable to predation, in which case reduced calling by moths from lit populations could present a beneficial strategy. In a field experiment, Van Geffen, Groot, et al. (2015) found fewer female moths on illuminated trunks than that on dark trunks, suggesting that they may actively seek darker locations.

While we did not find an effect of the interaction between ALAN at source location and light treatments on behaviour – which would have indicated adaptation to ALAN – we did find that male moths from lit locations fed more frequently than those from dark locations (Figure 2b), and we found small, marginally significant increased calling frequency in females from dark populations compared with lit populations (Figure 2c). We cannot exclude the possibility that these populations were adapted to a common driver other than ALAN. However, we suggest that it is unlikely that there is a similar selective pressure given the various settings and associated environmental conditions across our 10 source locations. Further study will have to elucidate whether such a change in the mean response to a stressor (in this case, ALAN), without a change in sensitivity, can or will ultimately result in adaptation of these behaviours.

We assumed that *Y. cagnagellus* is a dispersal-limited species. If gene flow was less limited than expected (i.e. if there was significant dispersal between illuminated and surrounding dark sites), then genetic mixing would dilute the effect of ALAN and reduce the rate of local adaptation. Moreover, our study does not allow for an estimate of this rate of local adaptation. While we know that the physical locations of the source populations had been dark or illuminated, respectively, for at least 10 years, that the distance from the dark source populations to the closest streetlight was on average 305 m (minimum 62 m), and that the host plant is a perennial species that was likely present there for a long time, we cannot be certain that the populations had been present at those locations for multi-generations. Despite these unknowns that should reduce the field response to ALAN, we still found signs of differences in calling and feeding behaviour between dark and illuminated source populations. Moreover, being a relatively dispersal-limited and conspicuous species, one could argue that *Y. cagnagellus* is one of the more vulnerable lepidopteran species to light pollution, which may result in a stronger response to ALAN and stronger adaptation, than other species. However, since it is also the only species that has been submitted to studies of behavioural adaptation to ALAN, such hypotheses can only be verified by an increase in the number of studies assessing the adaptation of behaviour that affects vital rates in different moth species and

other species groups. Further investigations may also assess the mitigation of moths' responses and adaptation to illumination of different spectra (e.g., Brehm et al., 2021).

CONCLUSION

We show that an ecologically relevant intensity of white light at night affects the phenotypical behaviour of *Y. cagnagellus* moths at night, resulting in a reduction of feeding behaviour by males, and calling behaviour of females, but has not resulted in adaptation. In order to halt the decline of insects and other species, we need to gain a full understanding of the potential for different species to adapt to the environmental conditions to which they are exposed, including light at night. The species studied here has shown adaptation of flight-to-light behaviour elsewhere (Altermatt & Ebert, 2016), and our study indicates an instantaneous response of female calling and male feeding behaviour to ALAN but does not evidence local adaptation. The importance of differential adaptation between traits in population dynamics remains to be better understood. Given the global increase in ALAN, its purported role in the decline of many moth species globally, lack of adaptation in (some of the) behaviour that significantly affects mortality and reproduction suggests that the declines in moth populations reported may continue or even be exacerbated. Increased research such as carried out here, in combination with assessments of fitness in trans-generational (field and lab) experiments, is required to understand and act to halt the decline of insects globally.

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CONFLICT OF INTEREST

All authors declare that they have no conflict of interest. There are no disputes over the ownership of the data presented in the paper and all contributions have been attributed appropriately.

AUTHOR CONTRIBUTIONS

Ellen Cieraad and Roy H. A. van Grunsven conceived of the study. Nienke Zwart and Florine van der Sman participated in the design, carried out the experiments and participated in initial data analyses and write up as part of their BSc student research projects, which were supervised by Ellen Cieraad and Roy H. A. van Grunsven and logistically supported by Frank van Langevelde. Ellen Cieraad reanalysed the data and drafted the manuscript based on reports written by Nienke Zwart and Florine van der Sman, and conceptual discussions with Roy H. A. van Grunsven, Krijn Trimbos, C. J.

M. Musters, Emily Strange and Frank van Langevelde. All authors critically revised the manuscript and gave final approval for publication and agree to be held accountable for the work performed therein.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

TABLE S1. Summary of glmmTMB model outputs assessing the effect of Light at location (lit/unlit), Light treatment (dark/dim/bright) and their interaction on the prevalence (binary response) of feeding and calling behaviour by female *Yponomeuta cagnagellus* moths ($n = 115$). Due to a mean feeding prevalence of zero for males from dark source locations exposed to bright light treatment ($n = 17$), modelled errors were inaccurate, and model results are not shown here.

Figure S1. Modelled effect of light treatment light at location on feeding (A-B) and calling (C) prevalence of *Yponomeuta cagnagellus* moths (males A, females B-C). Shown are estimated marginal means (± 1 SE) presented on a log-scale. Prevalence is the probability that the behaviour was observed (binary response). In (A), the feeding prevalence of male moths from dark source locations exposed to bright light treatment was 0 ($n = 17$) and is inserted here at the y-origin for visual purposes only, errors could not be accurately estimated.

File S1. This file contains the raw data that support the findings of this article. Each row in the dataset represents one individual, with their population location ("Location"), whether the population was located under a streetlight ("Locationlight", with 0 = no, 1 = yes), its sex ("Sex", Male or Female), which experimental night it was exposed to treatment ("Night", value 1 to 8), in which compartment it was housed during the experiment ("Compartment", value 1 to 21), which light treatment it was exposed to ("LuxF", one of "Dark", "Dim" or "Bright"), and how often Feeding or Calling behaviour was observed out of 20 observations in each experimental night ("FeedingY", "CallingY", value 0 to 20).

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