

MAJOR REVIEW

Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle

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Abstract. 1. The night-time environment is increasingly being lit, often by broad-spectrum lighting, and there is growing evidence that artificial light at night (ALAN) has consequences for ecosystems, potentially contributing to declines in insect populations.

2. Moths are species-rich, sensitive to ALAN, and have undergone declines in Europe, making them the ideal group for investigating the impacts of light pollution on nocturnal insects more broadly. Here, we take a life cycle approach to review the impacts of ALAN on moths, drawing on a range of disciplines including ecology, physiology, and applied entomology.

3. We find evidence of diverse impacts across most life stages and key behaviours. Many studies have examined flight-to-light behaviour in adults and our meta-analysis found that mercury vapour, metal halide, and compact fluorescent bulbs induce this more than LED and sodium lamps. However, we found that ALAN can also disrupt reproduction, larval development, and pupal diapause, with likely negative impacts on individual fitness, and that moths can be indirectly affected via hostplants and predators. These findings indicate that ALAN could also affect day-flying insects through impacts on earlier life stages.

4. Overall, we found strong evidence for effects of artificial light on moth behaviour and physiology, but little rigorous, direct evidence that this scales up to impacts on populations. Crucially, there is a need to determine the potential contribution of ALAN to insect declines, relative to other drivers of change. In the meantime, we recommend precautionary strategies to mitigate possible negative effects of ALAN on insect populations.

Key words. Artificial light at night, insect declines, Lepidoptera, meta-analysis, nocturnal, phototaxis, street lighting.

Introduction

Life on Earth has evolved over millions of years under predictable photic cycles, namely the daily light–dark cycle, seasonal variation in day length, and lunar periodicity. These natural cycles have become increasingly disrupted since the beginning of the 20th century by anthropogenic light (Gaston *et al.*, 2017). There is growing evidence that these changes can have profound impacts on biodiversity and associated ecosystem processes (Hölker *et al.*, 2010; Davies & Smyth, 2018; Sanders & Gaston, 2018).

It is estimated that 23% of the world's area experiences light-polluted skies (Falchi *et al.*, 2016), and the global area that is artificially lit grew by 2% per year between 2012 and 2016 (Kyba

et al., 2017). Urban green space, domestic gardens, and road verges are expected to be among the most frequently illuminated habitats, though light pollution is also encroaching into less human-influenced areas, including biodiversity hotspots (Guetté *et al.*, 2018; Koen *et al.*, 2018), as well as freshwater and marine systems (Perkin *et al.*, 2011; Davies *et al.*, 2014). Furthermore, rapid shifts are underway in the spectral composition of outdoor lighting (Kyba *et al.*, 2017; Davies & Smyth, 2018). Narrow spectrum lighting, such as sodium lamps (characterised by a warm, yellow-orange light), is being replaced by LEDs, which are more energy efficient but typically emit light over a broader range of wavelengths (producing a cool, white light) (Taguchi, 2008; De Almeida *et al.*, 2014).

Nocturnal and crepuscular species are expected to be most vulnerable to artificial light. More than 60% of invertebrates are estimated to be nocturnal (Hölker *et al.*, 2010), including 75–85% of Lepidoptera (Kawahara *et al.*, 2018). Adult moths

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famously fly towards light (positive phototaxis) and, consequently, this group has been comparatively well studied in the context of light pollution. Furthermore, moths are ecologically and evolutionarily diverse, functionally important across terrestrial ecosystems globally, and have decades of high-quality data on abundance and occurrence in certain parts of Europe. For these reasons, moths are uniquely placed for understanding the population-level impacts of ALAN on nocturnal insects more broadly.

Long-term declines in moth abundance have been reported from some parts of central Europe. In Great Britain, standardised monitoring has revealed that 34% of the 390 commonest macro-moths had statistically significant declines between 1970 and 2016, with a 25% decline in a 442-species abundance indicator over the same period (Randle *et al.*, 2019; Hayhow *et al.*, 2019) and there is evidence for similar declines in macro-moth abundance from the Netherlands (Groenendijk & Ellis, 2011; Hallmann *et al.*, 2020). The causes of these declines are incompletely understood, although climate change (Conrad *et al.*, 2002; Martay *et al.*, 2017) and habitat degradation are thought to be largely responsible (Fox, 2013; Fox *et al.*, 2014). Yet, there is growing concern that light pollution may have a role in moth declines (e.g. van Langevelde *et al.*, 2018), and artificial light has been suggested as a driver of insect declines more broadly (Grubisic *et al.*, 2018; Owens *et al.*, 2020).

Anthropogenic light is known to have wide-ranging effects on moth behaviour and physiology, and recent studies have found correlative evidence linking light pollution to the negative population trends of some European moths (van Langevelde *et al.*, 2018; Wilson *et al.*, 2018). However, field studies have delivered mixed conclusions on the effects of night-time lighting on moth communities (Spoelstra *et al.*, 2015; Plummer *et al.*, 2016; Macgregor *et al.*, 2017; White, 2018; Péter *et al.*, 2020). Thus, there is a clear need to elucidate the mechanisms by which ALAN might be affecting moth populations.

Here, we substantially build upon previous reviews on the effects of light pollution on moths (Frank, 1988; Macgregor *et al.*, 2015) and insects more broadly (Eisenbeis & Hänel, 2009; Owens & Lewis, 2018; Desouhant *et al.*, 2019), by adopting a holistic approach to consider the potential mechanisms by which light affects moths throughout their entire life cycle. We define 'mechanisms' as any way that ALAN can affect the physiology, behaviour, or processes of individual moths, and thereby potentially impact on moth populations. Relevant research from outside the context of ecological light pollution is synthesised (e.g. within the pest control literature) with a growing number of newly published studies. We also conduct a network meta-analysis of studies to reveal which lighting technologies are the most effective at eliciting flight-to-light behaviour for both moths and all nocturnal insects. Having considered mechanisms, we then seek to determine the extent to which individual-level responses translate to the population level (including past applications of light for pest control) and so critically assess the quality of evidence linking ALAN with changes in moth assemblages or population trends. Finally, we consider the options for mitigating the disruptive impacts of lighting on moth behaviour and identify knowledge gaps for future research.

Methods

Scientific articles were located using Web of Science and Google Scholar, using an iterative process. Searches were conducted with the following terms: 'Moth' OR 'Lepidoptera' AND 'Light*' OR 'Phot*', followed by supplementary terms including circadian, activity, diel, attraction, phototaxis, behaviour, development, reproduction, diapause, predation, and parasitism. Additional articles were located through searching reference lists (snowballing) and subsequent citations (reverse snowballing). This was repeated until no new relevant articles were found. We deemed a systematic search to be inappropriate for this review given the very broad scope of relevant articles, spanning many disciplines, which we had already located.

In order to answer the specific question of which types of outdoor lighting technology induce the strongest flight-to-light responses for both moths and all nocturnal insects, a fully systematic search was conducted. Data from 14 qualifying studies were entered into two Bayesian network meta-analyses. Details of the search methodology, inclusion criteria, data extraction, and the meta-analysis models are given in the Supporting Information Appendix S1.

The thorough search of the literature produced evidence of direct and indirect impacts of ALAN throughout the moth life cycle, with evidence from fields as diverse as ecology, physiology, cellular biology, and pest management. We consider potential impacts sequentially from the adult stage to the egg (Figure 1), clearly describing the mechanisms and our assessment of the weight of evidence for each impact. We give priority to field or laboratory experimental studies focusing on moths, but also include observations and hypothesised effects (or effects demonstrated in other taxa). Where possible, the intensity and type of light (see Box 1) responsible for a result are reported.

Direct effects of artificial light at night on moths

Adult life stage

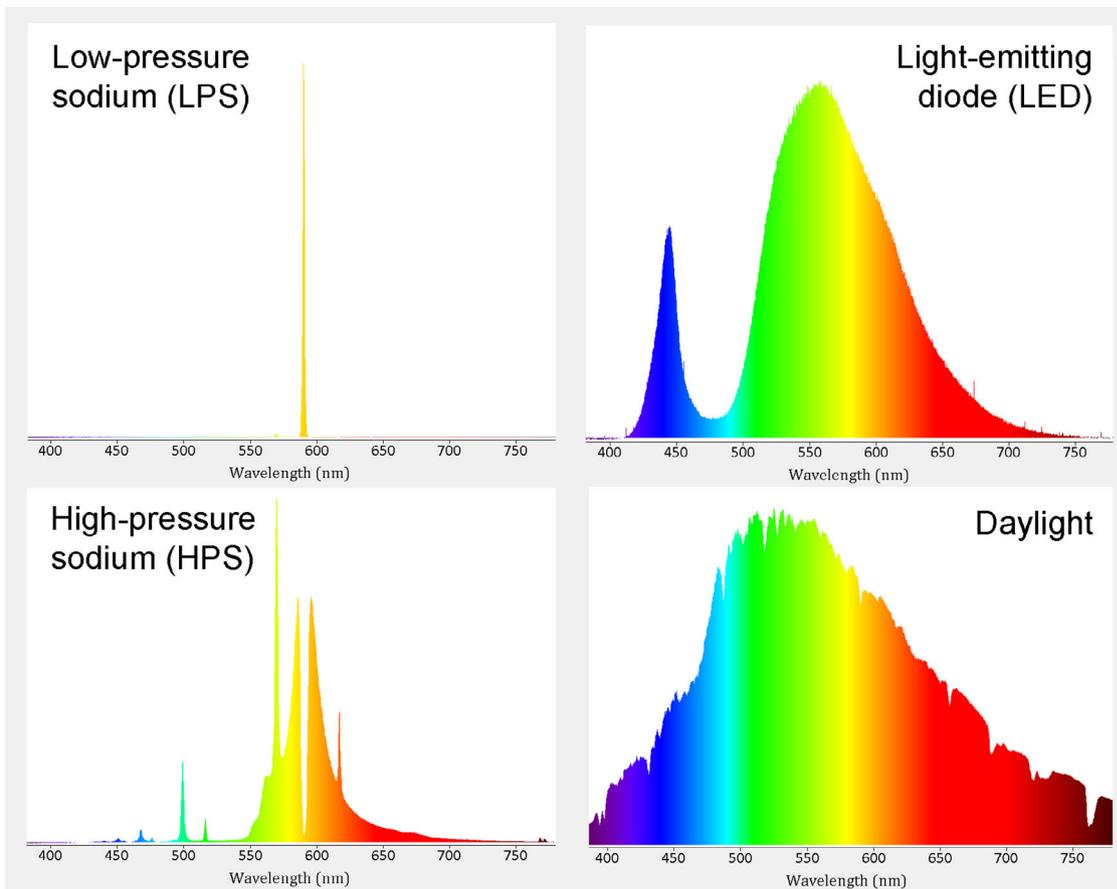
Moths are typically only adults for a small proportion of their entire life cycle; however, adults are responsible for reproduction, and in the vast majority of species, also dispersal. Consequently, there is disproportionate potential for ALAN to impact moth populations via mechanisms that affect adults.

Suppression of activity. There is clear evidence that artificial light can suppress the activity of adult moths, even at low levels, potentially preventing them from carrying out important behaviours. The onset of activity in nocturnal moths is often controlled by a drop in ambient light levels and laboratory experiments have found that the critical light level at which moths become active is typically below 1 lux (Persson, 1971; Dreisig, 1980). This means that moths resting in the vicinity of night-time lighting could fail to commence nocturnal activity. Experimentally illuminating oak tree trunks with LEDs at 10 lux strongly reduces the numbers of female *Operophtera brumata* (Linnaeus; Geometridae) caught in funnel traps (relative to

BOX 1. THE INTENSITY AND SPECTRAL PROFILE OF OUTDOOR LIGHTING

The two most biologically significant properties of light are its intensity and its spectral composition. Lux is the SI unit of luminance, which is widely used by urban planners, as well as ecologists, despite it representing the intensity of light as perceived by the human eye. This means that lux not a good metric when examining ecological impacts, because potentially relevant spectral information is omitted (Longcore & Rich, 2004). For instance, two lamps might produce the same value of lux, while emitting this light over different parts of the spectrum. For insects, the spectral composition of night-time lighting may be more biologically significant than its intensity (Longcore *et al.*, 2015). Common outdoor lamp types varying significantly in their spectral output. Low-pressure sodium (LPS) is almost monochromatic (producing only orange light), while high-pressure sodium (HPS) produces light over a wide range of wavelengths (including some blue and green light). Light-emitted diodes can be any colour, but LEDs used for amenity lighting tend to emit light across the visible spectrum to produce white light. Mercury-vapour and metal halide lamps also produce white light, but with a significant amount of ultraviolet light. The former was previously commonly used for street lighting but has been widely phased out in Europe.

| Lux | Comparable value | References |
|--------------------------------|---|-------------------------------|
| 103 000 | Daylight – sunny day | Rich and Longcore (2013) |
| 1000–10 000 | Overcast day | Rich and Longcore (2013) |
| 400–600 | Office | Rich and Longcore (2013) |
| 100–300 | Home | Rich and Longcore (2013) |
| 10 | Lit parking lot | Rich and Longcore (2013) |
| 3.6 (range: 0.1–16, $n = 30$) | Verges and hedgerow adjacent to street lighting | D. H. Boyes, unpublished data |
| 0.1–0.5 | Skyglow | Eisenbeis (2006) |
| 0.1–0.3 | Full moon; clear sky | Rich and Longcore (2013) |
| 0.001 | No moon; clear sky | Rich and Longcore (2013) |



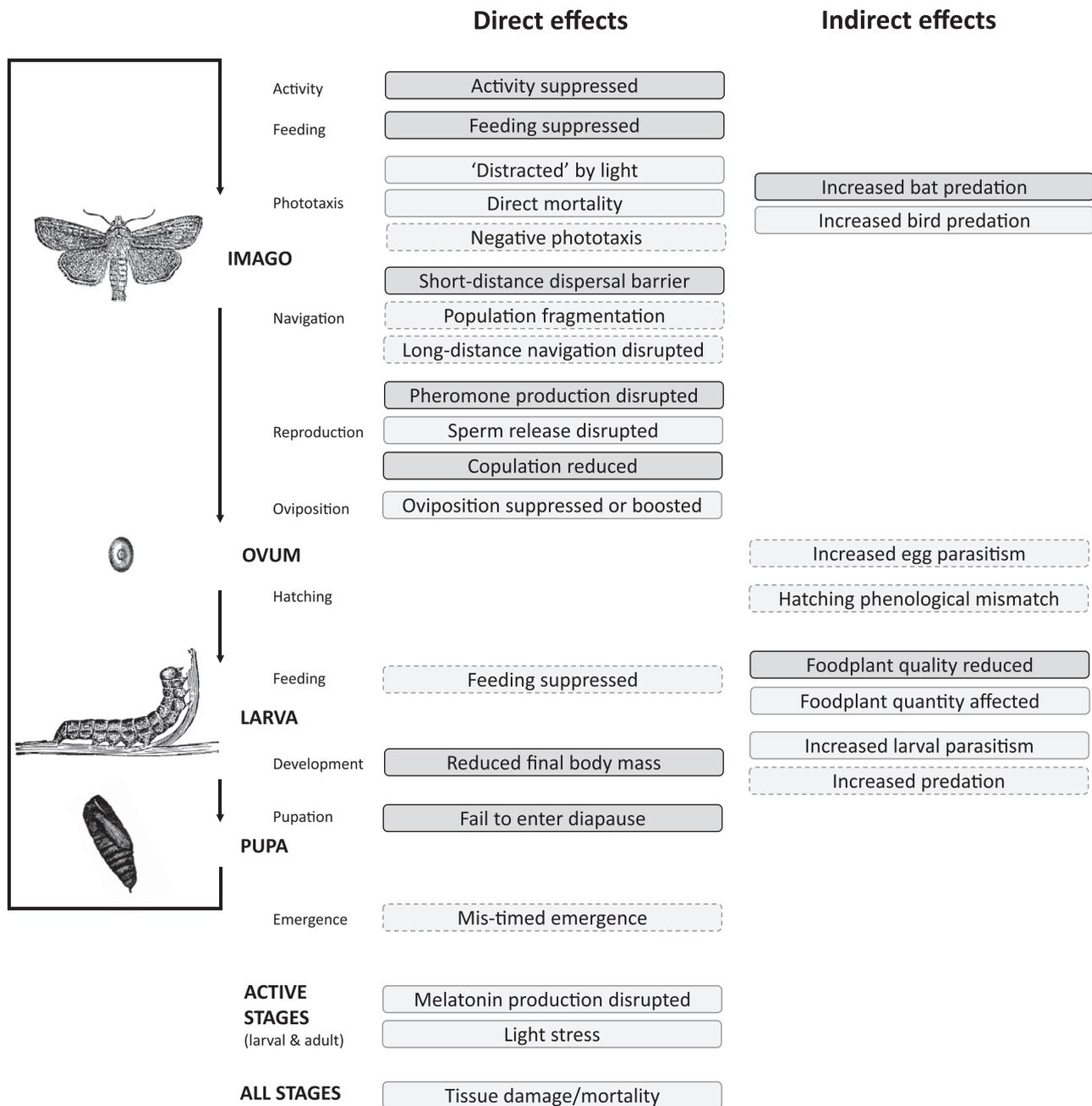


Fig. 1. Evidence for effects from artificial light on moths across the life cycle, as discussed in this review. Shaded boxes show effects with strong evidence, i.e. experimentally demonstrated in moths for at least one species in the field or laboratory, using field-realistic levels of light. Lighter boxes are effects with anecdotal evidence in moths, or effects documented at higher intensities of light, or strong evidence of a comparable effect in another insect taxon. Dashed boxes represent plausible effects but little or no evidence as yet.

controls), suggesting that light inhibits their activity (van Geffen *et al.*, 2015a). Moths that fly from darkness into an illuminated area can become inactive, sometimes remaining so for the rest of the night (Frank, 2006). This may be as the exposure to light triggers the day-time response of ceasing activity, possibly mediated through the light-adapted and dark-adapted states of

the compound eye in insects (Robinson, 1952; and see Walcott, 1969; Laughlin & Hardie, 1978). It has been proposed that a sudden change in light levels effectively blinds a moth until its eyes have readjusted (Frank, 1988), something that can take over 30 min in some species (Bernhard & Ottoson, 1960).

There is seemingly no evidence of the opposite phenomenon: diurnal Lepidoptera (day-flying moths or butterflies) becoming active at night in artificially lit environments, although this occupation of the 'night light niche' has been observed in other diurnal taxa, such as jumping spiders (Wolff, 1982; Frank, 2009).

Disruption of adult feeding. Many adult moths feed, typically on nectar from flowers, which increases their longevity and fecundity (Leather, 1984; Leahy & Andow, 1994; Tisdale & Sappington, 2001; Song *et al.*, 2007) and there is strong evidence that ALAN can disrupt his behaviour. Night-time feeding in four species of macro-moth was inhibited by artificial light at an intensity of 15 lux (produced by green, white, or red LEDs), compared to unlit controls (van Langevelde *et al.*, 2017). Consistent with the authors' expectations, shorter wavelengths of light (bluer) were most effective at suppressing feeding; however, even the red treatment (producing little light below 600 nm) reduced the probability of feeding by more than half. Negative impacts on feeding are irrelevant for the moth species that do not feed as adults (Norris, 1936; Frank, 1988); nevertheless, night-time lighting may have comparable effects on other key behaviours (e.g. reproduction).

Eliciting flight-to-light. Moths famously exhibit positive phototaxis (flight-to-light), though this is also found in many other insect groups. The consequences for an individual that has been attracted to a light range from a brief disruption of routine behaviours (small fitness cost) through to mortality (high fitness cost, especially if the individual had yet to reproduce); however, the costs of this behaviour at the population-level are poorly known.

Several explanations have been put forward to explain positive phototaxis in insects (summarised by Nowinszky, 2003). These include the light-compass theory, whereby lamps are being mistaken for a celestial cue used for orientation (Baker & Sadovy, 1978), and the idea that bright light simply dazzles night-flying insects (Robinson & Robinson, 1950). Upon encountering a light source, a moth can spiral around it, crash into it, settle some distance from it, or simply ignore it; no single theory successfully accounts for this diversity of behaviours (Frank, 2006).

Whilst the reasons for flight-to-light remain unresolved, different lamp types are known to elicit this behaviour to varying degrees. Shorter wavelengths of light, particularly ultraviolet, are the most effective at attracting moths (van Langevelde *et al.*, 2011; Barghini & de Medeiros, 2012). Taxonomic families of Lepidoptera do not respond uniformly to light (Merckx & Slade, 2014); for instance, Noctuidae are more strongly attracted to shorter wavelengths than Geometridae (Somers-Yeates *et al.*, 2013). Moths can also be sensitive to the polarisation of light (Belušič *et al.*, 2017). Polarised light pollution is thought to be particularly harmful to aquatic insects (Horváth *et al.*, 2009), though its potential effects on moths remain unexplored.

Many studies have compared the catches resulting from various types of bulbs commonly used for street lighting (Table 1). We included 14 studies in a meta-analysis; these either had data available or the effect sizes could be obtained from the

Table 1. Studies that have compared the number of moths and/or insects attracted to different bulb types commonly used for outdoor lighting. Note that some of these studies have compared additional bulb types not reported here (because these are not widely used for outdoor lighting, e.g. coloured LEDs).

| Study | Relevant bulb types compared | Results |
|--|---|--|
| Rydell (1992)* | MV; HPS; LPS | MV attracted more insects than HPS. LPS did not attract any insects, compared to unlit controls |
| Blake <i>et al.</i> (1994)* | MV; LPS | Eight times more insects seen around MV lamps than LPS |
| Eisenbeis (2006), and studies therein* | MV, HPS | MV attracted more insects than HPS |
| Huemer <i>et al.</i> (2010) | MH; HPS; warm and cool LED | All insects: MH > HPS > cool LED > warm LED. Moths: MH > HPS > cool LED = warm LED |
| Barghini and de Medeiros (2012) | MV; HPS | MV attracted more insects and more moths than HPS. |
| Somers-Yeates <i>et al.</i> (2013) | MH, HPS | In moths, MH was more attractive to Noctuidae than HPS. Geometridae showed no difference |
| Soneira (2013) | MH; LED | MH caught more insects and moths than LED. |
| Pawson and Bader (2014) | HPS; LED (of different colour temperatures) | LED caught more insects than HPS. Catches from different LEDs did not differ significantly |
| van Grunsven <i>et al.</i> (2014a) | MV; MH, LPS, LED | MV attracted many more insects than the other lamp types (which each attracted comparable numbers) |
| Longcore <i>et al.</i> (2015) | CFL; LED | CFL caught more insects and moths than LED |
| Poiani <i>et al.</i> (2015) | CFL; LED | CFL caught more insects and moths than LED |
| Justice and Justice (2016) | CFL; Warm and cool LED | No significant difference for neither all insects nor just moths |
| Wakefield <i>et al.</i> (2016) | CFL; Warm and cool LED | CFL attracted more insects than LEDs. No significant difference between warm and cool LEDs |
| Pintérné and Pödör (2017)* | MH; HPS | MH caught more moths than HPS |
| Wakefield <i>et al.</i> (2018) | MH, LED, HPS | MH caught five times as many insects than LED or HPS |
| van Grunsven <i>et al.</i> (2019) | MV; LED | MV caught twice as many insects as LED |

MV, mercury-vapour; HPS, high-pressure sodium; LPS, low-pressure sodium; MH, metal halide; LED, light-emitting diode; CFL, compact fluorescent lamp. * Asterisks indicate that the study was unable to be included in the quantitative meta-analyses (Figure 2; Supporting Information Appendix S1).

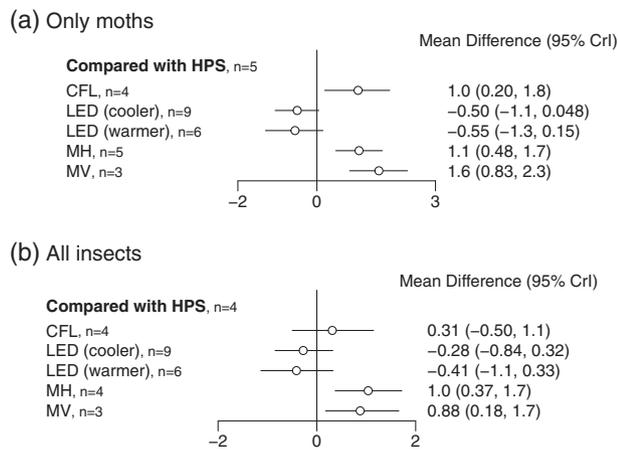


Fig. 2. Forest plots from network meta-analyses on the abundance of (a) Lepidoptera and (b) all insects attracted to different types of lamps commonly used for street lighting, relative to the incumbent technology: high-pressure sodium. Error bars show 95% credible intervals. Note that mean differences are on a \log_e scale, so each unit represents a 2.7-fold change in number. The number of contributing studies is shown for each treatment. LEDs with colour temperatures of 2700 k to 3500 k were grouped as ‘warmer’, while those of 4000 k to 6500 k were ‘cooler’. Abbreviations used in the plots: high-pressure sodium (HPS); compact fluorescent lamp (CFL); light-emitting diode (LED); metal halide (MH); mercury-vapour (MV). The methods are given in the Supporting Information Appendix S1, along with results for each treatment pairwise comparison; Supporting Information Appendix S2 reports the 39 studies found by the systematic search and the rationale for inclusion or exclusion; Supporting Information Appendix S3 lists the treatment estimates from the studies included in the meta-analyses.

publication (Supporting Information Appendix S1). High-pressure sodium (HPS) is the incumbent street light technology across much of Europe so we compared the capture rates of insects of HPS lamps to other bulb types, using capture rate as an indicator of the flight-to-light response. Relative to HPS, LED lamps with cool colour temperatures catch 0.6 times the number of moths on average than HPS (however, the 95% credible intervals (CrI) overlap slightly with no difference; range: -1.05–0.33; Fig. 2a). There was no detectable difference between the attractiveness of LEDs of cooler or warmer colour temperatures (Supporting Information Fig. S2). Metal halide (MH) and mercury-vapour (MV) lamps (both rich in ultraviolet light) attract three and five times more moths, respectively, than HPS.

Averaged across 10 studies that reported order-level data, Lepidoptera only made up 11% of the total insects attracted to light [the third most abundant order after Diptera (48%) and Coleoptera (11%)]. Despite this, moths show comparable responses to the catches of all orders pooled (Fig. 2; Fig. S2), with a strong correlation in the treatment pairwise mean differences between only moths and all insects (Pearson’s rho: 0.94, $n = 11$). This indicates that moths are a suitable model group for nocturnal insects more broadly (at least with respect to phototaxis).

These studies have implicitly or explicitly assumed that the number of insects attracted to a certain lighting type is a suitable

proxy for the bulb’s ecological impact. This may not necessarily be valid. For instance, a certain type of bulb may catch few insects because it is suppressing flight activity, not because insects are insensitive to it. Moreover, the approach fails to consider negative impacts on fundamental life processes (e.g. reproduction) and other life stages (Fig. 1).

Nonetheless, the number of insects drawn to a given lighting type may be a reasonable proxy for its ecological impact provided that a biologically significant portion of the individuals attracted either: (i) suffer direct mortality or (ii) remain effectively trapped, being unable to carry out normal behaviours. Direct mortality can occur due to collision with a hot bulb (although this is presumably only applicable to less energy-efficient lamps), or exhaustion if the moth continually circles the light. Another source of mortality is predation, which can be heightened around street lights (see section on indirect effects). It has been estimated that 33% of insects that are attracted to street lights perish (Eisenbeis, 2006); however, it is not clear how this figure was obtained. It remains unknown what proportion of the moths that are initially attracted to a street light die from collision with the bulb, succumb to exhaustion, are predated, or fly away unharmed.

A commonly discussed concern in the context of flight-to-light behaviour is trap effects (Macgregor *et al.*, 2015), or a ‘vacuum cleaner’ effect (Eisenbeis & Hänel, 2009). These hypothesise that moths are continually drawn in from the surroundings, depleting those populations, with the illuminated area forming a sink habitat. At present, there is little evidence to support this idea, though this could partly reflect the challenges of detecting it. A study in Japan found that the abundance and species richness of moths caught in a light trap does not increase over consecutive nights, suggesting that individuals can escape the lamp’s radius of attraction (Hirao *et al.*, 2008).

We believe it is useful to distinguish a trap effect from a concentration effect (Figure 3), whereby moths are drawn in from surrounding habitats but are otherwise not negatively impacted. Such outcomes are likely to be context-specific, for instance, a trap effect is more likely if the lit area comprises entirely unsuitable breeding habitat (e.g. car parks, airports, industrial units). An alternative idea is the disruption effect, whereby behaviour is impacted locally, but individuals are not drawn in from surrounding areas.

There are reasons why flight-to-light behaviour might be expected to have a limited impact at the population level. The distance at which moths are drawn to lamps is generally thought to be small (Frank, 1988; Nowinszky, 2004). The effective range of a 125 w mercury-vapour lamp has been estimated at 3–5 m (Baker & Sadovy, 1978), while others have reached a figure an order of magnitude greater (Robinson & Robinson, 1950; Robinson, 1960; Degen *et al.*, 2016). A mark-release-recapture study estimated the proportion of individuals recaptured when flying 0–1 m past a 6 w actinic light was only up to 10% for noctuids, 15% for geometrids, and 50% for erebids (Merckx & Slade, 2014), while a similar study using 15 w actinic lamps reported most recaptures occurred at release distances <30 m, and typically <10 m (Truxa & Fiedler, 2012) and another study found that only 25% of moths released 2 m from a 6 w actinic light were recaptured by the trap (van Grunsven *et al.*, 2014b).

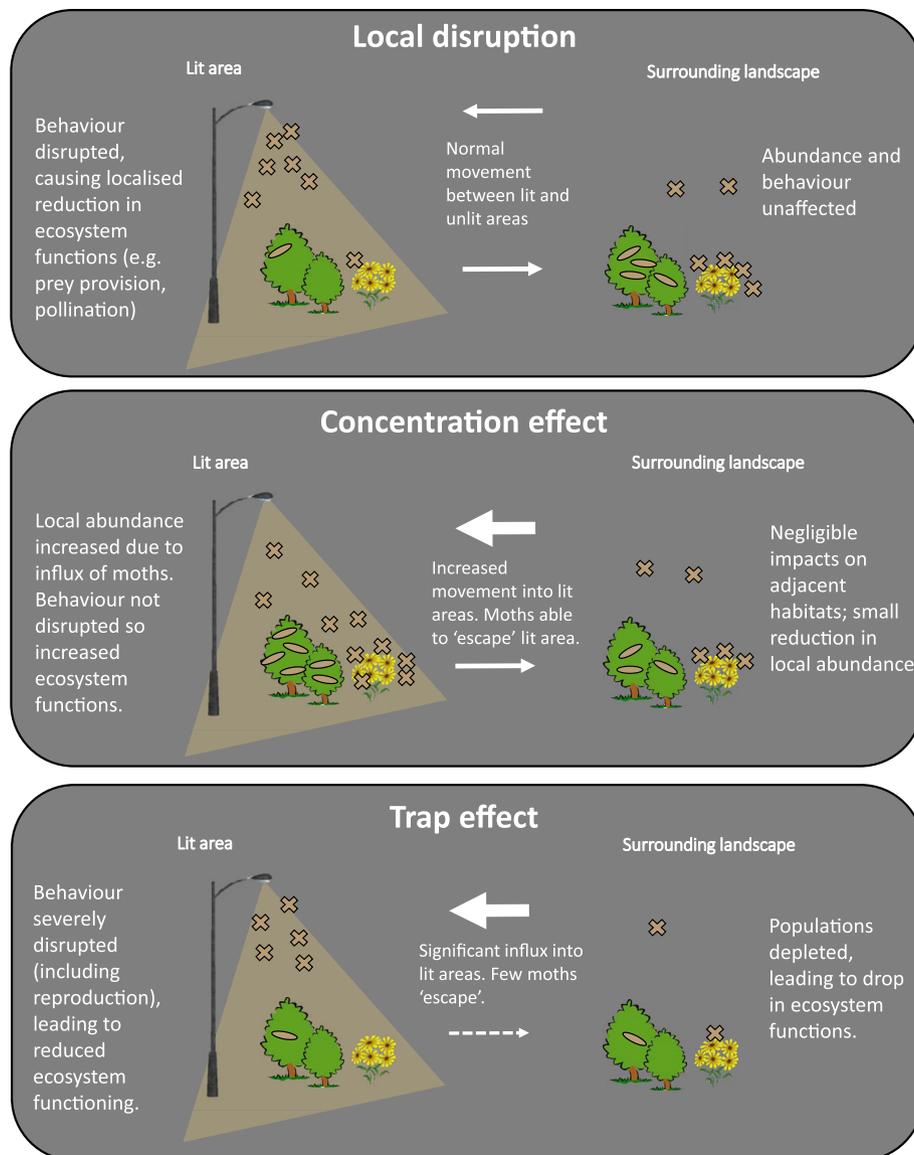


Fig. 3. Three hypothetical impacts of light on moths (adapted from Macgregor *et al.*, 2015), in terms of their populations and the ecosystem functions they provide. Crosses represent adult moths and ovals represent larvae. [Color figure can be viewed at wileyonlinelibrary.com]

These studies have investigated the lighting types used in moth traps. The radius of attraction of the lamps most commonly used for outdoor lighting (e.g. HPS, white LEDs) remains largely untested but might be expected to be lower as these emit little or no ultraviolet light. Thus, the idea that moths are routinely lured into urban areas over great distances (Eisenbeis & Hänel, 2009) seems unlikely.

The population-level ramifications of phototaxis by moths may also be limited by the fact that females are less strongly affected. A 4-year study using light traps found that males were more frequently captured for 45/51 species examined, with only 15% of the 9,926 individuals caught being female (Williams, 1939). The actual sex ratios of these moth populations are not known; however, experimental evidence for male-

biased flight-to-light behaviour has been reported, with males from two species being 1.6 times more likely to fly to light (Altermatt *et al.*, 2009). This is most likely because males are more mobile (thus are more likely to enter the radius of attraction), as opposed to being more strongly attracted to light (Degen *et al.*, 2016).

Evidence that flight-to-light behaviour can have negative population-level effects on moths comes from the discovery that individuals of the micro-moth *Yponomeuta cagnagella* (Hübner; Yponomeutidae) from urban areas appear to have evolved to be less attracted to light (Altermatt & Ebert, 2016). Larvae were reared in a common garden setting after being collected in north-western Switzerland and eastern France from five rural areas and five light-polluted sites (albeit all within a single city: Basel).

Adults from urban sites were 30% less likely to be caught by the light trap (6 w actinic lamp), which was 5.7 m away at the opposing end of a mesh cage. Further evidence to test the generality of this finding would be valuable. Evolution by moths in response to anthropogenic lighting has long been hypothesised (Frank, 1988) and may be expected given artificial light at night can represent a strong selective pressure (Hopkins *et al.*, 2018). If an evolutionary change towards reduced phototaxis was widespread among moths, light trap catches would be expected to decrease in light-polluted areas over time. Yet, in the Rothamsted Insect Survey (a UK-wide, long-term systematic monitoring scheme), abundance trends from locations where light pollution had increased from 1992 to 2000 were not more negative than trends at sites that remained dark (Conrad *et al.*, 2006).

Negative phototaxis. There is limited evidence that adult moths avoid illuminated areas at night, though this may be due to the challenges of studying the behaviour in insects. Certain vertebrate taxa are known to be repelled by artificial light at night, including some bats (Lewanzik & Voigt, 2017) and some authors consider it likely that certain moths exhibit comparable behaviour (Robinson, 1952). One species of moth, *Amphipyra tragopoginis* (Clerck; Noctuidae), is infrequently seen in light traps, compared to its abundance in suction samples, so is probably is poorly attracted to light (Taylor & Carter, 1961). Given the typical adult behaviour of this species is to scuttle for cover when exposed to light (Waring & Townsend, 2017), it is plausible the species may actively avoid lit areas at night.

Disruption of short and long-distance movements. It has been hypothesised that linear sections of street lighting may disrupt movement in moths, potentially leading to population fragmentation (Frank, 2006). A grid of 12 experimental street lights (4 × 3) fitted with flight interception traps found that the two lamps in the middle caught fewer moths than lights on the edge of the grid, which the authors propose is evidence that street lighting can interrupt short-distance moth dispersal (Degen *et al.*, 2016). However, the lamps in the centre may also have been less effective at attracting moths due to elevated background illumination from the surrounding edge lights (Bowden, 1982). Furthermore, the flight intercept traps were lethal, thus, movement is likely to be more significantly restricted than at regular street lights, where a proportion of the moths that were initially attracted would continue past unharmed.

Light pollution has been suggested as a potential issue for moths that use celestial cues to orientate during long-distance dispersal, such as *Noctua pronuba* (Linnaeus; Noctuidae) (Sotthibandhu & Baker, 1979) and *Agrotis exclamationis* (Linnaeus; Noctuidae) (Baker, 1987). These behaviours are only known to occur routinely in a select number of highly abundant moths, and it is questionable whether local populations of these species are dependent on effectively navigated long-distance movements. Celestial cues are not exclusively used for orientation, with some moths using a magnetic compass (Baker & Mather, 1982). Furthermore, migration in Lepidoptera typically occurs at high altitudes (Wood *et al.*, 2009) so is unlikely to be affected by direct illumination from artificial lights, although it

is plausible that diffuse anthropogenic light pollution ('sky-glow') could interfere with this process.

Impacts on reproduction. Reproduction in moths is closely linked to the natural light cycle and there is clear evidence that ALAN (especially at high levels) can impact reproduction through several different mechanisms. The synthesis and release of female sex pheromones in moths are typically timed using the day-night cycle (Groot, 2014). Overnight illumination of 17 lux inhibits pheromone production in female *Mamestra brassicae* (Linnaeus; Noctuidae), with only a third of the amount produced under shorter wavelengths (green LEDs), relative to dark controls (van Geffen *et al.*, 2015b). The same lighting treatments also significantly altered the chemical composition of the pheromone blend. This reduction in the quantity and quality of pheromones is hypothesised by the authors to correspond to reduced mating success.

Female pheromone production and 'calling' behaviour (during which the pheromones are released) is inhibited by continuous lighting in cultures of *Dioryctria abietella* (Denis & Schiffermüller; Pyralidae) (Fatzinger, 1973), and a similar effect is observed in *Helicoverpa assulta* (Guenée; Noctuidae) (Kamimura & Tatsuki, 1994). In *Trichoplusia ni* (Hübner; Noctuidae), the release of pheromones is increasingly inhibited by light intensity from 0.3 to 300 lux (Sower *et al.*, 1970). Calling in female *Plodia interpunctella* (Hübner; Pyralidae) is not suppressed by constant light, which may be because this is a pest of stored grain that has adapted to survive without natural day-night cycles (Závodská *et al.*, 2012; Groot, 2014). Yet, calling in female *Ephesia kuehniella* Zeller (Pyralidae), another stored grain pest, is suppressed by constant light, while the diel rhythm persists in continual darkness: a characteristic of circadian regulation (Závodská *et al.*, 2012). Similar circadian rhythms in sex activity have been demonstrated in several other moths from natural habitats (Groot, 2014).

The production of mature sperm in moths is also closely linked to the diel cycle and can be disrupted by ALAN. Under natural day-night cycles, sperm is released rhythmically through the reproductive tract towards the duplex (where it is stored until mating); however, continuous light can disrupt this sequential release of sperm, meaning little reaches the duplex and the males are effectively sterile (Giebultowicz *et al.*, 1990; Bebas *et al.*, 2001; Seth *et al.*, 2002). Male sterility, or significantly depressed fertility, in response to continuous light has been shown in laboratory cultures of moths from the families Noctuidae (Hagan & Brady, 1981; Bebas & Cymborowski, 1999), Pyralidae (Lum & Flaherty, 1970; Riemann & Ruud, 1974; Cymborowski & Giebultowicz, 1976), and Erebidae (Giebultowicz *et al.*, 1990). However, the phenomenon is not universal since *Cydia pomonella* (Linnaeus; Tortricidae) does not appear to show adverse impacts on male reproductive capacity from continuous lighting (Giebultowicz & Brooks, 1998).

Artificial lights may also disrupt moth reproduction by directly reducing the incidence of copulation. Mating is gradually inhibited by light levels above 0.3 lux in *T. ni* under laboratory conditions, although very bright light (>300 lux) is required to completely suppress the behaviour (Shorey, 1966). This process is temperature dependent in *Chilo suppressalis* (Walker; Crambidae); for instance, 5 lux is sufficient to suppress mating

at 30°C, but 600 lux is required at 15°C (Kanno, 1980). Light may also disrupt copulation by suppressing male flight activity, or cause males to exhibit positive phototaxis, diverting them away from females. Low levels of light (0.1–0.9 lux) cause male *Lymantria dispar* (Linnaeus; Erebididae) to fly less directly towards females (Keena *et al.*, 2001).

When oak trunks are illuminated with 10 lux, the proportion of mated *O. brumata* females drops by half under longer wavelengths (red LEDs) and a quarter under shorter wavelengths (green LEDs), relative to dark controls (van Geffen *et al.*, 2015a). This reduction may be due to disrupted pheromone production by females, inhibition of mating behaviour, suppression of male flight activity, or males being 'distracted' from females by flying towards light (or a combination thereof). The authors also deployed traps baited with synthetic female pheromone and found a smaller (but statistically significant) drop in males caught under the lighting treatments. This suggests that the male response to female pheromones is disrupted by light, but that the observed drop in mated females is likely to be predominately attributable to disrupted pheromone release or suppressed mating behaviour.

Artificial light might also affect oviposition in moths. Moderate light levels (8–40 lux) produced by an incandescent bulb significantly reduce the number of eggs laid by *P. interpunctella* (Sambaraju & Phillips, 2008). Suppression of oviposition by light has been demonstrated for several other species under laboratory conditions, though this has typically been tested with continuous bright light (>200 lux) (Broodryk, 1971; Henneberry & Leal, 1979; Skopik & Takeda, 1980; Ismail *et al.*, 1988). The opposite effect, whereby oviposition is concentrated around artificial lights, has been reported anecdotally (Frank, 1988). For instance, larval infestations of *Helicoverpa armigera* (Hübner; Noctuidae) in cornfields were several times higher in the vicinity of light traps (Martin & Houser, 1941). This may lead to reduced larval fitness through intensified intra-specific competition.

As ova

We found no evidence that artificial light, at the intensities normally found outdoors, can impact moth fitness during the egg stage. The diel timing of hatching is under circadian control in some moths, although constant light does not seem to prevent hatching (Minis & Pittendrigh, 1968). Furthermore, photoperiod is not an important cue for seasonality in moth ova; hatching is usually controlled by temperature (Du Merle, 1999; Visser & Holleman, 2001). The adult fecundity of three tortricids is affected by the photoperiods experienced by the ova and first instar larvae (Deseo & Saringer, 1975); however, it is not clear whether this effect would also occur at field-realistic levels of artificial light during the night.

Larval stage

Feeding and development. Many moth larvae are nocturnal feeders and we found some evidence that ALAN could affect

their physiology and behaviour, although several plausible mechanisms of ALAN on moth larvae remain to be tested.

Negative developmental effects from low levels of ALAN have been demonstrated experimentally in two noctuid larvae. Male *M. brassicae* larvae reared under 7 lux of white and green LEDs at night reached a lower final body mass, relative to dark controls (van Geffen *et al.*, 2014). No difference was observed for female larvae, nor males reared under red LEDs. In *Apamea sordens* (Hufnagel; Noctuidae), larvae experiencing dark nights achieved significantly higher body mass after 10 weeks, compared to those reared under HPS lamps (Grenis & Murphy, 2019). Larval survival was not affected in either study; however, the authors hypothesise that the reduction in final larval mass would translate to reduced adult fitness (e.g. reduced fecundity).

Moth larvae of many species feed predominately at night, when fewer predators and parasitoids are active (Porter, 2010). Positive phototaxis has been observed in the larvae of several moth species (De Ruiter & van der Horn, 1957; Buck & Callaghan, 1999), which could theoretically cause caterpillars to be drawn away from their hostplants. Outdoor lighting might also suppress feeding behaviour in nocturnal caterpillars (triggering the normal day-time response of inactivity), with knock-on effects for larval development, though this has yet to be tested.

Diapause and pupation. Diapause is a state of dormancy that enables insects to survive unfavourable conditions (e.g. winter) and we found evidence that lighting can readily disrupt diapause, although the impact on populations remains unknown. Night-time lighting can prevent multivoltine species from entering winter diapause, a process that is typically initiated by shortening day lengths (Adkisson, 1966; Peterson & Hamner, 1968; Bell *et al.*, 1975). White and green LEDs at an intensity of 7 lux inhibits *M. brassicae* larvae from entering diapause (van Geffen *et al.*, 2014), which instead enter a non-diapausing pupal stage. Fluorescent lamps extending daylength in field plots to 17 h results in 70% of *C. pomonella* and 76% of *Ostrinia nubilalis* (Hübner; Crambidae) failing to enter diapause, compared to 0% of larvae in plots with natural day-night conditions (Hayes *et al.*, 1970). The authors state that the larvae that fail to enter diapause would perish over the winter. In a greenhouse study, 60 lux of LED inhibited diapause in the leaf-miner *Cameraria ohridella* Deschka & Dimić (Gracillariidae), which the author concludes could lead to either increased outbreaks (more generations per year) or local extinction (if pupae that failed to enter diapause died over winter) (Schroer, 2019).

Pupal stage

We could find no documented effects of artificial lighting in the pupal stage, and we conclude that this unlikely to be an important mechanism whereby ALAN affects moths. It is plausible that outdoor lighting could cause mistimed adult emergence in temperate moths that use photoperiod cues to detect seasonality, which could disrupt population synchronicity. It has been suggested that the emergence of adults in some species is

synchronised with lunar periodicity, perhaps to maximise the chances of finding mates (Nemec, 1971; Nowinski *et al.*, 2010). There is little evidence of this, however, and cyclical dynamics appearing in light trap data are considered an artefact arising from the reduced sampling effectiveness around full moon (Williams *et al.*, 1956; Yela & Holyoak, 1997).

Diel emergence synchronicity could be theoretically disrupted by light pollution, as certain species tend to emerge at the same time of day (e.g. Bergh *et al.*, 2006; Calatayud *et al.*, 2007), provided the emergence cue involved is photic and not thermal. The reasons for this behaviour are unclear but may include promoting population synchronicity between males and females, as well as avoiding predation.

Molecular and physiological effects (on various life stages)

The physiological and molecular-level effects of ALAN on moths are not well known. Melatonin is a highly conserved hormone found in most living organisms, including insects (Hardeland & Poeggeler, 2003; Zhao *et al.*, 2019). Its synthesis and release typically happen during darkness and are suppressed during the daytime (Bloch *et al.*, 2013). Melatonin is involved in the circadian regulation of adult moths (Linn *et al.*, 1995; Lampel *et al.*, 2005), and the hormone has been found in moth larvae (Itoh *et al.*, 1995) where it is likely to perform a similar role. Melatonin is also a powerful antioxidant, having a protective role within cells (Reiter *et al.*, 2017). It is plausible, though untested, that light pollution could suppress melatonin synthesis in moths, leading to oxidative stress and cellular damage. The potential implications of this for moth fitness are unknown but might be limited given their short life cycles.

All insect life stages can be vulnerable to direct exposure to certain wavelengths of light. The negative effects of ultraviolet (UV) light at a cellular level are well known, for instance, its ability to damage DNA molecules (Sinha & Häder, 2002). In addition to its lethal effects on insects (Beard, 1972), UV light can cause changes in the expression of neuropeptides in adult moths (Wang *et al.*, 2018). Prolonged irradiance by shorter wavelengths of visible light can cause high mortality in various life stages of a fruit fly, a flour beetle, and a mosquito (Hori *et al.*, 2014). However, it is doubtful that many insects experience the requisite intensities from artificial lighting while outdoors.

Indirect effects of artificial light at night on moths

It is becoming increasingly apparent that effects mediated through other taxa must be considered to predict the impacts of global change. Indirect effects can be strong in ecological communities exposed to artificial light (e.g. Bennie *et al.*, 2018b; Sanders *et al.*, 2018); however, species interactions remain relatively poorly studied in the context of light pollution (Sanders & Gaston, 2018).

Moths may be indirectly affected by night-time lighting via plants; this could occur if artificial light modifies the quantity and quality of plants, or if ALAN creates a phenological

mismatch between moths and the plants they are reliant on. Such effects are most likely to act on the larval stage, which is entirely dependent on hostplants in the majority of lepidopterans, though weaker effects might also be observed in species with nectar-reliant adults. Top-down indirect effects can occur through predation and parasitism, as artificial light may locally concentrate prey and effectively extend photoperiods, potentially benefiting otherwise diurnal parasitoids and predators.

Bottom-up effects via hostplants

Night-time lighting can affect plants through a range of physiological and ecological mechanisms, though the topic has received relatively little attention (for reviews, see: Briggs, 2006; Bennie *et al.*, 2016; Singhal *et al.*, 2019).

Artificial light can modify the quantity of hostplants available for herbivores. For instance, mesocosm experiments have revealed negative bottom-up effects on aphid abundance due to reduced plant biomass and/or flowering under LED lighting (Sanders *et al.*, 2015; Bennie *et al.*, 2018b). Anthropogenic lighting can also change the quality of hostplants. For instance, carbon/nitrogen ratios in plants can be affected by lighting, with knock-on effects for herbivores (Vänninen *et al.*, 2010; Barber & Marquis, 2011; Bennie *et al.*, 2018b). Indirect effects on moth larvae due to ALAN altering the biochemistry of foodplants remain untested. However, negative developmental effects from HPS lighting have been found in *A. sordens* caterpillars, which appear to result from the hostplant being physically tougher, so less digestible, under lit conditions (Grenis & Murphy, 2019).

Outdoor lighting can also alter plant phenology, for instance, causing early budburst in deciduous trees (Ffrench-Constant *et al.*, 2016). This could result in phenological mismatch if moth ova use non-photoc cues (e.g. temperature) and therefore hatch after budburst. By this time, leaves can be too rich in phenols and tannins to be easily digestible by caterpillars (Feeny, 1970). Artificial light can alter the phenology of, or even suppress, flowering in some plants (Whitman *et al.*, 1998; Chen *et al.*, 2009; Vänninen *et al.*, 2010; Bennie *et al.*, 2018a). This could potentially impact upon moth larvae that consume flowers and seeds (Pettersson, 1991), as well as creating a mismatch between the phenology of flower-visiting adults and their nectar sources (Petanidou *et al.*, 2014; Macgregor *et al.*, 2015).

Top-down effects mediated by parasitoids and predators

Parasitoids can exert strong indirect effects on moths, as these typically cause the death of the host (either at the egg, larval or pupal stage). Night lighting may be predicted to affect parasitoid behaviour and populations in various ways. The potential for ALAN to cause elevated rates of parasitism in insects has already been demonstrated. Low levels of LED lighting (0.1–5 lux) in a field experiment doubled the parasitism rate of an aphid, relative to unlit controls (Sanders *et al.*, 2018). The authors hypothesise that the wasps predominately search for prey by day; thus, they can exploit the ‘night light niche’ under artificial light. Parasitoid wasps display positive phototaxis, so local densities could also

be boosted around outdoor lighting, leading to more parasitism. Conversely, night lighting can suppress parasitism. Bright LED light (10–100 lux) causes decreased parasitism of aphids, possibly because the wasps are drawn up towards lamps (Sanders *et al.*, 2018). Continuous night-time lighting might disrupt key demographic processes of the parasitoids themselves (perhaps via similar mechanisms to those described above for moths), causing local densities to decline. Lighting could also disrupt the synchronicity of the phenology of parasitoids and their hosts if photoperiod is used as a cue for emergence. To date, no research has been conducted on how night lighting affects parasitism rates in moths. The existence of hyper-parasitoids makes these indirect effects even more difficult to predict.

Bat predation of adult moths is commonly observed around street lights (Frank, 1988; Rydell, 2006). Some species of bat exploit the high prey densities gathered around lamps (Rydell, 1992; Minnaar *et al.*, 2015; Russo *et al.*, 2019). Furthermore, moths can fail to perform their usual anti-predation behaviours (e.g. evasive manoeuvres) in lit areas, rendering them even more susceptible to predation (Svensson & Rydell, 1998; Acharya & Fenton, 1999; Wakefield *et al.*, 2015). The elevated rates of bat predation around outdoor lighting might deplete local moth populations.

Birds represent important predators of both adults and larvae; however, the effects of light pollution on moth predation by birds have rarely been tested. Songbird activity can be altered by artificial lighting (Titulaer *et al.*, 2012; Dominoni *et al.*, 2014), potentially resulting in a longer period suitable for foraging in lit areas. As demonstrated by the famous example of *Biston betularia* Linnaeus (Geometridae), adult moths can be highly vulnerable to bird predation if their crypsis is disrupted (Cook *et al.*, 2012). Adults attracted to artificial lamps frequently remain in situ and may fail to show cryptic behaviour the following day, where they are readily predated (e.g. Collins & Watson, 1983). If light traps are run frequently in the same location, songbirds seem to learn that these will produce a high density of prey on the surrounding ground and vegetation at dawn (Randle, 2009). Yet, it is unknown whether this type of bird predation occurs when the light is not near the ground, for instance, around street lamps (where there are no proximate surfaces for moths to settle on).

The abundance of predatory invertebrates can be intensified around outdoor lighting (Davies *et al.*, 2012; McMunn *et al.*, 2019). Certain spiders preferentially construct webs near light sources (Heiling, 1999), while some diurnal species of jumping spider utilise the 'night light niche' by hunting by lamps at night (Frank, 2009). Social wasps (*Vespula* species) have been observed feeding on adult moths attracted to light (Warren, 1990). However, a field experiment has demonstrated that live moth larvae pinned to Styrofoam squares do not suffer higher rates of predation (predominately from ants, wasps, and spiders) under street lights (Grenis *et al.*, 2015) and lit spider webs can have lower rates of adult moth capture compared to unlit webs (Yuen & Bonebrake, 2017).

Mixed results from field-based and correlative studies on moth assemblages

Field-based studies, including both experimental and correlative analysis of observation data, are important for determining

whether behavioural and physiological changes due to artificial light at the individual-level (often demonstrated in laboratories) translate to population-level effects in the real world. Yet, field studies have generally provided mixed results on the effects of artificial light on moth assemblages.

An experimental study that installed LED street lights along the forest edge at seven sites in the Netherlands, found no effect on adult moth abundance after 1 year (Spoelstra *et al.*, 2015). A separate experiment as part of the same project found increased arboreal caterpillar biomass over several years in response to 7.6 lux from green and white LEDs, relative to red LEDs and dark controls (Welbers *et al.*, 2017), which the authors suggest resulted from adult moths being attracted to the lit areas. Conversely, in Hungary, caterpillar biomass was not correlated with varying levels of artificial light (predominately HPS lamps) across 36 urban trees (Péter *et al.*, 2020).

In a matched-pairs experiment, moth abundance at the ground level was found to be 0.5 times lower under HPS lamps, compared to unlit sites, while at the height of the light, flight activity was 1.7 higher at lit sites (Macgregor *et al.*, 2017). Lit sites also had significantly lower species richness than unlit sites. This provides evidence of a local disruption effect (Fig. 3), as opposed to concentration or trap effects, whereby moths would be drawn in from surrounding areas. In contrast, a before-after-control-impact study found that a change from LPS to HPS street lights led to increased species richness (Plummer *et al.*, 2016), which the authors attribute to moths being drawn in from surrounding areas. However, this study had limited temporal replication and was spatially pseudoreplicated.

In East Lansing (USA), macro-moth abundance and species richness were not predicted by levels of light pollution across 32 urban sites (White, 2018), though this could be explained by adaptation to ALAN by moths in urban areas. In the United Kingdom, there was no detectable difference in long-term trends of the abundance of macro-moths at sites that had witnessed an increase in light pollution, compared with sites that had remained dark (Conrad *et al.*, 2006). Furthermore, if light pollution were the main driver of moth declines, one would expect urban areas to be most affected; however, since the early 1980s, moth biomass in the United Kingdom has declined more steeply at woodland and grassland sites, compared to those in urban areas (Macgregor *et al.*, 2019b).

Two correlative studies have hinted at the importance of light pollution for explaining population trends in European macro-moths. In the Netherlands, diurnal moths show more positive trends than nocturnal moths, and moths that are classed as not attracted to light also tend to be faring better (van Langevelde *et al.*, 2018). Yet, the groups that showed a significant difference in trends contained only a small number of the 481 species tested (23 classed as diurnal, and 20 grouped as not attracted to light). Furthermore, diurnal moths could be faring better due to factors not related to light pollution (e.g. climatic changes) and determining the extent to which nocturnal moths are attracted to light is not straightforward. This was based on expert assessment in the study and not measured quantitatively. In Great Britain, the abundance ratio of certain species between gardens with low and medium levels of light pollution was correlated with national abundance trends (Wilson *et al.*, 2018). Species that are

relatively less abundant in gardens with higher levels of light pollution tended to have more strongly negative national trends. In the Czech Republic, it has been noted that many endangered Noctuidae are rare or absent from areas with higher light pollution (Tihelka, 2019). Whilst both studies made efforts to disentangle the effects of urbanisation from light pollution, it is not clear whether this was achieved successfully in either case. Isolating the effects of ALAN from its confounding factors must be a priority for researchers (Hopkins *et al.*, 2018)

Artificial light and pest moth populations

The purpose of this review is to document the unintentional impacts on moths from ALAN; however, it is interesting to note that in certain circumstances light has been intentionally used to suppress moth populations. The mechanisms and life stages involved are not always clear but may involve suppression of adult activity, or perhaps interference with specific behaviours linked to crop damage (e.g. oviposition). These control efforts have typically employed bright illumination. The impact of lower levels of ALAN (e.g. analogous to ecological light pollution) remains untested but might be expected to be small since direct artificial illumination of crops is not currently a common control strategy for insect pests.

Illuminating crops in fields and orchards has been reported as a method of controlling moth pests. In field experiments, illumination of cotton fields by incandescent lamps (producing 50 lux at crop height) reduced *Heliothis* oviposition by 85% (Nemec, 1969). Illuminating orchards can significantly reduce the damage made by fruit-piercing adult moths (Nomura, 1965; Whitehead & Rust, 1972; Bhumannavar & Viraktamath, 2013) and this can also limit larval damage by *C. pomonella* (Herms, 1929). Whilst such trials have often been effective at reducing crop damage, they have used high intensities of light and the associated energy expenditure typically outweigh any yield benefits (Herms, 1947). The desire to reduce pesticide use and the efficiency of LEDs may make constant illumination of crops a more viable option in the future (Shimoda, 2018).

Conversely, it has been suggested that outdoor lighting could increase pest outbreaks of *Grapholita molesta* (Busck; Tortricidae), as this species undertakes key reproductive behaviours between 3 and 500 lux (Li *et al.*, 2019).

Lethal light traps have been trailed as a method to directly control populations, with mixed success (Herms, 1947; Cantelo, 1974; Kim *et al.*, 2019). Unless a high density of traps is deployed over a large area, lethal light trapping might only be expected to have an appreciable impact on the populations of the least mobile species (Cantelo, 1974; Bowden, 1982; Vaisanen & Hublin, 1983).

Cascading effects and disruption of ecosystem function

The potential impacts of ALAN on moth assemblages and populations could cascade to other taxa with which moths closely interact. In moths, the ontogenetic niche change (Nakazawa,

2015), with herbivorous larvae (antagonistic) becoming pollinating adults (mutualistic), might have important consequences for predicting the indirect effects of ALAN on plant community dynamics. A third fundamental position occupied by moths within ecological networks is as prey for predators and parasitoids (see section on indirect effects above). Despite the significant potential for cascading effects from moths due to light pollution, few field studies have investigated these, with most focusing on pollination. The presence of HPS street lights in field margins is linked to lower rates of pollen transport in moths (Macgregor *et al.*, 2017). A field experiment using LED lamps found that lighting reduced nocturnal visits, with fewer species, and reduced pollination success, compared to dark controls (Knop *et al.*, 2017). This provides field-based evidence that moth feeding behaviour can be disrupted by lighting, which is in congruence with an earlier laboratory result (van Langevelde *et al.*, 2017). However, a similar field study found the opposite result: higher seed set under LED lighting (Macgregor *et al.*, 2019a), meaning that the impacts of ALAN on flower visitation by moths and the consequent cascading impacts on plant fitness may be context specific.

It has been suggested that larger moths may be more sensitive to light pollution, as they tend to be more strongly attracted to light, likely due to larger eye size (van Langevelde *et al.*, 2011) and also perhaps because they are more mobile (and therefore more likely to come into contact with lighting). This could lead to disproportionate impacts on ecosystem functioning if larger moths are particularly important, i.e. correlated effect and response traits (Larsen *et al.*, 2005).

Potential for adaptation in response to anthropogenic light

There has been highly consistent periodicity in light levels throughout evolutionary history, meaning there is significant potential for evolutionary change in response to anthropogenic light (Swaddle *et al.*, 2015). The short-term changes in pheromone composition and mating behaviour in moths due to artificial light (van Geffen *et al.*, 2015a, 2015b) raises the distinct possibility of divergent selection, and potentially speciation, in moths as a direct consequence of artificial light at night (Tierney *et al.*, 2017). If outdoor lighting acts as a dispersal barrier, this may cause effective population fragmentation, speeding up rates of evolution (Degen *et al.*, 2016).

The discovery that a species of micro-moth appears to have evolved reduced phototaxis in certain urban areas (Altermatt & Ebert, 2016) provides the first evidence that moths have adapted to anthropogenic light. In theory, this result could also mean trend data from light traps in urban areas are unreliable, as population sizes might become detached from light trap catches. Further work should be conducted to determine whether evolutionary adaptation to light has also occurred in moths from other geographical regions, and in other taxonomic families. The rapid shifts in lighting technologies (e.g. switch from narrow to broad-spectrum lamps) could mean that insects that have successfully adapted to one lighting type are not adapted to others.

Insects in the arctic do not experience large cycles in the intensity of light and daily activity is typically controlled by temperature (Downes, 1965; Danks, 2004). Species of moth that are nocturnal in Denmark are able to persist successfully in Greenland, where they appear to have acclimated to the radically different photic conditions (Dreisig, 1981). The process of acclimation and/or adaptation involved is not clear, nor is it known how rapidly insects can respond to altered photic regimes, but these findings do suggest that some moths that are nocturnal at lower latitudes can survive in the absence of dark nights. There is evidence that other Arctic fauna entrain their circadian rhythm using diel shifts in the spectral composition of light, instead of changing intensity (Krüll *et al.*, 1985; Nordtug & Mela, 1988).

Mitigation of the disruptive effects of outdoor lighting

Finding ways to mitigate the ecological impacts of ALAN is an interdisciplinary challenge. Outdoor lighting carries numerous societal benefits, such as preventing traffic collisions (Wanvik, 2009; Yannis *et al.*, 2013), reducing crime (Welsh & Farrington, 2008) and increasing perceived public safety, particularly for marginalised groups (Trench *et al.*, 1992; Painter, 1996). Conversely, concerns about the impacts of light pollution on astronomy (Riegel, 1973) and human health (Cho *et al.*, 2015) mean that reducing light pollution has the potential to deliver a win-win for both biodiversity and people.

A raft of mitigation measures has been advocated for outdoor lighting, many of which are relatively easy to implement, such as turning off or dimming lights for part of the night, and adding shielding to street lights to restrict the area illuminated (Gaston *et al.*, 2012; Davies & Smyth, 2018). It is generally thought that broader spectrum lighting (e.g. LEDs) has the potential for greater ecological impacts than narrow-spectrum lighting (e.g. LPS), as the wider range of wavelengths emitted can affect a greater range of taxa and biological processes (Davies *et al.*, 2013; Longcore *et al.*, 2018). The energy efficiency of LEDs means that it is unlikely that older lamp technologies will be retained, so adjusting the spectral composition of LEDs to reduce the intensity of the most biologically disruptive wavelengths, while still maintaining the benefits to people, could be a more feasible mitigation strategy (Gaston *et al.*, 2012). Whilst no difference has been detected in the number of moths attracted to LEDs of varying spectral profiles (Pawson & Bader, 2014; Supporting Information Fig. S2), longer wavelengths (red LEDs) have been shown to partially mitigate the negative impacts on key behaviours in moths to varying degrees (van Gefen *et al.*, 2014, 2015a,b).

Understanding which wavelengths of light moths are sensitive to may be crucial for designing successful mitigation strategies. The eyes of nocturnal moths typically have three maxima in their sensitivity; for instance, *Deilephila elpenor* (Linnaeus; Sphingidae), has photoreceptors with peak sensitivities in the ultraviolet (350 nm), violet (440 nm), and green (525 nm) regions (Schwemer & Paulsen, 1973; Schlecht, 1979). These visual sensitivities have been compared to spectral outputs to predict the ecological impacts of different street light technologies (Davies

et al., 2013; Longcore *et al.*, 2018; Seymoure *et al.*, 2019). Yet, adult moths also possess extraocular photoreceptors, including in the brain and reproductive organs (Page, 1982; Giebultowicz *et al.*, 1989). The perception of photoperiod appears to rely on extraocular receptors in some adult moths (Saunders, 2008). Transplant experiments have revealed that photoreceptors in the brain are responsible for diapause regulation in the larvae of a hawkmoth and silkmoth (Bowen *et al.*, 1984; Hasegawa & Shimizu, 1987), and it is thought that red wavelengths of light are most important for the regulation of diapause (Saunders, 2012). Thus, the disruption of certain biological processes (e.g. those related to circadian rhythm) by artificial light will not necessarily correspond to the visual sensitivity of moths and wavelengths of light that moths are visually insensitive to could still be harmful.

Elucidating the mechanisms by which lighting could disturb moth populations is also likely to be important for designing effective mitigation measures. For instance, if negative effects occur from moths incorrectly perceiving longer photoperiods in lit areas, then turning off the lamps part way through the night may be equally harmful, as the perceived photoperiod remains artificially extended. Conversely, if disrupted adult behaviour around lamps is a significant factor, then part-night lighting might be effective in enabling key behaviours to proceed for some of the night. This may be taxon-specific, as different species fly at different times of the night (Williams, 1939), with crepuscular groups (e.g. Hepialidae) potentially receiving little benefit, compared to species that fly later in the night.

Conclusions and future directions

We have detailed the multitude of mechanisms by which artificial lighting could impact moth populations and how it potentially acts on every stage of the life cycle (Fig. 2). However, we conclude from our detailed review that, as yet, there is limited evidence that light pollution is exerting negative effects at the population level. We believe that some studies have prematurely attributed insect declines to ALAN (e.g. Owens *et al.*, 2020), although we acknowledge that the lack of direct evidence could reflect the relatively small number of studies that have examined changes to moth assemblages or population trends in the context of ALAN (to date, 11 studies, as discussed above). This paucity of direct evidence could also reflect the challenges in detecting causal effects. We therefore advocate that the precautionary principle is invoked and emphasise the need for further research into this topic. Crucially, there is a need to consider the effects of light pollution in the context of other drivers of change, such as agricultural intensification and climate change (Fox, 2013); does light pollution represent a major threat, or is its contribution effectively negligible when placed in the context of other anthropogenic drivers?

Commonly, studies have taken the number of adult insects attracted to a light source as a proxy for its ecological impact (e.g. Pawson & Bader, 2014; Wakefield *et al.*, 2018; van Grunsven *et al.*, 2019). Results of our meta-analysis mean that historic trends in street lighting technology might be predicted to have benefitted moths. Mercury-vapour lighting elicits among the

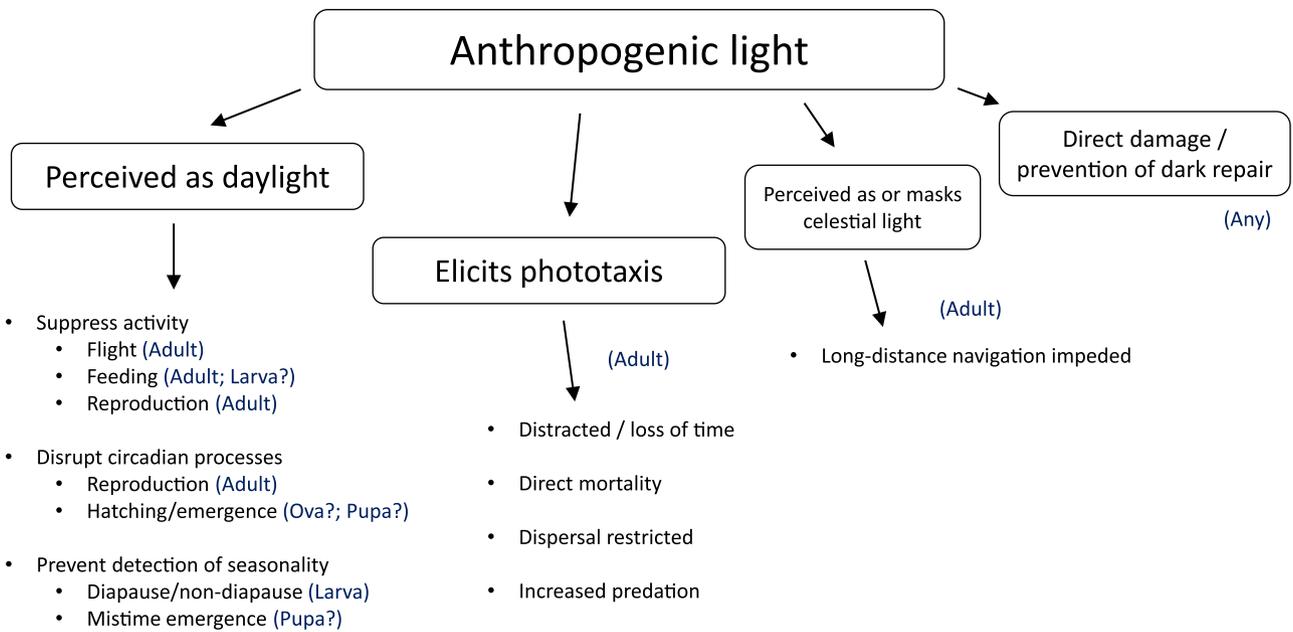


Fig. 4. Potential effects of artificial light on moths, grouped by the mode of mechanism. The life stages that could be affected are indicated. [Color figure can be viewed at wileyonlinelibrary.com]

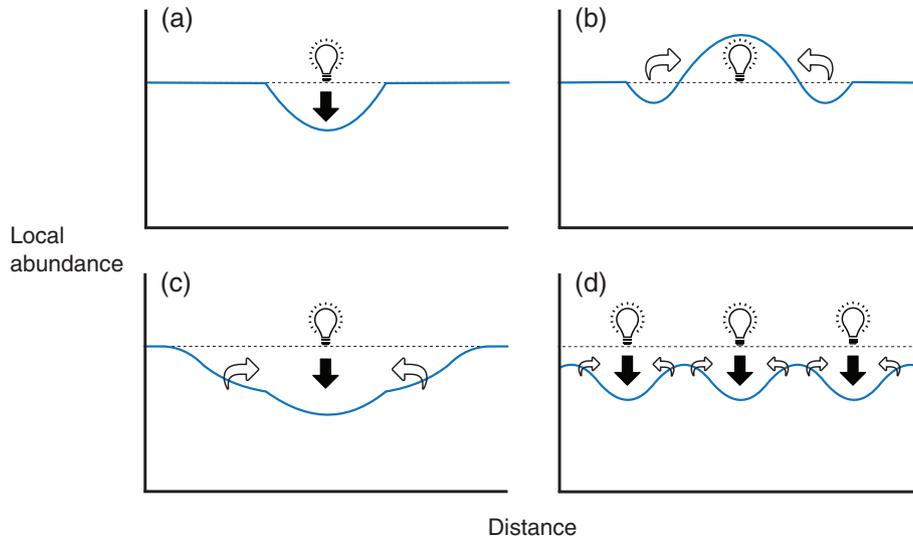


Fig. 5. Hypothesised relationships between local moth abundance and distance from a light source (bulb). Dotted horizontal line show moth abundance in the absence of light. The blue solid line is the hypothesised moth abundance. Filled downward arrows represent local depression of abundance due to light. Hollow sideways arrows show movement due to phototaxis. (a) Abundance suppressed locally due to light (negligible population-level effect). (b) Concentration effect, where abundance boosted around light due to moths being drawn in from surrounding areas, which are consequently slightly depleted (no population-level effect). (c) Strong local depression, combined with moths being drawn from surrounding areas (moderate population-level effect). (d) A large proportion of landscape directly lit, with concentration effects, causing overall population level to be suppressed (high population-level effect). [Color figure can be viewed at wileyonlinelibrary.com]

strongest phototactic response in moths and was commonly used in the United Kingdom during the middle of the 20th century, before being replaced by sodium street lights (McNeill, 1999). Moths are thought to be largely insensitive to low-pressure sodium lamps, so the switch to high-pressure sodium lamps possibly had

negative impacts, whilst the ongoing switch from high-pressure sodium to LED lighting is likely to have a minimal, or even positive, effect on moths (in terms of flight-to-light behaviour; Fig. 2). Yet, we are unconvinced that the attractiveness of a light source serves as a suitable proxy for ecological impact, given the many

Table 2. Outstanding research questions raised by this review.

| |
|---|
| Direct mechanisms |
| Over what scales are moths drawn in to (and affected by) lit areas? Do urban areas represent ecological traps for moths? |
| What are the rates of mortality of moths attracted to street lamps? |
| Do some moths exhibit negative phototaxis and actively avoid lit areas at night? |
| Are circadian processes (e.g. sperm release) routinely disrupted by intensities of light typically experienced by moths outdoors at night? |
| How does outdoor lighting affect oviposition? |
| Is the activity of nocturnal moth larvae suppressed by anthropogenic light? |
| Can very low levels of diffuse light pollution ('skyglow') exert negative effects on moths? |
| Indirect effects |
| Does light pollution affect rates of parasitism in moths? |
| Is bird predation, of adults or larvae, elevated in lit areas? |
| Is larval development in lit areas affected by biochemical changes that occur in foodplants? |
| Does artificial light engender phenological mismatch between plants and moths (either hostplants and larvae, or flowers and nectar-reliant adults)? |
| Population-level effects, evolutionary responses, and mitigation |
| Do behavioural effects and evidence of local disruption, scale up to population-level impacts? |
| What proportion of moth declines can be attributed to light pollution, relative to other drivers (e.g. climate change, agricultural intensification)? |
| Does artificial lighting interact with other drivers (e.g. warming due to climate change or urban heat effects)? |
| Are evolutionary changes in response to ALAN widespread across moth species? |
| Can policy interventions be effective in delivering win-wins by maintaining benefits to people while minimising disruptive impacts on insects? |

ways that anthropogenic light can affect moths (Figure 1) and caution against making policy recommendations from data that only examine one narrow impact on a single life stage.

It can be valuable to group the effects of ALAN within a mechanistic framework (Gaston *et al.*, 2013). For moths, the impacts of ALAN can be broadly categorised into four modes of action: light perceived as daylight, light eliciting phototaxis, light interfering with celestial cues, and light causing direct damage or preventing dark repair (Fig. 4). We consider that the first two modes of action as having the greatest potential for harm to moths.

It is important to consider the scale over which the mechanisms discussed above operate. The proportion of landscapes that are directly lit by anthropogenic lighting is typically relatively small. While diffuse skyglow covers a much greater area, there is currently no evidence that such low levels of artificial light affect moths. If direct illumination does exert strong negative local effects on moths, this could still be negligible at population-level (Fig. 5a), unless: (i) a high proportion of the landscape is directly lit (Fig. 5d); (ii) moths are drawn in from a wide radius, depleting surrounding populations (Fig. 5c; Fig. 3); and/or (iii) a species has limited dispersal.

Whilst moths were the focus of this review, we consider it likely that our findings and conclusions are broadly applicable

to most other groups of insects. Importantly, since the majority of the mechanisms discussed above do not involve adult phototaxis (Figs. 1 and 4), then there is the potential for diurnal insects (i.e. those active in the day in their adult stage, such as butterflies) to be negatively impacted by light pollution, for instance, through disruption of the circadian rhythm, or via a nocturnal larval stage.

Priorities for future research

Our review has revealed gaps in our understanding of how artificial light might affect moth populations (Table 2). Despite most moths only living as an adult for a small fraction of their lifespan, relatively few studies have investigated impacts on earlier life stages. Much of the work has been conducted on a small number of moth species (often of commercial importance).

Some of the laboratory studies discussed were not investigating light pollution, thus did not use conditions analogous to outdoor night lighting. For instance, continuous lighting in laboratory cultures typically remains unchanged over 24-hr periods. Yet, even the brightest artificial lighting will not completely mask the diel cycle in this way. As a result, there is a need for more experiments to use photic conditions that may be experienced under street lighting (e.g. van Geffen *et al.*, 2015a) to clarify whether the mechanisms involving an entrained circadian rhythm (e.g. sperm release) are affected by low levels of artificial light at night. Low levels of LED lighting can affect two processes controlled by photoperiod in *M. brassicae*: diapause in larvae and pheromone production in adults (van Geffen *et al.*, 2014, 2015b); therefore, bright light at night may not be necessary to disrupt processes dependent on circadian rhythm in moths.

The increasing extent and intensity of ALAN mean there is an urgent need for more well-replicated field studies to determine whether the disruptive effects demonstrated in behavioural studies (often with single species), scale up to real-world networks of interacting species under field-realistic levels of lighting. Ultimately, the relative contributions of individual anthropogenic factors, including light pollution, needs to be teased apart from the complex interplay of drivers that are likely to be implicated in the decline of European moths.

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Data availability statement

Data available in article supplementary material

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Methods used for network meta-analyses of flight-to-light responses to different light types.

Appendix S2: Studies located for the meta-analyses.

Appendix S3: Treatment estimates used in the meta-analyses.

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