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Like a moth to a flame: how artificial light at night attracts and influences moths, and possible ecosystem consequences

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Abstract

Light cycles play a vital role in the organization of the biological world. Increased and global use of artificial light sources at night may disturb these natural light cycles. Nocturnal animals likely suffer the most from artificial light at night. Moths are especially vulnerable because of their sensitivity to light. Moths play a crucial role as pollinator and prey. In this review, I examine how artificial light at night impacts moths and how this can affect other organisms. Moths are especially attracted to short wavelengths of light, with large moths and males showing the strongest attraction. This flight-to-light behaviour can cause direct mortality via, for example, burning. Due to increased selection pressure, urban moth populations already show decreased attraction to light. The exact mechanism for flight-to-light behaviour remain unknown. Moths show inhibited foraging behaviour under artificial light, subsequently reducing pollination and thereby affecting plants and diurnal pollinator communities. Anti-predator defences, including evasion and crypsis, are undermined by artificial light as well, increasing predation and thus mortality. Moreover, predator behaviours change with flight-to-light behaviour of moths, such as spiders building webs near lit sites. Reproduction is affected as well, with moths showing decreased pheromone sensitivity and fewer fertilizations. Moreover, development is influenced by low levels of light. Light decreases caterpillar mass and inhibits diapause. Light pollution appears to play a part in moth population declines. However, other factors like habitat fragmentation and pesticides also contribute and may interact with artificial light at night. Solutions include limiting illumination and removing short wavelengths from lamp radiation emission. It is necessary to further investigate the effects of artificial light on moths for conservation of both moths and indirectly affected species. Also, experimental evidence for cascading effects remains scarce. For successful conservation, further research on cascading effects and the mechanisms of flight-to-light behaviour is required.

Introduction

Light plays a key role in the organization of the biological world. The rotation of Earth divides time into a consistent cycle of day and night, while the tilted axis and the orbit around the sun cause seasonal variation. The monthly lunar cycle is the third periodic cycle in the light regime. Many plants use light for photosynthesis, directly or indirectly providing food to many trophic levels. Organisms use the cycle of light and darkness to partition activity between day and night. The biological clock, which controls biological rhythms, is entrained by this cycle as well. Vision and navigation are made possible by light, while darkness is thought to enhance critical processes in the repair and recovery of physiological processes (Owens & Lewis, 2018; Gaston, Bennie, Davies, & Hopkins, 2013).

Increasing urbanisation and population growth, as well as technological and economic development have led to a rapid and global increase in the use of artificial light sources at night. Light sources range from public street lights and traffic lights to massive billboards and domestic lighting, and often have a different spectral composition than natural light. Artificial light at night increases between 0% and 20% each year, depending on geographic location, averaging 6% (Gaston, Visser, & Hölker, 2015). The increased spatial, temporal and spectral distribution of artificial nocturnal light is known as light pollution (Gaston et al., 2013). Light pollution comes in two forms. The first form is direct light pollution, where a light source such as a street light directly illuminates the surrounding area. The second form is known as skyglow, which is caused by the scattering of light by the atmosphere. This affects large areas surrounding towns and cities, and its illumination can be of the same or greater magnitude as high-elevation summer moonlight (Gaston et al., 2013, 2015)

Especially nocturnal animals, making up 30% of vertebrates and 60% of invertebrates worldwide, must be affected substantially by light pollution (Owens & Lewis, 2018). The moth visual system is especially sensitive to light (Owens & Lewis, 2018). 71% of moth species showed a population decline in highly illuminated areas (Fox, 2013) and light pollution is thought to play a key role in this decline (Van Langevelde et al., 2018). Moths also have many interspecific interactions: they play the role of pollinator (Macgregor, Pocock, Fox, & Evans, 2015) and prey (Arlettaz, Godat, & Meyer, 2000). Therefore, I have chosen to focus this review on nocturnal and crepuscular moths. I do this by examining how artificial light at night impacts moths and how this can affect other species in the ecosystem.

Artificial light at night impacts a variety of mechanisms in moths, which can have cascading effects (See Figure 1, and Table 1 in Appendix A). Nocturnal and crepuscular moths are sensitive to light because of their to darkness adapted visual system (Owens & Lewis, 2018). Although the exact mechanisms remain unclear, this causes flight-to-light behaviour and direct mortality (Frank, Rich, & Longcore, 2006). Since moths are so sensitive to light, artificial light can disturb moths during their daily activities. Light pollution inhibits feeding and foraging behaviour (Van Langevelde, Van Grunsven, Veenendaal, & Fijen, 2017; Knop et al., 2017; Fenske, Nguyen, Horn, Riffell, & Imaizumi, 2018). Many moths feed on nectar and provide pollination services in return (Macgregor et al., 2015). Reduced feeding subsequently results in decreased pollination (Knop et al., 2017). Light interferes with anti-predator adaptations as well, increasing predation and thus mortality (Frank et al., 2006). In addition, light can interfere with mating (Van Geffen et al., 2015; Warrant, 2019) and development (Van Geffen, Van Grunsven, Van Ruijven, Berendse, & Veenendaal, 2014), reducing reproductive success.

Here I will provide an incomprehensive review of the literature on this subject to date. I will first describe vulnerability of moths to artificial light at night, then present two important ecological applications (pollination and predation), followed by the consequences of light pollution on reproduction and moth populations. In the first section, I will discuss insect vision as well as the mortality and proximate and ultimate causes of flight-to-light behaviour in moths. Here, I also review some experimental evidence of light attraction. In the next section, I will discuss the importance of moth pollination services, the reduced effectiveness of foraging under artificial light at night, and experimental evidence for cascading effects. In the third section, I review experimental evidence of how artificial light at night interferes with anti-predator adap-

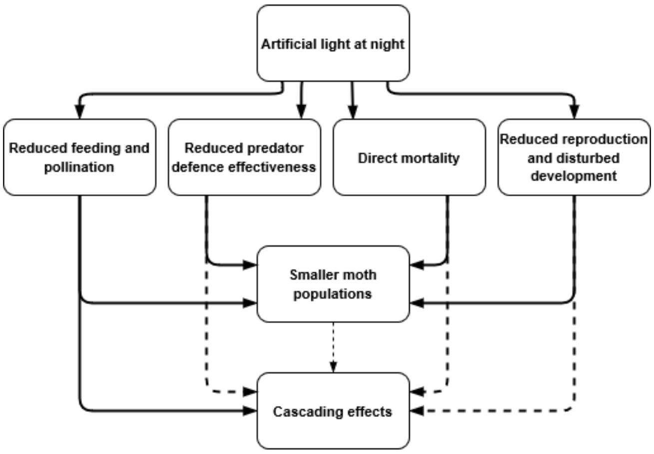

Figure 1: An overview of how artificial light at night affects moths, possibly leading to cascading effects. Dashed lines represent possible impacts, while solid lines represent impacts that are substantiated experimentally

tations and discuss some possible cascading effects. In the fourth section, I discuss how light can interfere with mating and development processes in moths. Then, I examine if and how artificial light at night affects moth populations, and the implications thereof. To conclude, I discuss the shortcomings of this review, speculate about the cascading effects, and I provide recommendations for future research.

Insect vision and flight-to-light behaviour

Many moths are attracted to light, a phenomenon known as positive phototaxis. When moths approach an artificial light source, they may start zigzagging towards it, circle around it, crash into it or ignore it completely. Many studies have investigated the effective range of street lights on the attraction of moths, and results ranged from 3 to 130 meters (Frank et al., 2006). Besides a reduction in mating and foraging and an increase in predation - which I will discuss later - moths suffer in a variety of ways when under artificial light at night. Moths tend to land in illuminated areas and remain inactive, sometimes even for the rest of the night. They can even stay for more than one day, which is quite significant considering most adult moths live a week at most. Also, moths become practically blinded by the light and it may take hours for their vision to return to normal (Owens & Lewis, 2018). However, light may also improve moth vision when staying far enough away from light sources (Frank et al., 2006). Moths completely dehydrate or burn when landing on heated lamp surfaces as well. In addition, they may lose body parts such as antennae when getting trapped inside lamp housings. When lamps are over water, moths may drown. Also, traffic lights lure moths towards oncoming vehicles (Frank et al., 2006; Frank, 1988). All these factors increase mortality greatly.

There are several theories which try to explain the seemingly suicidal behaviour. However, none of these theories fully explain the phenomenon. For example, the light-compass theory suggests that moths navigate by flying at a constant angle to a distant light source, like the moon (Altermatt, Baumeyer, & Ebert, 2009; Frank et al., 2006; Gandy, 2016). When moths approach a lamp, they mistake it for a distant light source and will fly towards it with a constant angle, resulting in the moth spiralling or circling towards the light. But light competes with other sensory information, including gravitational, geomagnetic and chemical cues (Frank et al., 2006). Another theory is the open space theory. This theory suggests that moths fly to open space, which is suitable for their activities. Open space is naturally brighter because of star or moonlight (Altermatt et al., 2009; Gandy, 2016). Yet, there is little resemblance between the diffuse light of the night's sky and the concentrated light from sources of artificial light (Gandy, 2016). A theory that fully explains the phenomenon remains to be seen.

Even though the ultimate cause remains somewhat of a mystery, the proximate cause is more well known. Ancestral insects are thought to have had three different photoreceptor opsins: one opsin sensitive to ultraviolet (UV) light (300-400nm), one to short wavelength light (400-480nm, blue) and one to long wavelength light (480-600nm, green-amber). Through evolution, nocturnal insects like moths lost one or more opsins for colour vision, but not for UV light, and subsequently lost spectral sensitivity. Besides the reduced capacity for colour vision, moths sacrificed spatial and temporal resolution by evolving special eyes, increasing overall visual sensitivity in low-light conditions by up to 1000x (Owens & Lewis, 2018). In short, moths are sensitive to short wavelengths and have increased sensitivity to light.

Therefore, one would expect both the overall light sensitivity of moths and the emitted wavelength of the light source to play a role in moth attraction to light. This is exactly what Van Langevelde et al. (2011) found. They tested whether artificial light with shorter wavelengths attracted a higher abundance of moths with a higher species richness. They also tested whether this was correlated to morphological characteristics of the moth. Eye size was of particular interest, since larger eyes have greater light sensitivity. They used six different lamps with varying spectral composition. They found that lamps that are dominated by shorter wavelengths attracted more moths with a greater species richness. A mean weighted wavelength of 382nm attracted the highest abundance and species richness, while a wavelength of 617nm attracted the fewest. They also found that larger species with larger eyes were attracted by the light in greater numbers (Van Langevelde, Ettema, Donners, WallisDeVries, & Groenendijk, 2011). This size-dependent attraction and subsequent mortality might have significant cascading effects. First, it is likely that smaller moth species are found in relatively greater abundance in lit areas, due to the selective pressure on larger moths. Second, it is likely that the possible change in size distribution of moth species will affect predators like particular birds and bats that rely on larger moth species to feed. Third, large moths are important pollinators, and the disappearance of these species may lead to a decline in density for certain plants (Van Langevelde et al., 2011).

Besides size-biased attraction, there is also experimental evidence for male-biased flight-to-light behaviour. A common observation during many field studies is the higher proportion of males caught in light traps. Altermatt et al. (2009) experimentally studied the flight-to-light behaviour of two moth species. They found that *Yponomeuta cagnagella* males were 1.6x more frequently attracted to light than females, which is a significant difference. Young and old *Ligdia adustata* males were 1.4 and 1.7x more frequently attracted to the light, respectively. This may suggest that young moths have a higher chance to reproduce, but the sample size for this species was rather small, so care should be taken when interpreting this result (Altermatt et al., 2009). A possible explanation for this sexual dimorphism may be the general behaviour of male moths. Males show greater flight activity in the search of potential mates whilst females are less active and lure males. The higher mobility of males increases the likelihood of encountering light sources where they may get "trapped". Male-biased attraction might therefore affect gene flow, resulting in a loss of genetic diversity. Populations living in highly lit areas may even become genetically isolated. A different, but not mutually exclusive, hypothesis would be that male moths simply have larger and more sensitive eyes. As explained previously, larger eyes cause greater attraction to light. Since moths attracted by light suffer higher mortality than moths that are not attracted to light, sex-biased attraction to light results in increased mortality for one sex. This alters population structure and reduces effective population size. Sex-biased attraction is especially harmful when combined with sex-biased predation or sex ratio distorting parasitism (Altermatt et al., 2009).

One experiment did not show increased attraction of moths to different colours of light compared to a dark control. Spoelstra et al. (2015) set up rows of lampposts on a forest edge for two years. Each row was assigned a different light colour: red, green, white or dark. Even though species composition varied greatly for each site, the total number of moths did not vary with treatment. Spoelstra et al. (2015) hypothesise that there might be an effect on individual moths, but the effect on a species level is small, and may only emerge after several more years (Spoelstra et al., 2015).

Due to the increased mortality near artificial light, it should come to no surprise that the positive phototaxis trait is under selection. Altermatt and Ebert (2016) report experimental quantification of reduced attraction to light of small ermine moths (*Yponomeuta cagnagella*) in urban populations with high levels of light pollution compared to low levels of light pollution populations. Overall, the moths were 30% less attracted to light in high light pollution conditions (Figure 2). Males showed a stronger response, with a 36% reduction compared to 28% for females. This may reduce mortality and other negative consequences caused by light pollution (Altermatt & Ebert, 2016).

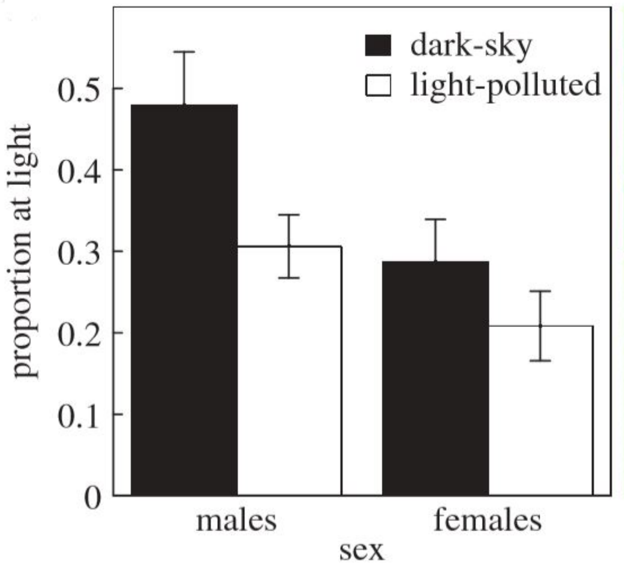

Figure 2: Bar plot illustrating the mean proportion of small ermine moths (*Yponomeuta cagnagella*) attracted to light under experimental conditions for light-polluted (white bars) and dark-sky (black bars) populations (Altermatt & Ebert, 2016).

Foraging and pollination

Nocturnal moths play a vital role as pollinators. In fact, moths are considered to be the second most important plant pollinators, next to bees (Macgregor et al., 2015). Macgregor et al. (2015) reviewed the role of moths on pollination. They found that plants from 75 different families were either partially or exclusively pollinated by moths. Moths visit flowers because of the energy-rich nectar, which they use as a food source. Plants, in turn, benefit from the pollination service provided by moths. Compared to diurnal pollinators, moth pollination provides increased interpopulation gene flow, longer-distance dispersal of pollen, higher quality pollination and more efficient pollination (Macgregor et al., 2015).

Since moths are attracted to light at night, one might expect that this disturbs their foraging behaviour. This is indeed the case. In an experiment by Van Langevelde et al. (2017), feeding behaviour for four moth species known to be attracted by light was observed under different light conditions. They found that green, white and red light reduced feeding on average by 82%, 72% and 63% respectively, compared to the dark control. They also found that large species were more disturbed than smaller species (Van Langevelde et al., 2017). This is in accordance with his previous research, in which moths were more attracted to low wavelengths of light and that larger species were affected more strongly (Van Langevelde et al., 2011). In contrast to the findings of Altermatt et al. (2009), both males and females were equally affected. Starving females produce less pheromones, lay fewer eggs and have a shorter lifespan, which all reduce reproductive success. Reduced feeding in males may decrease flight distance, possibly reducing gene exchange rates (Van Langevelde et al., 2017).

A possible explanation for the reduced foraging behaviour could be the biological clock. To attract specific pollinators, temporal control and oscillation of the flower's advertising traits (like smell) is of vital importance. Moths also have temporal restrictions on their activities, such as activity patterns and olfaction. However, detailed time recordings of moth pollination behaviour are rare. When the moth's biological clock is not aligned correctly with the time of day, they may experience a reduced effectiveness in foraging. (Fenske et al., 2018). Moths entrained to a light/dark cycle synchronized with a flowering plant's visited 63% of flowers within ten minutes, compared to only 10% for moths entrained to a reversed light/dark cycle. Even though the visitation decreased with time (Figure 3), these results suggest that moths may not be able to respond effectively to scent emitting flowers if their biological time is mismatched (Fenske et al., 2018).

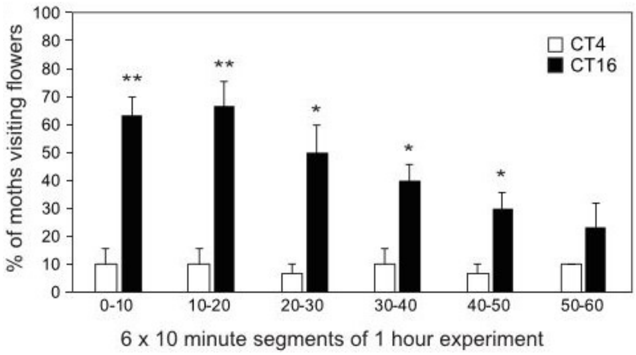

Figure 3: Percentage of moths showing foraging behaviour on flowers in different segments of the experiment. Moths were entrained to a light/dark cycle synchronised (black bars, CT16) or asynchronised (white bars, CT4) with the flowering plant (Fenske et al., 2018).

Many pollinator networks have complex interactions, so reduced insect feeding and consequently reduced pollination might have detrimental effects on ecosystem functioning (Macgregor et al., 2015; Knop et al., 2017). Indeed, experimental evidence reveals the negative effects of artificial light at night on moths result in a loss in reproductive success in plants, which can cascade to the diurnal pollinator community (Figure 4). Knop et al. (2017) analysed the interactions between plants and nocturnal pollinators in seven newly artificially lit meadows, while leaving another seven as control. They found a 62% decrease in the amount of flower visits in illuminated sites, and a 29% decrease in species richness. They also found that the amount of fruits on a model plant (which was visited the most by both diurnal and nocturnal species) decreased significantly in the illuminated areas. Because biomass was the same in both lit and dark areas, this is unlikely to be caused by the light itself. Reproductive output of the plant was reduced, and this could not be compensated by diurnal pollinators. This already happened for relatively low levels of light. Since this plant is an important food source for diurnal pollinators, the reduced plant fitness is likely to impact this group as well. This way, plants form indirect connections between diurnal and nocturnal pollinators (Knop et al., 2017). So artificial light negatively influences moth foraging, and indirectly impacts plants and diurnal pollinator communities.

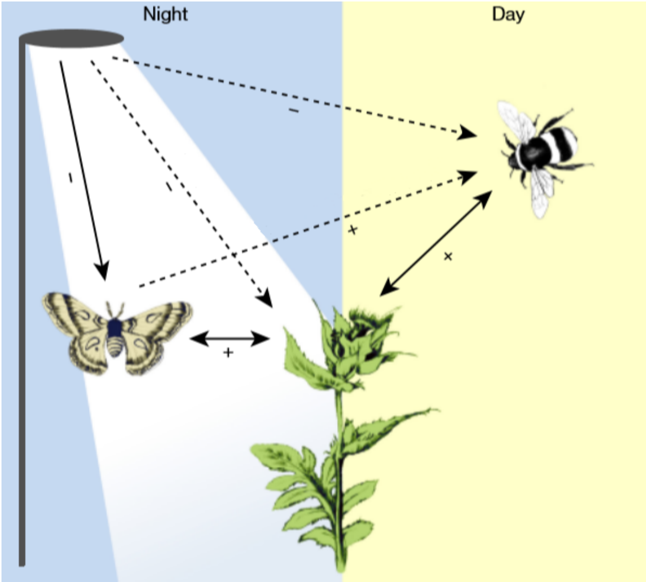

Figure 4: Interaction web showing how artificial light at night affects moths and can have cascading effects on diurnal pollinator communities. Dashed arrows indicate indirect effects, while solid arrows indicate direct effects. Signs (+ or -) refer to positive and negative effects respectively (Knop et al., 2017).

Anti-predator adaptations and predation

Due to their flight-to-light behaviour, moths become concentrated near streetlamps and other light sources, making them easy for predators to exploit. To counteract predation, moths can perform defensive manoeuvres, such as diving or changing directions. However, it has also become apparent that light interferes with moth's defence mechanisms. In an experiment, Svensson and Rydell (1998) show that light decreased the moth's evasive behaviours when exposed to electronic ultrasound (representing bat echolocation). In the dark control, 100% of moths reacted to the sound. However, when moths got closer to a mercury vapor lamp, this number decreased to 57% (Svensson & Rydell, 1998). Moths are virtually never exposed to bat echolocation sounds during daylight, while they are exposed to other ultrasounds like those from cicadas and grasshoppers. So when we assume that defensive manoeuvres come at a cost, this behavioural response to light makes sense. When moths reacted, the evasive behaviour did not differ between the two groups, suggesting there was no qualitative difference in the way moths evaded (Svensson & Rydell, 1998).

However, Wakefield, Stone, Jones, and Harris (2015) did find a qualitative difference in evasive manoeuvres, alongside the already established quantitative difference (Figure 5. Instead of mercury vapor lamps, they used street light LEDs. They found a significant decrease in the number of moth powerdives (a straight dive or spiralling flight towards the ground) but not direction changes under lit conditions when exposed to electronic ultrasound. Whilst 60% of moths performed powerdives during the dark ultrasound treatment, only 24% showed this response during LED ultrasound treatment (Wakefield et al., 2015). But qualitative difference or not, fact remains that due to their impaired acoustic responsiveness, moths near lamps become easy prey for bats.

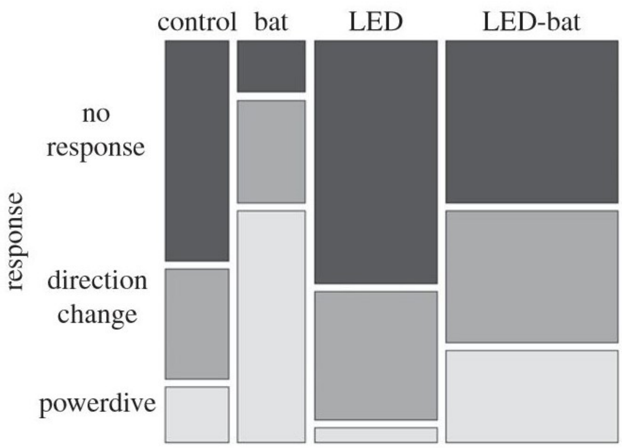

Figure 5: Mosaic plot illustrating the overall proportion of moth flight responses in relation to treatment type. Column widths are proportional to sample sizes (Altermatt & Ebert, 2016).

Even so, not all bats can profit from the easily exploitable food. Especially fast and straight flying bats that use long range echolocation are likely to feed under lamps, while more slow flying and manoeuvrable species that use short-range echolocation do not hunt around lamps. Bats from certain genera seem less affected by insect declines than others, implying that artificial light at night might have contributed to their success (Rydell, 1992). An example of this would be the common pipistrelle bat (*Pipistrellus pippistrellus*), which appears to outcompete the lesser horseshoe bat (*Rhinolophus hipposideros*). The diet of these species overlaps up to 81% during some months, with Lepidoptera forming an important part of their diet. Pipistrelle bats hunt under street lights, while the lesser horseshoe bat does not due to echolocation constraints. The attraction of prey to illuminated areas may deplete food in the surrounding area in which the lesser horseshoe bat hunts. This, in combination with the overlap in diet, results in interspecific competition and the subsequent decline of the lesser horseshoe bat (Arlettaz et al., 2000). Bats play important roles as predators, prey, parasite hosts, pollinators, seed dispersers and nutrient distributors. For example, bat species roosting in caves provide cave ecosystems with primary organic input. Cave flora and fauna, including cave-dwelling salamanders, fish and invertebrate communities, are highly dependent on bat guano (Kasso & Balakrishnan, 2013). So, the disappearance of bat species due to interspecific competition, partly due to artificial light at night effects on moths, might have far stretching ecosystem consequences. Yet again, the behavioural changes of moths due to artificial light at night have cascading effects.

But artificial light at night also interferes with other aspects of anti-predator mechanisms, such as crypsis. One form of crypsis is camouflage. Many moths are camouflaged, but this only works with a suitable background. Light interferes with moth behaviour that would normally match them to a suitable background. A dark moth resting on a white wall under a street light illustrates the problem. The large concentrations of moths around light also gives birds more experience in recognising camouflage patterns, enabling them to detect the moths outside of illuminated settings (Frank et al., 2006). One might argue that this helps birds in recognising unpalatable species, reducing predation. However, those moths are likely to be palatable for another species (Frank, 1988).

But other defence mechanisms, such as surprise, are also undermined by artificial light at night. For example, underwing moths (*Catocala*; Noctuidae) have camouflaged wings resembling tree bark, with bright orange or red hindwings. When resting on a tree, the hindwings are fully concealed, but when touched, the moth raises its forewings, exposing the bright underwings. This startles birds, giving the moth enough time to escape. However, under experimental conditions, this response in birds quickly diminished after repeated exposure. The visible aggregation of moths under artificial light likely decreases the startle response, further weakening moth anti-predator defence (Frank et al., 2006).

Bats and birds are not alone in adapting their behaviour in response to moth light attraction. Other predators include rats, reptiles and amphibians such as geckos or cane toads, and spiders (Owens et al., 2020). Reptiles and amphibians, some of which are classified as diurnal, hunt on the ground under street lights at night. They exploit several effects of artificial lighting: flight suppression, prey illumination, higher prey concentration and the diversion of prey on surfaces such as walls, which support these predators (Frank, 1988; Frank et al., 2006).

In an experiment by Heiling (1999), nocturnal orb-web spiders (*Larinioides sclopetarius*) chose artificially lit sites to construct their webs. The site for building a web is an important decision for spiders to make, because of the considerable cost of web construction and increased risk of predation during relocation. There is evidence that spiders build their webs on high quality foraging patches and move from areas with low prey density to areas with high prey density. Other factors such as age and predation affect web site choice as well. In lit areas, insect density was significantly higher compared to unlit areas, and the number of prey (mostly flies) captured per hour increased as a result. Spiders collected in the wild and laboratory-reared spiders accustomed to light actively chose artificially lit web sites 90% and 94% (Figure 6 of the time respectively, suggesting that this behaviour is genetically determined (Heiling, 1999). Even though this species feeds mostly on flies, it is likely that other spiders with a different diet show similar behaviour, resulting in an increased predation rate for moths as well.

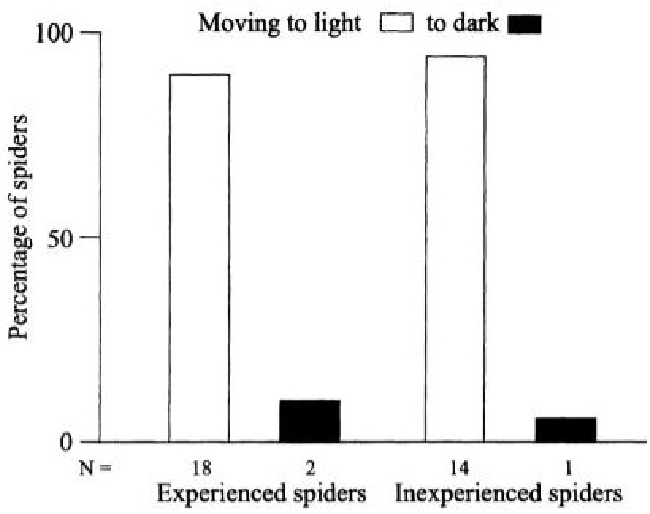

Figure 6: Bar plot showing the percentage of light-experienced (n = 20) and light-inexperienced (n = 15) adult female spiders choosing lit (white bars) or unlit sites (black bars) (Heiling, 1999).

Reproduction and development

A study by Van Geffen et al. (2015) showed that moths also suffer from a reduction in reproductive success when near artificial light. They used the winter moth (Opherophtera brumata). Female winter moths are unable to fly, but climb up the trunk of their host tree to mate. They attract males with pheromones. For this experiment, red, green, and white LEDs were placed in the proximity of trees, illuminating one side of the tree and shading the other. Since winter moths become more active during low light levels, Van Geffen et al. hypothesised that artificial light reduces activity and thus reduced female trunk ascension. Previous laboratory experiments also indicated that light inhibits sex pheromone release for females, as well as sex pheromone sensitivity for males, so artificial light might decrease male attraction as well. Another hypothesis was that shorter wavelength light sources would have a stronger effect, because of moth's previously mentioned sensitivity to UV light. And that is exactly what was found. Most female moths were captured in the dark control and on the shaded side of the tree under red light conditions. The number of captures decreased significantly with shorter wavelengths. The shaded side consistently had more moth trappings than the lit side, except for the dark control (Figure 7). In the dark control, 53% of females had mated, while only 13%, 16% and 28% had mated in the green, white and red light conditions respectively. The number of males attracted to pheromone traps was also significantly lower under light. Here, however, males were caught more often under green light than under white and red light, possibly due to the shorter wavelength of green light (Van Geffen et al., 2015). Since the light intensity in these experiments was lower than most street lights, the effects may be even stronger in many cases. Since light also had an effect on the shaded side of the trunk, the effective range of light extends to at least a few meters around the light source. Since males and females are both negatively affected, light at night has a negative synergistic effect on reproductive success in winter moths. Winter moth larvae form a vital bulk-food source for forest breeding birds in Northern Europe. A reduction in larvae numbers is also likely to result in a decrease in herbivory. So, reduced reproductive success for only one species of moth can impact a variety other species on higher and lower trophic levels (Van Geffen et al., 2015).

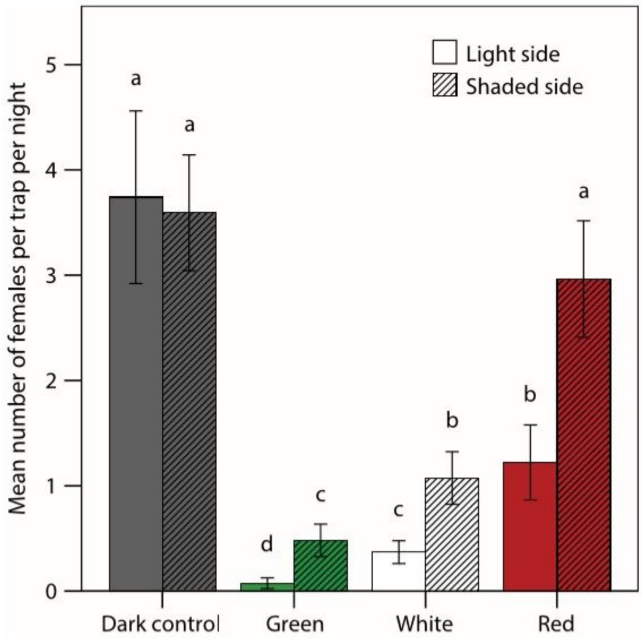

Figure 7: Bar plots showing the mean number of female winter moths (*Opherophtera brumata*) per trap on the light (open bars) and shaded (dark bars) side of a tree under different light conditions (Van Geffen et al., 2015).

Light may also interfere with courtship in moths with sexual dimorphism. Although rare, sexual dimorphic wing colouration is seen in nocturnal animals like moths. The recent discovery of a substantial difference between male and female wing colouration in the dot-underwing moth (*Eu-*

docima maternal) suggests that this plays a role in visual courtship behaviour at night. The differing patterns can be seen best when the wings are rotated about 20-30 degrees (Figure 8). Whether wing colouration is actually used during courtship by moths remains an open question, but it is highly probable due to their excellent night vision (Warrant, 2019). However, due to the negative effects of light on moths, such as functional blindness (Frank et al., 2006), it is also not hard to imagine that artificial light at night may interfere with courtship and subsequent mating in this species.

Figure 8: Optical signals in the Dot-underwing moth *Eudocima materna*. Male (A) wings (C, D) and female (B) wings (E, F) when horizontal (C, E), or rotated 23 degrees (D, F) (Warrant, 2019).

Besides impacting reproduction itself, artificial light at night can also impact the development of moth larvae. Unfavourable conditions during the larval stage can result in reduced growth rate, lower pupal mass and advanced pupation. This, as a result, can impact mate preference, longevity, flight ability, and female egg production. Because day length is often used by nocturnal caterpillars as the main cue for the decision to initiate pupal diapause, artificial light might impact the accuracy of this cue and subsequently affect the larval stage of moths (Van Geffen et al., 2014). Van Geffen et al. (2014) tested these hypotheses. They used cabbage moth (*Mamestra brassicae*) larvae and subjected them to relatively low intensities of red, green, and white light. Cabbage moths larvae overwinter as pupae so they can emerge in spring. They found that male caterpillars had a significantly lower mass under white light, compared to red light and the dark control. Green light had an intermediate effect. Males also pupated earlier under white and green light compared to the dark control, and pupal mass was lower under white light. Moths under green and white light emerged significantly earlier, by up to approximately 70 days, compared to the dark control, with red light having an intermediate effect. When the first moth from the dark control emerged, 85% from the green light, 83% from the white light and 25% from the red light condition had already emerged. Early emergence may cause moths to emerge in winter instead of spring, which they are unlikely to survive. Even though reduced development time may decrease the risk of death before reproduction, the reduction in mass can negatively impact longevity, sperm competition and flight ability for males. Females may suffer from strongly decreased egg production. So, disturbed development may lead to mortality and decreased future reproductive success (Van Geffen et al., 2014).

Population extinction and solutions

Depending on the theoretical framework, artificial light at night could be considered an ecological trap. An ecological trap is defined as "low in quality for reproduction and survival [that] cannot sustain a population, yet...is preferred over other available, high-quality habitats" (Battin, 2004). Ecological traps can lead to rapid extinction, depending on initial population size (Battin, 2004). The previously discussed open-space theory suggests that moths fly towards light because it signifies open space, which would be suitable for their activities (Altermatt et al., 2009; Gandy, 2016). This theory would suggest that illuminated areas are indeed perceived as high-quality habitats. However, when considering other theories, like the light-compass theory (Altermatt et al., 2009; Frank et al., 2006; Gandy, 2016), attraction to light may simply result from sensual confusion. Either way, the results are the same: moths suffer increased mortality from flying into light sources, caused by burning or exhaustion, or drowning when the light is near water; starvation or dehydration because of reduced foraging behaviour and a mismatched circadian rhythm; increased predation due to undermined crypsis and reduced evasive behaviours; and reduced reproductive success and changed development due to a variety of effects. And yet, moths keep flying towards it.

The increased mortality and loss in reproduction due to light pollution are responsible for declining moth populations. In the Netherlands, 71% of moths showed a negative population trend and one third of total moth abundance was lost between 1980 and 2009. Similar patterns were found for other countries like Great Britain (Fox, 2013). Van Langevelde et al. (2018) showed that ecological traits related to light explained the most variation in the decline of moth populations in a PCA, suggesting that light pollution plays a major role in moth decline. Species that were nocturnal or were more attracted to light showed the strongest response (Van Langevelde et al., 2018). Large moths are therefore extra vulnerable (Van Langevelde et al., 2011) and thus show the strongest declines (Fox, 2013).

The disappearance of moths might again have cascading effects on the ecosystem. A reduction in prey availability might cause more interspecific competition for certain insectivorous predators (Rydell, 1992; Arlettaz et al., 2000). The disappearance of a predator might cause an extinction cascade as it decreases top-down control, giving some prey a competitive advantage over others. In turn, this causes bottom-up control, where outcompeted prey affects specialist predators, resulting in more predator extinction (Sanders, Kehoe, & Van Veen, 2015). Moths also play crucial roles as pollinators. When moth populations become smaller, they pollinate less. Like mentioned previously, reduced pollination by moths affects plants and diurnal pollinator communities as well (Knop et al., 2017). Moreover, smaller populations likely produce fewer offspring. Fewer caterpillars result in fewer prey for breeding birds and could reduce herbivory (Van Geffen et al., 2015). So, not only does altered moth behaviour affect the ecosystem, their subsequent population decline may have many of the same effects as well.

Since the effects of positive phototaxis on moths are so detrimental, and the cascading effects widespread, it is of the utmost importance to find a quick and efficient solution. The most effective method of protecting moths from artificial light at night, is to just simply turn lights off. Owners of large illuminated structures like billboards, can save both moths and money by limiting illumination during hours in which people are least likely to pass (Frank et al., 2006). Removing light sources from structures in which moths can easily get stuck should prevent them from getting trapped. Dark patches along busy roads or other highly illuminated stretches of land may prevent populations from becoming isolated from each other. Vulnerable or rural regions could even remove street lighting altogether to provide moths with a light-free sanctuary. In addition to limiting the amount of light and the duration of use, using lamps with longer wavelengths will help in attracting fewer moths (see Figure 9 for an overview of spectral emissions of different lamp types). For instance, low-pressure sodium lamps emit light in the visible spectrum almost exclusively. However, this is presumably an expensive operation, both in terms of money and ecological footprint. Alternatively, equipping lamps with a UV filter which blocks short wavelength light may help in reducing moth attraction. Lamps should be equipped with reflectors so that they only illuminate the required areas, and fixtures should be tightly sealed to prevent moths from getting trapped. If all these options are not viable, placing lights within close proximity of each other might help in reducing moth attraction, since moths show an inverse relationship of lamp density and positive phototaxis, caused by interference with pathfinding (Frank et al., 2006). However, increasing the total number of lights is ill-advised, because of the possible increase in skyglow; low levels of light can already affect moths (Van Geffen et al., 2015). When adequate measures are taken, we might yet again see an increase in moth populations.

Discussion and conclusion

In summary, moths show positive phototaxis, directly or indirectly increasing their mortality and reducing their reproductive success, with subsequent cascading effects. Artificial light at night increases mortality due to direct attraction to light, increased predation and reduced feeding. It inhibits successful mating and development as well. It is arguable whether illuminated areas can be considered ecological traps, but results stay the same: a reduction in moth abundance and species richness. Behavioural and numerical changes could have cascading effects on a variety of trophic levels, including plants, predators and pollinators.

However, the scope of this review is limited, and many other factors play an important role as well. For example, artificial light at night can affect gene expression as well endocrine hormone production. This could lead to alterations in the biological clock, resulting in temporal changes in behaviour. In turn, this may cause, for example, niche overlap (Owens & Lewis, 2018; Owens et al., 2020). Parasitism was also not discussed, while artificial light does impact parasite-host interactions (Owens & Lewis, 2018). Other factors like pesticides, habitat fragmentation, invasive species and climate change all affect moths and other insects as well and might interact with artificial light at night (Fox, 2013). For example, effects of artificial light at night are known to interact with temperature changes (Miller et al., 2017). Thus, artificial light at night may have even greater or perhaps lesser impacts.

Cascading effects may be even more widespread than discussed in this review. Reduced pollination and seed dispersal services are likely to greatly impact plant communities, which form the basic building blocks of ecosystems. Plant density or biomass may decrease, and species exclusively pollinated by moths may become (locally) extinct. A reduction in leaves, stems, branches, and roots will reduce shelter and nesting opportunities. This will affect a broad range of species and may lead to further biodiversity declines. The fact that diurnal pollinator communities are impacted by the reduced pollination by moths (Knop et al., 2017) likely only aggravates these effects. Extinction of predators may disturb the delicate ecosystem balance and could cause explosive growth or decline in some species. However, all this remains speculative. Although studies on single species are very useful, implications for ecosystem structure and functioning should be interpreted carefully since species interactions and networks play an important role here. Experimental evidence of cascading effects and community-wide impacts (Knop et al., 2017) remains scarce.

It is important to note that the discussed experiments used different methods. Researchers used different moth species, which came from different parts of the world with presumably differing degrees of light pollution, which could result in differences in moth light attraction (Altermatt & Ebert, 2016). Some experiments were conducted in laboratory conditions, while others were done in the field. Also, a variety of different lamp types were used, including LEDs, mercury vapor lamps and fluorescent lights (See Table 1 in Appendix A for an overview of lamp types used). To further complicate matters, old- fashioned light bulbs often produce large amounts of heat, while some LEDs may emit ultrasonic frequencies, which could influence results (Owens et al., 2020). While using a variety of Lepidoptera, lights and locations in experiments may reveal the scope of the problem, it also com-

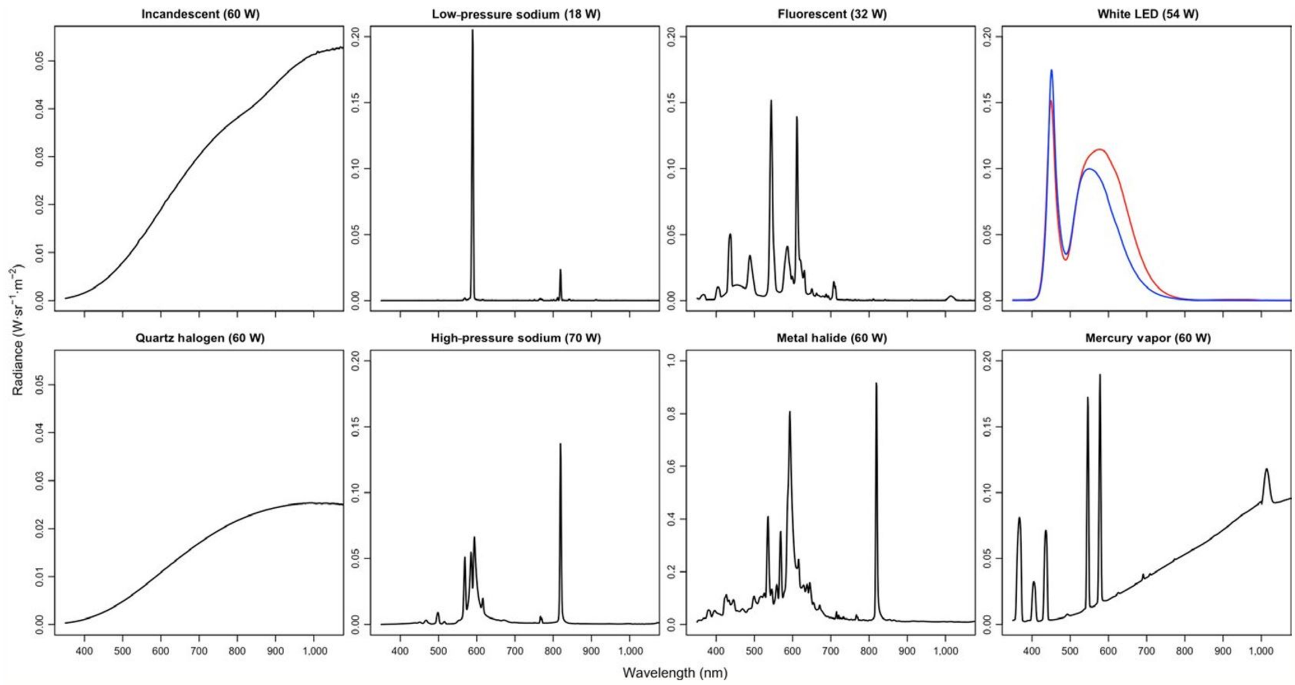

Figure 9: Spectral emission of different lamp types. Light sources such as mercury vapor lamps emit large amounts of UV radiation, while lamps such as low-pressure sodium lamps emit next to nothing. Neutral (red) and cool (blue) temperature white LEDs are plotted in the same graph (Owens & Lewis, 2018).

plicates generalizing results and mechanisms. For future research on moth populations and flight-to-light behaviour, I would advise against exclusively using light traps, as larger species are more sensitive (Van Langevelde et al., 2011) and urban populations may be less sensitive (Altermatt & Ebert, 2016).

The crucial roles of moths as prey or pollinator, their dramatic reduction in abundance and species richness (Fox, 2013; Van Langevelde et al., 2018), and cascading effects stress the importance in coming up with fast and efficient solutions. However, we still do not fully understand why moths are attracted to light (Frank et al., 2006) and finding a theory that explains their flight-to-light behaviour would help in taking the appropriate steps for further conservation efforts. Perhaps, a standardized method for testing the effects of artificial light at night on moths could be designed. Also, the effects of skyglow appear to be relatively understudied, so further research could provide valuable insights. Furthermore, research on species interactions and networks may provide experimental evidence on cascading effects and possible extinctions, revealing the true extent of the problem. In conclusion, I think it is about time we shed some more light on the matter, so moths may again have a (not so) bright future ahead of them.

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Appendix A

Table 1: A summary of experimental evidence for effects of artificial light at night on moths. Flight-to-light refers to the attraction of moths to light sources. Foraging refers to general feeding behaviour and pollination. Predator evasion refers to defensive manoeuvres made by moths to prevent capture by a predator. Reproduction refers to elements related to mating, such as mate attraction and successful copulation. Development refers to all elements before and during pupation. For information on spectral emissions for lamp types, see Figure 9.

Behaviour	Response	Lamp type	Species	Latin name	Citation
Flight-to-light	A greater abundance and diversity of on average larger moths is attracted to lamps with shorter wavelengths	Fluorescent	112 species	Species from Geometridae, Noctuidae and Pyralidae	Van Langevelde et al. (2011)
Flight-to-light	Male moths are more frequently attracted to light than female moths	Fluorescent	Small ermine moth, scorched carpet moth	*Yponomeuta cagnagella, Ligdia adustata*	Altermatt et al. (2009)
Flight-to-light	Moths from urban populations show a significant reduction in flight-to-light behaviour	Fluorescent	Small ermine moth	*Yponomeuta cagnagella*	Altermatt and Ebert (2016)
Flight-to-light	Moths show no measurable light attraction	LED	354 species	Species from Erebidae, Geometridae, Noctuidae, Notodontidae and Sphingidae	Spoelstra et al. (2015)
Foraging	Moths spend less time feeding when under lamps with short wavelengths compared to moths in darkness	LED	Cabbage moth, straw dot, small fan-footed wave, common marbled carpet	*Mamestra brassicae, Rivula sericealis, Idaea biselata, Dysstroma truncata*	Van Langevelde et al. (2017)
Foraging	Nocturnal pollinators pollinate less under artificial light at night, with cascading effects on plants and diurnal pollinators	LED	No information	No information	Knop et al. (2017)
Foraging	Moth circadian rhythms are mismatched under artificial light at night, inhibiting foraging behaviour	Fluorescent	Tobacco hornworm	*Manduca sexta*	Fenske et al. (2018)
Predator evasion	Moths under artificial light show a quantitative decrease in evasive manoeuvres compared to moths in darkness	Mercury vapor	Winter moth, northern winter moth	*Operophtera brumata (L.), Operophtera fagata*	Svensson and Rydell (1998)
Predator evasion	Moths under artificial light show a quantitative decrease and qualitative change in evasive manoeuvres compared to moths in darkness	LED	Not identified	Species from Geometridae, Noctuidae or Notodontidae	Wakefield et al. (2015)
Reproduction	Females under artificial light show decreased activity and males show decreased pheromone sensitivity compared to moths in darkness, resulting in inhibited mating	LED	Winter moth	*Operophtera brumata (L.)*	Van Geffen et al. (2015)
Development	Moths under under low levels of green or white artificial light emerge earlier and males have a lower mass and pupate earlier compared to moths in red light or darkness, increasing mortality	LED	Cabbage moth	*Mamestra brassicae*	Van Geffen et al. (2014)