

A REVIEW INFLUENCE OF LIGHT ON INSECT ACTIVITY AND BEHAVIOUR: SUSTAINABLE LIGHTING AND LIGHT POLLUTION

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Abstract: This paper reviews the influence of artificial light at night on insect activity and behaviour reported around the world with a focus on Malaysian insects. Insects, whether diurnal or nocturnal are the most diverse organisms on the planet and they play an important role in balancing the local ecosystems. However, their activities might be affected by light pollution, which inadvertently disrupts the natural order. This review found that insects were influenced by light in terms of photoperiod, direction, and mating. However, natural light such as sunlight and moonlight does not have any negative effect on insects while light pollution was found to be a major factor in altering insect activity and behaviour. Despite Malaysia being a megadiverse country with a huge variety of insect biota, not many studies have investigated the effects of light on insects. More studies are needed to investigate the consequences of light pollution, specifically on insect diversity in Malaysia.

Keywords: Artificial light at night, insects, light pollution, nocturnal insects, ecosystem.

Introduction

Insects are the most diverse and widespread organisms that can be found almost everywhere on Earth (Stork, 2018). Most insects can adapt to environmental changes (Lee, 1989). Light is one of the environmental changes that has a direct influence on insect behaviour, whether positively or negatively. Light has a positive affect when it is a natural occurrence such as sunlight and moonlight. On the other hand, artificial light affects the behaviour of insects negatively (Owens *et al.*, 2020). Light pollution is a condition where a naturally dark area is illuminated by artificial light (Cinzano *et al.*, 2000; Cinzano *et al.*, 2016). Most of the time, light pollution refers to astronomical light pollution where an artificial sky glow (Figure 1) is visible in the sky, which disrupts the view of other astronomical objects due to artificial light scattering across the atmosphere (Falchi *et al.*, 2016). Among the best (low light pollution) sites to observe celestial objects in Malaysia

are the Langkawi National Observatory (LNO) in Kedah and the KUSZA Observatory in Terengganu (Tahar *et al.*, 2017, Umar *et al.*, 2018; Baharim *et al.*, 2022).

Although researchers from disparate fields are now interested in light pollution, its magnitude is poorly known on a global scale because measurements are sporadically distributed across the globe. Thus, Falchi *et al.* (2016) has produced the world atlas of artificial sky luminance (Figure 2). Factors such as the transparency of the atmosphere, the upward emission function of cities, the spectrum of artificial light and the time of night when the phenomenon was observed were taken into account when computing the atlas. The more the actual conditions differs from these assumptions, the greater the deviation in artificial light will be compared with the atlas prediction.

The first column in Table 1 contains the ratio between artificial brightness and natural background sky brightness (assumed to be



Figure 1: Example of skyglow over Bukit Maras, Batu Rakit, Kuala Nerus, Terengganu, Malaysia. The photo was taken by research assistant, Ahmad Najmuddin Zulkeflee

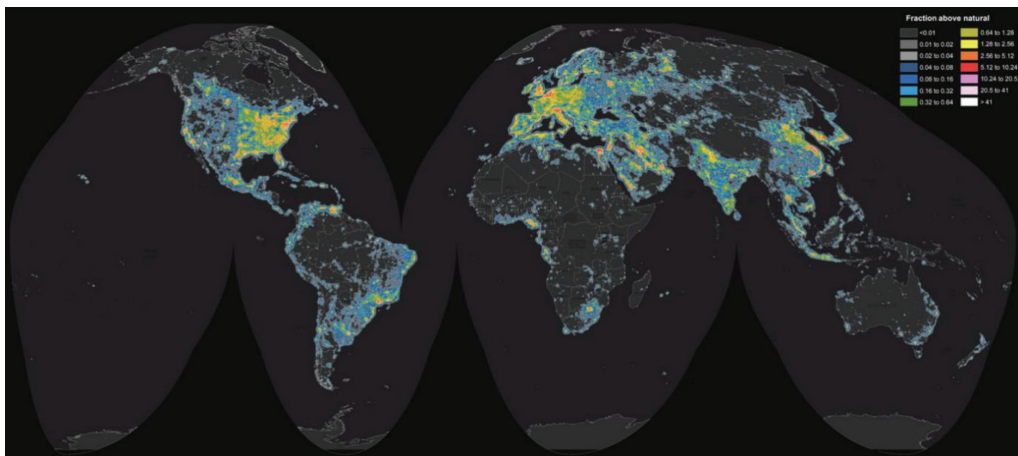


Figure 2: World map of artificial sky brightness by Falchi *et al.* (2016)

174 $\mu\text{cd}/\text{m}^2$). Meanwhile, the second column contains the artificial brightness ($\mu\text{cd}/\text{m}^2$). In addition, the third column contains the approximate (assuming a natural background of 22 mag/arcsec²) total brightness (mcd/m²) whereas the fourth and fifth columns contain the colours (Falchi *et al.*, 2016).

As many reports have shown that light pollution has a big impact on the natural ecosystem and has changed the activity and

behaviour of many organisms, we have gathered literature on related information. This review focused on the influence of natural daylight and nightlight on insect activity and behaviour. It also touches on the effect of ecological light pollution, such as sun and moon eclipses, as well as artificial light pollution on insects' activities and behaviour. Information about the effect of light pollution on insect activity and behaviours reported in Malaysia was also gathered in this

Table 1: Colour levels used in the maps

Ratio to Natural Brightness	Artificial Brightness ($\mu\text{cd}/\text{m}^2$)	Approximate Total Brightness (mcd/m^2)	Colour	
<0.01	<1.74	<0.176	Black	
0.01 – 0.02	1.74 – 3.48	0.176 – 0.177	Dark grey	
0.02 – 0.04	3.48 – 6.96	0.177 – 0.181	Grey	
0.04 – 0.08	6.96 – 13.9	0.181 – 0.188	Dark blue	
0.08 – 0.16	13.9 – 27.8	0.188 – 0.202	Blue	
0.16 – 0.32	27.8 – 55.7	0.202 – 0.230	Light blue	
0.32 – 0.64	55.7 – 111	0.230 – 0.285	Dark green	
0.64 – 1.28	111 – 223	0.285 – 0.397	Green	
1.28 – 2.56	223 – 445	0.397 – 0.619	Yellow	
2.56 – 5.12	445 – 890	0.619 – 1.065	Orange	
5.12 – 10.2	890 – 1780	1.07 – 1.96	Red	
10.2 – 20.5	1780 – 3560	1.96 – 3.74	Magenta	
20.5 – 41	3560 – 7130	3.74 – 7.30	Pink	
>41	>7130	>7.30	White	

review as Malaysia is one of the countries identified as having a megadiverse biodiversity by Conservation International (Skouloudis *et al.*, 2019). A country's level of megadiversity is judged by the number of endemic species in that country. Malaysia, being one on the list shows that any factor that has an ecological impact on its biodiversity should not be taken lightly. Similar to other developed countries, Malaysia also suffers from light pollution due to urbanisation. Thus, this information will reveal whether light pollution has also become an important variable from an ecological perspective in the country.

Insects: Diurnal and Nocturnal

There are two categories of insects: Diurnal and nocturnal. Diurnal insects are active during the day while nocturnal insects are active during the night. Compared with nocturnal insects, diurnal insects are more drawn to visual and olfactory stimuli (Riffel, 2020). On the other hand, nocturnal insects are more drawn to chemical and olfactory cues rather than visual cues (Borkakati *et al.*, 2019). Both insect categories

usually have two types of eyes: Simple eyes or ocelli and compound eyes.

Ocelli are different from compound eyes as they only have one single structure. They are sometimes referred to as 'simple' eyes. Every adult insect with compound eyes also has ocelli, which are often seen on the face or back of their body. For example, dragonfly nymphs have both compound and ocelli. However, when they turn into an adult, their compound eyes are more prominent and the ocelli appears as small swellings. Insects can have two to three simple eyes that are more effective at detecting changes in light than at differentiating between visual images.

Compound eyes are made up of multiple ommatidia and each one is used to gather visual data. The ommatidia are essentially a separate eye containing a lens, a cone, pigment cells, and visual cells that are sensitive to light. Thousands of ommatidia are present in an insect's compound eyes and each one gathers visual data that is then combined in the insect's brain. During light reception, rays from a small area of

the field of view fall on a single facet and is then concentrated upon the rhabdom of the retinula cells. The degree of detail in the image depends on how many ommatidia are present in the compound eyes. Since each point of light differs in brightness, all ommatidia that form the retina receive a crude mosaic of the field of view. The ommatidia of some insects possess pigments that enable them to distinguish between colours like yellow-green, blue, and ultraviolet light. In addition, each ommatidium is commonly shielded by a curtain of pigmented cells that prevents the spread of light to neighbouring ommatidia. This is called an apposition eye.

Nocturnal insects have developed a remarkable ability to visually navigate at night despite having tiny eyes and brains. While some nocturnal insects utilise celestial compass cues like the moon or stars to stay on a straight route, others use visual landmarks to get to and from their nest (Mandal, 2018). These impressive visual abilities occur at light levels when only a trickle of photons is being absorbed by each photoreceptor thanks to their highly sensitive compound eyes and unique visual processing techniques in the brain. For nocturnal insects, the pigment can be withdrawn so that light received from neighbouring facets overlaps to some extent. This is called a superposition eye. The image formed is brighter but not as sharp as that formed by the apposition eye. In addition to perceive brightness, the eyes of nocturnal insects can perceive colour as well as some other properties of light.

Scientific journals have reported that nocturnal insects' behavioural responses like dispersal, foraging, defence against predation, location of food, hosts, oviposition sites, resting sites, and mating are governed by vision. However, these behavioural responses of insects are related to light intensity (adaptation), circadian periodicity and photoperiodism. In addition, the effects of environmental (e.g., light intensity, exposure time of light, polarisation, weather and season) and physiological (e.g., sex, mating status, age, and adaptation to the dark) factors as well as other anthropogenic activities

(e.g., intensive agricultural practices) may affect an insect's activity and behaviour.

Effect of Natural Daylight on Insect Activity/Behaviour

The most important source of light for all living organisms on this earth is the sun, as it provides natural daylight for all living things. The basic role of sunlight is an indicator of the day and night cycle, which is a significant factor for insects as some insects use the length of day as an environmental cue for diapause (Beck, 2012). For example, Critical Photoperiod (CCP) of *Aedes albopictus* in Guangzhou, China was observed both in the laboratory and in the wild to determine the length of exposure to daylight that induces diapause. In the laboratory, the CCP of *A. albopictus* was estimated to be 12.312 hours of light. In the wild, the population is at the lowest from December to February, during which time, it was recorded that the day was 12.111 hours long in 2016 and 12.323 hours long in 2017 that contributes to diapause in the species (Xia *et al.*, 2018).

Effect of Sunlight on Insect Direction

Sunlight, acting as a light compass for insects has been studied for a long time, yet, there are numerous findings concerning various species and other factors that need to be taken into consideration such as light polarisation, temperature, humidity, and light intensity. The study about sunlight as a light compass goes way back to Santchi in 1911. In Santchi's experiment, two species of ants from the genus *Cataglyphis* and *Monomorium* were able to find their nests in the right direction despite being surrounded by tubular screens made of blackboards. The ants were able to navigate properly when there was an unblocked view of the sky but became lost when entering a tube (Vowles, 1950). These observations of ants were later generalised to insects by von Buddenrock (1917). However, Wellington argued that insects do not use light as a compass but rather the insect is affected by it. His study showed that *Archips cerasivorana*

larvae changed direction when temperature and polarisation also changed (Wellington, 1955).

Recent studies showed that the polarisation of light could be an important navigation tool for insects. el Jundi reviewed several studies about the relationship between insects' neural networks and the polarisation of the sky. Desert locusts, monarch butterflies, field crickets, and honeybees were found to have neural networks related to the sky compass due to the presence of specific polarisation -sensitive eye regions (el Jundi *et al.*, 2014).

Effect of the Solar Eclipse on Insect Behaviour/Activity

A solar eclipse is a phenomenon where the sun is either totally or partially covered by the moon. Solar eclipse affects insects' behaviour in many ways because of the change in light intensity and temperature (examples as listed in Table 2). In 1954, when a solar eclipse occurred in Southern Sweden, Kullenberg took the opportunity to carry out a biological observation on behavioural changes in various organisms. In his observations, various species of insects were found to be affected by the eclipse. Some wasps from the Cabronidae group such as *Gorytes mystaceus*, *Nysson spinosus*, *Crabro cribrarius* and *Ectemnius continuus* and other heliophilus Hymenoptera could not be found on flowers during the ecliptic twilight. Meanwhile, a female mason wasp, *Odynerus melanocephalus*, descended on his sweeping net to sleep. *Melitaea cinxia* settled on a *Scabiosa* flower while a chafer beetle, *Cetonia aurata* also settled to sleep. Some Acrididae were also observed getting into position to rest (Kullenberg, 1955).

However, this is merely an observation without any discussion or analysis on what caused behavioural changes in these insects. Despite having the temperature and light measured, there was no discussion on the correlation between changes in biological activities and sudden environmental changes. However, his data showed that a sudden decrease in temperature and lux (light) during the eclipse did occur and

both of these factors were probably a major cause of behavioural change in insects. In 1976, a total solar eclipse occurred in Snobs Creek in Victoria, Australia. A study on aquatic organisms was carried out to observe the changes in the activities of aquatic invertebrates. Data was collected a day before, during and the day after the eclipse. During the study, both air and water temperature were measured before, during and after the eclipse where air temperature showed a sudden decrease, while the water temperature remained almost constant. Some insects showed no change in activities, some Baetidae and *Trinotoperla* sp. nymphs were absent and did not appear until sunset. Some aquatic insect larvae showed changes in activity, while some Scirtidae larvae and two species of Leptoceridae were more abundant during sunset and increased (samples) during the eclipse between 1700 and 1800. Meanwhile, *Cricotopis* sp. larvae provided opposite responses where they were less active during sunset and also decreased in the number of samples (Cadwallader & Eden, 1977). This showed that eclipses affect both nocturnal and diurnal insects. Since there was no change in water temperature during eclipses, insects that exhibited no change in activity may have been used to the temperature as an indicator for their circadian rhythm, while those that exhibited changes in activity must have used light as an indicator. On 21 August 2017, a total solar eclipse occurred in North America, which provided an opportunity to study flight activities of foraging bees using acoustic monitoring. The recorded audio showed that some flight activities had ceased during totality. However, flight activities did not change during the dimming of sunlight during the partial phase of the solar eclipse (Galen *et al.*, 2018). Foraging and homing activities of honeybees, *Apis mellifera* had changed during the eclipse. The foraging activities of *A. mellifera* had decreased but not completely. As for homing activities, drones were the most affected, whereby, only 35% of drones returned to the hive before totality. Generally, the number of workers and drones increased in the hive when approaching totality (Waiker *et al.*, 2019). Decreased light intensity

Table 2: Example of insects affected by solar eclipse

No.	Location, Date and Duration of Solar Eclipse	Insect	Activities During Eclipse	References
1	Woodside, California October 23, 2014 3 hours	Honeybee: <i>Apis mellifera</i> L	Increased the departing and returning flights corresponding to the eclipse peak, followed by a gradual restoration of normal activity during eclipse resolution	Hains & Gamper, 2017
2	Lore Lindu National Park (Lat.: 1.4364°S Long.:120.1317°E), Indonesia March 9, 2016 2 hours 32 minutes	Dung beetles: <i>Paragymnopleurus planus</i>	Reduction in the speed of movements during the first and second partial eclipses. The movement stopped during the maximum eclipse and beetles buried themselves inside the ground in the cower-sleep position	Wiantoro, 2019
3	Kilombero Valley, south-eastern Tanzania [8°23'3.74"S, 36°40'26.66"E] September 1, 2016 3 hours 26 minutes	Mosquitoes: <i>Anopheles</i> sp.	Both male and female mosquitoes increase their activity	Brydegaard <i>et al.</i> , 2020
4	Pacific Coast, Rocky Mountain and Midwest regions of North America August 21, 2017 90 minutes	Bees: <i>Bombus latreille</i> <i>Megachile latreille</i> <i>Halictus robertson</i> <i>A. mellifera</i> L.	Bees ceased flying during complete darkness at totality. Flights of bees during partial phases of the eclipse lasted longer than flights made under full sun	Galen <i>et al.</i> , 2019
5	Central Platte River Valley of Nebraska August 21, 2017 3 hours	Field cricket Tree crickets Ground crickets	Increased call activity Decreased/ceased call activity	Buckley <i>et al.</i> , 2018
6	143 weather radar stations across the continental United States August 21, 2017 92 minutes	Flying insect	Diurnally active insects were landing	Nilsson <i>et al.</i> , 2018

7	Cherry Farm Insectary at Clemson University (34.67° N, 82.84° W) August 21, 2017 3 hours	Honeybees: <i>Apis mellifera</i> L.	Foraging activity was most severely reduced during and directly after the total eclipse but did not stop completely Drones returned faster during the eclipse than during the morning period	Waiker <i>et al.</i> , 2019
8	Informal observations of animal behaviour during solar eclipse from social media (i.e., March for Science Facebook discussion) August 21, 2017	Ant, Dragon flies, Fireflies, Gnats, Mosquitos Bees Cicadas, Crickets, Locust Grasshopper Nocturnal insects	Activity increased Activity increase but vocalization decreased Vocalization increased Activity decreased Vocalization and activity increased	Ritson <i>et al.</i> , 2019
9	Missouri to North Carolina August 21, 2017	Firefly: <i>Photinus pyralis</i> L.	More flashing activity	Branham & Faust, 2019

may have affected their internal circadian rhythms and caused the bees to return to the hive earlier.

A solar eclipse undoubtedly affects the behaviour of various insects, whether directly through the intensity of light or indirectly, due to the sudden change in humidity and temperature. Nevertheless, more systematic research needs to be done regarding solar eclipse and insect behaviour by including data on humidity and temperature.

Effects of Natural Nightlight on Nocturnal Insect Activity/Behaviour

While natural daylight affects insects in numerous ways, natural nightlight such as moonlight, affects both, insect behaviour and activities. They are influenced by the polarisation of moonlight for direction or difference in light intensity in different lunar phases or numerous other factors. A study on the effects of the phases of the moon on insect activities may

have started with Hora (1927) when he observed that some mayflies' nuptial flights occurred in definite periods of the lunar phases. However, the investigation of the effect of moon phases on animal behaviour generally could have started before that time by Fox (1924), who focused on the effect of lunar phases on some sea urchins and the growth rate of fruits. The study was influenced by a belief that sea urchins and crabs are 'full' during the full moon and 'empty' during the new moon. More systematic studies on the effect of moon phases on insect activity were carried out by Williams (1936) using light traps. The study showed that insects captured during a new moon were greater in number as compared with insects captured during the full moon, especially Noctuidae, who always fly in the middle of the night. A night with full clouds also increased the number of insects captured. In his study, it is clear that moonlight can reduce the number of flying insects. Williams claimed that the change in numbers was due to the insect's physiological behaviour and not

because of the reduction in efficiency of the light trap. However, Provost (1959) continued the study on the number of mosquitoes captured on a light trap in relation to the lunar cycle. Two different traps were used in the experiment; one was the non-attractant flying insect trap and the other was a light trap. The result showed that the non-attractant flying trap did not show any changes in numbers in relation to moon periodicity but the change was obvious in the light trap. Provost concluded that the change in numbers using the light trap was not due to the insect's physiological behaviour, but rather because of the physical change in the efficiency of the light trap during the full moon. Nemec (1971) also made a similar light trap collection of Bollworm Moths during different lunar phases. The results were similar to previous light trap experiments during the lunar cycle, whereby, the number of moths peaked during the new moon phase and declined during the full moon. Nemec argued that the number was a result of the insect's physiological behaviour. This argument was supported by a preliminary laboratory study where moths that were kept under full illumination were less active while moths kept in darkness were very active.

Arguments about the efficiency of the light trap remains controversial and there is no definite answer on whether lunar phases reduces the efficiency of the light trap. Nowinszky (1979; 2010) took a different approach by comparing the data on pheromone traps during lunar cycles from 1982 to 1988 and 1993 to 2007 in Hungary, which gave mixed results. Some species such as *Lobesia botrana*, *Grapholita molesta* and *Cydia pomonella* had a maximum catch rate during the new moon, similar to the light trap results. As for the other species, the collections were higher during the last quarter or the waxing period from the new moon to the full moon. These results created a new understanding of how different species act differently during different lunar phases. Kasili *et al.* (2010) found that the influence of lunar cycles on sandflies had negative results, whereby, there was no difference in the number of sandflies captured during the new moon and the full moon. Gunn

and Gunn (2012) studied the bioluminescence of glow worms, *Lamprys noctiluca*, in relation to lunar cycles. Surprisingly, the glow from the larva reduced during a full moon and increased gradually and peaked during the new moon. However, the activity of an adult female remained insignificant during the lunar cycles. More research is proposed by measuring environmental changes. Nada (2012) made light trap collections of *Helicoverpa armigera* during different lunar cycles and found that the population of moths peaked during the new moon and the first quarter. Recently, a study found that insect activity during lunar cycles reduced significantly, which was probably due to a reduction in the efficiency of the light trap during the full moon. Another reason is that lunar phases are natural occurrences and do not have a negative impact on the ecosystem, which renders the topic insignificant. However, from an agriculture perspective, observations on changes in insect activity due to lunar phases could help determine the right time to start agriculture activities in any given month. Even though most of the activity is seasonal, determining the exact moment and location where a specific pest for a specific plant appears will be helpful since the plant is most vulnerable in its early growth stages. More research needs to be carried out in correlation to agricultural activities.

Effect of the Moon Eclipse on Insect Behaviour/Activity

There is a lack of studies about the relationship between a solar eclipse and insect behaviour as the solar eclipse phenomenon rarely occurs and only occurs at certain places for a very short period. Comparatively, the lunar eclipse occurs very frequently in numerous places and lasts for a long time. Studies about the effect of a lunar eclipse on insect behaviour are almost non-existent. One recent study showed that the polarisation of the sky changes significantly during the lunar eclipse (Yang *et al.*, 2020). Since insects have a polarisation-sensitive eye region (el Jundi *et al.*, 2014) and dung beetles use the polarisation of the sky for direction

(Foster *et al.*, 2019), it is possible that the lunar eclipse significantly affects insect behaviour.

The Effect of Artificial Light on Insect Behaviour/Activity

The effect of artificial light on insects is very well known (examples as listed in Table 3). Many researchers took advantage of this phenomenon as a method for collecting insects, which is light trapping, a method that has been used for an exceptionally long time. Tucker (1905) mentioned that artificial light is a regular method used for collecting insects at night besides using bait. Early studies on the effect of artificial light on insects mainly focused on the responses of insects and not on ecological consequences. Curtis Riley (1912) carried out an ecological study about the effects of artificial

light on dragonfly nymphs and found that they tend to move away from light sources. Plant (1916) also noted that water scorpions react positively to artificial light and will move forward into the light source. In 1921, Curtis Riley studied water striders and found that they were attracted to artificial light. Studies about the attraction of insects to light are relevant for maintaining the ecosystem. Poiani *et al.* (2015) explored the effects of energy-saving lamps on insects and found that LEDs had a lesser effect on insects and could benefit the whole ecosystem. Nowadays, the consequences of artificial light on the ecosystem has become more apparent where modern research has focused on the consequences of artificial light or light pollution on insects ecosystems.

Table 3: Example of the insects' activity and common behaviour changes affected by artificial lights

No.	Insect	Effect of Artificial Light	References
1	Flesh fly: <i>Sarcophaga similis</i>	Failed to enter diapause	Mukai <i>et al.</i> , 2021
2	Crickets: <i>Teleogryllus commodus</i>	Reduced life span	Jones <i>et al.</i> , 2015
3	Aphid	Reduced the size of colony	Sanders <i>et al.</i> , 2018
4	<i>Phalerisida maculata</i> Kulzer	Altered the normal locomotor activity, forcing insects to remain buried in the sand for extended periods of time; thus, reduced the feeding time	Quintanilla-Ahumada <i>et al.</i> , 2021
5	Firefly: <i>Photuris versicolor</i>	Reduced flashing activities	Firebaugh & Haynes, 2016
6	Spider: <i>Pachygnatha clercki</i> , <i>Trochosa</i> sp. <i>Opiliones</i>	Increase the density Their activity was extended into the day	Manfrin <i>et al.</i> , 2017
7	Nocturnal ground beetles (Carabidae)	Decrease in density	Manfrin <i>et al.</i> , 2017
8	Grasshoppers	Attracted the migration of grasshopper to the city; thus, increase their population abundance	Tielens <i>et al.</i> , 2021
9	Mosquitoes: <i>Culex pipiens</i>	Female mosquitoes avert diapause	Fyie <i>et al.</i> , 2021

10	Firely: <i>Photuris</i> sp. <i>Photinus obscurellus</i>	Affected the development and movement. Accelerate weight gain in early-instar of <i>Photuris</i> larvae Insects are more likely to burrow beneath the soil surface, rather than disperse across it	Owens & Lewis, 2021
11	Moth: <i>Yponomeuta cagnagellus</i>	Lack of local adaptation of feeding and calling behaviours	Cieraad <i>et al.</i> , 2022
12	Black field cricket: <i>Teleogryllus commodus</i>	Reduces the cellular immune response	Durrant <i>et al.</i> , 2020
13	Triatominae: <i>Panstrongylus geniculatus</i> <i>Panstrongylus lignarius</i> <i>Panstrongylus</i> <i>Rufotuberculatus</i> <i>Rhodnius robustus</i> <i>Rhodnius pictipes</i> <i>Rhodnius amazonicus</i> <i>Eratyrus mucronatus</i>	Attract the Chagas disease vector to the residential areas and may cause disease transmission to human	Castro <i>et al.</i> , 2010
14	Moth: <i>Mamestra brassicae</i> L. <i>Rivula sericealis</i> <i>Idaea biselata</i> <i>Dysstroma truncata</i>	Reduced feeding activity	Van Langevelde <i>et al.</i> , 2017
15	<i>Mamestra brassicae</i> L.	Inhibited diapause and changed sex-specific life history	van Geffen <i>et al.</i> , 2014

The Effect of Artificial Light on Insect Mating Behaviour

Like many living organisms, insects need to reproduce to ensure their species do not go extinct. However, artificial light has become ubiquitous and many studies have shown that light pollution directly affects insects' mating behaviour (examples as listed in Table 4). Firebaugh and Haynes (2016) carried out field experiments on fireflies. Fireflies are important specimens for light pollution studies since their mating behaviour uses bioluminescent flash to attract mates. In this experiment, four pairs of plots were chosen in a place with no sky glow and light pollution. One plot was randomly chosen in each pair and was exposed to artificial light while the others remained in the dark as a control. The results showed artificial light had indeed reduced the number of female firefly courtship flashes and successful mating as no mating occurred in

the plot exposed to artificial light. Even though the abundance of local fireflies was not affected by light pollution, the number may reduce in the long run due to failure in the mating process. Botha *et al.* (2017) studied the effect of artificial light on cricket courtship and mating behaviour using different intensities of light from 10 to 100l x to simulate different environments. As a result, crickets that were exposed to 100l x of light had a higher probability of successful mating and there was no change in singing or calling behaviour even with different intensities of light. This study showed that some insects may not even be affected by light pollution. Firebaugh and Haynes (2019) continued the study of light pollution on fireflies by including prey and predator relationships. Some elements that were explored in the study were the attraction of fireflies to artificial light, courtship behaviour in lit and unlit plots and predatory-

Table 4: Example of insects' mating behaviour changes affected by artificial lights

No.	Insect	Effect of Artificial Light	References
1	Firefly: <i>Photinus pyralis</i>	Reduced courtship behaviour and mating success	Firebaugh & Haynes, 2016
2	Mosquitoes: <i>Culex pipiens</i>	Become reproductively active	Fyie <i>et al.</i> , 2021
3	Winter moth: Operophtera: Brumata	Disrupts reproductive behaviour	van Geffen <i>et al.</i> , 2015
4	Black soldier flies: <i>Hermetia illucens</i>	Influences mating and oviposition	Zhang <i>et al.</i> , 2010
5	Crickets: <i>Teleogryllus commodus</i>	Affected mate choice and efficiency	Botha <i>et al.</i> , 2017
6	Fly: <i>Drosophila melanogaster</i>	Decreases fecundity and adult survival	McLay <i>et al.</i> , 2017
7	Moth: <i>Mamestra brassicae</i>	Disrupts sex pheromone and altered the chemical composition of the pheromone blend	van Geffen <i>et al.</i> , 2015

prey relationship to prey mating behaviour. The first result showed that fireflies were attracted to artificial light, whereas, both prey and predator firefly species were found more on lit traps than on unlit ones. In regards to courtship behaviour, female fireflies never flashed in lit plots while all 11 females flashed in unlit plots at least once. The presence of predators did not affect the number of flashes of the prey firefly. Fireflies have proven to be affected by direct light pollution. Future studies should focus on one species of firefly to determine whether the population as a whole in both rural and urban areas is affected by similar conditions such as humidity and temperature. All of these studies have shown that some insects' mating behaviour may be affected directly by light pollution while some may not be affected at all. Insects that are directly affected by light pollution may reduce in numbers in places affected by light pollution due to a failure to reproduce.

Indirect Effect on Nocturnal Pollinators

One of the important functions of insects is to act as a pollinator. Some plants require assistance from insects to pollinate them and produce seeds. Some plants require nocturnal pollinators because flowering only occurs at night. There is

a possibility that light pollution could drive away or redirect insects away from night-flowering plants, which affects plant reproduction.

Altermatt and Ebert (2016) examined flight-to-light behaviour in moths since moths are the main nocturnal pollinators. Surprisingly, the result showed that moths reared in light-polluted areas are less likely to have flight-to-light behaviour than moths reared in places with no light pollution. This is probably because of the adaptation mechanism in moths that increases their survivability. This shows that artificial light has a significant effect on moths, which acts as the main pollinator. Knop *et al.* (2017) investigated whether light pollution directly affects the pollination of plants. *Cirsium oleraceum* was chosen as the study sample in this experiment for analysing fruit production from 100 plants distributed equally in five illuminated sites and five dark sites. 10 plants were paired on each site and one of the paired plants was bagged to exclude flower visitors. As a result, the number of fruits from exposed (not bagged) plants in dark sites was higher than the number in illuminated sites. Meanwhile, the bagged plants seemed to have almost similar fruit productivity, regardless of being in dark sites or illuminated sites. The study also suggested that disruption

in pollination may already occur in low light intensity. In addition, the results showed that streetlamps can also reduce the number of pollinations from nocturnal insects, which substantiates existing information on how light pollution affects plant pollination. However, MacGregor *et al.* (2019) found contradicting results when using different variables of light exposure such as full-night light, part-night light, and unlit on *Silene latifolia*. The study found that pollination increased in full-night light, while part-night light and unlit night had similar numbers. The study went on to explain that it could probably be because the full night light could have attracted lots of moths into the plots. However, while the result may seem positive, it still showed that a plot exposed to full-night light will cause an imbalance in the ecosystem. This study also showed that part-night light is the solution to this problem since the number of pollinations remained the same as unlit night and there was no disruption to the ecosystem. A review by MacGregor (2020) showed that some nocturnal pollinators play an important role in the pollination of commercial crops, such as bats to durian trees, thrips to oil palm, jasmine and coffee plants, moths to oil palm and nocturnal beetles to nutmeg plants.

Thus, it can be concluded that nocturnal pollinators are directly affected by light pollution. Some of those insects are important pollinators of commercial plants, wild plants and endangered plants. For example, nocturnal moths are important pollinators of *Platanthera bifolia* and some nocturnal thrips seemed to be very important pollinators of *Ocotea porosa*, which are plants listed as vulnerable in the International Union for Conservation of Nature's (IUCN) Red List.

Disruption Caused by Light Pollution on the Food Pyramid

Since insects are the main food source for insectivorous bats and birds, the possibility that light pollution could directly or indirectly affect both these species cannot be ignored.

Insectivorous bats are known to reduce or increase their activity in response to prey availability (Richards, 1989). Azam *et al.* (2016) examined the national scale and found that artificial light has a more significant effect on bat activity compared to impervious surfaces and intensive agriculture. The decrease in bat activity may increase the nocturnal population in light polluted areas and may be the reason for the increasing pollinating rates of *Silene latifolia* (MacGregor *et al.*, 2019). A bats' reaction to artificial light may vary between species due to different foraging strategies. Bats are not sensitive to light hence; they can exploit the insect's attraction toward light and use it as a main foraging spot. Conversely, light-sensitive bats tend to stay away from artificial light and live in the dark. Insects' attraction to light may reduce the number of insects available to light-sensitive bats (Haddock *et al.*, 2019). Another study noted that most insectivorous bat species have been found near artificial light, which is better for their foraging (Frank *et al.*, 2018).

Conclusion

Much evidence has shown that artificial lights have altered the natural ecosystem of insects and these changes are expected to have substantial cascading consequences for ecosystems. Thus, we need to minimise the use of artificial light or at least to improve the lighting system worldwide in minimising the negative impact on insect populations as well as linked ecosystem processes at marginal costs. More research on this topic should be done in future to save the planet for the next generation.

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