



IMPACTS OF ARTIFICIAL LIGHT AT NIGHT ON NOCTURNAL AND DIURNAL INSECT BIOLOGY AND DIVERSITY

RENEE M BORGES

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, Karnataka, India

Email: renee@iisc.ac.in

ABSTRACT

Artificial light at night (ALAN) is leading to light pollution on local and global scales. Reflected and scattered light contributes to skyglow over cities and large industrial complexes. ALAN is one of the key drivers of insect declines in the Anthropocene era. This is the likely consequence of perturbations in circadian clocks by extension and even abolition of the dark phase of the diel cycle, which affect reproduction and foraging. Bioluminescent insects that use light as sexual signals are severely affected by ALAN and may be under sexual selection for even brighter signals. The phototactic response of insects to light is also causing mortality due to increased predation and altered activity. Mitigatory measures are urgently needed to stem insect declines and to 'protect' the role of insects in community ecology. New satellite technology for ALAN measurement is urgently required. There are many research gaps, such as the effect of ALAN on diurnal insects and on interaction networks, that need to be filled.

Key words: ALAN, biological clocks, circadian rhythms, light pollution, nocturnal pollination, bioluminescence, phototaxis

The length of one diel cycle of Earth's rotation has varied from 6 h in the Archean eon (4 Gy ago), increasing to 21 h in the Paleo-Proterozoic (2.5 Gy ago) and finally reaching the present-day 24-hour cycle in the Neo-Proterozoic (1 Gy ago) in the Precambrian era (Bartlett and Stevenson 2016; Spalding and Fischer 2019). Early life that arose in the Precambrian, therefore, experienced a cycle of 21-24 hours, and it is possible that this period has consequently been entrenched in the physiology of life forms (Paranjpe and Sharma 2005; Nikhil and Sharma 2017). Before the formation of the ozone layer, the photic period with the downwelling of ultraviolet radiation during the day presented a threat to DNA replication and repair especially in aquatic organisms such as photoautotrophic Cyanobacteria that require light for photosynthesis; these organisms therefore temporally segregate damage-sensitive activities such as DNA synthesis, cellular maintenance and nutrient storage into the dark portions of the diel cycle (Nikhil and Sharma 2017). That the diel period could, using photic cues, be efficiently divided into activity and non-activity periods for various behavioural, cellular, and physiological processes was a clear advantage in the evolution of life; consequently, there are no known organisms lacking circadian rhythms that do not suffer survival disadvantages (Daan and Aschoff 1982). Circadian rhythms and their extension into circannual cycles governed largely by variation in day length and photoperiods, based on the earth's orbit around the

sun, are vital for reproductive success; fitness declines have been demonstrated in all forms of life either when organisms have impaired circadian clocks or when the in-built clocks do not match with the expected diel cycles (Green et al., 2002; Emerson et al., 2008; Nikhil and Sharma 2017; Horn et al., 2019; Koritala et al., 2020; Liao and Rust 2021).

Between the Tropics of Cancer and Capricorn, the daily photoperiod remains approximately at 12 h through the year; however, above and below these latitudes towards the poles, the photoperiod increases progressively towards summer and decreases in winter. Since the earth's orbit is invariant, organisms that are resident between the tropics and the poles adapt to the dynamic, but predictable changes in photoperiod during the year. While temperatures are also dynamic, they are unpredictably variable from year to year. Therefore, organisms use the change in photoperiod to inform them of a likely change in temperature and thereby prime themselves for physiological activities such as diapause in resident organisms or migration in those that leave their breeding or feeding areas in a seasonal manner (Hut et al., 2013; Helm et al., 2017). Consequently, unseasonal changes in photoperiod, as happens with continuous artificial light during the expected night, may induce physiologies and behaviours at inappropriate times with detrimental effects (Kronfeld-Schor et al., 2017). Besides the inappropriate scheduling of seasonal events, artificial light at night can disrupt

rest and sleep that are vital for normal functioning (but see Geissmann et al., 2019); even organisms that are in continuous movement for extended periods of time, that could last for weeks, as in great frigatebirds or swimming sharks, engage in unihemispheric sleep such that only one hemisphere of the brain is awake while the other is quiescent (Rattenborg et al., 2016; Mascetti 2021). Therefore, periods of rest and sleep have evolved as adaptations for survival in many life forms. Most insect circadian rhythms have been investigated using *Drosophila melanogaster* (Diptera: Tephritidae) that has served as a model in understanding human sleep disorders (Donelson and Sanyal 2015). However, there is need to investigate non-model insects (Beer and Helfrich-Förster 2020), since its will inform us about the level of plasticity and/or variation available in diel and annual rhythms (Helm et al., 2017) for insect survival under various perturbations including light pollution during the Anthropocene.

Artificial light at night (ALAN)

The phenomenon of ALAN is pervasive and ubiquitous in many parts of the world. It is largely a phenomenon of urban and industrial areas, but road and rail stretches between urban areas could also be illuminated, as also small towns and villages. With the invention of light-emitting diodes (LEDs), and the economical and longevity benefits of LEDs, illumination is shifting from the more monochromatic yellow lighting to the broader spectrum white-light LEDs, which have a more pronounced blue spectral coverage and higher intensity (Elvidge et al., 2010; Longcore et al., 2018; Alaasam et al., 2021). Cool-white LEDs with a spectral maximum at 450 nm are optimised for humans since its spectrum confers maximum suppression of melatonin and thereby induces maximum alertness in humans (Mills et al., 2007). With increasing demand for indoor and outdoor illumination, dark nights are absent in many areas, and global maps of ALAN demonstrate the scale and severity of the problem (Kyba et al., 2017).

Although the lux differential between day and a full moon night is a million-fold (full moon = 0.1 lux; starlight = 0.001 lux) (Davies and Smyth 2018; Borges et al., 2016), even dim ALAN is sufficient to disrupt quite a few biological activities. For example, dim ALAN depresses the cellular immune response of *Teleogryllus commodus* (Orthoptera: Gryllidae) (Durrant et al., 2020). Light under a commonly used LED streetlight is 1-2 lux in a radius of 10-20 m, while that from floodlights in a stadium, for example, is usually in the order of 100 lux (Sanders et al., 2021).

Besides the effect of direct light on organisms, indirect light contributes to skyglow, which is the result of light directed upwards, reflected and scattered by atmospheric particles; the intensity of skyglow is 0.1-0.5 lux, which is brighter than a full moon (Eisenbeis 2006). Skyglow extends around areas with a high density of lights such as cities and metropolises.

Currently, the best available option for measuring ALAN is via the day—night band (DNB) of the satellite-mounted visible infrared imaging radiometer suite (VIIRS) (Lee et al., 2014; Barentine et al., 2021). However, there are several shortcomings of this sensor technology, especially its insensitivity in the blue region of the spectrum and its spatial resolution that is limited to 750 m (Kyba et al., 2017). The sensitivity lacuna is particularly important with the increased use of white LEDs that have a considerable blue component. Consequently, new mission-mode satellite technology is urgently required, along with extensive ground-truthing to determine the correspondence between satellite readings and light measurements on ground (Levin et al., 2020; Barentine et al., 2021).

Insect traits that increase vulnerability to ALAN and anthropogenic change

Insects as small-sized ectotherms have modulated their biology and life history to match their environments (Saunders 2009; 2020). Being ectotherms, they are most vulnerable to high and low temperatures and are predicted to be metabolically at high risk owing to human-induced changes of the Anthropocene, such as warming (Wagner et al., 2021). Insects are active either at dawn, or dusk, or during day or night. While inactive they must retire to resting places with conducive temperatures where predation risk is minimal. Insects that inhabit relatively arrhythmic environments, characteristic of high latitudes, may also exhibit lack of rhythmic clock activity but may also be sensitive to other environmental variables, such as temperature, which interact with clock-gene expression to produce activity rhythms adapted to local conditions (Bloch et al., 2013; Kobelkova et al., 2015; Bertolini et al., 2019; Helfrich-Förster et al., 2020). When conditions are predictably unsuitable for insect survival, insects either migrate or enter diapause so that the diapausing dormant stage can survive through the harsh conditions. These transitions between developmental stages are usually regulated by hormones, which are under the control of biological clocks that are in turn entrained by zeitgebers (synchronizers, *sensu* Jürgen Aschoff), such as light levels and temperature (Beer and Helfrich-Förster 2020). Disruptions in these environmental-

time cues can have major effects on life-histories and consequently impact on the demographics (van Langevelde et al., 2018). Addressing the causes and consequences of these stressors on insects is important, given their importance in the functioning as components of aquatic and terrestrial communities, and their catastrophic decline, which is underway in many parts of the earth (Wagner et al., 2021).

Effect of ALAN on nocturnal insects

ALAN has a wide variety of impacts on insects through interference with such vital traits as mating, foraging, melatonin production, and offspring development time, including many other aspects of their biology (see Desouhant et al., 2019 for a comprehensive review). For example, ALAN affects reproduction, resulting in the alteration of the pheromone blend by increasing repellent compounds and decreasing mate attractants, demonstrated in many species of Noctuidae (Lepidoptera) (Van Geffen et al., 2015). Light pollution also inhibits the feeding behaviour of adult Noctuidae (van Langevelde et al., 2017). Most insects exhibit a dorsal light reaction and show positive phototaxis towards light (Jander 1963). They are attracted towards either polarised or unpolarised light sources or their reflections (Robertson et al., 2017); however, this attraction also depends on the light spectrum with blue and red light evoking less attention (Donners et al., 2018; Robertson and Horváth 2019). However, the Noctuidae are strongly attracted by ultraviolet and blue regions of the spectrum (Brehm et al., 2021).

Many nocturnal insects have impaired mate detection, courtship and related reproductive behaviours under light pollution. Australian populations of *Teleogryllus commodus* were slow to initiate movement towards calling mates in the presence of ALAN either in the laboratory or under streetlights, but they did engage in sexual behaviour suggesting that ALAN was not entirely detrimental to their reproduction (Thompson et al., 2019). In another example, lifetime rearing of *Gryllus bimaculatus* (Orthoptera: Gryllidae) under 12 h light and 12 h of ALAN of intensities varying from 2, 5, to 40 lux revealed that although there was a greater impact of higher ALAN intensities, all experimental light intensities at night affected locomotory and stridulatory rhythms (Levy et al., 2021). There was greater asynchrony between individuals in calling activity and locomotion, all of which are likely to have critical effects on mating as well as foraging activity.

ALAN has particularly serious effects on bioluminescent insects that produce light. In the nocturnal

Lampyrus noctiluca (Coleoptera: Lampyridae), males experienced difficulty in locating dummy light-emitting females when LED light was facing upwards such that the lights had maximum spread; this difficulty was reduced with distance away from the light source (Van den Broeck et al., 2021a). The study recommended the reduction of LED lights and their intensities in areas where *L. noctiluca* were usually abundant. Under ALAN, *L. noctiluca* females are more likely to attract males if their signal was bright, suggesting sexual selection for brighter females under conditions of light pollution (Elgert et al., 2021). However, when light-emitting *L. noctiluca* females were exposed directly to ALAN, they neither moved to darker areas where their signal would be more conspicuous nor delayed their light emission, suggesting that *L. noctiluca* lack the ability to be flexible in signalling strategies under light pollution (Elgert et al., 2020). Female glow worms in dark areas stopped glowing after one night while those in areas lit by artificial light continued glowing for several nights, suggesting that the latter females were unsuccessful at attracting males under lit conditions (Van den Broeck et al., 2021b). The effects of ALAN are not restricted to adult stages of bioluminescent insects. The aquatic larvae of *Aquatica ficta* (Coleoptera: Lampyridae) suffered enhanced mortality when experiencing ALAN; furthermore, under ALAN, there was a down-regulation of genes controlling spermatid development, oogenesis and neuron differentiation, and an up-regulation of genes responsible for hormonal production and ecdysteroid metabolism (Chen et al., 2021). Owing to its disruption and interference with the reproductive biology of light-emitting insects, light pollution is considered the most critical contributor to the decline of populations of the Lampyridae in Brazil's Atlantic Forest (Vaz et al., 2021).

Light pollution also affects pestiferous insects such as *Culex pipiens f. molestus* (Diptera: Culicidae) in temperate regions; in response to long photoperiods because of ALAN, females delay diapause and are active for longer periods thus biting humans later in the season when they should no longer be active (Fyie et al., 2021). Such females diverted energy from fat bodies into production of larger egg follicles and thus extended the yearly risk period for disease spread (Fyie et al., 2021). Similarly, *Aedes albopictus* (Diptera: Culicidae), which has invaded many parts of the world, also delays diapause with light pollution (Westby and Medley 2020). Whether extended ALAN periods also extend the diel-biting periods of this day-biting mosquito is not yet known but could also affect disease spread by this vector of arboviral diseases, such as dengue and

chikungunya (Paupy et al., 2009).

While the impacts of ALAN on insects have usually been studied using terrestrial insects, data are presently accumulating on the effects of light pollution on aquatic insects that have flying adult stages; Ephemeroptera and Trichoptera were caught by traps that were located near portable LED lights in an effort to mimic realistic ALAN conditions at different distances from riparian areas (Carannante et al., 2021). While the Ephemeroptera and Trichoptera catches were greater in traps set near rivers, the Diptera were trapped at all distances from the river. Carannante et al. (2021) recommended that LED lighting should be placed at 40-60 m from riverbanks to prevent the attraction of adult aquatic flying insects. The larvae of aquatic insects were also attracted to mid-regions of the spectrum, and the Ephemeroptera larvae did not exhibit phototaxis towards blue light (Kühne et al., 2021).

Several insects use celestial and lunar cues in the night sky for navigation. The South-African Scarabaeoidea (Coleoptera) use the polarisation patterns in the night sky coupled with the Milky Way to navigate (Dacke et al., 2004; 2013); however, skyglow due to light pollution is obscuring the night sky and its celestial cues. Consequently, the Scarabaeoidea are resorting to using available artificial lights as guides and exhibiting impaired navigation, resulting in increased competition from similarly disoriented beetles (Foster et al., 2021). Similarly, adult flying aquatic insects find water bodies at night through the horizontally polarised reflection of moonlight from water surfaces, including reflection of polarised ultraviolet light (Robertson et al., 2017; Fraleigh et al., 2021); this ability is being severely disrupted by light pollution (Haynes and Robertson 2021). That skyglow and light pollution are extending into protected areas and biodiversity-rich areas (Garrett et al., 2020; Mu et al., 2021) is a matter of great concern for the long-term survival of these specialized navigation capabilities.

Effect of ALAN on diurnal insects

Little research has been done measuring the impact of ALAN on diurnal insects (Desouhant et al., 2019). In diurnal *D. melanogaster*, sustained exposure to dim ALAN (> 1 lux) reduced fecundity and adult survival (McLay et al., 2017). ALAN extends the foraging time of diurnal moths, e.g., *Tegeticula maculata* (Lepidoptera: Prodoxidae) that pollinates the *Hesperoyucca whipplei* (Asparagaceae) (Wilson et al., 2021) with as yet unknown longterm consequences for

this mutualism between a seed-eating pollinator and the plant that it services. The diurnal *Apis mellifera* (Hymenoptera: Apidae) has a pronounced nocturnal sleep rhythm (Kaiser and Steiner-Kaiser 1983); whether this sleep rhythm is compromised by light pollution in *Apis dorsata* or *A. florea*, that nest in the open, and not in cavities, also needs to be determined. *Apis dorsata* is often found in cities (Saravanan et al., 2020) where it is likely to be affected by light pollution. *Apis dorsata* increases its activity into the night in the waxing or waning period of the moon between half-moon and full moon cycles (Dyer 1985; Young et al., 2021), since that quantity of moonlight is above the illumination threshold required for the optimal functioning of its optical system. Still, the impact of ALAN on this *A. dorsata* is presently unknown. It is possible that this aggressive bee with its large worker force could dominate night-blooming flowers under conditions of light pollution. In a study in which unmanaged meadows were treated with ALAN or left as dark controls, 19% of plant species were affected by the light treatment and received either more or less diurnal pollinator visitation compared with the dark controls (Giavi et al., 2021). The reasons for this variation in effect on plant species are as yet unknown.

ALAN also affected a diurnal endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae) that parasitises the larvae of the Pyralidae, by extending its activity level into the night (Gomes et al., 2021); females of *V. canescens* exposed to low level ALAN also demonstrated a transgenerational effect with increased development time and increased latency for feeding in their offspring. In a massive collective phototactic response, 45 million individuals of *Trimerotropis pallidipennis* (Orthoptera: Acrididae), that are usually diurnal, were attracted to city lights in Las Vegas, USA (Tielens et al., 2021) during one of the perennial population outbreaks. Consequently, phototaxis can have devastating effects on even diurnal insect populations by triggering inappropriate behavioural activity.

ALAN and insect interaction networks

While flower opening times for nocturnal and diurnal flowering plants are under strict circadian pattern (Ren et al 2021), whether ALAN affects flower opening times is not yet known. But it is likely that this effect will be demonstrated, and that such changes may also affect insect visitation to those flowers. Diurnal insects such as species of *Heliconius* (Lepidoptera: Nymphalidae) can associate floral rewards such as nectar with morning

or afternoon time periods (Toure et al., 2020) and adjust their visitations accordingly. Whether nocturnal pollinators, such as the Heterocera, also do the same is not known. While amber LEDs and even high-pressure sodium lamps attract low numbers of insects and are less damaging compared with white broad-band LEDs with more of blue emission, a modelling study using known values of colour receptor sensitivities showed that white broad-band LEDs were more similar to moonlight in their effects on colour contrasts in the visual system of the nocturnal *Deilephila elpenor* (Lepidoptera: Sphingidae) (Briolat et al., 2021). Therefore, the nature of ALAN could affect Heterocera's visitation frequency at flowers of varied colours and contrast against their leaf background during nights.

Using 3D-printed flowers and illumination levels to match moonlight (0.1 lux) and dawn/dusk light conditions (50 lux), the nocturnal *Manduca sexta* (Lepidoptera: Sphingidae) took longer to find flowers and efficiently locate the nectary at 50 lux compared with lower light levels (Deora et al., 2021) indicating that those visual systems that are adapted to perform at low light levels will encounter difficulties at higher light levels. The consequences of this for foraging efficiency and thereby reproductive success of the Heterocera and their pollination services under light pollution is unknown. The circadian rhythms of plants and pollinators are often delicately matched, e.g. in the interaction between *Manduca* and *Petunia*, the circadian rhythm of scent production of *Petunia* matches that of the antennal sensitivity of *Manduca*, whose activity peaks about 4 h after sunset (Fenske et al., 2018). Therefore, the disruption of these timed activities by ALAN would have serious consequences for existing plant-pollinator interactions. In a specialised nursery pollination system, the nocturnal species of *Hadena* (Noctuidae) pollinates and lays eggs in the night-opening flowers of *Silene latifolia* (Caryophyllaceae); plants had higher seed predation owing to moth oviposition in dark, unlit control sites compared with lit areas; however, dark areas adjacent to lit areas had spillover effects of the light, and here also seed predation was increased compared to the lit areas (Giavi et al., 2020) suggesting that light can have effects that are carried over onto adjacent unlit areas as well.

Modelling of visual systems also revealed that the perception of colours on the wings of the Sphingidae that may be used in sexual selection or mate attraction displays or anti-predation strategies was affected by amber but not white LEDs. In an investigation of 14

species of the Sphingidae in the UK, Briolat et al. (2021) found that since nocturnal moths choose settling backgrounds at night for camouflage against diurnal predators such as blue tits, colour contrast using amber LEDs would give hawkmoths inappropriate information about the colour of substrates used for resting and affect their choice of backgrounds. This mismatch between colours perceived under ALAN and those perceived under natural light available at night (moonlight and/or starlight), can result in wrong choice of substrates, leading to greater conspicuousness and thereby greater predation risk during diurnal resting periods. These authors therefore stress the importance of knowledge of the visual ecology and sensory biology of insect pollinators, the colour spectrum of their floral resources, and the colour discrimination abilities of their predators in assessing the impact of ALAN on networks of interactions.

Light pollution can affect tritrophic and higher levels of interaction. In a multitrophic experiment with plants, aphids and parasitoids, although plant biomass increased with ALAN, there was a differential effect on the aphids and parasitoids. The day-active parasitoids were able to extend their activity into the 'night-time' with moderate intensity ALAN but parasitoid activity declined with high intensity ALAN; consequently, the density of aphids declined with moderate ALAN but their numbers remained high under strong ALAN owing to the lower activity of the parasitoids (Sanders et al., 2018). Therefore, low levels of ALAN increased predation of aphids but this effect was not occurring at high levels. Similarly, insectivorous birds such as mockingbirds were able to prey upon insects and feed their nestlings after nightfall owing to ALAN (Stracey et al., 2014), which could result in greater predation on insects under these conditions. Since many insects show attraction to artificial light especially those emitting blue light, congregations of insects at lights are affecting their predation rates by nocturnal predators such as geckoes and bats that are also attracted to these light sources (Rowse et al., 2016; Pauwels et al., 2021). While biological management of pestiferous insects is successful in some instances, in general, there are negative impacts of ALAN on agroecosystems affecting the efficiency of pestiferous arthropod management (Grubisic et al., 2018).

Combined effects of ALAN and other anthropocene effects

Diapause in insects is usually optimally timed to coincide with the onset of harsh conditions such as

winter. The reaction norm of diapause in response to photoperiod will respond to increasing temperatures by advancing development thereby having more time for growth including an increase in voltinism (having multiple breeding episodes within the same season). On the other hand, ALAN will result in longer artificial photoperiods, and thereby a delay in moving into diapause; this will result in development prior to diapause occurring at inappropriate times (Merckx et al., 2021). Diapause in an urban population of blowflies *Sarcophaga similis* in Japan was delayed under ALAN such that flies had not yet entered diapause in autumn compared to rural populations (Mukai et al., 2021). Noise pollution is also another consequence of the Anthropocene. At low urban noise levels, the frequency of a species of *Corethrella* sp. (Diptera: Corethrellidae) decreased with increasing ALAN intensity; however, at higher noise pollution levels, these midges were absent at all experimental light levels (McMahon et al., 2017), indicating that noise and light levels have counteracting effects.

Unanswered questions

The light environment is the single most reliable cue available to life on earth, and insect circadian rhythms and utilisation of habitats at specific times of the day or night are guided by this periodicity of light availability (Denlinger et al., 2017; Tierney et al., 2017). While studies record population declines of insects under light pollution, the mechanisms that cause these declines need investigation (Boyes et al., 2021a, b); a mechanistic understanding will have impact on selection of appropriate strategies for insect conservation (Stewart 2021). There is a need for interdisciplinary research on the effect of ALAN on insects and their interacting trophic guilds (Kalinkat et al., 2021). This interdisciplinary research must encompass radiometry, satellite technology, regular insect monitoring, critical experiments using model insect species and an outreach component which also attempts to provide scientifically validated solutions to mitigate the effects of ALAN.

Among the many questions that need to be answered is the impact of ALAN on dawn, dusk, and twilight levels. The duration of these transitions between day and night varies with latitude (Borges et al., 2016). The contribution of ALAN to matutinal and vespertine light levels will also depend on the timing of switching on and off of lights. There is no information on ALAN magnitude at these times at a local or global level, although the data may be available and need to be

extracted and analysed. The impacts are likely to be most profound for those organisms that show matutinal and/or crepuscular behaviour. For example, only the largest foragers *Bombus terrestris* (Hymenoptera: Apidae) leave the nest at low light levels at the onset of dusk because these are likely to have the largest eyes and therefore the greatest photon catch ability that enables them to fly under these light conditions (Hall et al., 2021); these large foragers occur in low frequency in the nest presumably due to the cost of their maintenance. Whether the abolition of dawn by ALAN will result in negative selection against large size in these bumblebees remains to be investigated. Similarly, in a Neotropical dim-light-foraging bee community, light intensity limited their foraging activity; these bees needed a certain threshold of light intensity to forage, but also avoided foraging in bright light (Liporoni et al., 2020). *Xylocopa tranquebarica* (Hymenoptera: Apidae) has colour vision under starlight conditions and only flies under nocturnal conditions, avoiding even crepuscular flights) (Somanathan et al., 2008; 2020). How bees like *X. tranquebarica* will respond to ALAN is not known. Nocturnal moths are being increasingly recorded as important pollinators of wild plants even in agricultural landscapes (Walton et al., 2020); the myriad negative impacts of ALAN on different Heterocera does not auger well for the long-term sustainability of this interaction. Whether mismatches between the circadian clocks of flowering plants and their insect pollinators will have cascading effects on the structure of communities is not known but requires attention (Bloch et al., 2017; Kronfeld-Schor et al., 2017).

Many nuisance insects, such as those of the Blattodea, have a pronounced nocturnal activity rhythm, and a period of immobility when lights are switched on (Tobler and Neuner-Jehle 1992); will ALAN result in reduced activity by such arthropods or will they evolve to compensate for longer light availability periods? Since the foraging time of insectivorous species is extended by ALAN, how this may affect predation on diurnal insects is also unknown. Since light pollution affects sexual attraction especially in insects that use light signals, e.g. bioluminescence, is it possible that new sexual signals will evolve (Broder et al., 2021)?

Several detailed plans have been drawn up to mitigate the impact of ALAN especially in protected areas (Jägerbrand and Bouroussis 2021). For example, in Hungary, researchers have successfully reduced attraction of many species of the Ephemeroptera to light by optimising the spectrum of beacon lights

on a bridge such that the adults do not show a mass phototactic response (Mészáros et al., 2021). Since adult Ephemeroptera live only for a few hours, and spend their development stages in water, the judicious adoption of such mayfly-protecting lights near water bodies is a practical mitigation measure. Insects are often caught in evolutionary sensory traps by ALAN; research must be directed towards disarming such traps (Robertson and Blumstein 2019). Yet, arriving at a spectrum of lighting that will have the least negative impact on all taxa will be a daunting task as also shown by studies with fireflies wherein each species is impacted by the spectral peak of its own bioluminescence (Owens and Lewis 2021); these naturally vary between sympatric species in a habitat as a consequence of competition for light spectral space. Reducing the blue spectrum of light has however shown to be most beneficial towards reducing insect attraction to LEDs in a lowland forest site in the Peruvian Amazon (Deichmann et al., 2021). In many parts of the world, citizen groups have led the way with regard to changing policies on light pollution and lighting innovations (Zielińska-Dabkowska et al., 2020). Such recommendations are also valid for lighting of public spaces, and monuments, especially when they are enclosed by woodlands (Kobav et al., 2021); such a situation is particularly germane to countries rich in heritage structures such as India. Illuminating such monuments excessively and inappropriately will result in islands of light surrounded by darkness; such light islands may serve as attractors to insects and disrupt local community processes of which insects are an integral part.

Since conservation can have greater success when it is informed by sensory ecology (Dominoni et al., 2020), it is necessary that more attention is paid to insect sensory biology. There have been calls for making the mitigation of light pollution a major research goal in the 21st century (Davies and Smyth 2018) since its effects are pervasive (Gaston et al., 2021). ALAN needs a comprehensive framework within which its individual effects as well as its effects on diurnal-nocturnal trophic cascades and the dynamics of communities may be investigated (Grubisic and van Grunsven 2021). Borges et al. (2016) suggested that owing to the stresses involved with diurnal flowering under global warming, it is possible that plants will shift their flower opening times to the cooler nocturnal hours, as may also happen with animals that may shift activity to the night (Levy et al., 2019). However, this flowering shift into the night will only be successful if suitable pollinators are available during the night. Since light pollution is responsible for serious declines of nocturnal insects

(Owens et al., 2020), this is unlikely to be a successful evolutionary trajectory.

The ‘normal’ night in the absence of artificial light is fraught with its own constraints for plant and insect activity (Borges 2018; Gaston 2019; Somanathan et al., 2020). It would be valuable to be able to predict which interactions will prevail under the combined stresses of global warming, light pollution, noise, and atmospheric pollution. There are a multitude of questions that demand answers, if we are to successfully conserve insect diversity and their vital role in functioning ecosystems.

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REFERENCES

- Alaasam V J, Kernbach M E, Miller C R, Ferguson S M. 2021. The diversity of photosensitivity and its implications for light pollution. *Integrative and Comparative Biology*. Doi: 10.1093/icb/icab156.
- Barentine J C, Walczak K, Gyuk G, Tarr C, Longcore T 2021. A case for a new satellite mission for remote sensing of night lights. *Remote Sensing* 13: 2294.
- Bartlett B C, Stevenson D J. 2016. Analysis of a Precambrian resonance-stabilized day length. *Geophysical Research Letters* 43: 5716-5724.
- Beer K, Helfrich-Förster C. 2020. Model and non-model insects in chronobiology. *Frontiers in Behavioral Neuroscience* 14: 601676.
- Bertolini E, Schubert F K, Zanini D, Sehadová H, Helfrich-Förster C, Menegazzi P. 2019. Life at high latitudes does not require circadian behavioral rhythmicity under constant darkness. *Current Biology* 29: 3928-3936.
- Bloch G, Barnes B M, Gerkema M P, Helm B. 2013. Animal activity around the clock with no overt circadian rhythms: patterns, mechanisms and adaptive value. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130019.
- Bloch G, Bar-Shai N, Cytter Y, Green R. 2017. Time is honey: circadian clocks of bees and flowers and how their interactions may influence ecological communities. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160256.
- Borges R M. 2018. Dark matters: Challenges of nocturnal communication between plants and animals in delivery of pollination services. *Yale Journal of Biology and Medicine* 91: 33-42.
- Borges R M, Somanathan H, Kelber A. 2016. Patterns and processes in nocturnal and crepuscular pollination services. *Quarterly Review of Biology* 91: 389-418.
- Boyes D H, Evans D M, Fox R, Parsons M S, Pocock M J. 2021a. Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conservation and Diversity* 14: 167-187.

- Boyes D H, Evans D M, Fox R, Parsons M S, Pocock M J. 2021b. Street lighting has detrimental impacts on local insect populations. *Science Advances* 7: eabi8322.
- Brehm G, Niermann J, Jaimes Nino L M, Enseling D, Jüstel T, Axmacher J C, Warrant E, Fiedler K. 2021. Moths are strongly attracted to ultraviolet and blue radiation. *Insect Conservation and Diversity* 14: 188-198.
- Briolat E S, Gaston K J, Bennie J, Rosenfeld E J, Troscianko J. 2021. Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. *Nature Communications* 12: 4163.
- Broder E D, Elias D O, Rodríguez R L, Rosenthal G, Seymoure B M, Tingham R M. 2021. Evolutionary novelty in communication between the sexes. *Biology Letters* 17: 20200733.
- Carannante D, Blumenstein C S, Hale J D, Arlettaz R. 2021. LED lighting threatens adult aquatic insects: Impact magnitude and distance thresholds. *Ecological Solutions and Evidence* 2: e12053.
- Chen Y R, Wei W L, Tzeng D T, Owens A C, Tang H C, Wu C S, Lin S, Zhong S, Yang E C. 2021. Effects of artificial light at night (ALAN) on gene expression of *Aquatica ficta* firefly larvae. *Environmental Pollution* 281: 116944.
- Daan S, Aschoff J. 1982. Circadian contributions to survival. *In Vertebrate Circadian Systems* (Aschoff J, Daan S, Groos G A eds.) (pp. 305-321). Springer, Berlin, Heidelberg.
- Dacke M, Baird E, Byrne M, Scholtz C H, Warrant E J. 2013. Dung beetles use the Milky Way for orientation. *Current Biology* 23: 298-300.
- Dacke M, Byrne M J, Scholtz C H, Warrant E J. 2004. Lunar orientation in a beetle. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 361-365.
- Davies T W, Smyth T. 2018. Why artificial light at night should be a focus for global change research in the 21st century. *Global Change Biology* 24: 872-882.
- Deichmann J L, Ampudia Gatty C, Andía Navarro J M, Alonso A, Linares-Palomino R, Longcore T. 2021. Reducing the blue spectrum of artificial light at night minimises insect attraction in a tropical lowland forest. *Insect Conservation and Diversity* 14: 247-259.
- Denlinger D L, Hahn D A, Merlin C, Holzapfel C M, Bradshaw W E. 2017. Keeping time without a spine: what can the insect clock teach us about seasonal adaptation? *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160257.
- Deora T, Ahmed M A, Brunton B W, Daniel T L. 2021. Learning to feed in the dark: how light level influences feeding in the hawkmoth *Manduca sexta*. *Biology Letters* 17: 20210320.
- Desouhant E, Gomes E, Mondy N, Amat I. 2019. Mechanistic, ecological, and evolutionary consequences of artificial light at night for insects: review and prospective. *Entomologia Experimentalis et Applicata* 167: 37-58.
- Dominoni D M, Halfwerk W, Baird E, Buxton R T, Fernández-Juricic E, Fristrup K M, McKenna M F, Mennitt D J, Perkin E K, Seymoure B M, Stoner D C. 2020. Why conservation biology can benefit from sensory ecology. *Nature Ecology & Evolution* 4: 502-511.
- Donelson N C, Sanyal S. 2015. Use of *Drosophila* in the investigation of sleep disorders. *Experimental Neurology* 274: 72-79.
- Donners M, van Grunsven R H, Groenendijk D, van Langevelde F, Bikker J W, Longcore T, Veenendaal E. 2018. Colors of attraction: Modeling insect flight to light behavior. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329: 434-440.
- Durrant J, Green M P, Jones T M. 2020. Dim artificial light at night reduces the cellular immune response of the black field cricket, *Teleogryllus commodus*. *Insect Science* 27: 571-582.
- Dyer F C. 1985. Nocturnal orientation by the Asian honey bee, *Apis dorsata*. *Animal Behaviour* 33: 769-774.
- Eisenbeis G. 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. *In Ecological Consequences of Artificial Night Lighting* (Rich C, Longcore T, eds.) (pp. 191-198). Island Press, Washington, DC.
- Elgert C, Hopkins J, Kaitala A, Candolin U. 2020. Reproduction under light pollution: maladaptive response to spatial variation in artificial light in a glow-worm. *Proceedings of the Royal Society B* 287: 20200806.
- Elgert C, Lehtonen T K, Kaitala A, Candolin U. 2021. Sexual selection for bright females prevails under light pollution. *Current Zoology* 67: 329-331.
- Elvidge C D, Keith D M, Tuttle B T, Baugh K E. 2010. Spectral identification of lighting type and character. *Sensors* 10: 3961-3988.
- Emerson K J, Bradshaw W E, Holzapfel C M. 2008. Concordance of the circadian clock with the environment is necessary to maximize fitness in natural populations. *Evolution* 62: 979-983.
- Fenske M P, Nguyen L P, Horn E K, Riffell J A, Imaizumi T. 2018. Circadian clocks of both plants and pollinators influence flower seeking behavior of the pollinator hawkmoth *Manduca sexta*. *Scientific Reports* 8: 2842.
- Foster J, Tocco C, Smolka J, Khaldy L, Baird E, Byrne M J, Nilsson D E, Dacke M. 2021. Light pollution forces a change in dung beetle orientation behavior. *Current Biology* 31: 3935-3942.
- Fraleigh D C, Heitmann J B, Robertson B A. 2021. Ultraviolet polarized light pollution and evolutionary traps for aquatic insects. *Animal Behaviour* 180: 239-247.
- Fyie L R, Gardiner M, Meuti M E. 2021. Artificial light at night alters the seasonal responses of biting mosquitoes. *Journal of Insect Physiology* 129: 104194.
- Garrett J K, Donald P F, Gaston K J. 2020. Skyglow extends into the world's key biodiversity areas. *Animal Conservation* 23: 153-159.
- Gaston K J. 2019. Nighttime ecology: the "nocturnal problem" revisited. *American Naturalist* 193: 481-502.
- Gaston K J, Ackermann S, Bennie J, Cox DT, Phillips B, Sánchez de Miguel A, Sanders D. 2021. Pervasiveness of biological impacts of artificial light at night. *Integrative and Comparative Biology* 61: 1098-1110.
- Geissmann Q, Beckwith E J, Gilestro G F. 2019. Most sleep does not serve a vital function: Evidence from *Drosophila melanogaster*. *Science Advances* 5: eaau9253.
- Giavi S, Blösch S, Schuster G, Knop E. 2020. Artificial light at night can modify ecosystem functioning beyond the lit area. *Scientific Reports* 10: 11870.
- Giavi S, Fontaine C, Knop E. 2021. Impact of artificial light at night on diurnal plant-pollinator interactions. *Nature Communications* 12: 1690.
- Gomes E, Rey B, Débias F, Amat I, Desouhant E. 2021. Dealing with host and food searching in a diurnal parasitoid: consequences of light at night at intra-and trans-generational levels. *Insect Conservation and Diversity* 14: 235-246.
- Green R M, Tingay S, Wang Z Y, Tobin E M. 2002. Circadian rhythms confer a higher level of fitness to *Arabidopsis* plants. *Plant Physiology* 129: 576-584.
- Grubisic M, van Grunsven R H. 2021. Artificial light at night disrupts species interactions and changes insect communities. *Current*

- Opinion in Insect Science 47: 136-141.
- Grubisic M, van Grunsven R H, Kyba C, Manfrin A, Hölker, F., 2018. Insect declines and agroecosystems: does light pollution matter? *Annals of Applied Biology* 173: 180-189.
- Hall K, Robert T, Gaston K J, Hempel de Ibarra N. 2021. Onset of morning activity in bumblebee foragers under natural low light conditions. *Ecology and Evolution* 11: 6536-6545.
- Haynes K J, Robertson B A. 2021. A transdisciplinary research agenda for understanding insect responses to ecological light pollution informed by evolutionary trap theory. *Current Opinion in Insect Science* 45: 91-96.
- Helfrich F, Förster C, Bertolini E, Menegazzi P. 2020. Flies as models for circadian clock adaptation to environmental challenges. *European Journal of Neuroscience* 51: 166-181.
- Helm B, Visser M E, Schwartz W, Kronfeld-Schor N, Gerkema M, Piersma T, Bloch G. 2017. Two sides of a coin: ecological and chronobiological perspectives of timing in the wild. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372: 20160246.
- Horn M, Mitesser O, Hovestadt T, Yoshii T, Rieger D, Helfrich-Förster C. 2019. The circadian clock improves fitness in the fruit fly, *Drosophila melanogaster*. *Frontiers in Physiology* 10: 1374.
- Hut R A, Paolucci S, Dor R, Kyriacou C P, Daan S. 2013. Latitudinal clines: an evolutionary view on biological rhythms. *Proceedings of the Royal Society B: Biological Sciences* 280: 20130433.
- Jägerbrand A K, Bouroussis C A. 2021. Ecological impact of artificial light at night: Effective strategies and measures to deal with protected species and habitats. *Sustainability* 13: 5991.
- Jander R. 1963. Insect orientation. *Annual Review of Entomology* 8: 95-114.
- Kaiser W, Steiner-Kaiser J. 1983. Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature* 301: 707-709.
- Kalinkat G, Grubisic M, Jechow A, van Grunsven R H, Schroer S, Hölker F. 2021. Assessing long-term effects of artificial light at night on insects: what is missing and how to get there. *Insect Conservation and Diversity* 14: 260-270.
- Kobav M B, Erzen M, Bizjak G. 2021. Sustainable exterior lighting for cultural heritage buildings and monuments. *Sustainability* 13: 10159.
- Kobelkova A, Goto S G, Peyton J T, Ikeno T, Lee Jr R E, Denlinger D L. 2015. Continuous activity and no cycling of clock genes in the Antarctic midge during the polar summer. *Journal of Insect Physiology* 81: 90-96.
- Koritala B S, Wager C, Waters J C, Pachucki R, Piccoli B, Feng Y, Scheinfeldt, L B, Shende S M, Park S, Hozier J I, Lalakia P. 2020. Habitat-specific clock variation and its consequence on reproductive fitness. *Journal of Biological Rhythms* 35: 134-144.
- Kronfeld-Schor N, Visser M E, Salis L, van Gils J A. 2017. Chronobiology of interspecific interactions in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372: 20160248.
- Kühne J L, van Grunsven R H, Jechow A, Hölker F. 2021. Impact of different wavelengths of artificial light at night on phototaxis in aquatic insects. *Integrative and Comparative Biology* 61: 1182-1190.
- Kyba C C, Kuester T, De Miguel A S, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge C D, Gaston K J, Guanter L. 2017. Artificially lit surface of Earth at night increasing in radiance and extent. *Science Advances* 3: e1701528.
- Lee S, Chiang K, Xiong X, Sun C, Anderson S. 2014. The S-NPP VIIRS day-night band on-orbit calibration/characterization and current state of SDR products. *Remote Sensing* 6: 12427-12446.
- Levin N, Kyba C C, Zhang Q, de Miguel A S, Román M O, Li X, Portnov B A, Molthan A L, Jechow A, Miller S D, Wang Z. 2020. Remote sensing of night lights: A review and an outlook for the future. *Remote Sensing of Environment* 237: 111443.
- Levy K, Wegrzyn Y, Efronny R, Barnea A, Ayali A. 2021. Lifelong exposure to artificial light at night impacts stridulation and locomotion activity patterns in the cricket *Gryllus bimaculatus*. *Proceedings of the Royal Society B* 288: 20211626.
- Levy O, Dayan T, Porter W P, Kronfeld-Schor N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecological Monographs* 89: e01334.
- Liao Y, Rust M J. 2021. The circadian clock ensures successful DNA replication in cyanobacteria. *Proceedings of the National Academy of Sciences USA* 118: e2022516118.
- Liporoni R, Cordeiro G D, Prado P I, Schlindwein C, Warrant E J, Alves-dos-Santos I. 2020. Light intensity regulates flower visitation in Neotropical nocturnal bees. *Scientific Reports* 10: 15333.
- Longcore T, Rodriguez A, Witherington B, Penniman J F, Herf L, Herf M. 2018. Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329: 511-521.
- Mascetti G G. 2021. Adaptation and survival: hypotheses about the neural mechanisms of unihemispheric sleep. *Laterality* 26: 71-93.
- McLay L K, Green M P, Jones T M. 2017. Chronic exposure to dim artificial light at night decreases fecundity and adult survival in *Drosophila melanogaster*. *Journal of Insect Physiology* 100: 15-20.
- McMahon T A, Rohr J R, Bernal X E. 2017. Light and noise pollution interact to disrupt interspecific interactions. *Ecology* 98: 1290-1299.
- Merckx T, Nielsen M E, Heliölä J, Kuussaari M, Pettersson L B, Pöyry J, Tiainen J, Gotthard K, Kivelä S M. 2021. Urbanization extends flight phenology and leads to local adaptation of seasonal plasticity in Lepidoptera. *Proceedings of the National Academy of Sciences USA* 118: e2106006118.
- Mészáros Á, Kriska G, Egri Á. 2021. Spectral optimization of beacon lights for the protection of night-swarming mayflies. *Insect Conservation and Diversity* 14: 225-234.
- Mills P R, Tomkins S C, Schlangen L J. 2007. The effect of high correlated colour temperature office lighting on employee wellbeing and work performance. *Journal of Circadian Rhythms* 5. Doi: 10.1186/1740-3391-5-2.
- Mu H, Li X, Du X, Huang J, Su W, Hu T, Wen Y, Yin P, Han Y, Xue F. 2021. Evaluation of light pollution in global protected areas from 1992 to 2018. *Remote Sensing* 13: 1849.
- Mukai A, Yamaguchi K, Goto S G. 2021. Urban warming and artificial light alter dormancy in the flesh fly. *Royal Society Open Science* 8: 210866.
- Nikhil K L, Sharma V K. 2017. On the origin and implications of circadian timekeeping: An evolutionary perspective. *In Biological Timekeeping: Clocks, Rhythms and Behaviour*. (Kumar V. ed.) (pp. 81-129). Springer, New Delhi.
- Owens A, Lewis S M. 2021. Narrow-spectrum artificial light silences female fireflies (Coleoptera: Lampyridae). *Insect Conservation and Diversity* 14: 199-210.
- Owens A C, Cochard P, Durrant J, Farnworth B, Perkin E K, Seymoure B. 2020. Light pollution is a driver of insect declines. *Biological Conservation* 241: 108259.

- Paranjpe D A, Sharma V K. 2005. Evolution of temporal order in living organisms. *Journal of Circadian Rhythms* 3: 7 Doi: 10.1186/1740-3391-3-7.
- Paupy C, Delatte H, Bagny L, Corbel V, Fontenille, D. 2009. *Aedes albopictus*, an arbovirus vector: from the darkness to the light. *Microbes and Infection* 11: 1177-1185.
- Pauwels J, Kerbiriou C, Yves B A S, Valet N, Isabelle L E. 2021. Adapting street lighting to limit light pollution's impacts on bats. *Global Ecology and Conservation* 28: e01648.
- Rattenborg N C, Voinin B, Cruz S M, Tisdale R, Dell'Omo G, Lipp H P, Wikelski M, Vyssotski A L. 2016. Evidence that birds sleep in mid-flight. *Nature Communications* 7: 12468.
- Ren Y, Gao Y, Zhang Q. 2021. Morning and evening alarm of the circadian clock for flower opening times in *Hemerocallis*. *Plant Science* 311: 110992.
- Robertson B A, Blumstein D T. 2019. How to disarm an evolutionary trap. *Conservation Science and Practice* 1: e116.
- Robertson B A, Campbell D R, Durovich C, Hetterich I, Les J, Horváth G. 2017. The interface of ecological novelty and behavioral context in the formation of ecological traps. *Behavioral Ecology* 28: 1166-1175.
- Robertson B A, Horváth G. 2019. Color polarization vision mediates the strength of an evolutionary trap. *Evolutionary Applications* 12: 175-186.
- Rowse E G, Lewanzik D, Stone E L, Harris S, Jones G. 2016. Dark matters: the effects of artificial lighting on bats. *In Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 187-213). CC Voight and T Kingston (eds). Springer, Cham.
- Sanders D, Frago E, Kehoe R, Patterson C, Gaston K J. 2021. A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution* 5: 74-81.
- Sanders D, Kehoe R, Cruse D, van Veen F, Gaston K J. 2018. Low levels of artificial light at night strengthen top-down control in insect food web. *Current Biology* 28: 2474-2478.
- Saravanan S, Kamaladhasan N, Maruthupandian J, Basu M J, Chandrasekaran S. 2020. Beehive removal practices in urban India: Bane of bee's life? *Materials Today: Proceedings*. <https://doi.org/10.1016/j.matpr.2020.10.060>.
- Saunders D S. 2009. Circadian rhythms and the evolution of photoperiodic timing in insects. *Physiological Entomology* 34: 301-308.
- Saunders D. 2020. Insect photoperiodism: Seasonal development on a revolving planet. *European Journal of Entomology* 117: 328-342.
- Somanathan H, Borges R M, Warrant E J, Kelber A. 2008. Nocturnal bees learn landmark colours in starlight. *Current Biology* 18: R996-R997.
- Somanathan H, Krishna S, Jos E M, Gowda V, Kelber A, Borges R M. 2020. Nocturnal bees feed on diurnal leftovers and pay the price of day-night lifestyle transition. *Frontiers in Ecology and Evolution* 8: 288.
- Spalding C, Fischer W W. 2019. A shorter Archean day-length biases interpretations of the early Earth's climate. *Earth and Planetary Science Letters* 514: 28-36.
- Stewart A J. 2021. Impacts of artificial lighting at night on insect conservation. *Insect Conservation and Diversity* 14: 163-166.
- Stracey C M, Wynn B, Robinson S K. 2014. Light pollution allows the northern mockingbird (*Mimus polyglottos*) to feed nestlings after dark. *The Wilson Journal of Ornithology* 126: 366-369.
- Thompson E K, Cullinan N L, Jones T M, Hopkins G R. 2019. Effects of artificial light at night and male calling on movement patterns and mate location in field crickets. *Animal Behaviour* 158: 183-191.
- Tielens E K, Cimprich P M, Clark B A, DiPilla A M, Kelly J F, Mirkovic D, Strand A I, Zhai M, Stepanian P M. 2021. Nocturnal city lighting elicits a macroscale response from an insect outbreak population. *Biology Letters* 17: 20200808.
- Tierney S M, Friedrich M, Humphreys W F, Jones T M, Warrant E J, Wcislo W T. 2017. Consequences of evolutionary transitions in changing photic environments. *Austral Entomology* 56: 23-46.
- Tobler I, Neuner-Jehle M. 1992. 24-h variation of vigilance in the cockroach *Blaberus giganteus*. *Journal of Sleep Research* 1: 231-239.
- Toure M W, Young F J, McMillan W O, Montgomery S H. 2020. Heliconiini butterflies can learn time-dependent reward associations. *Biology Letters* 16: 20200424.
- Van den Broeck M, De Cock R, Van Dongen S, Matthysen E. 2021a. Blinded by the light: Artificial light lowers mate attraction success in female glow-worms (*Lampyrus noctiluca* L.). *Insects* 12: 734.
- Van den Broeck M, De Cock R, Van Dongen S, Matthysen E. 2021b. White LED light intensity, but not colour temperature, interferes with mate-finding by glow-worm (*Lampyrus noctiluca* L.) males. *Journal of Insect Conservation* 25: 339-347.
- Van Geffen K G, Groot A T, Van Grunsven R H, Donners M, Berendse F, Veenendaal E M. 2015. Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology* 40: 401-408.
- Van Langevelde, F, Braamburg-Annegarn M, Huigens M E, Groendijk R, Poitevin O, van Deijk J R, Ellis W N, van Grunsven R H, de Vos R, Vos R A, Franzén M. 2018. Declines in moth populations stress the need for conserving dark nights. *Global Change Biology* 24: 925-932.
- Van Langevelde F, Van Grunsven R H, Veenendaal E M, Fijen T P. 2017. Artificial night lighting inhibits feeding in moths. *Biology Letters* 13: 20160874.
- Vaz S, Manes S, Gama-Maia D, Silveira L, Mattos G, Paiva P C, Figueiredo M, Lorini M L. 2021. Light pollution is the fastest growing potential threat to firefly conservation in the Atlantic Forest hotspot. *Insect Conservation and Diversity* 14: 211-224.
- Wagner D L, Grames E M, Forister M L, Berenbaum M R, Stopak D. 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences USA* 118: e2023989118.
- Walton R E, Sayer C D, Bennion H, Axmacher J C. 2020. Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Biology Letters* 16: 20190877.
- Westby K M, Medley K A. 2020. Cold nights, city lights: Artificial light at night reduces photoperiodically induced diapause in urban and rural populations of *Aedes albopictus* (Diptera: Culicidae). *Journal of Medical Entomology* 57: 1694-1699.
- Wilson A, Seymoure B M, Jaeger S, Milstead B, Payne H, Peria L, Vosbigian R A, Francis C D. 2021. Direct and ambient light pollution alters recruitment for a diurnal plant-pollinator system. *Integrative and Comparative Biology* Doi: 10.1093/icb/icab010.
- Young A M, Kohl P L, Rutschmann B, Steffan-Dewenter I, Brockmann A, Dyer F C. 2021. Temporal and spatial foraging patterns of three Asian honeybee species in Bangalore, India. *Apidologie* 52: 503-523.
- Zielińska-Dabkowska K M, Xavia K, Bobkowska K. 2020. Assessment of citizens' actions against light pollution with guidelines for future initiatives. *Sustainability* 12: 4997.