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Biological Conservation xxx (xxxx) xxxx

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Short communication

Light pollution is a driver of insect declines

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ARTICLE INFO

Keywords:
ALAN
Light pollution
Skyglow
Insect apocalypse
Insect declines
Insect conservation

ABSTRACT

Insects around the world are rapidly declining. Concerns over what this loss means for food security and ecological communities have compelled a growing number of researchers to search for the key drivers behind the declines. Habitat loss, pesticide use, invasive species, and climate change all have likely played a role, but we posit here that artificial light at night (ALAN) is another important—but often overlooked—bringer of the insect apocalypse. We first discuss the history and extent of ALAN, and then present evidence that ALAN has led to insect declines through its interference with the development, movement, foraging, and reproductive success of diverse insect species, as well as its positive effect on insectivore predation. We conclude with a discussion of how artificial lights can be tuned to reduce their impact on vulnerable populations. ALAN is unique among anthropogenic habitat disturbances in that it is fairly easy to ameliorate, and leaves behind no residual effects. Greater recognition of the ways in which ALAN affects insects can help conservationists reduce or eliminate one of the major drivers of insect declines.

1. Introduction

Over the last two decades, researchers have uncovered steep declines in insect diversity and biomass (Dirzo et al., 2014; Potts et al., 2010) across geographically distinct areas including Germany (Hallmann et al., 2017), the Netherlands (van Langevelde et al., 2018; van Strien et al., 2019), Sweden (Franzén and Johannesson, 2007), the British Isles (Powney et al., 2019; Shortall et al., 2009; Wilson et al., 2018), Puerto Rico (Lister and Garcia, 2018), and Costa Rica (Janzen and Hallwachs, 2019). This alleged "insect apocalypse" (Jarvis, 2018) has generated an appropriate amount of public concern: insects are a critical component of all terrestrial and freshwater food webs (Baxter et al., 2005; van Veen et al., 2006) and provide important ecosystem services (Schowalter et al., 2018). Their absence would have devastating consequences for life on this planet. If insect decline is indeed a global phenomenon (see Wagner, 2019), the question then becomes: What is the problem, and how can we best address it? One recent review of insect decline has sought to identify the main causes by ranking potential drivers in order of their frequency of mention within relevant literature (Sánchez-Bayo and Wyckhuys, 2019). The authors found, as indeed have we, that habitat loss, chemical pollution (especially pesticide use), invasive species, and climate change are the most well-described threats to insect persistence. However, we do not agree that relative degree of scientific consideration reflects importance in this case. Instead we posit that "diurnal bias"—a preference among ecologists for studying daytime phenomena (Gaston, 2019)—has led insect conservationists to overlook another widespread habitat disturbance, pollutant, and method of insect control: artificial light at night (ALAN).

Although discrete sources of anthropogenic light have been used to kill insects since *circa* 60 CE (Beavis, 1995), the modern phenomenon of ecological light pollution began in earnest with the invention of the arc lamp in the early 1800s (Dillon and Dillon, 2002; Saunders, 1887). Soon after, dedicated "light traps" were adopted as a common method of pest control (U.S. Patent, 4808), and are indeed still used for this purpose today (Johansen et al., 2011; Pawson et al., 2009; Shimoda and Honda, 2013); around the 1950s, light traps became popular among entomologists for use in surveying insect biodiversity (Leather, 2015). More recently, as lighting technology has advanced and the cost per unit of brightness declined, both the intensity and quantity of artificial light installations have increased worldwide (Kyba, 2018; Kyba et al.,

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https://doi.org/10.1016/j.biocon.2019.108259
Received 26 April 2019; Received in revised form 26 August 2019; Accepted 20 September 2019
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Please cite this article as: Avalon C.S. Owens, et al., Biological Conservation, https://doi.org/10.1016/j.biocon.2019.108259

2017; Tsao et al., 2010). Modern light pollution is no longer confined to urban centers, but radiates outwards through the atmosphere and along road networks that run into or around otherwise pristine areas (Gaston et al., 2015; Gaston and Holt, 2018; Guetté et al., 2018). Since 1992, levels of light pollution have doubled in high biodiversity areas, and are likely to continue to rise (Koen et al., 2018; Kyba et al., 2017). By 2014, over 23% of the land surface of the planet experienced artificially elevated levels of night sky brightness (Falchi et al., 2016); by comparison, agricultural crops cover approximately 12% (FAO, 2012). Insect conservationists now frequently lament, as do we, the dearth of insects to be found swarming around artificial lights (*e.g.* Janzen and Hallwachs, 2019), yet rarely consider that the lights themselves may be an issue.

Artificial light at night is a potent evolutionary trap (Schlaepfer et al., 2002; Altermatt and Ebert, 2016; Hopkins et al., 2018). Most anthropogenic disturbances have natural analogs: the climate has warmed before, habitats have fragmented, species have invaded new ranges, and new pesticides (also known as plant defenses) have been developed. Yet for all of evolutionary time, the daily cycle of light and dark, the lunar cycle, and the annual cycle of the seasons have all remained constant. Until now (Altermatt and Ebert, 2016), insects have had no cause to evolve any relevant adaptations to ALAN. And so some species retreat from streetlights (Farnworth et al., 2018) while others for unclear reasons perch beneath them, stunned, or circle around them until claimed by injury, exhaustion, or predation (Frank, 1988; Owens and Lewis, 2018). While the total fitness impact of an artificial light source will depend on its intensity, direction, spectral distribution (Elvidge et al., 2010), and flicker rate (Inger et al., 2014), as well as the time of day and structure of nearby surfaces (Horváth et al., 2009; Szaz et al., 2015), the light output of most common fixtures is more than enough to radically disturb the entire habitat of small-bodied animals such as insects. Insects that manage to escape the cone of light beneath a fixture can still be affected by skyglow, which emanates far beyond urban centers at levels sufficient to obscure or alter vital environmental cues including polarized moonlight, starlight, moon phase, and day-length (Davies et al., 2013b; Kyba et al., 2011a; 2011b).

A growing body of research demonstrates that ALAN can impact the fitness of plants and animals (Bennie et al., 2016; Gaston et al., 2013), and more recent reviews have catalogued its broadscale effects on insects in particular (Desouhant et al., 2019; Grubisic et al., 2018; Owens and Lewis, 2018; Seymoure, 2018). Some estimates suggest that one third of insects attracted to stationary artificial light sources die before morning, either through exhaustion or predation (Eisenbeis, 2006; Frank, 2006; Yoon et al., 2010); insects attracted to vehicle headlights likely die immediately (Frank, 2006; Gaston and Holt, 2018). This "fatal attraction" has been estimated to result in 100 billion insect deaths per summer in Germany (Eisenbeis and Hänel 2009) and had the potential to swiftly eliminate isolated populations of *Hydraecia petasitis* moths in Finland (Väisänen and Hublin, 1983; see also Cantelo et al., 1972). Insects that escape immediate death may still become trapped in a "light sink," unable to engage in behaviors vital to fitness (van Langevelde et al., 2017). The potential for individual deaths to compound into large-scale declines (Kokko and Sutherland, 2001) has been borne out by the results of a 30 year survey of Dutch macromoths (van Langevelde et al., 2018), during which time positively phototactic and nocturnal species underwent steeper declines than diurnal species not attracted to light. A similar survey of macromoths in the UK and Ireland found greater losses at light polluted sites (Wilson et al., 2018), even after controlling for urbanization (Bates et al., 2014), and that nocturnal species once again underwent disproportionate declines (Coulthard et al., 2019). However, a small number of studies have found disproportionate declines in day-active insect species instead (Franzén and Johannesson, 2007).

One complicating factor is the fact that temporal niche partitioning between diurnal and nocturnal species has become less extreme in response to human activity (Ditchkoff et al., 2006; Gaynor et al., 2018; Levy et al., 2019). At the same time, deforestation and habitat fragmentation have reduced the availability of dark refuges for all species (reviewed in Seymoure, 2018). If ALAN is contributing to a worldwide decline of entomofauna, insects that occupy open habitats should be more threatened than those that occupy closed habitats, and terrestrial and aquatic species more so than fossorial species—as indeed they are (Coulthard et al., 2019; Fox et al., 2014; Franzén and Johannesson, 2007; Guerra Alonso et al., 2019; Paukkunen et al., 2018; Potocký et al., 2018; Sánchez-Bayo and Wyckhuys, 2019; van Strien et al., 2019), although few have viewed these trends with light in mind.

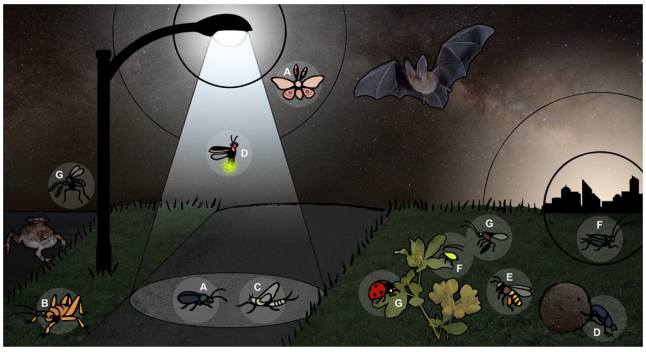

Fig. 1. Both local sources of artificial light (**left**) and diffuse skyglow (**right**) can impact the physiology, behavior, and fitness of insects. Positively phototactic insects, including macromoths and beetles, exhibit a "fatal attraction" to ALAN (**A**), while negatively phototactic insects such as weta avoid it (**B**). ALAN also amplifies polarized light pollution, causing mayflies and other aquatic insects to oviposit on non-aquatic flat surfaces (**C**). Skyglow obscures natural nocturnal light sources (**D**), including the astronomical cues used by dung beetles to navigate and the bioluminescent signals produced by fireflies and other insects, with consequences for foraging and reproductive success in these species. In the short term, ALAN can alter circadian patterns of activity and rest (*E*), causing diurnal pollinators and insectivores to extend their foraging bouts into the evening, while fully nocturnal insects delay their nightly emergence. Over the long term, these repeated perturbations have been shown to alter the development and phenology of crickets and aphids (**F**). The resulting phenological mismatches between host plants, predators, and prey will have cascading effects on pollination success, host-parasite interactions, and eventually entire food webs (**G**). Textures modified from Creative Commons Attribution 2.0 Generic licensed images (Wikimedia Commons, Flickr; Milky Way: John Fowler; túngara frog: Geoff Gallice; Townsend's big-eared bat: National Parks Service).

We argue here that ALAN impacts the vital biological functions of nocturnal and diurnal insects alike in ways both related and unrelated to flight-to-light behavior (Fig. 1). ALAN can cause immediate behavioral change, or more complex behavioral expression of physiological changes induced by external timekeeping signals (*i.e.Zeitgebers*); both changes may be triggered by certain wavelengths of light only. ALAN can also interact with other anthropogenic disturbances such as climate change or noise pollution in complex ways (McMahon et al., 2017; Miller et al., 2017; Walker et al., 2019). For example, pollinator insects pushed from agricultural fields to road verges by pesticides will be more exposed to streetlights and vehicle headlights (Phillips et al., 2019). Impacts on single species will have downstream effects on other members of the food web, the outcome of which can be extremely difficult to predict (Sanders and Gaston, 2018). To keep this review in scope, we focus here on the way in which ALAN impacts several vital fitness-related behaviors of insects on the individual level. We also discuss some of the potential consequences for insect populations, many of which are just now becoming apparent (Table 1)

2. Movement

Large-scale seasonal migration and small-scale daily movements in pursuit of food or habitat both play a crucial role in maintaining the fitness of insect species (Hammock and Wetzel, 2013; Rankin, 1985),

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Table 1
Examples of the effects of ALAN on vital fitness-related behaviors in diverse insect taxa. **RESPONSE to ALAN** adapted from Owens and Lewis (2018): positive and negative phototaxis refer to impulsive movement towards or away from a light source; spatial disorientation connotes an impaired ability to navigate due to altered environmental cues; temporal disorientation arises from the disruption of circadian rhythms; altered recognition refers to the impact of additional and/or spectrally unnatural illumination on the perception of visual cues; indirect effects are the bottom-up or top-down effects of ALAN on food plants, prey, hosts, or natural enemies. Citations given **in bold** have directly shown the described impact of ALAN on insect fitness; while other citations show a clear potential for the described impact, ALAN was not a focus of these studies.

BEHAVIOR	RESPONSE to ALAN	FITNESS COST	EXAMPLE TAXON	citation(s)
development	*temporal disorientation*	juvenile insects exposed to ALAN experience accelerated, slowed, or impaired growth	field crickets	**Durrant et al., 2018**
movement	*positive phototaxis*	insects caught in the orbit of artificial lights are trapped, unable to advance or retreat	macromoths	**Somers-Yeates et al., 2013**
	negative phototaxis	insects that avoid moving through or around lit areas are unable to effectively disperse	aquatic insects	Perkin et al., 2014a,
	spatial disorientation	ALAN obscures orientational cues such as the moon or stars, and thus impedes navigation	sand hoppers	Ugolini et al., 2005
	temporal disorientation	ambient illumination inhibits nocturnal activity, including locomotion, in night-active insects	leafhoppers	Shi et al., 2017
foraging	*positive phototaxis*	insects trapped around or under artificial lights do not engage in normal foraging behavior	insect pollinators	Knop et al., 2017
	negative phototaxis	insects that avoid lit areas are unable to capitalize on the foraging opportunities within	tree and cave weta	Farnworth et al., 2018
	temporal disorientation	insects that shift to new temporal niches are physiologically unprepared to forage therein	dung beetles	Caveney et al., 1995
	altered recognition	unnatural spectra obscure the visual signals insects use to identify food sources or hosts	parasitoid wasps	Cochard et al., 2017
	indirect effects	the impact of ALAN on plant growth decreases food availability for herbivorous insects	pea aphids	Bennie et al., 2018a
reproduction	*sex-biased phototaxis*	disproportionate attraction to ALAN skews the effective sex ratio in insect populations	winter moths	van Geffen et al., 2015b
	temporal disorientation	physiological effects of ALAN lead to sterility or decreased fecundity of adult reproductives	fruit flies	McLay et al., 2017
	altered recognition	ALAN obscures or masks the visual signals that insects use to find and court potential mates	firefly beetles	Owens and Lewis, 2018
predation	*positive phototaxis*	insects trapped around or under artificial lights are vulnerable to exploitation by predators	giant water bugs	Yoon et al., 2010
	altered recognition	unnatural spectra obscure aposematic coloration and/or camouflage in prey insects	*Heliconius* butterflies	Seymoure, 2016
	indirect effects	increased illumination allows visually guided insectivores to hunt more effectively	lady beetle prey	Miller et al., 2017

and are necessary to the recovery of at-risk metapopulations (Schultz et al., 2019). The attractive and repulsive effects of discrete sources of artificial light are well known to prevent natural patterns of movement (Allema et al., 2012) and alter the distribution of insects in a landscape away from the evolved baseline (Degen et al., 2016; Macgregor et al., 2017; Manfrin et al., 2017; Manríquez et al., 2019; Šustek, 1999; but see Grenis et al., 2015; White, 2018). The fitness repercussions of "fatal attraction" are described above, and not covered in any more detail here. Lines of closely spaced streetlights, as are found along most major roads, can also act as a barrier to the movement of positively and negatively phototactic species alike (Degen et al., 2016; Eisenbeis, 2006), effectively fragmenting major swaths of otherwise suitable habitat. For example, the drift rates of negatively phototactic immature aquatic insects are significantly lower in the presence of riverside lighting (Henn et al., 2014; Perkin et al., 2014a), and their adult forms prevented from moving between streams or colonizing new streams (Perkin et al., 2014b).

Nocturnal light signals serve an important role in the orientation of many insect species (reviewed in Foster et al., 2018; Owens and Lewis, 2018). For example, *Scarabaeus satyrus* dung beetles use the stars and dim patterns of polarized starlight to efficiently navigate away from dung piles (Dacke et al., 2013), while *Talitrus saltator* sand hoppers maintain a route parallel to the shoreline on their nightly excursions by moving with respect to the moon (Ugolini et al., 2005). These signals can be partially or fully obscured in light polluted habitats (Davies et al., 2013b; Kyba et al., 2011a; 2011b); lunar signals also face competition from overhead sources of artificial light (*e.g.* streetlights; Sotthibandhu and Baker, 1979). Upwelling light (*e.g.* path lighting) can further disorient flying insects such as wasps and dragonflies that maintain a horizontal position in the air by keeping the more illuminated half of their visual field always overhead (Berry et al., 2011; Goodman, 1965). In fact, both upwelling and downwelling artificial lights are intentionally used in agriculture to suppress the movement and abundance of pest insects (Loughlin, 2014; Miller et al., 2015; Shi et al., 2017; Shimoda and Honda, 2013), yet we wonder why more desirable species have stopped visiting our increasingly illuminated backyards.

3. Foraging

Artificial light at night can interfere with efficient acquisition of food, vital to the developmental and reproductive success of insects (Wenninger and Landolt, 2011), in several ways. Diurnal and crepuscular insects that move their foraging activity into the "night light niche" (Garber, 1978) must endure cold stress (Caveney et al., 1995; Urbanski et al., 2012), while nocturnal insects that continue to forage alongside may experience reduced rates of growth due to increased competition and/or what is effectively a reduction in their spatial niche (Duarte et al., 2019). Insects avoid profitable foraging patches under illumination due to perceived (Skutelsky, 1996) or actual increases in their risk of predation by invertebrate (Heiling, 1999; Miller et al., 2017), avian (Dwyer et al., 2013, and mammalian insectivores (Rydell, 2006). For example, the reduced presence of tree (*Hemideina thoracica*) and cave (Rhaphidophoridae sp.) weta at artificially illuminated sites is thought to be in avoidance of geckos and other nocturnal predators (Farnworth et al., 2018).

Nocturnal insects that postpone foraging until their habitat is sufficiently dark (Dreisig, 1980) are likely to be negatively affected by a reduction in temporal niche (Tierney et al., 2017). For example, in laboratory environments exposure to dim ALAN is linked to less frequent feeding in several moth species (van Langevelde et al., 2017). *Orchestoidea tuberculata* sand hoppers consume less food under ALAN, and grow less (Luarte et al., 2016). Tasmanian cave glow-worms (*Arachnocampa tasmaniensis*) extinguish their bioluminescent lures when exposed to artificial light (Merritt and Clarke, 2013), and could therefore starve under constant cave lighting. In the field, pollinators that

delay their nightly forage due to the day lengthening effects of skyglow are likely to become desynchronized from their food plants, especially in cases where flower opening is cued by temperature instead of light (Seymoure, 2018; Somanathan et al., 2008; van Doorn and Van Meeteren, 2003). Differences in the environmental cues used to guide development of insects and their food plants result in increasingly exaggerated desynchronization over the course of the growing season (Forrest and Thomson, 2011; Laube et al., 2014) and decrease pollinator effectiveness (Rafferty and Ives, 2012).

Artificial light at night might also cause unexpected trophic cascades through its effects on plants (Bennie et al., 2016; Schroer et al., 2019) or insect natural enemies (see Predation). For example, ALAN stunts the growth of larval cutworms (*Apamea sordens*) by increasing the cuticle toughness of their smooth brome host plants (Grenis and Murphy, 2018). By decreasing the flower abundance of pea plants (Bennie et al., 2018a, 2016), ALAN has also been shown to impact pea aphids (*Acyrthosiphon pisum*) (Bennie et al., 2018b) as well as the parasitoid wasps (*Aphidius* megourae; *Lysiphlebus fabarum* and *Aphidius ervi*) that prey upon them (Sanders et al., 2018, 2015). When food is available, and foraging insects present and active, ALAN can still impact foraging success. Unnatural spectra may obscure the particular visual cues that tobacco hornworm moths (*Manduca sexta*) and other insects use to identify flowers, plants, or prey (Cutler et al., 1995; Davies et al., 2013a; Streinzer et al., 2019). For example, monochromatic red illumination has been found to decrease the rate at which parasitoid wasps encounter their pea aphid hosts (Cochard et al., 2017; 2019a, 2019b). Finally, ALAN can incapacitate positively phototactic insects such as giant water bugs (*Lethocerus deyrolli;*Choi et al., 2009; Yoon et al., 2010) and macromoths (Somers-Yeates et al., 2013) that might otherwise spend the evening engaged in foraging activities, including nocturnal pollination (Knop et al., 2017; Macgregor et al., 2015).

4. Reproduction

ALAN can delay or eliminate the window of time during which night-active insects engage in courtship and mating (Dreisig, 1975; Lall, 1993; Li et al., 2019). The corn earworm moth (*Helicoverpa zea*) never mates when ambient light levels are above that produced by a quarter moon (Agee, 1969), and other strictly nocturnal insects are likely similarly sensitive, but understudied. The insects that manage to maintain a nightly routine within light polluted habitats may still have difficulty locating suitable mates. Firefly beetles are one unique example: the courtship of most fireflies requires the exchange of bioluminescent signals, which are obscured or inhibited by artificial illumination (Firebaugh and Haynes, 2016; Owens et al., 2018) to the point that receptive *Lampyris noctiluca* females perched underneath streetlights are never visited by male conspecifics (Ineichen and Rüttimann, 2012). In certain cases, these females must compete with the streetlights to attract males (Bek, 2015). Other insects may see but be unable to recognize conspecifics: male crepuscular horned beetles (*Coprophanaeus lancifer*) have a coloration that reflects the purplish light of dusk, and will be less apparent to females when lit by artificial light of a different spectral composition (Davies et al., 2013a; Kelley et al., 2019; Théry et al., 2008).

ALAN can also impact the reproductive success of insects directly through its various effects on development and physiology (Honnen et al., 2016). Exposure to constant light is known to sterilize males (Bebas et al., 2001; Giebultowicz et al., 1990), suppress female sex pheromones (Fatzinger, 1973; van Geffen et al., 2015a), and interfere with oviposition in moths (Nemfc, 1971; Yamaoka and Hirao, 1981) – likely a result of its disruption of the circadian timing of reproductive development or behavior. Similarly, exposure to dim ALAN decreases the fecundity of *Drosophila melanogaster* (McLay et al., 2017). Exposure to different ratios of blue or red light at night significantly alters the sex ratio of parasitoid wasps (Cochard et al., 2019a, 2019b), and may impact other insect species as well. The effective sex ratio of surviving reproductives can be further altered by the differential impacts of ALAN on behavior: for example, male tree weta avoid illuminated areas but female tree weta do not (Farnworth et al., 2018), and female winter moths (*Operophtera brumata*) avoid illuminated tree trunks (van Geffen et al., 2015b). In general, female moths tend to be less strongly attracted to artificial lights than males of the same species (Altermatt et al., 2009; Garris and Snyder, 2010; van Geffen et al., 2015b). Those that can be found at light traps are often gravid (Frank, 1988) and may be compelled to oviposit in the immediate area regardless of habitat suitability. Perhaps most dramatically, polarized light pollution frequently misleads aquatic insects into ovipositing on non-aquatic, impermeable surfaces (Szaz et al., 2015; Villalobos Jiménez and de, 2017), efficiently decimating subsequent generations.

5. Predation

Insects that become caught in the orbit of artificial lights can be readily exploited by insectivores. This may be why predatory arthropods tend to be disproportionately represented in illuminated habitats (Davies et al., 2017, 2012; Eccard et al., 2018; Manfrin et al., 2017), just as insectivorous bats (Jung and Kalko, 2010; Minnaar et al., 2015; Russo et al., 2019; Rydell, 2006), rats (Yoon et al., 2010), shorebirds (Dwyer et al., 2013), geckos (Zozaya et al., 2015) and cane toads (González-Bernal et al., 2016) are often found feeding around artificial lights. Orb-web spiders prefer to build their webs near artificial lights, where they net more prey (Czaczkes et al., 2018; Heiling, 1999; Yuen and Bonebrake, 2017). Diurnal predators such as jumping spiders (Frank, 2009; Wolff, 1982) and anoles (Garber, 1978) have also been described hunting for insects at lights at night (Manfrin et al., 2018), while birds are known to feed on aquatic insects trapped by polarized light pollution (Robertson et al., 2010). In general, prey insects do not appear able to defend against the increased predation pressure. To the contrary, a wide variety of moth species willingly approach streetlights monitored by foraging bats (Acharya and Fenton, 1999), where they are less able to execute their normal evasive flight behavior (Minnaar et al., 2015; Svensson and Rydell, 1998).

Predators do not only benefit from the dense aggregation of insect prey under artificial lights, but also the increased visibility, which is thought to benefit visually oriented vertebrate insectivores including some birds (Dwyer et al., 2013; Santos et al., 2010) and fish (Meyer and Sullivan, 2013). Other invertebrate predators may also benefit: pea aphids are more frequently predated by visually oriented lady beetles (*Coccinella septempunctata*) under ALAN, but not by lady beetles that use non-visual cues to hunt (Miller et al., 2017). When light levels are too bright, however, some predatory and parasitoid insects themselves succumb to its suppressive effects on foraging behavior (Eccard et al., 2018; Sanders et al., 2018, 2015). Finally, alterations to the intensity and spectra of the nocturnal light environment can interfere with visual signals, which play an important role the predator-prey arms race. The aposematic glows of larval fireflies (Branham and Wenzel, 2003; Leavell et al., 2018) and the aposematic coloration of *Heliconius* butterflies (Seymoure, 2016) are likely to become less apparent under ALAN, as these and other warning signals have evolved to maximize visibility within particular natural light environments. Camouflage has also evolved within environments illuminated solely by natural sources (Davies et al., 2013a; Delhey and Peters, 2017), and could become ineffectual when viewed under ALAN. In some cases, intelligent predators given the opportunity to observe insects perched beneath artificial lights may become better at recognizing them in natural light environments (Frank, 2006). Whenever evolutionary traps increase predation risk in this way, they are likely to cause the rapid extinction of affected species (Kokko and Sutherland, 2001; Robertson et al., 2018).

6. Development

Artificial light at night can interfere with the development of

immature insects by directly inhibiting or promoting nocturnal or diurnal foraging activity (see **Foraging**), or by interfering with the production of a suite of endocrine hormones (Ouyang et al., 2018; Russart and Nelson, 2018a) and the processes that they regulate, including circadian rhythms (Aulsebrook et al., 2018; Dominoni et al., 2016) and metabolic function (Gaston et al., 2017; Marcheva et al., 2013). One insect hormone particularly affected by environmental light – especially short wavelength light (Aubé et al., 2013; Lampel et al., 2005) – is melatonin. Melatonin is an active antioxidant (Durrant et al., 2019; Jones et al., 2015; Tan et al., 2010) and key biological signal (Hardeland and Poeggeler, 2003), which is primarily produced in darkness and suppressed by blue light. Its daily oscillation helps to regulate circadian rhythms of activity as well as circannual photoperiodism (Desouhant et al., 2019; Evans et al., 2007; Tan et al., 2010).

Previous research into the circadian rhythms of insects has used regimens of constant darkness or light to elucidate the fitness costs of total arrhythmicity (Winfree, 1974), which include impaired immune function, reduced fecundity, and a shorter lifespan (Durrant et al., 2015; Kouser and Palaksha Shakunthala, 2014). Other subtler fitness costs may arise from the mistiming of crucial life history events. For example, many insect species synchronize certain developmental activities with particular times of day: for example, *Drosophila jambulina* fruit flies eclose before dawn when ambient temperature and humidity are optimal (Thakurdas et al., 2009), while intertidal midges (*Pontomyia oceana* and *Clunio* spp.) eclose during periods of low tide (Neumann, 1989; Soong et al., 2011); improper timing could cause fruit flies to desiccate and intertidal midges to drown.

Artificially lengthened photoperiods delay the development of insects that overwinter as juveniles, including locusts (*Locusta migratoria;* Tanaka et al., 1993) and thrips (*Megalurothrips sjostedti;* Ekesi et al., 1999), while accelerating the development of multivoltine lady beetles (*Coelophora saucia*; Omkar and Pathak, 2006), aphids (*Megoura viciae;* Kehoe et al., 2018) and flower bugs (*Orius sauteri;* Wang et al., 2013). By effectively lengthening photoperiod, and potentially suppressing melatonin production, ALAN prolongs juvenile development in black field crickets (*Teleogryllus commodus;* Durrant et al., 2018), but accelerates development in orb-web spiders (*Eriophora biapicata;* Willmott et al., 2018). Short-wavelength light speeds up the pupal development of cabbage moths (*Mamestra brassicae;* van Geffen et al., 2014), while red light has no effect. ALAN also causes aphids that exhibit seasonal polyphenism to maintain their summer form well into autumn (Sanders et al., 2015), and horse-chestnut leafminers (*Cameraria ohridella*) to undergo more generations per season (Schroer et al. 2019); both of these changes likely lead to cold stress. Whether ALAN slows or speeds development in a certain species is ultimately immaterial: whenever insects are desynchronized from their external climate, conspecifics, host plants, food sources, *etc*., the survival, reproduction and general fitness consequences are catastrophic (Boggs and Inouye, 2012; Bosch et al., 2010; Buckley et al., 2017; Conrad et al., 2003; Konvička et al., 2016; Kudo and Ida, 2013; Miller-Rushing et al., 2010; Schenk et al., 2018).

7. Recommendations

We still have yet to fully understand how diverse insect taxa respond to artificial light of varying spectral composition, intensity, polarization, and flicker. To make matters more complicated, old fashioned bulb types often release large amounts of heat (Elvidge et al., 2010), while some modern LED fixtures emit ultrasonic frequencies that could have compounding effects on insect fitness (John Swaddle, *pers. comm.*). A combination of insect electroretinography and thoughtfully controlled behavioral studies (Cronin et al., 2014) may reveal ways of reducing the ecological consequences of ALAN on insects while still maintaining sufficient levels of nighttime illumination for human safety and enjoyment. In general, efforts to mitigate ALAN driven declines in insect diversity and biomass should take a spectral, spatial, and temporal approach (Bruce-White and Shardlow, 2011).

Monochromatic LEDs can be engineered to produce light of any desired spectral composition (Pimputkar et al., 2009). Therefore, once we know the specific wavelength affinities of insects, we can in theory design lights with minimal output in the wavelengths that most affect insect fitness. Many insects are capable of perceiving ultraviolet wavelengths, but are fairly insensitive to red, deep red, and infrared (Briscoe and Chittka, 2001; Lind et al., 2017). Long wavelength light (amber or red) tends to induce relatively low levels of flight-to-light behavior across insect groups (Donners et al., 2018; Longcore et al., 2018; Seymoure et al., 2019; Spoelstra et al., 2015), and has the least suppressive effect on melatonin production (Dauchy et al., 2016; Do et al., 2009; Russart and Nelson, 2018b), which may reduce impacts on insect physiology and development (Desouhant et al., 2019; Do et al., 2009; Jones et al., 2015; Russart and Nelson, 2018b; Saunders, 2012). However, the spectral needs of certain insect (Bek, 2015; Pacheco et al., 2016; Spoelstra et al., 2015; van Langevelde et al., 2017) and non-insect taxa such as plants, fish, and birds (Bennie et al., 2016; Dominoni, 2015; Seymoure et al., 2019) do not always align. Furthermore, many monochromatic LED fixtures on the market today are so bright, with such a broad full width at half maximum (FWHM, a measure of the proportion of photons emitted on either side of the peak wavelength), that their color as stated is not particularly relevant.

In many cases, it is far easier, quicker, and cheaper to shield, dim, or turn off a light source than it is to find the particular bulb type or narrow bandpass filter that makes its emissions visible to humans alone. Spatial mitigation of ALAN must involve the installation of proper shielding, but shielding alone is insufficient: it may block glare at human eye level and reduce atmospheric skyglow, but it will not prevent downwelling light from affecting insects in the immediate habitat; stationary insects, including pond-dwelling aquatic species and most female fireflies, may be completely incapacitated by a perfectly shielded streetlight. Rather than focusing overly much on shielding, insect conservation efforts should instead be directed towards the following methods of spatial mitigation: limiting illumination to desired areas such as sidewalks or roads; dimming light sources to the lowest acceptable intensity; and—perhaps most importantly—reducing the number of fixtures installed in and around ecologically vulnerable areas. In ecotourist hotspots, path lights might be shielded from the top *and* the bottom to minimize their impact on nearby biodiversity. Increased understanding of how insects are affected by “invisible” qualities of light including polarization (Egri et al., 2017; Száz et al., 2016) and flicker rate (Barroso et al., 2017; Inger et al., 2014; Shields, 1989) can further inform the design of low-impact fixtures as well as their surrounding surfaces. Finally, temporal approaches comprising motion activation and/or automatic timers that extinguish lights when they are not needed, or when vulnerable species are likely to be most affected (*e.g.* during the two month long courtship season of the common glow-worm; (Gardiner, 2011), can greatly improve insect survivorship.

8. Conclusion

Some estimates predict that one million species, including up to 40% of insects, will go extinct within the next several decades (IPBES, 2019; Sánchez-Bayo and Wyckhuys, 2019). It is urgent therefore that we seek to identify the range of threats that insects face, and understand how to best address them. In light of the evidence presented above, we strongly believe that ALAN—in combination with habitat loss, chemical pollution, invasive species, and climate change—is driving insect declines. The relative lack of research into its ecological impact is likely a reflection of diurnal bias (Gaston, 2019), and not due to an inherent lack of importance. Quite the contrary: light is the source of all life on this planet, a fundamental part of the perceptive ability of most animal taxa, and an environmental cue of time of day and year that has been constant throughout all of evolutionary history. Anthropogenic changes

to the natural light environment should be predicted to affect all life that has evolved within it—that is to say, almost all life on Earth.

In this paper we have summarized numerous studies demonstrating the ways in which ALAN impacts nocturnal and diurnal insects through effects on movement, foraging, reproduction, predation risk, and development. We would like to emphasize that ALAN is not merely a subcategory of urbanization: the ecological consequences of light pollution are not limited to urban and suburban centers, but widespread along roadways and around protected areas. Although there is obviously no single cause of insect declines, each threat identified is an opportunity for better informed management practices. Furthermore, unlike other potential drivers of insect declines, ALAN is relatively straightforward to reverse, and doing so could greatly reduce insect losses immediately. Our aim in sharing our perspective is thus to urge policy makers and land managers to incorporate the known consequences of ALAN into their insect conservation agendas. Meanwhile, more research is needed to further document the role of ALAN in insect declines, as well as to engineer more insect friendly lighting technology.

Declaration of Competing Interest

The authors have no conflicts of interest to declare. Furthermore, this manuscript has not been submitted to any other journals.

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