

Review

Current evidence in support of insect-friendly lighting practices



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Anthropogenic light pollution is an emerging threat to natural ecosystems with myriad effects on insects in particular. Insect conservationists are increasingly interested in mitigating this driver of insect declines via sustainable lighting practices. Current recommendations often follow the five principles for responsible outdoor lighting developed by DarkSky International, a nonprofit organization founded by astronomers. While these principles unquestionably increase star visibility, their ecological costs and benefits remain relatively unexplored. Herein, we review recent research into the effects of each principle on insect fitness broadly defined. Most studies test the efficacy of spectral tuning, followed by dimming, although both mitigation methods seem generally ineffective in practice. In contrast, both shielding and motion detectors show promise as mitigation methods but remain remarkably understudied. Nonetheless, a preponderance of evidence now demonstrates that removing unnecessary light sources from natural habitats can reverse their varied impacts on diverse insect taxa and greatly benefit insect conservation.

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Introduction

As anthropogenic light pollution continues to intensify [1] both within and outside of urban centers [2], insect conservationists have become increasingly concerned

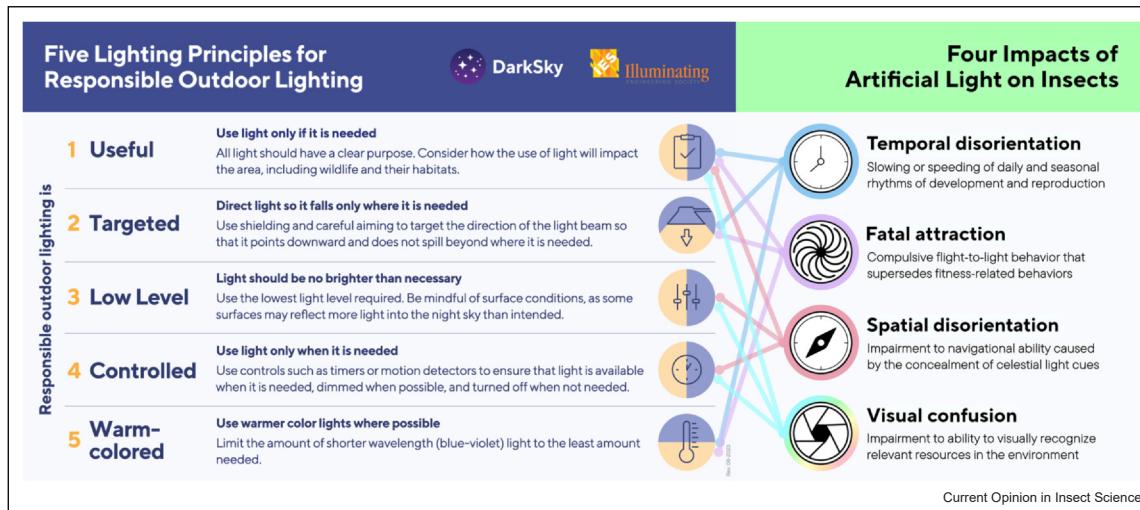
with the ways in which artificial light obscures or outcompetes natural cues guiding insect development, movement, foraging, and reproduction (Figure 1; see Ref. [3] for an in-depth review). By causing disorientation in time and space, concealing visual cues of environmental resources, and inciting detrimental flight-to-light behavior, artificial light radically disrupts normal functioning in insects.

The conservation consequences for individuals, populations, and communities [4,5] are now being documented across a broad range of nocturnal and — increasingly — diurnal insect taxa including termites [6], ants [7,8], parasitoid wasps [9], psyllids [10], and monarch butterflies [11,12]. Recent research has not only deepened appreciation for the effects of artificial light on diurnal taxa but also highlighted the relative abundance and ecological importance of nocturnal taxa [13], which are especially at risk [14], including the moths and other insects that provide crucial pollination services at night [14].

Along with a growing awareness of light pollution as an ecological threat has come regulatory interest in reducing harm via sustainable lighting practices that balance the needs of humans and nature [15]. Five simple guidelines for 'responsible outdoor lighting' (Figure 1) have been developed and popularized by DarkSky International, a nonprofit organization active in 24 countries that has worked since 1987 'to restore the nighttime environment and protect communities and wildlife from light pollution'. These 'five principles' to restore the night are well established to reduce skyglow and increase star visibility, reflecting the origin of the dark sky movement among amateur and professional astronomers. Ecologists, in contrast, have only recently begun to investigate how the same practices may ameliorate (or aggravate) the effects of light pollution on wildlife.

In this review, we summarize recent advances in our understanding of how each of the five principles for responsible outdoor lighting (addressed in reverse order) might benefit insect conservation (Table 1). We conclude by highlighting several areas of growing research interest as well as remaining knowledge gaps.

Figure 1



Five commonly recommended methods of reducing the impacts of light pollution developed and promoted by DarkSky International (left: infographic from darksky.org, used with permission) and four fundamental effects of artificial light on insects (right: icons from thenounproject.com). Lines connecting a lighting principle to a lighting impact suggest a higher potential for the former to mitigate the latter. First principles suggest that shielding (2) will most effectively limit temporal disorientation and fatal attraction, dimming (3) will most effectively limit spatial disorientation and visual confusion, timers and motion detectors (4) will most effectively limit spatial disorientation and visual confusion, and spectral tuning (5) will most effectively limit temporal disorientation and fatal attraction. Removal of unnecessary light (1) will eliminate all effects.

Table 1

Recent studies that explicitly test whether responsible outdoor lighting principles can mitigate the impacts of artificial light on insects. Here, positive phototaxis refers to fatal attraction and negative phototaxis to its opposite, light avoidance. Dimming (3) is considered effective only when dimmed treatments measure 5 lux or above at ground level, as illumination below this level is likely to be too dim to meaningfully support human use and enjoyment of outdoor spaces at night.

Responsible outdoor lighting principle	Citation	Lighting impact on insects in question	Evidence for mitigation?
1 Useful	All	All	Yes (highly effective)
2 Targeted	Bolliger et al., 2022 Dietenberger et al., 2024 van Koppenhagen et al., 2024	Positive phototaxis Positive phototaxis Positive phototaxis	Yes Yes No
3 Low level	Moubarak et al., 2023 Owens and Lewis, 2022 Levy et al., 2024 Levy et al., 2023 Cieraad et al., 2022 Dyer et al., 2023 van Koppenhagen et al., 2024 Jägerbrand et al., 2023	Visual confusion Visual confusion Temporal disorientation Temporal disorientation Temporal disorientation Temporal disorientation Positive phototaxis Positive phototaxis	Yes Yes Yes No No No Mixed
4 Controlled	Dietenberger et al., 2024 Hao et al., 2023 Kasai and Hironaka, 2024 Heinen et al., 2023	Positive phototaxis Positive phototaxis Positive phototaxis Community effects	No No No No (harmful)
5 Warm colored	Hao et al., 2023 Kunhe et al., 2021 Owens et al., 2022 Spoelstra et al., 2023 van Koppenhagen et al., 2024 Bolliger et al., 2022 Schofield et al., 2023 Mészáros et al., 2022 Sanders et al., 2022 Cieraad et al., 2022 Owens et al., 2022	Positive phototaxis Positive phototaxis Positive phototaxis Positive phototaxis Positive phototaxis Positive phototaxis Positive phototaxis Negative phototaxis Community effects Community effects Visual confusion	No No No No No Yes Yes Yes Yes Yes Mixed No (harmful)

Principle 5. Limit the amount of short-wavelength light

Each artificial light source produces a characteristic mix of wavelengths, known as its spectral distribution, and each animal has a tendency to detect certain wavelengths over others, known as its spectral sensitivity. Spectral sensitivities vary widely across taxa, with insects tending to be most sensitive to short-wavelength light [16]. Spectral distributions of modern LEDs are easily modified (e.g. [17,18]), leading some researchers to wonder whether intentional spectral tuning of artificial light might reduce its impact on insect species of conservation concern.

Recent studies confirm that short-wavelength UV and, to a lesser extent, blue light are most attractive to light-attracted insects [7,17,19]. Shifting to longer wavelengths can therefore ameliorate or even eliminate flight-to-light behavior (positive phototaxis), one of the better understood detrimental effects of artificial light on insects (but see counterexamples in Refs. [20,21]). Be that as it may, there remains scant evidence for any substantial difference in insect attraction to cool white versus warm white LEDs [17,22–24], probably because the two often vary only slightly in the amount of blue light they emit. However, monochromatic red light has repeatedly proven minimally attractive to light-attracted insects [17,20], most of which lack red photoreceptors [16].

Other colors of monochromatic light have been shown to either attract (blue light [25]) or repel (green light [18]) particular insect species of interest, leading to the restructuring of insect communities [19] (but see Ref. [26]). Combinations of monochromatic light can achieve an even more targeted effect [18], either increasing (UV and green; [27]) or decreasing (green and amber; [28]) the attraction of particular insect species relative to broad-spectrum white light while also enabling human color vision. To humans, combinations of monochromatic red, green, and blue components are indistinguishable from broad-spectrum cool white light but significantly reduce mosquito attraction and the risk of mosquito-borne disease transmission [29].

Relatively few studies address how spectral tuning might be used to reduce the impacts of artificial light on insects beyond flight-to-light behavior. The results of these studies tend to be highly species, system, and habitat dependent. For example, monochromatic blue or green light decreases the parasitism efficiency of diurnal parasitoid wasps without inducing flight-to-light behavior [30], increasing populations of their aphid hosts. Monochromatic red [31] or green [30] light increases plant growth while lowering plant defenses, culminating in greater overall insect herbivory. Relative to natural darkness, artificial light of unnatural spectral distribution can also radically alter the visibility of moths [32] and

moth-pollinated plants [33], with unknown but potentially far-reaching consequences for ecosystem function.

Principle 4. Use light only when it is needed

Automatic timers and motion activators, referred to together as lighting controls, limit the use of artificial lights to periods of greatest human activity. Timers are often set to automatically dim or extinguish their associated light sources later in the evening, often around midnight, when fewer people are likely to be active outdoors. So-called part-night lighting schemes likely have limited benefit for most nocturnal flying insects, which are disproportionately active around and just after dusk [34]. The majority of light-attracted insects aggregate between 1 and 3 hours after sunset [17,35] when timer-controlled light sources would still be lit. Part-night lighting could perhaps allow uninjured insects to escape from their orbit earlier than they otherwise would. Part-night lighting likely has even greater benefits for the subset of insects, primarily some moths, that aggregate around artificial lights 5–6 hours after sunset [35].

As noted previously, flight-to-light behavior is far from the only consequential effect of artificial light on insects. Physiological disruptions to the internal clock can alter daily, monthly, and yearly cycles of development and behavior in both nocturnal and diurnal taxa. Part-night lighting produces a highly unnatural pattern of intense daylight fading into relatively dim anthropogenic light followed by an immediate switch to darkness; full-night lighting reduces brightness contrast between day and night but maintains a natural cycle of light and relative darkness. The consequences of this distinction are largely unexplored but may help explain why some aphid colonies perform worse under part-night than full-night lighting [36].

Motion activators briefly activate their associated light sources in response to a movement trigger, dramatically reducing the total amount of artificial light in the environment over time, especially in natural and semi-natural areas where fewer people are active at night. Insects are far too small to trigger most motion detectors and, in such areas, should be able to perform nocturnal behaviors largely undisturbed. Note, however, that even brief pulses of light are capable of disrupting the internal clocks of insects (specifically crickets) in the laboratory [37]. As motion activators come into greater use, future studies should seek to understand the effects of intermittent light exposures on insect physiology and behavior in the field.

Principle 3. Light should be no brighter than necessary

Artificial light sources, especially LEDs, tend to be far brighter than they need to be to support human activity

and safety. Dimming them to the lowest acceptable intensity can greatly reduce the total amount of artificial light in the environment. Dimming artificial light only slightly (to < 30 lux) is sufficient to ameliorate or reverse its inhibitory effects on courtship and mating in fireflies [38,39] by allowing for successful transmission of bioluminescent signals. However, the benefits of dimming for other insect groups are much less clear, especially as the lowest acceptable intensity for humans may still be far too bright for most nocturnal insects.

Nocturnal insects tend to have extremely sensitive eyes capable of rapidly adapting to the ambient light environment (summarized in Ref. [40]). This is likely why recent studies have shown that even severely dimmed artificial light (< 5 lux) still significantly alters foraging patterns in ground beetles [41] and inhibits feeding behavior, pheromone release [42], and diapause induction [43] in moths while also inducing flight-to-light behavior [44]. Severe dimming does however ameliorate the impact of artificial light on the oviposition patterns of diurnal wasps [9]; see also Refs. [37,45], suggesting that the conservation benefits of dimming may depend on the temporal niche of the insect species in question.

Principle 2. Direct light so it falls only where it is needed

At their most basic, shielded fixtures prevent artificial light from going directly up into the atmosphere and reducing star visibility. In addition to these benefits for astronomy, shielding could have real ecological benefits: recent work suggests that upwelling light is especially disorienting to light-attracted insects [46], which tend to orient themselves in flight such that the brighter half of their visual field is kept overhead. Yet, the degree to which shielding actually reduces flight-to-light behavior, especially given that many insects are active below the height of a standard streetlight, is just beginning to be tested [22,24,47]. Its effects on the high-altitude navigation of migrating insects, known to orient with respect to natural light sources [48], remain entirely unexplored.

Modern shielded fixtures are increasingly designed to direct artificial light at particular areas of the ground, such as walking paths, and minimize light trespass onto bordering vegetation [49] and into rivers [23], where it has been shown to dramatically alter the local distribution of insects. One recent test compared fixtures that were individually tailored to minimize light leakage against conventional streetlights of the same intensity and spectral distribution and found that careful direction of artificial light alone can significantly reduce flying insect attraction [47]. Similar tests of fixtures that focus artificial light in a single direction against those that diffuse it outward have seen significant declines in the attraction of flying insects [22] but not ground dwellers

[24], with mixed influence of the intensity and spectral distribution of the artificial light source itself [22]. While more research is needed to understand how factors such as fixture type, fixture height, and surface reflectance influence effectiveness, shielding certainly appears to be a ‘no regrets’ action for insect conservation.

Principle 1. Use light only if it is needed

Relative to fully dark controls, artificial light of all colors, timings, shapes, and intensities has profound impacts on insect behavior and fitness, many of which are still being discovered. For example, recent studies show that disproportionate numbers of predators, parasitoids, scavengers, and parasites aggregate around artificial lights [50], threatening herbivorous caterpillars [51,52], while others show that artificial light disrupts circadian pathways [53–55] in mosquitoes [56] and crickets [53]. The simplest method of mitigating these and other fitness consequences discussed above (Figure 1) is also by far the most effective: removal of unnecessary light and restoration of natural darkness.

Conclusion

The past decade has seen a burgeoning of research into the behavioral impacts of artificial light on insects. Most studies still focus on either alterations to movement activity (especially flight-to-light behavior) or disruptions to ecological functioning (especially insect–plant interactions), and standard study systems have emerged for each impact type: adult moths for flight-to-light behavior, crickets for circadian disruption, and aphids and their natural enemies for community effects. While knowledge gaps persist regarding, for example, the movement ecology of light-averse taxa [57], the developmental physiology of pre-adult insect life stages (but see Ref. [53]), and the cascading effects on ecological communities, the overall message is clear: unrestricted use of artificial light poses a threat to insects.

Recent research by entomologists relevant to the five principles for responsible outdoor lighting has focused mostly on spectral tuning and, to a lesser extent, dimming. Yet neither of these mitigation measures have turned out to be sufficiently effective methods of reducing insect flight-to-light behavior or ameliorating other impacts of artificial light on insects. Nor does the relatively scant body of existing research (including that on the timing of nocturnal insect activity) clearly support the use of part-night lighting. Remarkably little research has been done on the benefits of either shielding or motion detectors, which is especially striking because both evidence and theory suggest that these mitigation measures are likely to be highly effective methods of minimizing the total exposure of insects to artificial light.

Clearer communication of the nuanced, widespread, and alarming impacts of artificial light on insects is urgently

needed to inform outdoor lighting policy, which, when addressing light pollution at all, currently prioritizes practices that have been conclusively demonstrated to prevent artificial light from illuminating the night sky. Truly responsible outdoor lighting should offer a win-win: allowing people to safely use and enjoy outdoor spaces at night while retaining both star visibility and the ability for humans and insects to coexist within natural spaces.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

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This paper collates and summarizes 331 quantitative comparisons of insect abundance throughout the day and night. The authors find that insect activity is over 30% higher on average during the night, lending support to previous estimates that approximately 60% of insect species are primarily active at night. The authors also find that insects in warm and/or aquatic habitats tend to exhibit more nocturnal activity.

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This paper collates published records of the spectral sensitivities of over 300 animal species, including over 100 insect species, and compares trends across groups. The resulting database is intended to help inform efforts to mitigate the effects of artificial light on natural ecosystems via spectral tuning, as the benefits to some species are likely to come at the cost of others.

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This study thoroughly explores patterns of flying insect attraction to two broad-spectrum and seven monochromatic colors of artificial light. The authors find that insects are more attracted to short wavelengths than to medium wavelengths and minimally attracted to long wavelengths but show no preference for cool white versus warm white light. The authors also find that insect flight-to-light behavior peaks between 90 min to 3 hours after sunset.

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This study reveals that diffuse fixtures, which spread light out 75 degrees more than standard fixtures, attract 16% more insects regardless of color temperature. The effects are highly taxon specific with Coleoptera, Heteroptera, and Diptera significantly more attracted to diffuse over directional lighting but insectivorous bats significantly more attracted to directional lighting.

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In this study, the authors test how artificial light of a range of color temperatures, at a range of distances from a river, varies in its attractiveness to flying insects, primarily locally abundant caddisflies. The authors find that caddisflies are much more attracted to cool white than to warm white lights and that their attraction declines rapidly with distance, such that the majority of caddisflies are attracted to artificial lights placed within 20 m of the river edge.

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This paper shows that, relative to broad-spectrum cool white LEDs, white LEDs that emit only monochromatic blue and yellow components are more attractive to mosquitoes while those emitting red, green, and blue components (RGB) are less attractive. As the three lighting types are indistinguishable to humans, RGB LEDs can be used to reduce the risk of mosquito-borne disease transmission at no cost.

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Here, the authors investigate predation rates on plasticine adult moth models under LED streetlights, HPS streetlights, and unlit control poles in an urban environment. Moth models under HPS streetlights have the

highest survival, likely due to lowered visual contrast of the moth model against the background.

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