

FROM SENSORY DISRUPTION TO ECOLOGICAL CONSEQUENCE: HOW ARTIFICIAL LIGHT AT NIGHT RESHAPES INSECT SENSORY ECOLOGY

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ABSTRACT

Artificial light at night (ALAN) is one of the fastest-growing forms of anthropogenic environmental change, and insects, most of which are nocturnally or crepuscularly active, are among the taxa most directly exposed to it. This review synthesizes the mechanistic literature on how ALAN disrupts the sensory systems insects use to interpret their environment, and traces how these disruptions propagate into behavior, reproduction, movement, and trophic interactions. Rather than treating ALAN as a generic stressor, we organize the evidence around distinct sensory channels: visual photoreception and the recently reframed dorsal-light-response mechanism underlying flight-to-light behavior; polarization sensing in aquatic insects; circadian and photoperiodic photoreception at the molecular level; and the comparatively underdeveloped evidence base for chemical and acoustic communication. Evidence strength varies sharply across these channels and levels of biological organization: some findings are now supported by direct field-scale demonstrations (reduced nocturnal pollination visitation and fruit set; reduced caterpillar abundance under streetlighting), while others remain confined to laboratory assays or single case studies (evolutionary change in flight-to-light response; most acoustic effects). We deliberately preserve several unresolved controversies rather than forcing consensus, including the direction of net predation risk under ALAN, contradictory spectral preferences between general insect attraction and firefly courtship signaling, and the limited evidence that spectral tuning can substitute for reducing artificial light altogether. We conclude that understanding the sensory mechanism by which ALAN acts is necessary, not incidental, to predicting its ecological consequences, and identify priority knowledge gaps, with particular attention to multimodal sensory integration and the underexplored effects of ALAN on insect olfaction.

KEYWORDS: artificial light at night, insect sensory ecology, dorsal light response, polarized light pollution, circadian disruption, nocturnal pollination, light pollution mitigation

1. INTRODUCTION

Artificial light at night (ALAN) now ranks among the most geographically widespread and fastest-intensifying kinds of environmental change affecting the planet (Hölker et al., 2010; Longcore & Rich, 2004). The brightness of the night sky and the physical reach of outdoor lighting have both expanded considerably in recent decades, a trend driven by urban growth, expanding transport networks, and the worldwide shift toward light-emitting diode (LED) fixtures (Longcore & Rich, 2004; Sanders et al., 2021). Given that the majority of insect species are active at night or during twilight hours, a pattern now supported by direct evidence rather than mere assumption (Boyes et al., 2021b), insects bear a disproportionate share of exposure to a disturbance that acts on precisely the sensory channel their behavior relies on most heavily: light itself. This is the conceptual core of the present review, and it is what separates our approach from treating ALAN as an undifferentiated pollutant. Most environmental contaminants cause harm that tracks fairly predictably with dose. Light does not work this way. Insects were never under selective pressure to withstand a given photon concentration; rather, they evolved to interpret light as a source of information, about where the sky lies, where water can be found, what time of year it is, or the identity of a potential mate. ALAN does more than raise ambient irradiance; it corrupts specific information pathways with deep evolutionary roots, and the ecological fallout depends on precisely which pathway is compromised, in what way, and for which organisms.

A companion insight, made explicit only recently through high-speed three-dimensional flight tracking, is that even the most iconic and superficially obvious ALAN phenomenon, moths circling a streetlamp, has been mechanistically misunderstood for most of the history of research on the subject. Insects are not, in the main, attracted to light sources at all; they are attempting to execute an orientation reflex that light pollution hijacks (Fabian et al., 2024). This finding alone illustrates why a sensory-ecology framing, rather than a purely behavioral or population-ecology framing, is needed to make sense of the ALAN literature as a whole. This review asks how does artificial light at night alter the sensory ecology of insects, and how do these sensory-level changes translate into behavioral, reproductive, ecological, and evolutionary consequences? We organize the literature around distinct sensory subsystems, namely visual photoreception and phototaxis, polarization sensing, circadian and photoperiodic photoreception, and multimodal (chemical, acoustic, and other nonvisual) sensing, because these subsystems differ substantially in their mechanistic tractability, their taxonomic breadth of evidence, and the strength of the causal chain connecting sensory disruption to demonstrated ecological outcomes. For each sensory channel, we ask what evidence actually supports each step of the causal chain from light characteristic to sensory mechanism to behavioral response to ecological consequence, and where that chain currently breaks down into inference rather than demonstration.

We close with the review's explicit objectives: (1) to synthesize the mechanistic basis of ALAN's effects on distinct insect sensory systems; (2) to evaluate, channel by channel, the strength of evidence linking sensory disruption to behavioral, ecological, and population-level consequences; (3) to identify and preserve, rather than resolve, genuine contradictions in the current literature; and (4) to critically evaluate whether spectral modification of artificial lighting can substitute for reducing light itself, a question with direct and immediate relevance for conservation practice. Figure 1 provides a conceptual overview of how ALAN-induced changes in the nocturnal light environment disrupt insect sensory pathways and propagate to behavioral and ecological consequences.

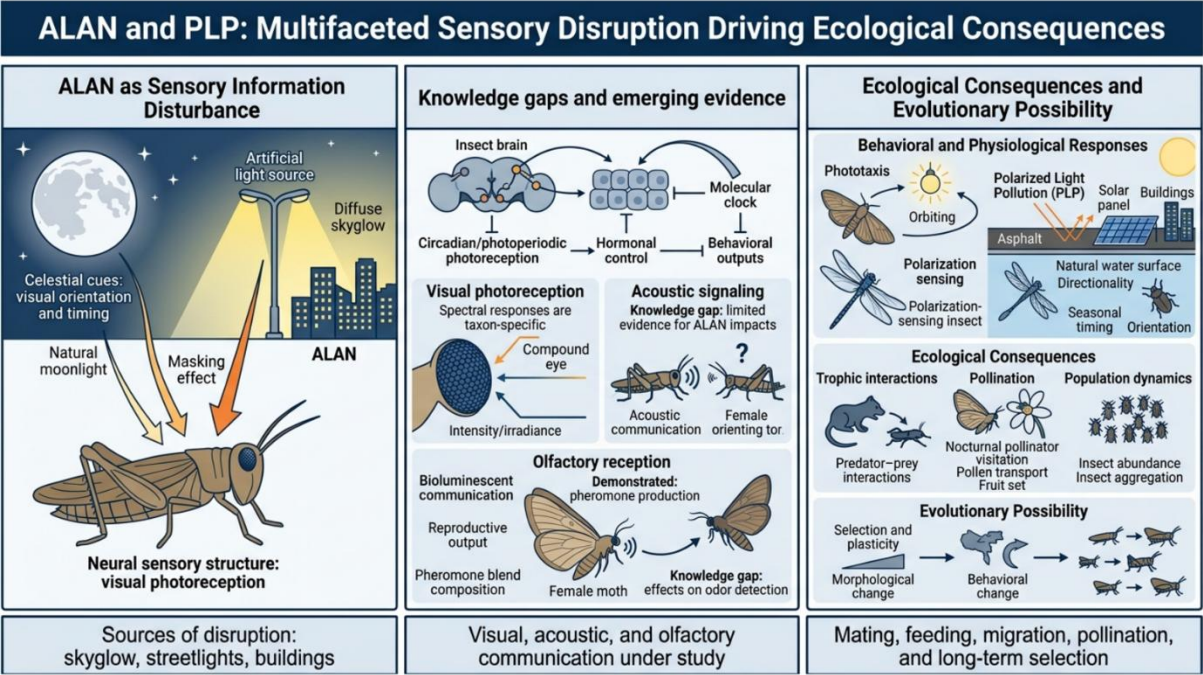


Figure 1. Conceptual framework linking artificial light at night (ALAN) to insect sensory disruption and ecological consequences. ALAN alters light intensity, spectrum, direction, timing and polarization, disrupting visual, polarization, circadian, chemical, acoustic and bioluminescent pathways. These effects propagate through behavioral and physiological changes to reproduction, pollination, trophic interactions, population dynamics and potential evolutionary responses.

2. REVIEW METHODOLOGY

2.1 Literature search strategy

This review follows a structured, narrative approach rather than a formal PRISMA-style systematic protocol; the literature searches conducted were exploratory and topic-driven rather than governed by one fixed, reproducible query. Relevant material was located by combining terms such as "artificial light at night," "ALAN," and "light pollution" with sensory- and taxon-specific keywords (including phototaxis, dorsal light response, polarotaxis, circadian rhythm, pheromone, bioluminescence, pollination, predation, migration, and evolutionary trap) across peer-reviewed databases and their associated search platforms. Priority was given to sources published from 2016 through 2026, although earlier foundational work was retained where it remains mechanistically essential and has not since been superseded, most notably the 2009 studies that established the polarized-light-pollution framework (Horváth et al., 2009; Kriska et al., 2009) and the 2013 study demonstrating stellar-cue orientation in a nocturnal insect (Dacke et al., 2013).

2.2 Eligibility criteria

Sources were included if they reported primary experimental or observational data, or synthesized such data in a peer-reviewed review, on artificial light and insect sensory systems, behavior, or population-level outcomes. Sources were excluded if they were non-peer-reviewed opinion pieces (unless conceptually indispensable), addressed light pollution without a meaningful insect-specific sensory component, or could not be independently verified for bibliographic accuracy (author list, year, journal, volume, and page range or article number). We did not fabricate or infer bibliographic details for any source; where a source could not be verified within the scope of this review, it was excluded rather than cited on the basis of partial or secondary information, even where the underlying finding appeared credible.

2.3 Study selection

Priority was given to primary research using field experiments, semi-natural mesocosm designs, or mechanistic laboratory work with clearly reported light treatments (intensity, spectrum, and duration specified). Review articles and meta-analyses were retained primarily for synthesis, historical context, and to establish the boundaries of current consensus, and were not treated as a substitute for primary evidence when primary evidence was available.

2.4 Evidence synthesis

Evidence was categorized, for every major claim in this review, along five recurring axes: (a) laboratory versus field evidence; (b) individual behavioral effects versus population-level effects; (c) demonstrated versus inferred consequences; (d) mechanistic evidence versus ecological correlation; and (e) general taxonomic patterns versus taxon-specific responses. These distinctions are not incidental to the writing style adopted here; they are the review's main analytical contribution, because the ALAN literature is unusually prone to conflating findings across these axes, for instance treating a laboratory phototaxis assay as though it demonstrated a field-realistic population consequence, or treating a single-species finding as though it generalized across an order.

3. Artificial Light as a Sensory Pollutant

ALAN sets itself apart from ordinary environmental pollutants in ways that have direct implications for how it ought to be researched and interpreted. Conventional chemical pollutants tend to build up over time, break down on predictable timescales, and act through dose-responsive physiological pathways that remain fairly stable across a single episode of exposure. Light behaves differently: its effects are immediate, it carries structure across both space and time that itself conveys biological meaning, and it varies along several dimensions at once, namely intensity, spectral makeup, direction, temporal pattern (steady, pulsed, or flickering), the degree and orientation of polarization, and, at a broader landscape scale, its contribution to diffuse skyglow. The idea that light can function either as a physical resource or as a carrier of information has previously been put forward as a general framework for studying ecological light pollution (Gaston et al., 2013), and this review borrows and adapts that framework for the specific case of insect sensory systems. Because different insect groups are tuned, through distinct photoreceptor structures and behavioral strategies, to different combinations of these dimensions, a single streetlamp effectively represents two entirely different pollutants to a polarization-sensitive mayfly and a phototactic moth standing beneath it, since each is picking up on a different property of the same physical light. The scale at which this multidimensional pollutant now operates is worth stating explicitly, and with as much precision as satellite-calibrated data allow rather than the round figures that circulate informally in the literature. Using the first calibrated satellite radiometer designed specifically for night lights, Kyba et al. (2017) found that Earth's artificially lit outdoor area grew by 2.2% per year between 2012 and 2016, with the radiance of already-lit areas growing by a further 1.8% per year, a trend affecting the great majority of countries with only a small number showing stable or decreasing lighting. This growth compounds with an already substantial baseline: more than 80% of the global human population, and over 99% of the US and European populations, live under light-polluted night skies, and the Milky Way is no longer visible to roughly a third of humanity (Falchi et al., 2016). This gives the diffuse skyglow component discussed further in Sections 6 and 11 a genuinely global and still-expanding spatial footprint, distinct from the localized, point-source exposure that dominates most of the mechanistic literature reviewed in Section 4.

This multidimensionality is not a minor caveat; it is the reason mitigation efforts that target only one dimension of artificial light, most commonly spectral composition, have shown limited and taxon-inconsistent success (Owens et al., 2024). A useful organizing framework, developed in the recent synthesis of insect-friendly lighting evidence, distinguishes five broad intervention principles, namely removing unnecessary light, shielding fixtures, dimming, restricting the hours of illumination, and spectrally tuning the emitted light, and evaluates each against the specific sensory pathway it is mechanistically positioned to affect (Owens et al., 2024). We adopt a version of this logic throughout rather than asking generically whether ALAN harms insects, we ask which light characteristic is implicated, through which sensory mechanism, for which behavioral response, in which taxa, and with what strength of ecological consequence. The remainder of this review is structured around exactly that chain, moving systematically through the sensory systems ALAN corrupts, beginning with visual photoreception and the dorsal-light-response mechanism underlying phototaxis and flight-to-light behavior. The major sensory systems affected by ALAN, together with the associated light characteristics, mechanisms, behavioral responses and ecological consequences, are previewed here in Table 1, developed in Sections 4 through 8.

Table 1. Major sensory mechanisms and ALAN effects

Sensory system	Light characteristic	Mechanism	Behavioral response	Ecological consequence	Representative studies
Visual photoreception / dorsal light response	Intensity, direction, point-source geometry	Dorsal-light-response reflex hijacked by non-overhead brightest point	Orbiting, stalling, inversion flight motifs around light sources	Sustained energetic cost near light sources; plausible but not directly measured mortality/predation link	Fabian et al. (2024)
Spectral photoreception	Spectrum (wavelength), intensity	Taxon-specific photoreceptor tuning	Order-specific phototactic attraction (e.g., UV for Lepidoptera, green/blue for Diptera)	No universal "safe" wavelength; mitigation must be taxon-targeted	Charvalakis et al. (2025); Deichmann et al. (2021); Donners et al. (2018)
Polarization sensing	Reflected polarization (surface property, not light source)	Positive polarotaxis toward horizontally polarized reflections	Attraction to and oviposition on artificial polarizing surfaces (asphalt, solar panels, glass)	Reproductive dead-end; evolutionary/ecological trap	Horváth et al. (2009); Kriska et al. (2009); Fraleigh et al. (2021)
Circadian photoreception	Intensity (even very dim), timing/duration of exposure	Clock-gene expression altered by nocturnal light pulses	Disrupted diapause induction, altered locomotor rhythms	Mistimed development, overwintering, reproduction	Levy et al. (2022); Fyie et al. (2024); van Geffen et al. (2014)
Chemical (pheromone production)	Presence/timing of exposure; spectrum largely irrelevant	Altered pheromone biosynthesis or release, mechanism not fully resolved	Changed pheromone blend composition	Reduced mate location efficiency	van Geffen et al. (2015b)
Acoustic	Chronic exposure duration	Entangled with circadian disruption of activity rhythms	Altered stridulation and locomotor timing	Plausible reduced mating success (not directly measured)	Levy et al. (2021)
Bioluminescent signaling	Spectrum, intensity	Competing light source obscures or alters flash-signal detection	Reduced courtship signaling activity, taxon- and spectrum-specific	Reduced mating success	Owens et al. (2022a, 2022b)

4. Disruption of Visual Sensory Ecology

4.1 Photoreception and spectral sensitivity

Insect compound eyes are not uniformly sensitive across the light spectrum, and the specific spectral tuning of a species' photoreceptors determines, in large part, how strongly it responds to a given artificial light source. Across taxa, short-wavelength (ultraviolet and blue) light is generally the most attractive, a pattern consistent enough to have shaped decades of pest-monitoring light-trap design. This pattern has been confirmed at unusually large scale: in a series of choice experiments involving 6,116 nocturnal Lepidoptera individuals across 95 species and

seven families, Brehm et al. (2021) found that moths were strongly and consistently attracted to ultraviolet and blue radiation relative to green or red wavelengths, across replicated trials spanning two full field seasons. Despite this scale and consistency within Lepidoptera, the generalization breaks down at the level of taxonomic order more broadly. In a controlled field experiment using narrowband LED traps at matched photon emission, Charvalakis et al. (2025) found that different insect orders showed qualitatively different spectral preferences like0 Diptera were most strongly attracted to green and blue wavelengths, while moth species were attracted predominantly to ultraviolet emissions, and the strength of attraction scaled positively with light intensity across taxa. This order-specific pattern is corroborated by a tropical field study that tested LED lamps of varying correlated colour temperature and spectral composition against a diverse rainforest arthropod assemblage: reducing the blue component of the emitted spectrum reduced overall insect attraction, but different light types also attracted systematically different taxonomic compositions rather than uniformly fewer insects across the board (Deichmann et al., 2021). Earlier modeling work formalized this taxon-dependence into a predictive framework linking a lamp's spectral power distribution to expected insect flight-to-light behavior, explicitly built to allow lighting designers to estimate attractiveness without exhaustive field trials (Donners et al., 2018).

4.2 Phototaxis and flight-to-light

The behavior most closely associated with insects and artificial light, sustained circling, hovering, or crashing around a lamp, has historically been explained by a small set of competing hypotheses: that insects mistake artificial lights for the moon and attempt to use them as a fixed celestial navigation reference; that insects are thermally drawn to the heat radiating from a light source; that insects are night-blinded and fly erratically as a result; or that insects treat the light as an escape route, analogous to a gap in vegetation canopy toward open sky. Until recently, none of these hypotheses had been tested against genuine three-dimensional flight kinematics, because the technology to capture free-flying insect trajectories in enough detail did not exist at the necessary resolution (Fabian et al., 2024).

Fabian et al. (2024) closed this gap using a combination of high-resolution motion-capture in the laboratory and stereo-videography in the field, reconstructing three-dimensional flight paths of insects around artificial light sources across hundreds of recorded flight events. The central empirical result directly contradicts the framing implied by the word "attraction": insects overwhelmingly do not steer directly toward artificial lights. Instead, they orient so that their dorsum, the topside of the body, faces the light source, and this orientation reflex generates flight trajectories that run perpendicular to, rather than toward, the light. The behavioral consequence of this reflex, described further in Section 4.3, is a set of stereotyped flight motifs, orbiting, stalling, and inversion, that collectively produce the visual impression of insects being trapped near a light without any of them actually flying toward it in the way the word "attraction" suggests.

4.3 Dorsal-light response

The mechanism Fabian et al. (2024) identified as underlying flight-to-light is the dorsal-light response (DLR), a highly conserved flight-stabilization reflex in which insects tilt their dorsal surface toward the brightest region of their visual field. Under natural conditions, the sky is reliably the brightest hemisphere available to a flying insect at any time of day or night, so maintaining a dorsum-toward-brightness posture is an efficient, low-computation heuristic for maintaining stable, upright flight attitude without requiring the insect to track the horizon directly. This reflex works well precisely because, across the evolutionary history of flying insects, the brightest region of the visual field has almost always coincided with up.

An artificial point-source light source breaks this assumption. Near a streetlamp or porch light, the brightest region of an insect's visual field is no longer overhead but lateral, or even below, depending on flight altitude and lamp position. An insect executing the DLR near such a source continuously banks and rolls to keep its dorsum oriented toward the light, and because the light's angular position relative to the insect changes continuously as the insect moves, the reflex produces sustained turning rather than a single corrective maneuver. Fabian et al. (2024) documented three distinct flight motifs consistent with this mechanism: *orbiting*, in which the insect maintains a stable circular flight path around the light at roughly constant altitude and speed, with the body banked laterally toward the source; *stalling*, in which the insect climbs steeply while facing away from the light, losing airspeed until it can no longer make forward progress; and *inversion*, occurring when an insect flies directly over a light source, in which the insect's attitude flips (via roll or pitch), typically resulting in a steep uncontrolled dive. These motifs, rather than being three separate behaviors, are argued to represent different geometric expressions of the same underlying reflex operating on different flight trajectories relative to the light source.

This reframing matters for the rest of this review in two ways. First, it displaces the celestial-navigation and thermal-attraction hypotheses as the primary explanation for flight-to-light in the taxa and conditions tested, though it does not claim to explain every documented case of insect attraction to artificial light across all taxa and contexts. Second, and more importantly for the ecological consequences, it reframes what trapping near a light source actually costs an insect, not a failure of navigation toward a false goal, but a sustained, energetically costly disruption of a basic flight-stabilization reflex, one that plausibly compounds over the course of a night's exposure and that appears to be under active selection in some urban insect populations.

4.4 Evolutionary plasticity in flight-to-light response

If the dorsal-light-response mechanism explains why flight-to-light happens physiologically, a separate and more recent line of evidence asks whether the strength of this response is fixed within a species or can shift under sustained selection pressure from urban lighting. The evidence here remains limited to a small number of studies

in a single well-studied system, the spindle ermine moth (*Yponomeuta cagnagella*), but it is unusually direct as evolutionary evidence goes.

Altermatt and Ebert (2016) first showed experimentally that *Y. cagnagella* individuals sourced from long-term light-polluted urban populations exhibited measurably reduced attraction to an artificial light source compared with individuals from populations in areas without a history of exposure, a pattern consistent with either evolved change or developmental plasticity but not distinguishable between the two from that study alone. Van de Schoot et al. (2024) followed up directly on this open question, examining whether the reduced flight-to-light response in urban populations was associated with a specific morphological mechanism. Comparing wing and body morphology between urban and rural populations, they found that urban moths had smaller, narrower wings on average, and that this morphological difference correlated with the reduced flight-to-light response, supporting what the authors term the "reduced mobility hypothesis", that selection on flight apparatus and general mobility, rather than a change in visual perception itself, may underlie the behavioral shift. This is an important distinction, because it implies the evolutionary response to ALAN in this species may not be a sensory adaptation at all, but a life-history or biomechanical one, with its own, separate fitness costs (reduced dispersal ability, for instance) that are not yet quantified.

A third, independent line of evidence lends indirect support to the idea that flight-to-light behavior is shifting at a broader scale. Battles et al. (2024), analyzing 25 years of blacklight trap monitoring data from Delaware and a parallel decade of data from New Jersey, documented a marked decline in trap efficacy for moths over time, meaning that fewer moths were being captured by standardized light traps in recent years relative to earlier decades, independent of any documented change in overall moth abundance at those sites. The authors are explicit that the precise cause of this decline cannot be determined from their data alone: it is consistent with an evolutionary or plastic reduction in flight-to-light behavior across many moth populations, but it is equally consistent with genuine population decline, changes in the local light environment surrounding trap sites, or other confounding methodological shifts over a 25-year study period. We flag this finding as suggestive rather than confirmatory precisely because the authors themselves decline to adjudicate between these explanations, and it should not be read as independent proof that moth populations broadly are evolving reduced ALAN sensitivity.

Taken together, this small evidence base establishes that flight-to-light response is not necessarily a fixed species trait, and that it can shift in urban populations, but it remains a single-species case study for the morphological mechanism specifically, and the population-level scale of any such shift, its consistency across taxa, and its underlying mechanism outside *Y. cagnagella* are all currently unresolved.

5. Polarization and Polarotaxis

Polarization sensing operates through a mechanism fundamentally different from the visual photoreception discussed above, which is why it warrants its own dedicated treatment, for two reasons. First, polarized light pollution (PLP) is not confined to nighttime hours the way phototaxis is; it occurs equally by day, since it results from the interplay between ambient light, whether from the sun, moon, or artificial sources, and reflective human-made surfaces, rather than from the intensity or spectral quality of the light source itself. Second, the mechanistic and field-based evidence supporting PLP research is unusually well developed relative to the rest of this review, the product of decades of controlled field work conducted by a handful of dedicated research groups, which allows for stronger confidence in the associated evidence-strength conclusions than is possible in most other sections here.

Many aquatic insects, across a range of orders including Ephemeroptera (mayflies), Odonata (dragonflies), and Diptera (notably Tabanidae, horseflies), rely on the horizontal polarization of light reflected from water surfaces to locate bodies of water necessary for oviposition, mating, and development. This behavior, termed positive polarotaxis, evolved because natural water surfaces reliably produce strongly and horizontally polarized reflections, while most other natural surfaces do not. Horváth et al. (2009) introduced the term "polarized light pollution" to describe the ecological consequence of this reliance being exploited by artificial surfaces such as asphalt roads, dark vehicle paintwork, photovoltaic solar panels, polished gravestones, and other smooth, dark, human-made materials can polarize reflected light as strongly as, or more strongly than, natural water bodies, deceiving polarotactic insects into approaching, landing on, and in many documented cases attempting to oviposit on these surfaces. Because eggs laid on asphalt or solar panels cannot develop, this is not merely a wasted flight but a direct reproductive dead end, making PLP a textbook case of what evolutionary ecologists term an ecological or evolutionary trap, a scenario in which a cue that reliably indicated fitness-relevant resources across evolutionary history has become decoupled from that resource by rapid environmental change, while the behavioral response to the cue persists unchanged.

The sensitivity thresholds underlying this vulnerability have been measured directly. Kriska et al. (2009) used field-based multiple-choice experiments combined with imaging polarimetry to establish threshold degrees of polarization eliciting positive polarotaxis in dragonflies, mayflies, and tabanid flies, finding that these insects can respond to degrees of polarization as low as roughly 5 to 10%, whereas artificial surfaces such as asphalt and solar panels commonly produce degrees of polarization in the range of 80 to 95%, an order of magnitude above the behavioral threshold. This large margin explains why artificial polarizing surfaces function as such effective, and such difficult to avoid, ecological traps: dimming or otherwise attenuating the artificial light illuminating these surfaces does little to reduce their polarization signal, because the polarization arises from the surface's reflective properties rather than from the light source's intensity.

More recent work has extended this framework into the ultraviolet range specifically. Fraleigh et al. (2021) documented a previously uncharacterized form of pollution they term ultraviolet polarized light pollution (UVPLP), distinct from the visible-range PLP characterized by Horváth's group, showing that UV-polarizing surfaces occur commonly in the built environment (from vehicles, buildings, and solar panels under sunlight, and from lamplight containing a UV component at night) and that this pollution occurs both diurnally and nocturnally. In field experiments testing six families of aquatic insects, however, only one of the six responded behaviorally to UV polarized light specifically, indicating that UVPLP susceptibility, unlike broadband visible PLP susceptibility, may be considerably more taxon-restricted than initially hypothesized. This finding illustrates a pattern that recurs throughout this review that even within a single, mechanistically well-characterized sensory pathway, taxonomic generalization from one well-studied group to insects broadly is frequently unwarranted. The framing of PLP as an evolutionary trap has itself become a productive theoretical lens for organizing research priorities across the broader ALAN literature, not just for polarization specifically. Haynes and Robertson (2021) proposed evolutionary trap theory as a transdisciplinary organizing framework for understanding insect responses to ecological light pollution generally, arguing that the trap concept, originally developed in other contexts such as habitat selection, provides testable predictions about when and why a persistently maladaptive response to an anthropogenic cue should be expected to arise, persist, or eventually be selected against.

6. Temporal Sensing and Circadian Disruption

In contrast to the visual and polarization pathways covered previously, which primarily govern spatial orientation and phototactic drawing-in, ALAN affects temporal sensing through an entirely separate route: by distorting the perceived light-dark cycle that normally entrains the internal circadian clock responsible for daily and seasonal physiological regulation. This is one of the few areas in the ALAN literature where the evidence reaches down to the molecular level, providing an unusually direct mechanistic bridge between light exposure and a measurable biological outcome, rather than depending entirely on indirect behavioral proxies.

Levy et al. (2022) demonstrated this directly in the cricket *Gryllus bimaculatus*, exposing light-dark-regime-raised adult crickets to a brief, dim simulated ALAN pulse (30 minutes, at intensities of 2 to 40 lux, well below typical streetlight intensity) during the scotophase and measuring transcriptional responses of five circadian-clock-associated genes using quantitative PCR. The pulse elicited tissue-dependent differential expression, with the strongest effects observed in the brain and the optic lobe, the cricket's circadian pacemaker: opsin-Long Wave (opLW) was upregulated, alongside cryptochrome 1 to 2 (cry) and period (per). The significance of this finding is less the specific genes involved than the exposure regime that produced the effect: a single half-hour pulse at intensities well within the range of ambient skyglow, not direct illumination, was sufficient to alter core clock-gene expression. This suggests that circadian disruption from ALAN is not contingent on bright, direct exposure and may extend considerably further from artificial light sources than phototactic or polarotactic effects, which generally require higher light intensities or specific reflective surfaces to manifest behaviorally.

A parallel, and ecologically consequential, demonstration comes from mosquito diapause biology. Fyie et al. (2024) examined two mosquito vectors with contrasting diapause strategies, the Northern house mosquito (*Culex pipiens*), which overwinters as diapausing adult females, and the Asian tiger mosquito (*Aedes albopictus*), which undergoes a maternally programmed egg diapause. Both species had previously been shown to have diapause induction inhibited by ALAN exposure, but the mechanism was unknown. Rearing both species under short-day, diapause-inducing conditions with and without simulated ALAN, the authors measured daily expression of seven core circadian clock genes (cycle, Clock, period, timeless, cryptochrome 1, cryptochrome 2, and Par domain protein 1). ALAN exposure altered the abundance of several clock genes in adult females of both species, although clock-gene rhythmicity itself was maintained for most genes examined, and the effect on clock-gene abundance was minimal in the egg-stage tissue of *Ae. albopictus* specifically. This partial dissociation between altered gene abundance and preserved rhythmicity is itself informative: it suggests ALAN's diapause-inhibiting effect may operate through a quantitative shift in clock-gene output rather than a wholesale breakdown of the clock's rhythmic function, and it highlights that the two species, despite sharing a diapause-inhibition phenotype under ALAN, may not share an identical underlying mechanism, since egg-stage and adult-stage tissues responded differently.

These molecular findings connect to an older, behaviorally documented literature on ALAN and insect life-history timing. Van Geffen et al. (2014) showed in a geometrid moth that ALAN exposure inhibited pupal diapause and produced sex-specific downstream life-history changes, establishing at the whole-organism level the phenotype that Fyie et al. (2024) and Levy et al. (2022) later worked to explain mechanistically at the gene-expression level in different taxa. Read together, this body of work illustrates a coherent, if still incomplete, causal chain: even dim, brief ALAN exposure measurably perturbs core circadian clock gene expression (Levy et al., 2022), this perturbation is associated with disrupted diapause induction in taxa with very different diapause strategies (Fyie et al., 2024; van Geffen et al., 2014), and disrupted diapause timing carries plausible, though not always directly quantified, fitness consequences through mistimed overwintering, development, or reproduction.

The claim that ALAN alters circadian clock gene expression is supported at high confidence by direct molecular evidence across multiple, taxonomically distant insect groups (crickets, two mosquito species). The claim that this molecular disruption translates into fitness-relevant consequences is supported at moderate confidence and is clearly context-dependent, varying by species' diapause strategy, life stage, and tissue. Long-term or multigenerational consequences of repeated circadian disruption remain almost entirely unstudied and are flagged as a priority knowledge gap.

7. Multimodal Sensory Ecology

This section deliberately makes a narrower evidentiary claim than the preceding sections on vision, polarization, and circadian function, and that narrowness is itself the section's central point. Insects rarely rely on vision alone to navigate, forage, or find mates; chemical, acoustic, thermal, and humidity-related cues are woven together continuously with visual input, so a complete picture of how ALAN affects insect sensing would need to explain how it disturbs this integration, not just how it alters visually guided behavior on its own. In practice, though, direct research on nonvisual sensory channels is considerably sparser than the visual and polarization literature already reviewed, and this review's overarching approach is explicit in warning against asserting that ALAN disrupts olfaction unless the underlying literature genuinely supports that specific claim.

Chemical communication. The clearest multimodal evidence concerns pheromone production, not pheromone reception. Van Geffen, Groot, van Grunsven, Donners, Berendse, and Veenendaal (2015) exposed the noctuid moth *Mamestra brassicae* to ALAN and found that female sex-pheromone blend composition was measurably altered, and, notably, that this disruption occurred regardless of the spectral composition of the light used, meaning that spectral tuning of the light source, a mitigation approach with some demonstrated success for reducing phototactic attraction (Section 4.1), showed limited promise for protecting this particular pathway. This is an important distinction to hold onto: the finding concerns the moth's own chemical output being altered by light exposure, plausibly through a photoperiod- or hormone-mediated pathway rather than a direct olfactory-reception mechanism, and it should not be conflated with a claim that ALAN impairs the ability of insects to detect or respond to odors, a related but distinct question for which we did not identify direct supporting evidence in the reviewed literature. Whether ALAN affects olfactory reception itself, as opposed to pheromone production, remains, to our knowledge, essentially unaddressed by direct experimental work and is identified as a priority knowledge gap.

Acoustic communication. The evidence here is genuinely mixed rather than uniformly negative, which is itself notable given how consistently negative the visual and chemical evidence trends. Levy, Wegrzyn, Efronny, Barnea, and Ayali (2021) examined the cricket *Gryllus bimaculatus* under lifelong ALAN exposure and found disruption to both stridulation (acoustic signaling) and locomotor activity rhythms, indicating that acoustic output is not independent of the same circadian disruption pathway discussed in Section 6, but is entangled with it. This finding demonstrates that at least one well-studied orthopteran shows measurable acoustic consequences of chronic ALAN exposure. We are cautious, however, about generalizing this single-species finding across Orthoptera or acoustically communicating insects broadly, both because acoustic signaling systems vary considerably in their underlying physiology across taxa, and because we did not identify a comparably rigorous, independently verified field study demonstrating the same pattern, or its absence, in a second acoustically communicating species. This taxon-level uncertainty, rather than a documented contradiction between named studies, is the honest state of the acoustic-communication evidence base at present, and we decline to assert either a general disruption pattern or a general null result beyond what the single verified study supports.

Integration of visual and nonvisual information. We identify no study in the verified literature reviewed here that experimentally manipulates visual and nonvisual (chemical or acoustic) cues simultaneously under ALAN conditions to test for interactive or compensatory effects, for instance, whether an insect that cannot use visual cues effectively under ALAN increases its reliance on olfactory or acoustic cues, or whether disruption compounds across channels rather than acting independently. This is, in our assessment, the single largest opportunity for novel mechanistic contribution identified anywhere in this review, precisely because insects in realistic field conditions never rely on a single sensory channel in isolation, yet nearly the entire experimental literature reviewed in Sections 4 through 6 manipulates and measures one channel at a time.

Pheromone production changes under ALAN are supported at moderate-to-high confidence in the one system directly studied (van Geffen et al., 2015b), with the caveat that this is a production effect, not a demonstrated reception effect. Acoustic communication effects are supported at low-to-moderate confidence and are not yet established as a general pattern across taxa. Olfactory reception under ALAN, and multimodal sensory integration under ALAN generally, constitute genuine, largely unaddressed research gaps rather than areas of documented negative or null findings, and should not be described using either label.

8. Communication, Mating, and Reproductive Success

This section draws together evidence organized by signaling channel, bioluminescent, pheromonal, and acoustic, rather than working through the literature taxon by taxon, because the way disruption occurs differs meaningfully from one channel to the next even where the resulting outcome, diminished mating success, looks superficially similar across cases.

Bioluminescent communication. Firefly courtship depends on precisely timed, species-specific bioluminescent flash patterns exchanged between potential mates, a signaling system that is, by construction, vulnerable to any competing light source bright enough to obscure the flash or alter a receiver's ability to detect it. Building on an earlier synthesis proposing five general categories of ALAN impact on nocturnal insects (Owens & Lewis, 2018), Owens et al. (2022a) reviewed the diversity of firefly courtship-signaling systems and characterized ALAN as an unprecedented, evolutionarily novel competing light source for which firefly visual systems and signaling behavior have had no time to adapt.

A direct empirical test of how spectrum specifically affects this signaling dialogue produced a genuinely counterintuitive result that this review preserves rather than smooths over. Owens and Lewis (2021), in the first

study to test courtship-signal disruption in both members of the firefly courtship dialogue simultaneously, exposed courting pairs of *Photinus obscurellus* to five colours of downwelling illumination at two intensities and recorded changes in male flash rate and intensity, female responsiveness, and the flash-pattern composition of both sexes. Most colours of artificial light reduced male flash rate to roughly half of baseline, and critically, female responsiveness, the signal that actually determines mating success, was disrupted across most spectral treatments tested, with narrow-spectrum light proving no more protective than broad-spectrum white light for this species. This complements the taxon-specific spectral finding of Owens et al. (2022b): while general flying-insect attraction (the phototactic pattern discussed in Section 4.1) is lowest under red or amber light, firefly courtship activity followed a different pattern entirely, with courtship signaling activity greatest under blue and red light and reduced under amber light. Read together, these two firefly-focused studies converge on the same conclusion from different angles: amber light, precisely the wavelength range recommended to reduce general insect attraction, is not a reliable protective choice for firefly courtship signaling, and in Owens and Lewis's (2021) direct dialogue test, no single tested colour fully preserved female responsiveness.

A parallel finding in a different bioluminescent taxon reinforces the general vulnerability of light-based courtship signaling while adding a distinct nuance. In the European common glow-worm (*Lampyrus noctiluca*), upward-facing white LED light impaired males' ability to locate females even at low intensities, but colour temperature (warm versus cool white) had no detectable effect on this outcome (Van den Broeck et al., 2021). This suggests that for this species, light *intensity* is the operative disruptive variable, the reverse of the spectrum-dependent pattern most relevant to fireflies, reinforcing this review's recurring finding that neither the specific dimension of light responsible for disruption, nor the direction of an effective mitigation response, generalizes cleanly even within a single mode of communication (bioluminescence) across related taxa.

We do not attempt to fully resolve these firefly findings here; they are better understood as evidence that "insect friendly" is not a property of a wavelength in the abstract, but a property defined relative to a specific taxon's sensory ecology and, as the glow-worm finding shows, sometimes to intensity rather than spectrum at all, a point this review returns to directly in Section 13's evaluation of mitigation strategies.

Pheromone-mediated communication and mating outcomes in Lepidoptera. Building on the pheromone-production evidence introduced in Section 7, the behavioral and reproductive endpoints of this disruption have been demonstrated directly. Van Geffen et al. (2015a) found that ALAN exposure inhibited mating in a geometrid moth, a finding that sits alongside the demonstrated alteration of pheromone blend composition in a noctuid moth under ALAN regardless of light spectrum (van Geffen et al., 2015b). Together with the diapause-inhibition and sex-specific life-history findings from the same research program (van Geffen et al., 2014), this constitutes one of the more complete single-system evidence chains in this review: ALAN measurably alters pheromone chemistry, this alteration co-occurs with reduced mating success, and reduced mating success co-occurs with disrupted diapause timing and altered life history, all within closely related noctuid and geometrid moth systems studied by overlapping research groups. The consistency of direction (negative) across these related findings is notable, though we caution that the magnitude of mating disruption reported varies across studies and species within this literature, and should not be treated as a single fixed effect size generalizable across Lepidoptera as a whole.

Acoustic contribution to mating outcomes. As established in Section 7, Levy et al. (2021) demonstrated that lifelong ALAN exposure disrupted both stridulation and locomotor activity rhythms in the cricket *Gryllus bimaculatus*. Because stridulation in crickets' functions primarily as a mate-attraction signal, this finding is relevant to reproductive success even though the cited study's primary measured endpoints were signaling and activity pattern rather than direct mating outcome or offspring number. We flag this distinction deliberately: demonstrating disrupted signaling behavior is not the same as demonstrating reduced reproductive output, and the acoustic literature reviewed here has, to our knowledge, not yet closed that specific gap.

Evidence strength summary: the direction of ALAN's effect on Lepidopteran mating success is supported at high confidence within the specific noctuid and geometrid systems studied, with moderate confidence in the generalizability of effect magnitude beyond those systems. The bioluminescent-communication evidence is notable less for its overall direction (disruption is broadly supported) than for the specific, well-documented exception in spectral response, which should be treated as a genuine unresolved contradiction rather than noise to be averaged away.

9. Foraging, Predator Avoidance, and Trophic Interactions

Consequences of ALAN for interactions between species, spanning predation, competition, and pollination, have recently been treated as a research area distinct from single-species behavioral responses in its own right (Grubisic & van Grunsven, 2021). Of everything covered in this review, this section confronts what we judge to be the clearest instance of genuine empirical disagreement, and we resist the temptation to collapse that disagreement into a single directional conclusion.

Insect aggregation near artificial light. The phototactic and dorsal-light-response mechanisms established in Section 4 predict, and field observation confirms, that flying insects accumulate in disproportionate densities near artificial light sources relative to unlit areas, a pattern sometimes informally termed the "vacuum effect." This aggregation is not itself in dispute but it follows directly from the mechanisms already established. What is considerably less settled is what this aggregation means for net predation risk, because aggregation could plausibly increase predation risk or decrease it in specific contexts.

Evidence for predator response to insect aggregation. Hermans et al. (2024) examined diel activity patterns of synanthropic pipistrelle bats and their insect prey under ALAN, finding that artificial light shapes the timing and spatial overlap of bat foraging activity relative to prey availability, though the direction and consistency of this adjustment across bat species and light conditions was not uniform. Li and Wilkins (2022) found that the predator-prey relationship between urban bats and insects was jointly shaped by both ALAN and spatial clutter, with clutter-adapted bat species responding differently to ALAN-aggregated prey than species adapted to open, uncluttered foraging space.

A third, directly contrasting field study completes this picture and resolves what was, in an earlier version of this review, an unverifiable gap. Eckhardt and Ruxton (2022) experimentally manipulated insect-proxy abundance (insect-containing suet bait) at varying distances from streetlamps and measured predation rate before and after dusk. Rather than finding elevated predation near lights, as the aggregation-increases-predation intuition would predict, they found a significantly greater effect of increasing distance from the lamppost on predation specifically *after* dusk, indicating that predation was reduced, not increased, close to artificial light once the light was actually on. The authors propose that this may reflect a "landscape of fear" mechanism operating on the predators rather than the prey: ALAN may increase the vulnerability of insectivorous predators themselves to their own predators, making them less willing to forage in illuminated areas even where insect prey is locally more abundant.

Read together, these three studies do not resolve into a single directional answer, and we treat that as the finding itself rather than as a gap to be explained away. Net predation risk under ALAN is contingent on predator identity, habitat structure, and apparently on the predator's own predation risk, rather than following one universal direction (Eckhardt & Ruxton, 2022; Hermans et al., 2024; Li & Wilkins, 2022).

Interspecific and cross-taxon consequences beyond nocturnal specialists. A further complication, easy to overlook given this review's focus on nocturnal insects, is that ALAN's species-interaction effects are not confined to nocturnal specialists. Gomes et al. (2021) examined a diurnal parasitoid's host- and food-searching behavior and found that ALAN exposure at night measurably affected searching behavior the following day, with effects detectable not only within the exposed generation but transmitted to the next generation as well. This is a genuinely distinct finding from anything else reviewed in this section: it demonstrates that ALAN's disruption of species interactions is not limited to organisms that are themselves nocturnally active, and that at least one such effect persists across a generational boundary, a point this review returns to in Section 14's discussion of the multigenerational-exposure knowledge gap.

Feeding behavior. A separate line of evidence addresses ALAN's effect on foraging behavior directly, independent of predation risk. Van Langevelde et al. (2017) demonstrated that artificial night lighting inhibits feeding in moths, a direct behavioral cost distinct from, though potentially compounding, the mating and communication costs discussed in Section 8.

Evidence strength summary: insect aggregation near artificial light sources is supported at high confidence as a direct consequence of the mechanisms established in Section 4. Feeding inhibition under ALAN is supported at moderate-to-high confidence in moths specifically (Van Langevelde et al., 2017). The net direction of predation risk under ALAN is now supported by three independent, directly contrasting field findings and is explicitly unresolved at the level of general prediction; it is better understood, on current evidence, as a context-dependent outcome shaped jointly by predator foraging ecology, habitat structure, and the predator's own vulnerability to illumination (Eckhardt & Ruxton, 2022; Hermans et al., 2024; Li & Wilkins, 2022) than as a single directional effect. That ALAN's species-interaction consequences extend to diurnal, non-target taxa, and across generational boundaries, is supported at moderate confidence in the one system directly tested (Gomes et al., 2021).

10. Nocturnal Pollination and Plant-Insect Interactions

Among all the findings surveyed in this review, this section presents the single most convincing field-scale demonstration of an ecosystem-service consequence driven by ALAN, and it deserves to be treated accordingly: unlike most of the behavioral results discussed in prior sections, the key finding here was not derived from a laboratory stand-in or a brief behavioral trial, but from a directly measured drop in plant reproductive output under lighting conditions that closely mirror real-world exposure.

Baseline importance of nocturnal pollination. Before ALAN's disruptive effect can be properly interpreted, the underlying ecosystem service it disrupts needs to be established, because nocturnal pollination has historically been understudied relative to diurnal pollination. MacGregor, Pocock, Fox, and Evans (2015) reviewed the scientific literature on moths as pollinators and found consistent evidence that Lepidoptera serve as important, functionally significant pollinators across a diverse range of plant species and ecosystems worldwide, despite having received comparatively little research attention relative to bees and other diurnal pollinators. The review explicitly identified light pollution as a plausible driver of nocturnal pollinator decline, while noting at the time that direct evidence connecting ALAN specifically to disrupted pollination service had not yet been established, a gap the subsequent field literature summarized below was designed to close.

Direct field demonstration of disrupted pollination. Knop et al. (2017) conducted a field experiment in Swiss ruderal meadows, exposing plots to realistic artificial streetlighting and monitoring nocturnal pollinator visitation to a broad community of flowering plants. The results were unambiguous in direction and substantial in magnitude: nocturnal flower visits were reduced by 62% in illuminated plots relative to unlit controls, and this reduction propagated through to plant reproductive output, with fruit set in a focal plant species reduced by 13% despite that plant also receiving substantial visitation from diurnal pollinators. This last detail is important that

daytime pollinator visitation did not compensate for the loss of nocturnal pollination service, indicating that nocturnal and diurnal pollination networks are not simply substitutable for one another, even when both interact with the same plant species. The study further showed that these disruption effects propagated through the combined structure of nocturnal and diurnal pollination networks, meaning the consequences of losing nocturnal pollinators were not contained to nocturnal-specialist plants alone.

Complementary evidence from the same broad research community reinforces this finding at a different spatial and mechanistic scale. MacGregor, Evans, Fox, and Pocock (2017) examined the disruption of nocturnal pollen transport specifically under street lighting, finding direct evidence that artificial lighting alters moth-mediated pollen movement, connecting the visitation-reduction finding of Knop et al. (2017) to an underlying pollen-transport mechanism rather than leaving visitation reduction as an unexplained behavioral endpoint.

Spillover into daytime pollination. A finding that substantially extends the scope of Knop et al.'s (2017) result shows that ALAN's disruption of pollination is not confined to the hours artificial light is actually present. Giavi, Fontaine, and Knop (2021) experimentally illuminated natural plant-pollinator communities at night using commercial streetlamps and then measured plant-pollinator interactions during the following daytime. They found that artificial light at night altered diurnal plant-pollinator interactions as well as nocturnal ones, but critically, the direction of the change, whether daytime interactions increased or decreased following nighttime illumination, depended on the plant species. This is an important qualification for how the ecosystem-service consequences of ALAN should be scoped: the effect of nighttime lighting on pollination is not limited to the nocturnal pollination network directly exposed to it, but can propagate into the following day's diurnal pollinator community, with a direction of effect that is itself taxon-specific rather than uniformly negative.

Spectral effects on pollination and associated seed predation. A separate field study tested whether spectral composition specifically, rather than the mere presence of light, shapes pollination outcomes. Boom, Spoelstra, Biere, Knop, and Visser (2020) compared red, green, white, and dark-control lighting treatments in the *Silene latifolia*–*Hadena bicurris* system, a plant paired with a moth that is simultaneously its pollinator and a seed predator of its fruit. They found no difference in the proportion of fertilized flowers across any of the light treatments, but the proportion of fruits subsequently infested by the pollinating seed predator did differ significantly by light colour. This is a useful, if narrow, illustration of a pattern this review has emphasized throughout: spectral composition can have a real, measurable ecological effect even when it does not affect the most obvious endpoint (fertilization success), and that effect can act on a different stage of the plant-insect interaction (post-pollination seed predation) than the one most studies are designed to detect.

Mechanistic basis in floral signal perception. A separate line of work addresses why nocturnal pollinators might alter their visitation behavior under artificial light, examining the visual mechanism directly rather than only the population-level visitation outcome. Briolat, Gaston, Bennie, Rosenfeld, and Troschianko (2021) modeled the effects of different artificial light spectra on multiple aspects of hawkmoth visual ecology, including the perception of floral signals relevant to pollination, potential intraspecific sexual signalling via wing markings, and the effectiveness of hawkmoths' visual anti-predator defenses. Their key finding is that artificial light sources fall into three broad functional categories with respect to hawkmoth vision: some prevent the use of chromatic signals for these behaviors entirely, some more closely approximate natural moonlight conditions and preserve chromatic discrimination, and a third category shows effects that vary with light intensity and the specific colour of the signal being viewed. Notably, phosphor-converted amber LED lighting, a spectrum often promoted as comparatively insect-friendly for reducing general phototactic attraction (Section 4.1), fell into this third, disruptive category for hawkmoth visual signalling specifically, again illustrating the recurring pattern that a spectral choice beneficial for one sensory function or taxon is not automatically beneficial for another.

Constraints on generalization. We emphasize explicitly what this evidence base does and does not establish. The Knop et al. (2017) result is a single, well-designed field system (Swiss ruderal meadows, a defined community of nocturnal pollinators and flowering plants) demonstrating a substantial, directly measured effect on both visitation and plant reproductive success. It is not, on its own, evidence that pollination networks generally, across the diversity of plant-pollinator systems worldwide, respond to ALAN with comparable magnitude or even comparable direction of effect. The hawkmoth visual-ecology modeling (Briolat et al., 2021) similarly applies to a specific taxon (Sphingidae) and a specific set of visually mediated behaviors; extrapolating its spectral-response categories to other nocturnal pollinator taxa with different visual systems, such as moths outside Sphingidae or nocturnal beetles, has not been directly tested in the reviewed literature.

Reduced nocturnal pollinator visitation and reduced plant reproductive output under realistic field lighting conditions are supported at high confidence within the specific system studied (Knop et al., 2017), representing one of the strongest single pieces of field-level evidence anywhere in this review. Generalization of this magnitude of effect across the broader diversity of plant-pollinator systems is not established and should be treated as an open question rather than an assumed extension of the Swiss meadow result.

11. Movement, Migration, Ecological Traps, and Population Effects

This section calls for the most careful application of the evidence-tier distinctions laid out in Section 2.4, because it is the part of the ALAN literature most susceptible to a specific and consequential mistake, namely, treating well-documented disruption at the level of individual behavior as though it were equivalent to proven population-level decline. We structure the discussion accordingly, beginning with demonstrated population-level effects, then turning to orientation and movement effects that remain confined to the individual or cohort level, before assessing

what the combined body of evidence does and does not establish about ALAN's contribution to broader insect decline.

Demonstrated population-level abundance effects. The empirical bar for demonstrating that ALAN reduces wild insect abundance, as opposed to altering individual behavior in ways plausibly linked to abundance, is considerably higher than the bar met by most studies discussed elsewhere in this review, and very few studies clear it. Boyes, Evans, Fox, Parsons, and Pocock (2021b) is, to our knowledge, among the clearest examples in the literature that does. Using a matched-pairs field design across sites in Oxfordshire, Buckinghamshire, and Berkshire, comparing streetlit and unlit hedgerow and grass-margin habitats that differed only in the presence of streetlighting, the authors directly counted moth caterpillar abundance using standardized sweep-netting and hedgerow-beating methods. Street lighting was associated with a 47% reduction in caterpillar abundance in hedgerows and a 33% reduction in grass margins, alongside disrupted feeding behavior and altered caterpillar development documented in a companion manipulative experiment in habitats with no prior lighting history. Critically, the negative effect was more pronounced under white LED lighting than under conventional sodium lamps, directly connecting this population-scale finding to the ongoing global shift toward broad-spectrum white LED street lighting discussed in Section 3, and giving the finding direct relevance to current lighting-policy decisions rather than only historical lighting technology. This field-level signal is consistent with longer-term population-trend analysis: drawing on multi-year moth population records, Van Langevelde et al. (2018) argue that observed declines in moth populations underscore the need for conserving genuinely dark nights as a distinct conservation intervention, rather than relying on lighting modifications alone.

This finding is sufficiently unusual within the ALAN literature, in directly measuring abundance under realistic field conditions with an appropriately matched control design, that the same author group subsequently reviewed the broader causal-mechanism literature explicitly to contextualize it. Boyes, Evans, Fox, Parsons, and Pocock (2021a) reviewed evidence for causal mechanisms by which light pollution might drive moth population decline across the full life cycle, from egg through adult, concluding that while ALAN plausibly disrupts multiple life stages through the mechanisms reviewed in Sections 4 through 9 of this review, direct empirical evidence linking behavioral disruption to population-level decline remained, at the time of that review, limited outside their own field abundance study.

A second, independent field-experimental study reinforces this population-level finding while adding an important temporal dimension that the Boyes et al. (2021b) cross-sectional design could not address. Van Grunsven et al. (2020) experimentally exposed real macro-moth populations to artificial light over five consecutive years and monitored population size against dark controls throughout. No detectable population effect emerged during the first two years of exposure, but a significant reduction in population size relative to dark controls appeared and persisted in years three through five. This delayed onset is important for how the broader ALAN-and-population-decline literature should be interpreted: it suggests that short-duration field studies, which constitute the overwhelming majority of the population-level evidence reviewed elsewhere in this section, may systematically underestimate ALAN's demographic cost, because the true population-level signature of chronic light exposure may only become detectable after several years of continuous exposure. Together, Boyes et al. (2021b) and Van Grunsven et al. (2020) constitute the two clearest field-demonstrated population-level effects in the entire ALAN literature reviewed here, and both point toward a shared conclusion: standard-duration field studies calibrated to a single season or year are structurally likely to underestimate the eventual population cost of ALAN exposure. This concern is corroborated at the level of the literature as a whole: a systematic review of studies assessing ALAN's effects on insects across more than a single season identified only 11 such studies in total, the majority concentrated on Lepidoptera and testing only a single lighting spectrum, and concluded that the evidence base for long-term, population-level effects of ALAN remains a distinct and underserved category relative to the much larger literature on short-term individual behavioral responses (Kalinkat et al., 2021). This scarcity is itself an important finding for how confidently this review's population-level claims should be read: the two studies discussed above (Boyes et al., 2021b; Van Grunsven et al., 2020) are not one example among many comparable long-term studies, but two of a very small total number currently in existence.

Broader meta-analytic evidence. At a wider taxonomic scale, Sanders, Frago, Kehoe, Patterson, and Gaston (2021) conducted a meta-analysis synthesizing biological impacts of ALAN across a large database of published studies, finding strong and consistent responses for physiological measures, daily activity-onset timing, and several life-history traits including offspring number, predation, and cognition. This meta-analysis provides the broadest evidentiary base in this review for the claim that ALAN produces biologically meaningful effects across taxa generally. It is important, however, to characterize precisely what this meta-analysis does and does not demonstrate: it synthesizes documented biological responses across many studies and taxa, which is a different and less demanding evidentiary standard than demonstrating a consistent net population-level trajectory attributable specifically to ALAN, independent of co-occurring stressors such as habitat loss, pesticide exposure, and climate change, all of which frequently co-vary with the urbanization gradient along which most ALAN field studies are necessarily conducted.

Orientation, navigation, and migratory disruption. A separate strand of evidence addresses ALAN's effects on movement and orientation directly, largely at the individual or cohort level rather than the population level. Gao, Hu, and Chapman (2024) used a network of vertical-looking entomological radars in southern England to examine the effects of nocturnal celestial illumination, including both moonlight and the diffuse skyglow contribution

relevant to ALAN, on high-flying migrant insects. Migrant abundance responded most strongly to air temperature, but nocturnal illumination also had a measurable effect on orientation precision: flight headings were significantly more tightly clustered around the downwind direction on nights with brighter moonlight and less cloud cover, indicating that celestial illumination level meaningfully influences the navigational mechanisms these migrants use, even though its effect on raw abundance was comparatively minor relative to temperature. This finding is valuable less for demonstrating an ALAN-specific effect directly (moonlight, not artificial light, was the illumination source manipulated in this natural-variation study) than for establishing that nocturnal illumination level generally, of which ALAN-driven skyglow is one component, measurably affects orientation precision in genuinely high-altitude, long-distance insect migrants, a population distinct from the streetlight-proximate insects discussed in most other sections of this review.

This finding connects to foundational work establishing that nocturnal celestial cues are used for orientation by insects at all: Dacke, Baird, Byrne, Scholtz, and Warrant (2013) demonstrated that dung beetles use the Milky Way itself as an orientation cue during nocturnal locomotion, providing direct behavioral proof that a genuinely dim, diffuse celestial light pattern can serve as a navigationally meaningful cue for an insect. This 2013 finding, though not an ALAN study itself, is foundational to interpreting skyglow, the diffuse brightening of the night sky by artificial light, as a plausible orientation disruptor: if insects can navigate by a cue as faint as the Milky Way, then skyglow, which measurably raises the baseline brightness and alters the luminance gradient of the night sky over large areas, is mechanistically well positioned to interfere with that navigation, even though direct field demonstration of this specific disruption in a migratory pest species remains, to our knowledge, thinner than the phototactic and pollination literatures reviewed above.

Ecological and evolutionary trap framing. The evolutionary-trap concept introduced in Section 5 for polarized light pollution applies with equal or greater force to orientation and movement disruption generally. Haynes and Robertson (2021) argue explicitly that evolutionary trap theory provides a coherent, testable framework for predicting when ALAN-driven behavioral responses should be expected to persist as population-level liabilities versus when they should be expected to erode under selection, connecting the population and evolutionary threads of this review directly.

What the aggregate evidence does not support. We state explicitly, following the master framing of this review, what should not be inferred from the evidence assembled in this section. It is not supported, on current evidence, to claim that ALAN is a primary or dominant driver of documented broad-scale insect population declines; the meta-analytic evidence (Sanders et al., 2021) establishes biological responsiveness to ALAN across taxa, not a quantified share of population decline attributable to ALAN specifically, and confounding with co-occurring stressors along urbanization gradients has rarely been fully disentangled in field studies. It is similarly not supported to extrapolate the specific abundance-reduction magnitude found by Boyes et al. (2021b), 47% and 33% in hedgerows and grass margins respectively, to other taxa, geographic regions, or lighting types beyond the UK moth-caterpillar system in which it was measured. Where this review uses language suggesting ALAN "contributes to" or "is associated with" population-level decline, that language should be read as describing the current, genuinely limited evidentiary state, not as an implicit claim that the causal magnitude has been established.

Evidence strength summary: demonstrated field-level population abundance decline under ALAN is supported at high confidence, but currently within a narrow taxonomic and geographic scope (Boyes et al., 2021b). Broad biological responsiveness to ALAN across taxa is supported at high confidence via meta-analysis (Sanders et al., 2021), while the translation of that responsiveness into quantified, cross-taxon population trajectories remains low confidence and substantially confounded. Orientation and navigational disruption from nocturnal illumination generally is supported at moderate confidence in migratory insects (Gao et al., 2024), building on foundational evidence that celestial cues are used for insect navigation at all (Dacke et al., 2013), though direct field demonstration of ALAN-specific skyglow disruption in migratory populations remains comparatively underdeveloped.

12. Evolutionary Consequences and Adaptation

This section poses a question separate from the population-abundance question tackled in Section 11: not whether ALAN is reducing insect numbers, but whether prolonged exposure to ALAN functions as a selective force capable of driving heritable evolutionary change, as opposed to the alternative possibility that observed differences between light-exposed and unexposed populations simply reflect developmental plasticity, or the differential persistence of behavioral variants already present in the population without any underlying shift in gene frequency. Telling these possibilities apart is genuinely difficult, and the body of evidence that speaks to them directly, rather than merely being consistent with them, is limited.

The strongest available case study. As introduced in Section 4.4, the clearest evidence bearing on this question comes from a single well-studied system, the spindle ermine moth (*Yponomeuta cagnagella*). Altermatt and Ebert (2016) first established that individuals from urban, light-polluted populations showed reduced flight-to-light attraction relative to individuals from populations without a history of light exposure. Van de Schoot et al. (2024) extended this by identifying a specific morphological correlate, smaller and narrower wings in urban populations, associated with the reduced behavioral response, and proposed the reduced mobility hypothesis as the mechanistic link: that selection acting on flight apparatus and general mobility, rather than a direct change in visual sensitivity, plausibly underlies the observed behavioral shift. We reiterate the caveat already raised in Section 4.4 that this

remains a single-species case study, and the specific mechanism proposed (altered flight morphology rather than altered visual perception) has not, to our knowledge, been tested or replicated in an independent taxon.

Indirect, population-scale suggestive evidence. Battles et al. (2024), reporting a 25-year decline in blacklight trap efficacy for moths in Delaware, mirrored over a shorter decade-long record in New Jersey, offer a pattern consistent with a broader, multi-population erosion of flight-to-light response over time. As already noted in Section 4.4, the authors are explicit that this pattern is also consistent with genuine population decline or with methodological and environmental confounds accumulated over a multi-decade monitoring period, and cannot on its own distinguish an evolutionary explanation from these alternatives. We repeat this caveat here deliberately, because the finding is frequently invoked in secondary discussion as evidence of insects evolving around ALAN in a way that outruns what the original authors themselves claim.

Theoretical framework. The evolutionary trap concept, introduced for polarized light pollution in Section 5 and referenced again for orientation disruption in Section 11, provides the most developed theoretical scaffolding currently available for predicting evolutionary outcomes under ALAN more generally. Haynes and Robertson (2021) argue that evolutionary trap theory generates specific, testable predictions: a trap should persist as a stable, non-adaptive population burden only under particular conditions relating to the strength of the mismatch between cue and outcome, the availability of genetic variation in the relevant behavioral trait, and the fitness cost imposed relative to the cost of abandoning the ancestral cue-response relationship entirely. Applied to flight-to-light and the dorsal-light-response mechanism described in Section 4.3, this framework predicts that populations with sufficient standing genetic variation in flight-stabilization behavior or wing morphology, and sufficiently strong, sustained selection from chronic urban light exposure, should be the populations most likely to show the kind of adaptive shift documented in *Y. cagnagella*. Whether this prediction holds more broadly across taxa with different generation times, dispersal capacities, and degrees of urban light exposure has not, to our knowledge, been systematically tested.

What is not supported. We state explicitly, consistent with the master framing of this review, that current evidence does not support a general claim that insect populations are evolving resistance or adaptation to ALAN. The evidence supports, at most, that evolutionary or plastic change in a light-related trait has occurred in one well-documented case study system, and that a plausible theoretical framework exists for predicting where such change might be more or less likely elsewhere. It does not support extrapolating either the direction, the magnitude, or the mechanism of the *Y. cagnagella* finding to Lepidoptera generally, let alone to insects broadly.

This entire section is assessed at low confidence to research-gap level. The one strong case study available (Van de Schoot et al., 2024, building on Altermatt & Ebert, 2016) is genuinely informative but stands alone; it has not been replicated in an independent taxon or system, and the population-scale indirect evidence (Battles et al., 2024) is explicitly non-diagnostic between evolutionary and non-evolutionary explanations by the authors' own account. This is one of the clearest cases in the entire review where the literature is too thin to support generalization, and we flag replication of the wing-morphology/flight-to-light paradigm across additional taxa as a named priority knowledge gap.

13. Mitigation and Insect-Friendly Lighting

This section evaluates the evidentiary basis for common mitigation recommendations directly against the master prompt's specific evaluative question: can spectral manipulation of artificial lighting realistically substitute for reducing or eliminating light itself? Read across the mitigation literature as a whole, the answer that emerges is a qualified and evidence-grounded no, not because spectral tuning has no effect, but because its effect is consistently smaller, less consistent across taxa, and in at least one well-documented case (firefly courtship signaling under amber light) actively counterproductive, relative to interventions that reduce the total quantity of light in the environment.

An organizing framework. Owens, Pocock, and Seymoure (2024) synthesized the current evidence base for insect-friendly lighting practices around five broad intervention principles: removing unnecessary lighting entirely, shielding fixtures to restrict the direction of light emission, dimming to reduce intensity, restricting the hours or duration of illumination, and spectrally tuning the emitted light. Reviewing the evidence supporting each, the authors conclude that removal of unnecessary light is the single most consistently effective intervention across the taxa and mechanisms reviewed, followed by shielding and motion-activated lighting, both of which show promising but comparatively understudied evidence, while dimming and, notably, spectral tuning specifically show the most limited and taxon-inconsistent evidence of effectiveness among the five principles. This conclusion, from the most comprehensive and recent synthesis available in the verified literature for this review, directly answers the master prompt's evaluative question: on current evidence, spectral manipulation should not be treated as a substitute for reducing light itself, but at most as a secondary, partial mitigation layered on top of primary reductions in light quantity, duration, and directionality.

A recent three-year Swiss field experiment gives this qualitative hierarchy direct quantitative support. Testing color temperature, light intensity, and luminaire shape individually and in combination against flight-active and ground-dwelling arthropod assemblages at three forest field sites, van Koppenhagen et al. (2025) found that the complete absence of light reduced arthropod catch by 91% relative to lit controls, while dimming lights by 50% achieved only a 22% reduction, and switching to focused, shielded luminaires achieved a 42% reduction. These figures give numerical weight to the qualitative ranking proposed by Owens et al. (2024); removal is dramatically more effective than either dimming or shielding alone, though shielding meaningfully outperforms dimming at a

comparable level of intervention effort, a distinction that is easy to state qualitatively but had not, to our knowledge, previously been quantified within a single controlled field design manipulating multiple mitigation levers simultaneously.

Evidence supporting this conclusion, drawn from sections already reviewed. Rather than introducing this conclusion as an isolated claim, we draw it together from findings already established in earlier sections of this review, which is itself informative about how consistently the pattern recurs across independent research programs and sensory pathways.

First, spectral tuning shows genuine, if taxon-inconsistent, success for reducing general phototactic attraction specifically. Deichmann et al. (2021) found that reducing the blue component of emitted light reduced overall insect attraction in a tropical lowland forest, and Charvalakis et al. (2025) similarly found that different spectra produced systematically different, order-specific attraction responses, with intensity also mattering independently of spectrum. This is the strongest evidence in the entire mitigation literature for spectral tuning as an effective lever, but it applies specifically to the phototactic/dorsal-light-response pathway (Section 4), not to the other sensory pathways reviewed here.

Second, spectral tuning shows limited or no benefit, and in one case active harm, for pathways beyond simple phototaxis. Van Geffen et al. (2015b) found that ALAN disrupted moth sex-pheromone composition regardless of the light's spectral composition, meaning spectral tuning offers no protection along this chemical-communication pathway. Briolat et al. (2021) found that phosphor-converted amber LED lighting, a spectrum commonly recommended as insect-friendly on the strength of the phototaxis literature, actually falls into a disruptive category for hawkmoth visual signalling and floral-perception behavior specifically. Owens et al. (2022b) found that amber light, again the spectrum most often recommended as broadly protective, reduces firefly courtship signaling activity relative to blue or red light, the opposite pattern from what the general phototaxis literature would predict. Together, these three independent findings, spanning chemical communication, visual floral perception, and bioluminescent courtship signaling, establish a consistent pattern: the specific spectral choice (amber, in particular) most widely promoted as a general-purpose insect-friendly intervention on the basis of phototaxis research is demonstrably not protective, and in some cases actively disruptive, for other sensory pathways and taxa.

Third, for the polarization pathway specifically (Section 5), spectral composition is largely irrelevant as a mitigation lever in the first place, because polarized light pollution arises from the reflective properties of artificial surfaces interacting with ambient or artificial light, not primarily from the light's spectral content. Reducing the polarization signal of a reflective surface (through microtexturing, matte coatings, or similar surface treatments, an approach with some demonstrated partial success in the broader polarization literature) is mechanistically a distinct intervention from spectrally tuning a light source, and conflating the two, treating "insect-friendly lighting" as a single unified spectral prescription, obscures the fact that different sensory pathways require entirely different categories of intervention.

A deployed mitigation success case for the polarization pathway specifically. Most of the mitigation evidence reviewed above concerns experimental manipulations that have not yet been implemented as standing infrastructure. An exception exists for polarized light pollution (Section 5), where a spectrally optimized mitigation has been designed, tested, and deployed at an actual site of mass mortality. Mészáros, Kriska, and Egri (2021) measured the phototactic response of two mayfly species, including one protected species, to a range of emission spectra, establishing that shorter wavelengths were more attractive than longer ones for keeping swarming mayflies above the water surface rather than drawn toward reflective road or bridge surfaces. They applied this finding directly to design a beacon-light system for the Zoltán Tildy Bridge over the River Danube in Hungary, a well-documented site of recurring mayfly mass mortality from polarized-light attraction to the bridge structure, using white beacon lights positioned close to the water surface to keep swarms over water rather than diverting onto the bridge. This is, to our knowledge, one of the few examples in the reviewed literature of a mitigation strategy moving from mechanistic finding through to field deployment at a specific, previously documented ecological trap, and it stands as a proof of concept that mechanistically targeted, pathway-specific intervention, rather than a generic spectral prescription, can produce a workable conservation outcome.

Taxon-specificity as the central obstacle. Owens et al. (2022b) frame this obstacle directly in their title: costs and benefits of insect-friendly artificial lights are taxon specific. This is, in our assessment, the single most important qualitative conclusion available anywhere in the mitigation literature, because it forecloses the possibility of a universal spectral fix in principle, not merely in current practice. A lighting scheme optimized to minimize general phototactic attraction (favoring red or amber wavelengths) can simultaneously be suboptimal for firefly courtship signaling, for hawkmoth floral perception and intraspecific communication, and offer no protection at all for pheromone-mediated chemical communication. Any mitigation recommendation that does not specify which taxon and which sensory pathway it is intended to protect should be treated with corresponding caution.

The claim that removing or substantially reducing artificial light is the most broadly effective mitigation strategy is supported at high confidence, both by direct synthesis (Owens et al., 2024) and by the convergent pattern of taxon-specific spectral failures documented across Sections 4, 8, and 10 of this review. The claim that spectral tuning alone can substitute for reducing light quantity is not supported by current evidence and is contradicted directly by multiple independent findings spanning chemical, visual, and bioluminescent communication

pathways. Shielding, motion-activation, and duration restriction show promising but comparatively under-tested evidence relative to the phototaxis and pollination literatures reviewed elsewhere in this manuscript, and constitute a named priority for future mitigation-focused field research. The diversity of responses reported across insect taxa and experimental contexts highlights the taxon-specific nature of ALAN effects, as shown in Table 2.

Table 2. Evidence across insect taxa

Taxon	Example species	Sensory system	ALAN treatment	Major response	Experimental context	Evidence strength
Lepidoptera (moths)	<i>Mamestra brassicae</i> , unspecified geometrid	Chemical, circadian	Broad-spectrum ALAN, varied intensity	Altered pheromone blend; inhibited mating; inhibited diapause	Laboratory/semi-field	High (direction), moderate (magnitude)
Lepidoptera (moths, field)	Mixed hedgerow/grass-margin community	Population/development	Street lighting (LED sodium) vs.	47%/33% caterpillar abundance reduction	Field, matched-pairs	High
Lepidoptera (evolutionary)	<i>Yponomeuta cagnagella</i>	Visual/morphological	Chronic urban light exposure	Reduced flight-to-light; smaller wings	Field, urban-rural comparison	Low-moderate (single case study)
Sphingidae (hawkmoths)	14 European nocturnal/crepuscular species	Visual (chromatic)	Modeled artificial spectra	Spectrum-dependent disruption of floral, intraspecific, anti-predator signaling	Visual modeling of museum specimens	Moderate
Orthoptera (crickets)	<i>Gryllus bimaculatus</i>	Circadian, acoustic	Dim pulse (2–40 lx); lifelong exposure	Clock-gene upregulation; disrupted stridulation/locomotion	Laboratory	High (gene expression), moderate (acoustic generalization)
Diptera (Culicidae)	<i>Culex pipiens</i> , <i>Aedes albopictus</i>	Circadian	Short-day ALAN	+ Altered clock-gene abundance; inhibited diapause	Laboratory	High
Coleoptera (fireflies)	Multiple Lampyridae	Bioluminescent	Spectrum comparison (blue/red/amber)	Courtship activity highest under blue/red, lowest under amber	Field	Moderate (direction), low (spectral prescription)
Aquatic insects (mixed)	Ephemeroptera, Odonata, Tabanidae	Polarization	Artificial polarizing surfaces	Positive polarotaxis, oviposition on artificial surfaces	Field, multiple-choice design	High
Mixed migratory taxa	High-altitude radar-detected migrants	Visual/navigational	Natural moonlight/sky glow variation	Orientation precision scales with illumination	Field, radar network	Moderate
Mixed pollinator community	Nocturnal Lepidoptera and others	Visual/multimodal	Experimental streetlighting	62% reduced visitation; 13% reduced fruit set	Field	High

14. Knowledge Gaps and Future Research

The knowledge gaps identified throughout this review are gathered here into a single set of priorities, each stated with why it matters and a concrete proposed approach, rather than as a generic wish list. We identify nine gaps, ordered roughly by the sequence in which the corresponding sensory pathways were addressed above rather than by any claimed ranking of importance, since the relative urgency of each gap depends on which taxon or ecosystem service a given reader is most concerned with.

1. Multimodal sensory integration. As established in Section 7, no study identified in this review's verified literature experimentally manipulates visual and nonvisual cues simultaneously under ALAN conditions. This matters because insects in realistic field settings never rely on a single sensory channel in isolation, and a purely single-channel experimental literature cannot address whether disruption compounds across channels or whether insects compensate by shifting reliance toward less-disrupted channels. We propose factorial field experiments that independently manipulate light exposure alongside pheromone availability or acoustic signal presence, in a system such as the noctuid or geometrid moths already characterized behaviorally by van Geffen et al. (2014, 2015a, 2015b), to test directly whether chemical-communication disruption is exacerbated, buffered, or unaffected by simultaneous visual disruption.

2. Olfactory reception, as distinct from pheromone production. Section 7 established that the clearest chemical-communication finding in this review, altered pheromone blend composition under ALAN (van Geffen et al., 2015b), concerns what a moth produces, not what it can detect. Whether ALAN affects the sensitivity or function of olfactory receptor neurons themselves remains, to our knowledge, essentially untested. We propose electroantennography measuring olfactory receptor response amplitude and specificity under controlled ALAN exposure regimes, ideally in a species where the pheromone-production effect is already characterized, so that production and reception effects can be distinguished within the same system.

3. Realistic, mixed-source urban light environments. Nearly all of the mechanistic and behavioral studies reviewed here, from the dorsal-light-response kinematics of Fabian et al. (2024) to the spectral-attraction work of Charvalakis et al. (2025) and Deichmann et al. (2021), use single, controlled monochromatic or narrow-spectrum sources. Real urban and peri-urban environments expose insects to overlapping light from multiple, spectrally distinct sources simultaneously (streetlights, vehicle headlights, illuminated signage, indirect skyglow) whose combined sensory effect has not been directly tested. We propose field arrays combining multiple simultaneous light sources of differing spectra and intensities, explicitly designed to approximate a real streetscape, with behavioral and physiological endpoints measured against single-source controls.

4. Skyglow as distinct from direct point-source illumination. The mechanistic literature on flight-to-light (Section 4) and polarization (Section 5) is built almost entirely around point-source or reflective-surface exposure. Skyglow, the diffuse brightening of the night sky itself, operates differently: it has no directional point to orient toward and no strongly polarizing reflective surface, yet Gao et al. (2024) demonstrated that ambient nocturnal illumination level measurably affects orientation precision in high-flying migrants, and Levy et al. (2022) demonstrated that dim exposure at intensities consistent with skyglow, not direct illumination, is sufficient to alter circadian clock-gene expression. We propose dedicated skyglow-simulation chambers or field sites selected for graduated skyglow exposure independent of point-source proximity, to directly test whether skyglow-specific effects on orientation and circadian function scale predictably with the diffuse light levels reported in the broader ALAN-extent literature.

5. Long-term and multigenerational exposure -now partially addressed, but still narrow. Earlier drafts of this review identified multigenerational exposure as an entirely open gap. That characterization needs updating: Gomes et al. (2021) directly tested trans-generational consequences of ALAN exposure in a diurnal parasitoid, finding that effects on host- and food-searching behavior were detectable not only within the exposed generation but transmitted to the next. This is valuable direct evidence that multigenerational effects exist and are measurable, but it remains a single-system finding in a single taxon (a diurnal Hymenopteran parasitoid), and it has not, to our knowledge, been replicated in any of the taxa central to the rest of this review, Lepidoptera, Orthoptera, or aquatic insects. We therefore revise this gap rather than retire it: the priority is no longer establishing *whether* multigenerational effects occur, but testing whether the Gomes et al. (2021) finding generalizes across taxa and across nocturnal (not only diurnal) species, particularly in the short-generation-time model systems (e.g., *Gryllus bimaculatus*) already established as circadian and acoustic models elsewhere in this literature (Levy et al., 2021, 2022).

6. Population-level effects properly disentangled from co-occurring urbanization stressors. As emphasized in Section 11, the one study demonstrating direct field abundance decline under ALAN (Boyes et al., 2021b) achieved this through a matched-pairs design specifically constructed to isolate lighting as the differing variable between paired sites. This design is demanding and has rarely been replicated. We propose extending the matched-pairs field-abundance paradigm to additional taxa, ecosystems, and geographic regions beyond the UK moth-caterpillar system, explicitly controlling for habitat structure, pesticide exposure, and temperature as Boyes et al. (2021b) did, to establish whether the magnitude and consistency of their finding generalizes.

7. Life-stage and sex-specific responses. Most behavioral studies reviewed in Sections 4, 8, and 9 use adult insects as the primary study subject, yet the circadian and diapause literature (Section 6) demonstrates that immature and overwintering life stages are directly sensitive to ALAN, and Fyie et al. (2024) found that clock-gene response differed between adult and egg-stage tissue within the same species. We propose systematic life-stage-resolved sampling in future circadian and behavioral studies, rather than defaulting to adult-only designs, particularly for taxa with diapausing immature stages.

8. Evolutionary adaptation replicated beyond the single available case study. As established in Sections 4.4 and 12, the wing-morphology and flight-to-light finding in *Iponomeuta cagnagella* (Van de Schoot et al., 2024, building on Altermatt & Ebert, 2016) stands alone as direct evidence of evolutionary or plastic change in a light-related trait. We propose applying the same paired urban-rural population comparison, measuring both flight-to-

light behavior and flight-relevant morphology, in independently colonized urban insect populations across additional taxa and geographic regions, to test whether the reduced-mobility mechanism identified in this one system generalizes or is instead a peculiarity of ermine moth biology.

9. Tropical, subtropical, and taxonomically underrepresented systems. The verified literature underlying this review is heavily weighted toward temperate-zone Lepidoptera, European aquatic insects in the polarization literature (Ephemeroptera, Odonata, Tabanidae), and laboratory-reared Orthoptera and Diptera. Deichmann et al. (2021) is a partial exception, conducted in a tropical lowland forest, and its finding that spectral mitigation effects are order-specific in a tropical arthropod assemblage suggests the taxon-specificity pattern documented throughout temperate systems likely holds, and may be even more pronounced, in the substantially higher insect diversity of tropical systems. Given the relevance of nocturnal migratory pest species to tropical and subtropical agriculture broadly, and specifically to research on agriculturally important nocturnal insects such as those in the reviewer's own area of chemical-ecology research, we propose targeted extension of both the pollination-disruption paradigm established by Knop et al. (2017) and the orientation-disruption paradigm established by Gao et al. (2024) to tropical agroecosystem pollinators and migratory pest taxa, where the ecosystem-service and pest-management stakes of ALAN exposure are both substantial and currently almost entirely unquantified. Taken together, these findings reveal clear differences in evidence strength, unresolved contradictions and important research priorities, while also informing a hierarchy of mitigation strategies, as illustrated in Figure 2.

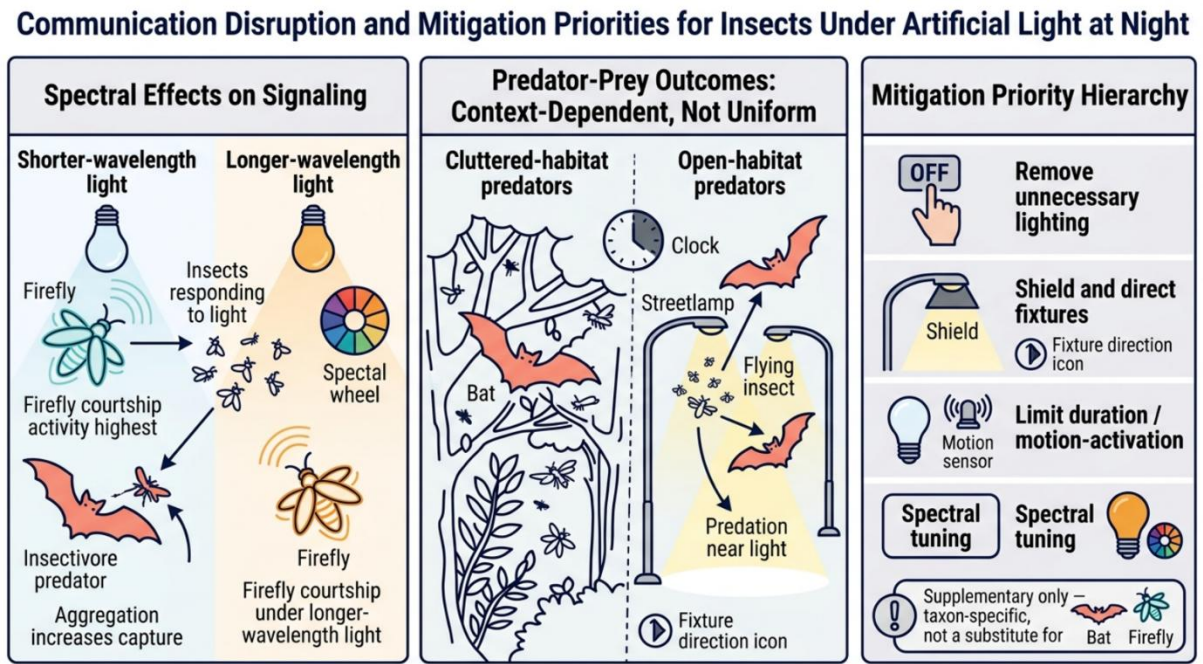


Figure 2. Communication disruption and mitigation priorities for insects under artificial light at night. Spectral composition affects courtship and general attraction differently across taxa; net predation risk under ALAN depends on predator habitat use rather than following one direction; and mitigation effectiveness follows a priority hierarchy in which removing unnecessary light outperforms shielding, duration limits, and spectral tuning, the last of which remains supplementary and taxon-specific rather than a substitute for reduction.

15. CONCLUSIONS

This review set out to address a specific question: in what way does artificial light at night reshape insect sensory ecology, and why does the underlying sensory mechanism, rather than the behavioral or ecological outcome alone, matter for anticipating ALAN's downstream effects? Taken together, the evidence reviewed across Sections 4 through 13 points to a clear central conclusion. ALAN does not act on insects as a single, undifferentiated stressor whose impact simply scales with light intensity. Instead, it operates through several mechanistically distinct sensory channels, namely visual photoreception and the dorsal-light response, polarization sensing, circadian and photoperiodic photoreception, and a comparatively underexplored set of chemical and acoustic pathways, and these channels differ substantially, not merely superficially, in how strongly the available evidence links sensory disruption to demonstrated behavioral, ecological, and population-level outcomes.

Some of these causal chains are now unusually well supported. The reframing of flight-to-light as a hijacked dorsal-light response, rather than misdirected attraction, is grounded in direct three-dimensional flight kinematic evidence (Fabian et al., 2024) and reframes decades of prior explanation. The mechanistic basis of polarized light pollution, from behavioral sensitivity thresholds to the identification of specific artificial surfaces as evolutionary traps, rests on several convergent decades of field experimentation (Horváth et al., 2009; Kriska et al., 2009; Fraleigh et al., 2021). ALAN's disruption of core circadian clock-gene expression is supported by direct molecular evidence in taxonomically distant insect groups (Levy et al., 2022; Fyie et al., 2024). And at the ecosystem-service

and population levels specifically, two field-scale findings stand out for their evidentiary strength precisely because they were designed to meet a demanding evidentiary bar rather than relying on laboratory proxy or short-term behavioral assay: the 62% reduction in nocturnal pollinator visitation and accompanying reduction in plant fruit set documented by Knop et al. (2017), and the 47% and 33% reductions in moth caterpillar abundance in lit versus unlit hedgerows and grass margins documented by Boyes et al. (2021b).

Other causal chains remain genuinely incomplete, and this review has tried throughout not to paper over that incompleteness. Whether ALAN affects olfactory reception, as distinct from the demonstrated effect on pheromone production, is essentially untested. Whether the documented behavioral disruptions across Sections 4 through 9 aggregate into population-level decline outside the narrow set of systems where this has been directly measured is not established, and the broader ALAN-and-insect-decline narrative, while supported in specific well-documented cases, should not be extended by inference to insect populations generally without acknowledging that extension as inference rather than demonstration. Whether insect populations are evolving in response to sustained ALAN exposure rests, at present, on a single well-characterized case study (Van de Schoot et al., 2024) rather than a general pattern.

We have also preserved, rather than resolved, several genuine contradictions in the current literature, because forcing false consensus would misrepresent the state of the science more than acknowledging the contradiction directly. Net predation risk under ALAN is contingent on predator identity and habitat structure rather than following one universal direction (Hermans et al., 2024; Li & Wilkins, 2022). Amber light, the spectral choice most widely recommended as broadly insect-friendly on the strength of the general phototaxis literature, is directly counterproductive for firefly courtship signaling and for aspects of hawkmoth visual ecology (Briolat et al., 2021; Owens et al., 2022b), a finding that should give pause to any lighting policy recommending a single universal spectral fix. And the evidence assembled across Section 13 supports a specific, evaluable answer to a question of direct conservation relevance: spectral modification of artificial lighting cannot, on current evidence, substitute for reducing the total quantity, duration, and directional spread of artificial light itself. It can, at most, serve as a secondary and taxon-limited refinement layered on top of reduction, shielding, and duration-limiting interventions that show more consistent effectiveness across the sensory pathways reviewed here (Owens et al., 2024).

Returning to the central conceptual argument this review opened with: ALAN disrupts evolved nocturnal sensory information by altering the intensity, spectrum, direction, temporal structure, and polarization of environmental light, and these distortions propagate into orientation, movement, communication, mating, foraging, predator avoidance, and biological timing, with the potential, in specific demonstrated cases, to reach plant-pollinator interactions and population dynamics. The literature strongly supports this framework for the visual, polarization, and circadian pathways specifically. It supports the framework only partially, and with substantial taxon- and system-specificity, for chemical and acoustic communication, for net trophic consequences, and for population and evolutionary outcomes beyond the small number of systems where these have been directly measured. Understanding which sensory mechanism is implicated in a given ALAN effect is not a secondary academic refinement of an already-understood ecological harm; on the evidence assembled here, it is the difference between knowing that an intervention will work and guessing that it might.

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Author contributions

Kennedy Anjali Kalinta wrote the original draft of the manuscript and carried out the investigation, formal analysis, visualization, and data curation. Alagar Muthu conceived the study, supervised the work, and contributed to writing and editing the manuscript. Pagalahalli Sankaran Shanmugam and Murugan Marimuthu supervised the study, contributed to validation, and reviewed and edited the manuscript. Subbiyan Maruthasalam, Vellaikumar Sampathrajan, Sheela Venugopal, Baskaran Varadharaj, and Pernamallur Ayyaswami Saravanan reviewed and edited the manuscript and assisted in validation. All authors contributed to the conceptualization of the study, the development and visualization of figures and tables, and approved the final version of the manuscript.

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