PNAS COMMENTARY

Harmonic radar suggests greater impact of light pollution for nocturnal insects

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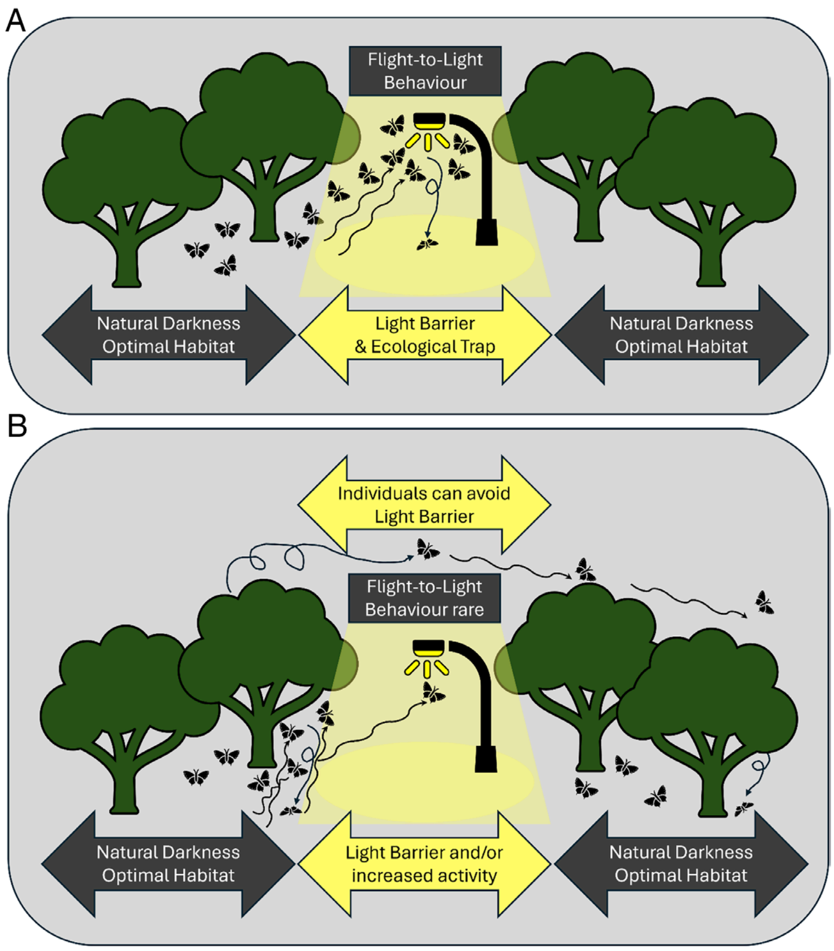

Fig. 1. The impact of light barriers and the flight-to-light response in insects. (*A*) Traditional understanding—the streetlight is both attractive and creates a light barrier that insects avoid crossing. Individuals that are attracted to the light source exhibit stereotypical flight-to-light behaviors that result in them orbiting until the light is turned off, or they are exhausted and drop to the ground. This scenario can result in a suitable unlit habitat beyond the light barrier being unused. (*B*) Adapted understanding using harmonic radar technology (9)—the probability that a streetlight will elicit a flight-to-light response is linked to flight trajectories but the presence of the light disrupts flight behaviors and may still act as a barrier to movement. Individuals that fly at higher altitudes (potentially lower altitudes, although not shown) are less likely to be attracted to the light allowing them to move through and beyond the light barrier to suitable unlit habitat. This results in fewer flight-to-light counts recorded and may suggest an apparent lack of light barrier between the two areas of suitable habitat. However, the presence of the light could still disrupt insect activity leading to more erratic and less efficient flight behaviors, which might be exacerbated if the light also acts as a barrier that disorients and reduces migration. These more subtle behaviors could be overlooked using the binomial flight-to-light response (attracted to a light, or not) leading to the impact of light at night being underestimated. This might be particularly critical if the disruption in flight behavior has fitness consequences as these could affect all individuals both close to, and potentially beyond, the light.

The presence of artificial light at night (ALAN) has dramatically increased in intensity and distribution over the past 150 y. Currently, it is estimated that more than 30% of terrestrial environments and 22% of global coastlines are affected by ALAN (1, 2). The impact of ALAN is exacerbated because light from point sources such as street- and other forms of urban lighting can scatter tens of kilometers resulting in skyglow in areas of otherwise darkness (3). At its core, ALAN alters the physical properties of the nocturnal environment increasing its brightness and often shifting its color to a blue-wavelength-rich

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spectrum (4). However, ALAN can also mask variations in natural light levels including the crepuscular transitions of the daily circadian light cycles; the waxing-to-full-to-waning moon of the circa-lunar cycle; and the small daily shifts in photoperiod that define the circa-annual light cycle (5). These natural light cycles are critical for cellular and circadian processes, and it is therefore unsurprising that ALAN is linked to a myriad of, largely detrimental, physiological and behavioral effects for animals (6, 7). On a global scale, the relationship between the presence of ALAN and biodiversity declines, particularly for nocturnal pollinators such as moths, has also been experimentally demonstrated (8). However, in their recent study in PNAS, Degen et al. (9) suggest that current methodological approaches may mean we are underestimating the influence of ALAN on animal behavior.

In their recent study in PNAS, Degen et al. suggest that current methodological approaches may mean we are under-estimating the influence of artificial light at night on animal behavior.

One of the most visible effects of street and other forms of artificial lighting is their ability to act as an attractant and potential ecological trap for many animals, including insects, birds, geckos, and bats (6, 10). Globally, the bright lights of major cities disrupt avian migration (11) and alter diel activity in the aquatic realm (12). Historically, the so called "flight-to-light" impact of ALAN has been estimated using light trapping along with manual and automated counts of animals observed at lights (Fig. 1*A*). However, these approaches often provide a binomial response: the flight-to-light effect is measured by whether an individual is attracted/trapped at a light source (be it a street light or within a light trap). While an invaluable metric of the impact of ALAN, this method is unlikely to capture more subtle, light-related, shifts in animal behavior including possible "light-barrier" effects (13) that may influence normal migration or activity in regions that are otherwise unlit. For strictly nocturnal species, which may be light-shy or completely photophobic, active avoidance of lit areas or a switch in movement behavior when nearing a light is a typical response (8, 14) (Fig. 1*B*). Without prior knowledge of a species' distribution or movement patterns, such shifts can go undetected. The need to monitor behaviors in relative darkness when considering the impact of ALAN is an obvious impediment, but technological advances in electronic miniaturization have facilitated an innovative approach to address this important knowledge gap. In their study, Degen et al. (9) used harmonic radar to assess experimentally the influence of ALAN on the flight behavior of moths. This novel application of existing technology allowed them to determine the immediate effect of nearby streetlights on moth movement patterns but also highlighted previously undetected ALAN-promoted behavioral changes far beyond the reach of the lights themselves.

Harmonic radar is a specialized radar system that has been used as a tool to track insect movement since the 1980s (15). In recent times, it has been applied to a range of ecological scenarios, including assessment of long-range migration (16), monitoring pest distributions (17), and observing mate-location behavior (18). The radar unit transmits a signal at a fundamental frequency, which is then reflected back by a passive transponder attached to the insect being tracked. The transponder is typically a small lightweight tag that contains a nonlinear component (such as a diode). When the transponder receives the radar signal, it "mixes" it and reflects it back at a higher harmonic frequency (often twice the original frequency) which facilitates signal detection against background noise. The radar receiver is then able to use the harmonic signal to calculate the location of the transponder and thus track the movement of the insect.

Underpinning the study by Degan et al. was the presumed strong flight-to-light response of many insects, including moths (Fig. 1*A*). To assess this response both within and beyond a light barrier, they deployed an array of six high-pressure sodium streetlights which emitted blue-reduced amber lighting (2000k), typical of the lights in their region of study (Großseelheim, Germany). Their study animals, comprising two groups of nocturnal moths, were field-caught using light traps adjacent to (Lappet moths) or beyond (Hawk moths) the experimental site. Captured moths were each fitted with a microtransponder before being released into the center of the street-light array. Individual flight paths were then tracked (either with the array of streetlights on or off) using harmonic radar until the individual was no longer detected in the area. Contrary to expectation, only 4% of moths exhibited a flight-to-light response when the lights were turned on. Moreover, the degree to which the flight paths of moths changed in the presence of ALAN (measured through the directionality of flight) was species-specific and context dependent. Hawk moths consistently left the array during their trial, likely flying over the streetlights and thus avoiding potential light barriers. However, the radar technology revealed that the direction of their flight was significantly disrupted when the visible moon was masked by the presence of ALAN, suggesting that it competed with the moth's ability to use celestial cues for navigation. In contrast, the Lappet moths displayed characteristic mate search behaviors beneath the streetlights and rarely left the experimental light array. However, their flight was also disrupted by the presence of ALAN when the moon was below the horizon suggesting that, for this species, ALAN may act as a disorienting light barrier in the absence of celestial cues.

The study by Degen et al. (9) broadens our understanding of the effect of ALAN for insect flight behavior, but it also highlights that current approaches that measure flight-to-light or light-barrier effects may significantly underestimate the disruptive potential of ALAN (Fig. 1*B*). Why most animals are attracted to light remains largely unclear, although a recent study found that some insects, including the Oleander hawk-moth, *Daphnis nerii*, tilt their dorsum toward the "brightest visual hemisphere" to facilitate maintenance of flight attitude and direction (19). Under natural conditions, this might be the distant sun or moon but, in the presence of a close-range light source, it can result in vast numbers of individuals perpetually orbiting and becoming trapped in a suboptimal location (a situation referred as an ecological trap) (20). The harmonic radar approach has revealed that these numbers may just be the tip of the iceberg: the majority of moths (who were all captured via light traps, and thus clearly attracted to a light source) did not exhibit this characteristic flight-to-light behavior to the presence of a 3.5 m light source (the height of the experimental streetlights). Instead, the likelihood of the response appears to be related to whether an individual moth flew at an altitude where the lamp was directly in their flight path. Nonetheless, the presence of ALAN was related to changes in flight activity and, for Lappet moths, appeared to create a barrier effect. These two scenarios could result in downstream fitness impacts. Crucially, these more subtle light-related disruptions to flight, including the first demonstration of a light barrier for an insect, would likely have been missed using traditional methods.

The degree to which these findings are applicable across species and with varied lighting technologies is untested. Future research should endeavor to replicate the approach used by Degen et al. (9) using next-generation blue-rich LED lighting, as these are rapidly replacing older lighting technology. Blue light, in particular, is likely to be disruptive to celestial navigators, as it masks moonlight more effectively, and may potentially be a more potent attractant. Nevertheless, Degen et al. (9) elegantly demonstrate the synergy of a multidisciplinary approach to understanding ALAN's impacts, while also highlighting the broader tension that exists between humans and biodiversity. Reducing light pollution is unarguably a problem that is readily solvable (we can simply switch it off), but humans have a seemingly indefatigable desire for night lighting. Indeed, just as comprehending the scale and impacts of ALAN requires collaborative efforts and emerging technology, so too will finding appropriate solutions to mitigate its various impacts.

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