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Effects of anthropogenic light on species and ecosystems

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Abstract

Anthropogenic light is ubiquitous in areas where humans are present and is showing a progressive increase worldwide. This has far-reaching consequences for most species and their ecosystems. The effects of anthropogenic light on natural ecosystems are highly variable and complex. Many species suffer from adverse effects and often respond in a highly specific manner. Ostensibly surveyable effects such as attraction and deterrence become complicated because these can depend on the type of behavior and specific locations. Here, we considered how solutions and new technologies could reduce the adverse effects of anthropogenic light. A simple solution to reducing and mitigating the ecological effects of anthropogenic light seems unattainable, because frugal lighting practices and turning off lights may be necessary to eliminate them.

Artificial light is ubiquitous in areas where humans are present and inevitably extends to our natural environment. This has far-reaching consequences for most species and their ecosystems. The ability of humankind to produce electric light has enabled us, a naturally diurnal species, to dispel darkness and extend our activities into the night. However, artificial light has serious side effects that are commonly referred to as light pollution. Light pollution is defined as the sum total of all of the adverse effects of artificial (hereafter referred to as anthropogenic) light (1). Ecological light pollution was originally defined as artificial light that alters the natural patterns of light and dark in ecosystems (2) that are caused by exposure to near and distant light sources and sky brightness. Light-polluted skies have become a global reality, affecting most of the world's economically developed areas (3). Sky brightness has increased over time, eroding natural darkness and encroaching on protected terrestrial and marine areas. Anthropogenic light not only worsens climate change through energy consumption but also poses serious challenges across species and ecosystems (4).

Over the past 15 years, there has been a substantial amount of research on the ecological effects of anthropogenic lighting across the globe (5, 6). Most of these studies have focused on direct light exposure. Research on broad-scale spatial patterns has become possible by combining remote sensing data on light emitted upward with digitalized biological data such as information on species occurrence and migration routes.

The deleterious effects of anthropogenic light have been reviewed for several species groups, including bats (7), insects (8–11), seabirds (12), fish (5), vertebrates (13), and marine, shoreline, and estuarine species (14–16). Effect sizes for numerous species have also been reviewed (6). These reviews line up numerous studies that have led to substantially more knowledge about the effects on different species groups, the diverse nature of such effects, and how they manifest across trophic levels, thereby increasing awareness about this environmental problem.

Commonly recommended solutions to mitigating the ecological effects of anthropogenic light include reductions or adaptations in light intensity, distribution, spectra, and duration. New technologies, such as light-emitting diodes (LEDs), can aid in reducing the effects of anthropogenic light on the natural environment. However, these solutions have limitations and may not safeguard against deleterious effects on all species.

Herein, we review the ways in which anthropogenic light affects species and ecosystems, discuss the research progress made in recent years, and describe various light pollution management solutions.

Effects of anthropogenic light on species groups

Birds

One of the most established effects of anthropogenic light on birds is their response to it during migration ([Fig. 1](#)). Many birds, including otherwise diurnal species, migrate at night. They are attracted to light and disoriented by it, especially strong light sources and bright spots in dark areas. This attraction to light can not only cause them to collide with buildings, lighthouses, oil rigs, and ships ([17](#)), but may also divert them from suitable stopover locations ([18](#)). Migratory routes are often close to illuminated urban areas ([19](#)). In areas with dark surroundings, such as islands, light sources attract seabird fledglings ([12](#)). These effects can directly result in high mortality and exhaustion. Many other effects are less pervasive but still problematic; for example, light may induce stress and disturb sleep ([20](#), [21](#)). Many bird species in temperate zones depend on the accurate seasonal timing of breeding and the accurate daily timing of song activity and foraging, so light disturbance of this temporal organization is problematic [[22](#), [23](#)]; [Fig. 2](#)].

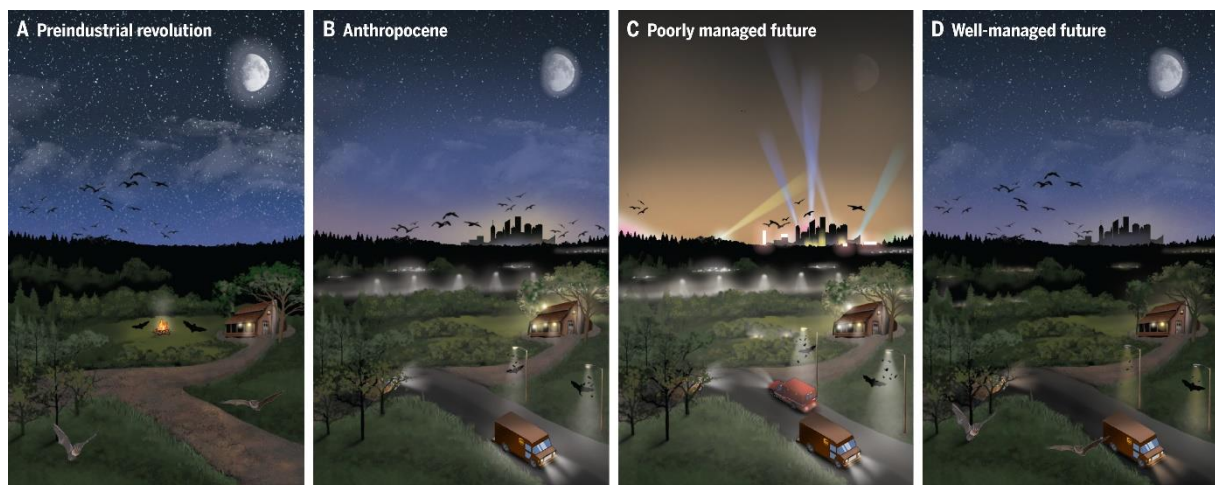


Fig. 1. Anthropogenic light through history and possible futures.

(A) During the preindustrial revolution, few light sources were used for outdoor activities during darkness. Natural light sources dominated the natural environment, bats foraged and commuted along forest edges, migrating birds were undisturbed by strong light sources, and there was no sky glow from cities. **(B)** In the Anthropocene, anthropogenic lighting is used where it is needed to enhance human activities, attracting insects, migrating birds, and foraging bats and causing visible sky glow. **(C)** As anthropogenic lighting is increasingly used, light pollution will also increase and result in higher mortality in insects and migrating birds, habitat loss for light-repelled bats, and increased foraging opportunities for synanthropic bats. Barrier effects and fragmentation of dark ecosystems will decrease habitat quality. **(D)** A well-managed future conserves dark areas and limits light use in several ways, thereby minimizing the effects of anthropogenic light on birds, insects, and bats and numerous other species.

ILLUSTRATION: K. HOLOSKI/SCIENCE, BASED ON ANNIKA K. JÄGERBRAND AND KAMIEL SPOELSTRA

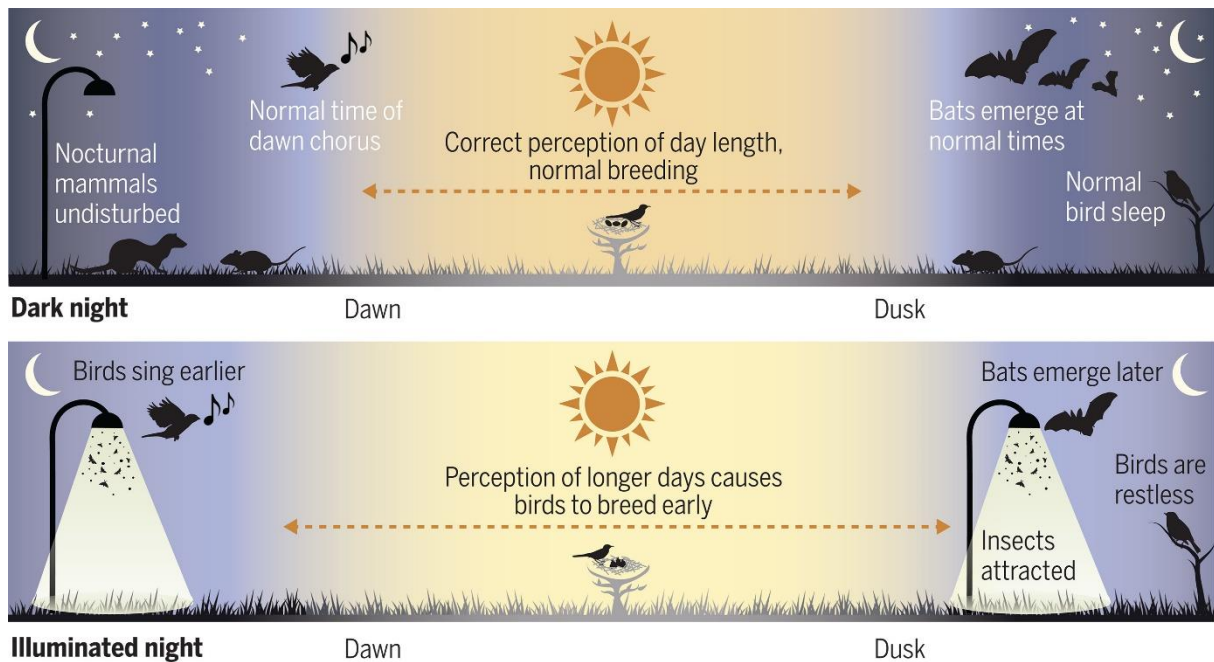


Fig. 2. Examples of disturbance of daily and seasonal rhythms by anthropogenic light.

Nocturnal rodents are less active, and diurnal species can be restless in illuminated nights. Birds advance their dawn song, and bats delay emerging until the evening. Light at night can disrupt the perception of day length in birds, causing them to breed earlier in spring.

ILLUSTRATION: N. CARY/SCIENCE, BASED ON ANNIKA K. JÄGERBRAND AND KAMIEL SPOELSTRA

Mammals

Most bat species are highly nocturnal and respond strongly to light. This response is driven by the fear of predators or the foraging ecology. For example, fast-flying, agile bats are less frightened by light and forage on accumulated insects around light sources, whereas slow-flying bats stay in sheltered locations (24) (Fig. 3). Bats are particularly vulnerable because they use linear landscape elements such as forest edges, hedgerows, and streams to guide them in foraging and commuting. Light along commuting and foraging routes can act as a barrier, thereby amplifying its negative effects by fragmenting habitat networks. Anthropogenic light in or near bat roosting sites can lead to delayed emergence or roost abandonment, which has negative consequences for the survival of populations (7).



Fig. 3. Light at night drives species interactions.

Many species are nocturnal because of fear of predators, for example by barn owls (*Tyto alba*). The middle and right species (Natterer's bat, *Myotis nattereri*, and the brown long-eared bat, *Plecotus auritus*) are examples of slow-flying bats that need to be extra wary of predators. These bats thrive in darkness, emerging late in the evening and foraging in sheltered places. The common pipistrelle (*Pipistrellus pipistrellus*) avoids light as well, but has a more agile flight and dares to forage on accumulated insects close to street lights.

ILLUSTRATION: K. HOLOSKI/SCIENCE, BASED ON ANNIKA K. JÄGERBRAND AND KAMIEL SPOELSTRA

A commonly accepted assumption is that, like bats, other nocturnal mammal species' responses to light are driven by fear of predators. A decrease in the activity of nocturnal species by light at night has been reported in numerous laboratory experiments. Many mammal species reduce activity in response to moonlight (25, 26) and show a comparable response to anthropogenic light (27). Likewise, anthropogenic light can change the spatial behavior of rodents (28) and, even in the absence of predation, reduce longevity and reproduction (29). Larger mammal species such as deer and predators may also change their spatial activity (30). On a larger scale, the deterrent effects of light on infrastructure may have far-reaching effects because mammals may stop using passage structures (31). As is the case with many other species, anthropogenic light can have profound effects on mammals' daily and seasonal rhythms of activity, physiology, and reproduction (32).

Invertebrates

The attraction of insects to light is a well-known phenomenon (Fig. 1). In naturally dark environments, insects can be attracted to low light intensities (33), and the extent of attraction to a light source depends on the presence of surrounding lights (34). Insect's flight-to-light may be a maladaptive response to the original orientation toward moonlight (35) and is related to color composition. Blue light (<500 nm) attracts more insects than the yellow and red parts of the spectrum (36). The attraction of insects to anthropogenic light may cause mortality and exhaustion, which may play a substantial role in global insect declines. This has been corroborated by the fact that phototactic

nocturnal species that fly toward light have shown strong population declines (37). Indeed, light posts have been found to affect local moth caterpillar abundance (38). Moreover, insect declines can be caused by the negative effects of light on reproduction and development (10). Insects that depend on bioluminescent signaling, such as fireflies, are especially vulnerable to anthropogenic light and are directly impaired in reproduction (11). Anthropogenic light deprives insects such as aquatic insects and dung beetles of their ability to use light cues for orientation (39). For several other invertebrate groups, the effects of light are well documented, including opportunistic foraging around light sources by spiders (40) and slugs (41). Finally, anthropogenic light can change species composition in invertebrate communities (42).

Amphibians

Early field observations have provided evidence that anthropogenic light affects the reproduction, visual performance, and activity patterns of amphibians (2). In toads, exposure to anthropogenic light has been found to cause reduced activity levels, altered energy allocation, and decreased juvenile growth and metamorphic duration (13). Anthropogenic light can also alter breeding behavior and reduce the fertilization success of toads (43). In frogs, although mate choice behavior appears to be unaffected by anthropogenic light, it has been shown to shorten the calling season and shift the daily calling period (13).

Reptiles

Knowledge about the impact of anthropogenic light on reptiles in general is limited, but its effect on marine turtle populations is widely known. Hatchlings are highly susceptible to disorientation caused by light when crossing the beach to reach the sea, leading to high mortality rates. Furthermore, even at low levels, anthropogenic light can disrupt the on-beach orientation of turtles, resulting in suboptimal selection of nesting sites (14). Turtle nests have declined in lit areas across several species, with turtles using lit beaches less frequently or avoiding them altogether (15). Some diurnal reptiles, such as geckos, are able to forage at night in the presence of anthropogenic light (44). Likewise, green anole lizards (*Anolis carolinensis*) express part of their normal daytime foraging and display activity during the night (45).

Fish

Compared with terrestrial organisms, fish have received less attention in studies investigating the effects of anthropogenic light (5). Such light may affect fish populations through changes in survival rates, spawning, hatching success, and physiology, and can alter the temporal and spatial activity of fish and increase their energy expenditure. This can stimulate various behaviors such as nest-guarding activity, higher nocturnal activity, overall activity during both day and night, increased time spent in open areas, and maintaining position in an area. Fish species can be attracted or repelled by light. For example, positive phototaxis can lead to the aggregation of smaller fish around lighting, thereby providing easy prey for predatory fish. Some species may benefit from foraging under brighter conditions, but whether the benefits outweigh the costs over time is still being determined (5). Very low light levels can have effects on fish behavior. For example, rainbow trout (*Oncorhynchus mykiss*) are attracted to low levels of bridge illumination, which further depends on various environmental factors, making it a complex issue (46).

Plants

Although the effects of anthropogenic lighting on commercially grown plants are well documented, there is a gap in the knowledge about its effects on plants and plant-mediated responses in the natural environment. Lighting close to trees can lead to increased photosynthesis and morphological changes through the relocation of biomass from roots to leaves (47). In deciduous trees, exposure to

anthropogenic light advances the emergence of leaf buds and, together with temperature, delays the coloring of leaves (48). Species-specific variations in responses to anthropogenic light have also been demonstrated in herbs and grasses (49).

Ecosystem effects of anthropogenic light

Nocturnal environments are dominated by moonlight because it is the strongest and most abundant natural light source. Light from anthropogenic sources differs from natural light in magnitude, color composition, and temporal and spatial presence. Moonlight intensities at midlatitudes can be as high as 0.2 lux depending on the position above the horizon and the amount of cloud cover (50). In many areas, however, the amount of anthropogenic light surpasses moonlight.

Anthropogenic light sources usually have a spectral composition that differs substantially from natural nocturnal light: Outdoor LEDs typically have a peak in the blue spectral range, resulting in a cooler, white light compared with the yellowish light of the moon. Traditional light sources, such as high-pressure or orange low-pressure sodium lamps, are different from natural light because they have very little or no blue light. The intensity and distribution of natural nocturnal light vary as the night progresses and are also influenced by changes in the lunar phases and weather conditions. By contrast, anthropogenic light is often constant and concentrated around human settlements.

Terrestrial landscapes vary in topography and in the heights of physical objects, which result in variations in light distribution and exposure to organisms.

Forest ecosystems are generally darker as light is filtered through and absorbed by the vegetation, and only a small proportion of ambient light reaches the ground. Species that inhabit forests are believed to have adapted to darker nocturnal environments (51). In open environments, light can propagate far from the source, and even a single strong light can be a conspicuous element in the landscape, resulting in glare and difficulties in seeing details in the surroundings and stars in the night sky. In general, open environments are perceived as brighter when larger parts of the naturally lit sky and the ground can be viewed. Low-growing and light-green vegetation such as grasses, bushes, and herbs can reflect a high proportion of light, which increases the luminance of the landscape.

In aquatic ecosystems, anthropogenic light is reflected on water surfaces and thus has a high probability of propagating widely over open water and may affect large areas.

Many human structures in or near aquatic ecosystems, such as ports, ships, and oil rigs, use high-intensity lighting with insufficient restrictions, often resulting in large amounts of light spilling into the surroundings. In water, light changes with depth. Water and its particulates absorb and scatter light, reducing light intensity, altering color composition, and changing the degree of polarization. Clear ocean waters absorb ultraviolet, red, orange, and yellow wavelengths at the top of the water column, allowing blue light to penetrate the deepest, which results in a bluer color at greater depths. Coastal and freshwater systems often contain suspended particulates and phytoplankton, which selectively absorb the light, causing the water to appear more yellow-green, orange, or brown in color. Aquatic species have adapted their eye morphology to natural variations in intensity and color composition with photoreceptors that match the color of light, thereby increasing photon absorption (52). For example, deep-sea fishes have a visual pigment that matches the color of downwelling oceanic light, whereas fish species found in yellow-green coastal waters and inland freshwater lakes have photoreceptors with absorption peaks at longer wavelengths. Because light diminishes with depth, organisms in the mesopelagic zone have adapted to more dim light conditions with larger eye size and wider pupils. Aquatic species are expected to be vulnerable to anthropogenic light at night

because of their high photosensitivity at low illuminance (53), which is an adaptation to decreased light intensity as light is filtered out by water.

Effects of anthropogenic light on temporal organization

Light is the key driver of the most important temporal niches in nature. The contrast between high light levels during the day and low levels at night enables species to share the same habitat within a 24-hour cycle. For most species, photic conditions are essential for their ability to survive (24). Organisms need to optimally schedule activity, rest, and sleep in (species-specific) natural light conditions.

The disturbance of rhythms in natural systems by light at night has attracted increasing interest (54), particularly in laboratory studies. For example, great tits (*Parus major*) exposed to low light levels during the dark phase of the light cycle were found to advance the start of their daily activities [e.g., (55)]. Rhythms in laboratory mice were shown to be weakened by dim light at night, and their hormonal rhythms were affected (56). Light at night has also been shown to disrupt circadian gene expression in great tits (57). In the field, an advanced onset of dawn song has been observed for several bird species, and individual blackbirds (*Turdus merula*) exposed to higher levels of anthropogenic light begin their activity earlier in the day (58). By contrast, nocturnal species respond to light by delaying their activity. For example, least horseshoe bats (*Rhinolophus pusillus*) emerge later, when their roost is illuminated (59). Bird species that normally start their dawn song relatively early during still low light levels, such as the robin (*Erithacus rubecula*), respond more strongly to the presence of artificial light compared with other birds (e.g., the blue tit, *Cyanistes caeruleus*) that start dawn song later in the morning [(23); Fig. 2].

In temperate zones, anthropogenic light interferes with the annual cycle of species. Trees delay shedding leaves from branches close to streetlights (60). Anthropogenic light can advance reproduction in birds (22), delay reproduction in mammals (61), and prolong yearly reproduction in insects (62).

Anthropogenic light affects interactions and trophic levels

Changes in the population of a species caused by anthropogenic light inevitably cause changes in the food web. Light can facilitate foraging for predators by concentrating prey species, such as for synanthropic bat species that catch light-attracted flying insects (Fig. 3) (63). Such changes in the predator–prey interaction may, however, be part of a trade-off for bats because they need to prevent exposing themselves too much (64). Foraging may be further facilitated by providing better visual detection of prey, as was shown for burrowing owls (*Athene cunicularia*), which could expand their foraging habitat into urbanized areas using the presence of anthropogenic light (65). Conversely, prey species may avoid illuminated, otherwise suitable habitat or change foraging behavior. Such changes have been shown in jerboas (*Allactaga sibirica*), which spend less time searching for food in illuminated conditions (66). Likewise, in aquatic systems, light at night can counteract the benefits of shelter material for amphipods (*Gammarus fossarum*) seeking shelter from the predatory Eurasian perch (*Perca fluviatilis*) (67).

Complex effects have been reported about the interaction of urbanization with the response to light. In urban areas, mule deer (*Odocoileus hemionus*) use illuminated foraging grounds but are then exposed to predation by cougars (*Puma concolor*) (30), which potentially results in an ecological “trap” in which species may do worse in an ostensibly beneficial situation.

Trophic interactions can form the basis of key ecosystem services such as pollination by insects. Nocturnal pollination is strongly affected by anthropogenic light, and reduced nocturnal pollination

rates are compensated for by diurnal insects (68). The disturbance of trophic interactions by light at night in plant–herbivore communities can be complex and depend on species and color composition (69). To understand ecosystem-wide changes, a better understanding of trophic interactions is essential.

Anthropogenic light affects species at different time scales

The attraction of animals to light is a well-known direct response. Anyone who is attentive will notice the accumulation of insects around light sources. Attraction has been reported in many other species groups, such as marine turtles, birds, and amphibians, and often has direct consequences for survival (8, 12, 17) and subsequently for populations. Because the removal of light sources is very rare, it is important to assess effects that may only manifest after a long period of time. Several studies have shown indirect effects of anthropogenic light on many insect species (9). Adult fireflies survive light sources in proximity but fail to attract mates (70), which eventually results in population decline. Moth species, in addition to the agony of being trapped near light sources, are burdened by impaired reproduction and development (38). Light at night affects gonadal growth in blackbirds, which manifests only during the second year of exposure (71). Ultimately, light at night may cause adaptive changes, but evidence is limited to just a few studies (9). These include the examples of potential adaptation in spiders (*Larinioides sclopetarius*) with the innate preference for building webs around anthropogenic light sources (40) and in urban moths that show reduced flight-to-light behavior compared with rural conspecifics (72).

The way forward

Given the varied and substantial impacts of anthropogenic light, there are no simple solutions for its reduction and mitigation in natural systems. Continued increases in the nocturnal use of anthropogenic lighting will exacerbate its impact on our natural environment (Figs. 1C and 4, A to E), causing major changes to ecosystems, such as further declines in insect populations, loss of habitats of nocturnal mammals, and disruption of food web interactions. These changes will lead to the loss of biodiversity and potential feedback effects, including impaired ecosystem services such as the pollination of crops. Keeping natural areas dark, limiting light emissions from near and distant light sources, and thereby reducing sky brightness are therefore of utmost importance. Strategies to prevent light emissions into nature conservation areas are therefore proposed to be urgently implemented to ensure the long-term survival of protected species, preferably by combinations of different light mitigation measures (53, 73). To effectively implement these measures, both national and international collaborations are essential. In protected areas, the aim should be to reduce light emissions from anthropogenic light sources to natural nocturnal light conditions. Current international guidelines, such as the “Guide on the limitation of the effects of obtrusive light from outdoor lighting installations” (74), can be used as the first step in ensuring that light emissions are below the recommended threshold values in protected areas.

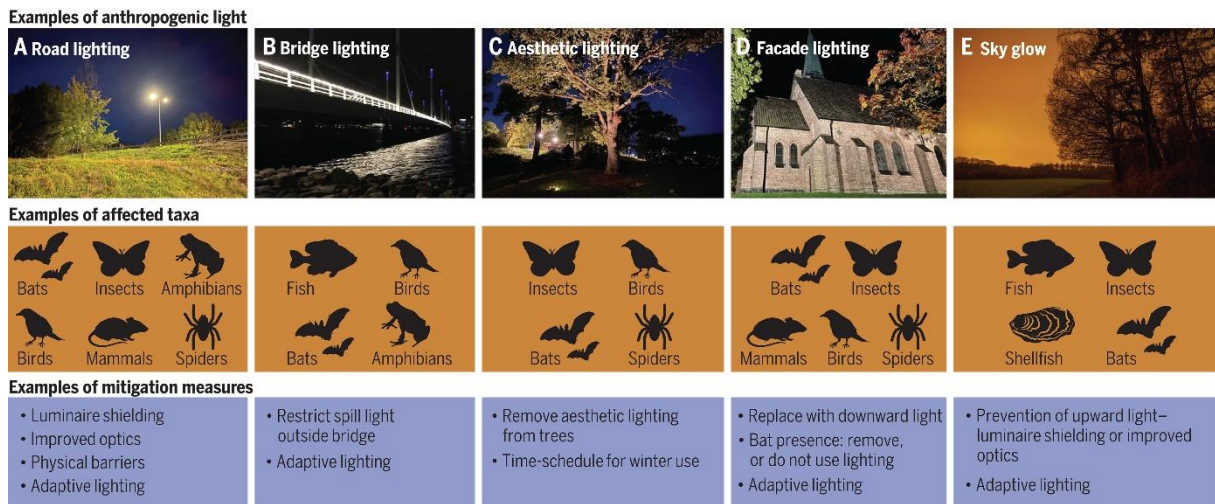


Fig. 4. Examples of anthropogenic light, affected taxa, and mitigation measures.

(A) Terrestrial species can be affected by road lighting, which can be reduced through various measures to control light spill. (B) Bridge lighting can affect both aquatic and terrestrial species, and light spill outside the bridge should therefore be restricted. (C) Aesthetic lighting on trees can affect species that use trees for habitats or foraging, so this lighting should be removed or time restricted. (D) Upward façade lighting on buildings can affect several terrestrial species, and downward lighting should be used instead unless bats are present. (E) Even low levels of sky glow—reflected light from remote anthropogenic light sources—can affect species in natural habitat.

PHOTOS: (A) TO (C) ANNIKA JAGERBRAND, (D) KAMIEL SPOELSTRA; ILLUSTRATIONS: N. CARY/SCIENCE

Several technical and practical adaptations of lighting designs can be used to reduce their effects on local ecosystems (53, 73). These include luminaire shielding, time-restricted and adaptive lighting, light intensity reductions, and tuning color composition.

Luminaire shielding or special optics can be used to prevent light being emitted in unwanted directions (53). Standardization to restrict spill light is urgently needed to prevent the negative effects of upward light and light outside of intentionally lit areas in vulnerable and exposed ecosystems such as open and aquatic environments (Fig. 4, A and B). Natural barriers, such as dense vegetation, can also be used to hinder light emission. The ecological benefit of time-restricted lighting may be limited, because the human demand for light during the first part of the night coincides with the peak activity of many nocturnal species. For example, bats are particularly active after dusk, reducing the potency of part-night lighting schedules (75). Adaptive road lighting is a promising solution to reduce ecological effects, but it is most effective for roads with low traffic. However, dedicated lighting schedules in more unique situations can be highly effective, for example, the intermittent off-switching of the lighting setup at the National 9/11 Museum’s “Tribute in Light” in lower Manhattan to release thousands of light-trapped migratory birds (17). Decreasing light intensity is essential to preventing its ecological effects because many species are highly photosensitive even at extremely low illuminance levels due to their adaptation to dark nocturnal ecosystems. However, little is known about the intensity thresholds of many species, which may vary according to exposure duration, life history stages, and habitat structure. The installation of dimmable LED lighting is therefore very important because light levels can be adjusted after installation. A good example is the city of Rotterdam in the Netherlands, where all 100,000 light posts are currently fitted with LED fixtures that can be remotely adjusted for light intensity at any time of night. Because of the problematic identification of threshold light intensity levels, a pragmatic approach may be to keep light levels

below lower moonlight illumination levels, which range from 0.05 to 0.1 lux (76). Finally, the color composition of light sources must be carefully chosen because it can modulate ecological consequences. The current worldwide transition to LED lighting poses both challenges and opportunities. White LED lamps often contain a high proportion of blue light (~450 nm) and, although the responses of species are diverse, there is a general tendency to caution against the high emission of blue light. By utilizing diodes that produce different colors, and with the application of phosphor conversion techniques, the amount of blue light in a light source can be reduced. This is effective in protecting animal species because the red part of the color spectrum attracts fewer insects (36) and has a less disturbing effect on the activity of bats (63). Highly adapted spectra should, however, be used cautiously because they may create ecological traps for species that are unable to sense the light and therefore think they are in a safe environment. In addition, technical and practical lighting design adaptations presumably need adjustments to better compensate for variations in ecosystem properties and topography.

International initiatives have been formed to establish policy frameworks aimed at reducing light pollution, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS). Work is underway in the International Commission on Illumination (Commission Internationale de l'Éclairage, CIE) to develop guidelines for minimizing the effects of anthropogenic lighting on the natural environment. Furthermore, some countries have implemented national guidelines aimed at reducing ecological light pollution. Currently, outdoor lighting is not included in the 2030 Agenda for Sustainable Development, which has been adopted by all the members of the United Nations. This is very unfortunate because many Sustainable Development Goals are markedly affected by outdoor lighting and light pollution. For ecological sustainable development, it should be an urgent priority to keep naturally dark environments dark and to protect species from the adverse effects of anthropogenic light. This should be a strong motivator for national and local governments to include effects of anthropogenic lighting in planning and decision making toward a sustainable future.

Future recommendations for ecological protection should aim to establish numerical threshold values on the basis of illuminance or luminance of current light sources and technologies. This will facilitate the translation of new research findings into practical guidelines for lighting design and the upgrading of existing lighting systems. Given the variation in species responses to both spectral differences and intensities, a simple solution to mitigating the effects of anthropogenic light on all species may be challenging. Therefore, investigating different types of mitigation measures and their effectiveness in different species and environments is an important mission for future research.

It is important to recognize that even when the most advanced current technologies are used, light can still spill into the natural environment and sky because of reflections from surfaces. This reflected light may affect aerial species and contribute to sky glow (Fig. 4E). However, guidelines for outdoor lighting or light pollution rarely address restrictions on reflected light. Given the difficulty of effectively reducing the ecological effects of anthropogenic light, it may be necessary to adopt more frugal lighting practices and, in some cases, turn off lights altogether, despite the potential discomfort to humans that this may cause.

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