Ecological and Organismic Effects of Light Pollution

Advanced article

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Since the invention of the electric light bulb in 1879, a significant portion of the planet has been transformed from experiencing a natural pattern of light and dark determined by the sun, moon, stars and occasional other transient lights to being subjected to intermittent and perpetual illumination from human civilisation that is unprecedented in the history of Earth. The pervasiveness of this phenomenon and its exponential growth has measurable and significant consequences for living organisms. The results of recent research have extended knowledge about the geographic scope and specific impacts of artificial night lighting on animal behaviour, physiological processes and ecological interactions across a range of taxa and its broader ecosystem effects.

Introduction

Even a cursory review of satellite-derived composite maps of nocturnal light emissions reveals the global reach of human-produced disruption of the night-time environment. Remotely sensed images can be used to discern city and other electric lights, fires, flares from hydrocarbon facilities and fishing boats (**Figure 1**). The influence of lights on surrounding terrestrial and aquatic habitats depends in large part on the total amount of light directed outwards and downwards and on the amount of cloud cover and particulates in the air that are available to scatter light that otherwise would propagate upwards (Kyba *et al*., 2011). The geographic rate of increase in outdoor lighting is estimated to be 6% per year (Hölker *et al*., 2010).

Light pollution within the context of the life sciences requires a context-dependent definition. From the perspective of evolutionary history and the environment to which all life has adapted, any human-generated light can be considered pollution in that it disrupts natural conditions. Such a definition is unsatisfactory, because nocturnal illumination is a hallmark of modern society and viewed as being indispensable to economic and social well-being. Consequently, a definition of light pollution could be limited to human-generated nocturnal lighting that is excessive or unnecessary or that has adverse impacts on particular species or species groups that are of concern. This definition is also subjective, because one person's excessive lighting is another's artistic expression. For practical purposes, therefore, a definition of light pollution is negotiated in a context-dependent manner that weighs the reality that all artificial lighting disrupts natural patterns of light and dark against the utility and desirability of that light for a range of human activities. The focus on impacts to either the natural environment or the human view of the night sky leads to recognition of 'ecological light pollution' and 'astronomical light pollution' (Longcore and Rich, 2004).

Light at night as an influence on biological processes is a global phenomenon that is highly spatially variable. Global night lights have been measured by satellites at a ~1 km resolution since 1992 and at a ~500 m resolution since 2012 (Kyba *et al*., 2015). These sensors measure the amount of light that escapes upwards, which is correlated with the amount of light that might be received by any person or organism in the environment. Across the globe, lighting visible from space is correlated with economic activity, population density, industrial production and other human activities. Night-time lights have their greatest concentration on continents and in the Northern Hemisphere but are highly variable within these regions (Gaston *et al*., 2014). The effects of lights extend far beyond locations where they occur because light is scattered and reflected in the atmosphere (Kyba *et al*., 2011). The resulting light visible on the ground is called *sky glow* and can reach intensities equal to the illumination from the full moon (**Table 1**). Extrapolation of satellite-measured night-time lights to the associated sky glow effects has shown that very few night skies in the world are entirely unaffected by scattered light from human sources (Cinzano *et al*., 2001).

The natural range of illumination between day and night is 11 orders of magnitude (**Table 1**). Illumination at a forest floor can be 10^{-4} or 10^{-5} lx or less, while a full moon usually produces around 0.1 lx (or more at high altitudes or near the equator) and full sunlight can exceed 10^5 lx. As a result of this variation, species have evolved powers of perception and navigation adapted to the large differences in ambient illumination between day and night. For example, some species have the ability to navigate, by sight, in conditions that are far darker than what

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Figure 1 The global extent and intensity of artificial night lighting is visible in this photograph of the India–Pakistan border taken from the International Space Station on August 21, 2011. The border itself is entirely illuminated with the characteristic orange light of sodium vapour floodlights installed by the Indian government. Photograph ISS028-E-029679 from NASA.

humans would consider complete darkness (Warrant and Dacke, 2010). Bioluminescent organisms have evolved to exploit the natural conditions of illumination for signalling, especially in the oceans and forests. Disruption of these natural conditions, even at light levels imperceptible to the human eye, therefore has adverse consequences on a range of species and interactions (Longcore and Rich, 2004) and, potentially, their evolutionary trajectories (Swaddle *et al*., 2015). These effects could be profound; even streetlights are a million times brighter than typical ambient night-time conditions (Perry *et al*., 2008).

Processes of Biological Disruption by Light Pollution

The degree to which artificial night lighting affects biological systems depends on the species involved and the type of disruption in question, combined with the characteristics of the light itself. Gaston *et al*. (2013) identified six biological and ecological processes that could be disrupted by light at night: photosynthesis, niche partitioning, dark repair and recovery, photoperiodism/circadian rhythms, visual perception and spatial orientation. The extent of impacts varies with the duration, intensity and wavelengths of light that are in the environment (Gaston *et al*., 2013; Longcore and Rich, 2016).

Photosynthesis

Photosynthesis under artificial lighting is desirable in greenhouse agricultural production, where large amount of energy from light that is concentrated in wavelengths at which plants are photosynthetically active (400–700 nm) is required. Little photosynthesis occurs under artificial lighting outdoors and it is limited to areas close to the light sources (Raven and Cockell, 2006). Lighting can affect photosynthesis indirectly as well, through triggering of other physiological responses in plants that influence photosynthesis (Skaf *et al*., 2010).

Niche partitioning

Niche partitioning associated with lighting levels has developed as a result of the historically predictable daily, monthly and annual patterns of light and dark. Diurnal animals that exploit artificial night lighting as a means to extend activity periods occupy the ‘night light niche’, thereby disrupting normal species interactions during the time locations are illuminated. Perry *et al*. (2008) provide an extensive list of diurnal reptiles and amphibians that exploit the night light niche, including geckos, iguanas, skinks, snakes, toads and treefrogs. This phenomenon was also measured for fishes around offshore platforms, where it was referred to as a ‘visual subsidy’ for the fishes exploiting the night light niche (Keenan *et al*., 2007). Although it is tempting to interpret use of the night light niche as being ‘good’ in some abstract sense, this is misleading; every species that benefits from day-like conditions at night intrudes into a niche already occupied by species adapted to natural patterns of light and dark.

Other species that are normally active between twilight and dawn can have their niches disrupted as well. Fireflies are active during particular ambient illumination conditions that sequentially separate the activity periods of different species (Lloyd, 2006). This temporal niche partitioning is vulnerable to changes in nocturnal lighting conditions.

The logical and predictable extension of the erosion of light as a means to maintain niche partitioning is that local species diversity

Table 1 Illumination from natural and artificial sources compared with ecological consequences across taxonomic groups

Magnitude (lx)	Natural and artificial illumination levels (lx)	Species responses with illumination levels (lx)
10^5	103 000 Full sunlight	
10^4	50 000 Partial sunlight	
	10 000 Cloudy	
10^3		
10^2	188 Sunset (Nowinszky, 2004)	
10^1	10 Parking lot	
10^0	1 Light pollution in urban marsh habitat	2.1 Reduction in seed set in short-day soya beans
		1 Initiation of downstream drift and emergence from winter substrate in fishes
10^{-1}	0.5 Illumination from urban sky glow (Kiel, Germany)	0.5 Maximum for foraging in some fishes
	0.1 Typical full moon (0.4 maximum	0.3 Melatonin reduced in Senegal sole (Oliveira *et al*., 2010)
	0.18–0.71 Light pollution on beaches (Taiwan) (Santos *et al*., 2010)	0.25 Disrupted melatonin, promoted tumour growth in rats
	0.178 Illumination from urban sky glow (Vienna)	0.2 Maximum illumination for most fireflies (Brazil) (Hagen and Viviani, 2009)
		0.1 Reduced foraging in rodents and schooling in fishes
		0.1 Desynchronisation of coral planula production (Jokiel *et al*., 1985)
10^{-2}	0.01 Lower limit of many commercial light meters	0.06 Prairie rattlesnakes forage more compared with 0.35 lx
	0.01–0.04 Crescent to half illuminated moon	0.04 Maximum illumination for activity in frogs
		0.01 Delayed foraging on forest floor (Wise, 2007) and increased number of visual threat displays in salamanders
10^{-3}	0.001 Instream illumination from billboards	0.003 Less activity and females hide nest in frogs
		0.001 Foraging in brown trout
		0.001–0.01 Most moth activity (Nowinszky, 2004)
10^{-4}	0.0005 Starry sky without moon	0.0006 Circadian rhythm of *Drosophila jambulina* influenced (Thakurdas *et al*., 2010)
		0.0001 Maximum for activity of *Ascaphus truei* frogs
10^{-5}		0.00001 Lower foraging limit in fishes
10^{-6}	0.000001 Dark night in forest	0.0000004 Negative phototaxis in phantom midge

Common sources of artificial light, including light reflected in the atmosphere (sky glow), produce illumination both brighter than many naturally occurring night-time conditions and above threshold levels to influence many biological phenomena. Sources in Rich and Longcore (2006) unless otherwise noted.

will decline when the full range of light and dark conditions no longer occurs and breadth of potential light-associated niches is reduced. **See also**: **Coexistence**

Dark repair and recovery

Dark repair and recovery refers to nocturnal physiological processes that are essential to healthy functioning of organisms inactive at night. Exposure to artificial lighting during these periods, even for short bursts, can disrupt these physiological processes and have adverse consequences. The production of the hormone melatonin during dark hours and the consequent repair benefits is an example (Liu *et al*., 2013). Melatonin is produced in organisms ranging from single celled to the most complex because of its early origins in evolutionary history (Jones *et al*., 2015). In vertebrates, its function as an antioxidant and scavenger of free radicals can be suppressed by exposure to light at night.

Suppression of melatonin production is greatest for wavelengths of light in the blue portion of the spectrum (Brainard *et al*., 2001). The response to light is dose dependent, with small reductions in melatonin production documented down to within the measurement accuracy of melatonin in the saliva or blood (Rea *et al*., 2010). The lower levels of illumination associated with measurable melatonin suppression in humans is on the order of magnitude of that provided by a streetlight shining directly through a window. The epidemiological studies of melatonin suppression and associated circadian disruption of humans by exterior lighting do suggest an effect; the brightness of human sleeping environments is associated with obesity (McFadden *et al*., 2014), breast cancer (Hurley *et al*., 2014) and prostate cancer (Kloog *et al*., 2009), with the intermediate mechanism of circadian disruption and melatonin suppression assumed. Such studies involve use of satellite imagery of night lighting at multiple scales and provide epidemiological indications that light pollution affects these chronic diseases in humans through interruption of dark repair and recovery.

Photoperiodism and circadian rhythms

Light is a signal that influences the timing of activities for organisms at several scales. Circadian rhythms are entrained daily by light and dark cycles for all organisms living in illuminated environments. Similarly, daylength signals trigger physiological responses associated with seasonal changes in environmental conditions for species living in seasonal environments.

Circadian clocks have evolved to synchronise physiology, metabolism and behaviour to the 24-h cycle of Earth (Vanin *et al*., 2012). In diverse organisms, circadian oscillators can be entrained to local time through the detection of an environmental cue, known as a zeitgeber, such that the endogenous timing of peaks and troughs stably corresponds to an environmental reference point, frequently dark-to-light transition, for which specialised photoreceptive and phototransductive mechanisms have evolved to be capable of functioning as pacemakers to synchronise downstream rhythmic events to the environment. **See also**: **Circadian Rhythms**

Studies of the effects of artificial lighting on photoperiodic responses are abundant, partly because of the implications for understanding human health (Zubidat *et al*., 2010). As a whole, they show that artificial lighting can entrain circadian rhythms and influence physiological functions such as immune response at relatively low levels (Bedrosian *et al*., 2011). For example, extremely dim light is sufficient to entrain rhythms in mice and can be done without affecting the other physiological indicators of light influence such as phase shifting or reduced melatonin production (Butler and Silver, 2011). For shorter wavelengths (blue and green), entrainment takes place at 10^{-3} lx. Adverse effects of mistiming have been documented on immune response, metabolism and stress associated with exposure to dim light at night (Bedrosian *et al*., 2011; Fonken *et al*., 2010; Zubidat *et al*., 2010).

Light pollution might reset interactions among species whenever synchronisation is important because entrainment requirements are different between species. For instance, plants 'anticipate' the dawn with a synchronised circadian clock and increase immune defence at the time of day when infection is most likely (Wang *et al*., 2011). The timing of resistance (R)-gene-mediated defences in *Arabidopsis* to downy mildew is tied to the circadian system such that defences are greatest before dawn, when the mildew normally disperses its spores (Wang *et al*., 2011). The importance of circadian rhythms in plants, for everything from disease response and flowering time to seed germination, and the potential for disruption by artificial night lighting, has not been explored widely (Resco *et al*., 2009). Some plants might use light-triggered circadian rhythms to synchronise expression of antiherbivory compounds with periods of peak herbivory, leading to increased loss from herbivory in out-of-phase plants (Goodspeed *et al*., 2012). **See also**: **Plant Circadian Rhythms**

In animals, research on timing of morning birdsong illustrates how lights can subtly influence reproductive behaviours through influences on circadian rhythms. For forest birds in Vienna, proximity to night lights advanced the morning chorus and resulted in more extrapair copulations than would be expected for younger Blue Tits (*Cyanistes caeruleus*) that were defending lower quality territories on forest edges adjacent to streetlights (Kempenaers *et al*., 2010). Other work has shown an earlier dawn chorus in light-polluted environments e.g., (Miller, 2006).

Artificial lighting can also induce or delay seasonal changes that are asynchronous with actual conditions, described as 'seasons out of time' (Haim *et al*., 2005). Such mistiming leads to failure of organisms to adjust appropriately to changing seasons, with a range of results that include plants not setting seed with shortened days or failing to drop leaves in the fall (Bennie *et al*., 2016) and disruption of reproductive synchronisation necessary to exploit environmental conditions (Robert *et al*., 2015). Integrating studies of circadian disruption on species in the wild with research on human and animal models is at the frontier of chronobiological research (Dominoni *et al*., 2016).

Visual perception

Artificial lighting can allow species to see at night that would otherwise not be able to do so. This has the potential to affect a whole range of behaviours and species interactions. Many studies link foraging activity with specific lighting conditions, presumably optimised to reduce predation risk while maximising foraging efficiency for each species. For example, onset of foraging time is delayed in lesser horseshoe bats (*Rhinolophus hipposideros*) when exposed to lighting and the lit areas of hedgerows were avoided (Stone *et al*., 2009). This pattern of delay is now seen in multiple taxa, from salamanders (Wise, 2007) to sugar gliders (*Petaurus breviceps*) (Barber-Meyer, 2007) to bats (Boldogh *et al*., 2007).

A driving force behind patterns of activity and foraging by animals influenced by artificial lighting is presumably the balance between rewards of foraging and risk of predation. The general pattern that has emerged is that increased light assists predators to locate prey. As a result, primary consumers that might otherwise forage under cover of darkness avoid illuminated areas. This general rule has an exception, which is that prey species with a communal predator defence, such as schooling or flocking, experience decreased risk of predation with additional light. Observations of individual species and of communities are consistent with this pattern. The insect community under streetlights has elevated proportions of predators (Davies *et al*., 2012), while schooling fish are aided by group vigilance afforded by additional light (Nightingale *et al*., 2006). A general review of nocturnal foraging suggests that birds and mammals are subject to less predation pressure at night and that the number of animals foraging together is greater at night, especially for clades that are not strictly nocturnal (Beauchamp, 2007).

Spatial orientation

The orientation of species relative to artificial light sources at night, or the inability of species to orient in the presence of artificial light sources, is perhaps the most visible impact of artificial lighting on ecology (Verheijen, 1985). For example, migratory birds are attracted to and collide with oil platforms, cruise ships, communication towers, buildings and athletic stadia and seabirds are attracted to lighted vessels (reviewed in Longcore and Rich, 2016). Hatchling sea turtles are unable to orient properly to crawl to the ocean in areas influenced by artificial lights (Salmon, 2003) and insects are attracted to artificial light sources (**Figure 2**).

Figure 2 Different light sources along a riverside meadow verge in Germany, including cold-white LED (light-emitting diode), halogen spotlight, neutral-white LED, high-pressure sodium vapour, mercury vapour and metal halide. Greatest numbers and species of insects were collected at traps affixed to lamps rich in blue and ultraviolet lights (mercury vapour and metal halide). LEDs, which did not contain ultraviolet light, attracted the fewest insects compared with other types of lighting, but among LEDs, cold-white LEDs attracted the greatest number of insects (Eisenbeis and Eick, 2011). Reproduced with permission from A. Hänel.

Movement and distribution of animals are limited by their ability to orient within the environment. Visual cues and light detection are used by almost all species except those living in perpetual darkness. The pervasiveness of light detection in orientation is shown by the discovery in *Drosophila* larvae of photoreceptors not associated with vision, which are found in each body segment and are sensitive in the ultraviolet, violet and blue wavelengths (Xiang *et al*., 2010). These are precisely the areas of the spectrum associated with light avoidance because daylight is rich in these spectra. Even those species that restrict their activities to the darkest, moonless nights have means of using available light to orient. Nørgaard *et al*. (2008) documented the visual ability of a nocturnal spider in the Namib Desert that presumably uses spatial and temporal summation to identify landscape structures, allowing it to orient and be active in the darkest conditions, thereby minimising predation risk.

The mechanisms by which artificial lighting influences spatial orientation of different taxa may differ. For nocturnally migrating songbirds, the disorientation of birds at lighted communication towers or tall buildings tends to occur when cloud cover has precluded navigation by celestial cues and the bird has encountered a bright light on the landscape. The behaviour is described as the bird being ‘trapped’ within the zone of influence of the lights. Studies show that flashing lights attract far fewer birds and that turning off a light temporarily allows birds to leave an area and continue on their migratory route. The process for insect attraction and disorientation is similarly described as the animal being ‘trapped’ or ‘dazzled’ at the light, with several hypotheses for the mechanism of the phenomenon. For hatchling sea turtles, experimental evidence has established that individuals move away from the horizon with dark silhouettes, which for most of evolutionary history would have been the onshore dune and beach vegetation. Artificial lighting onshore is inconsistent with that pattern and hatchlings either orient towards lights or do not have a fixed orientation (Salmon, 2003).

Synergistic Effects

The effects of light pollution may extend beyond directly observed impacts on physiology and behaviour. In humans, disturbance by light at night could lead to behaviours that increase circadian disruption such as turning on additional lights. In ecosystems, the behavioural or physiological changes caused by artificial night lighting could have cascading effects (Bennie *et al*., 2015). The ecological and evolutionary consequences that result from the global increase in night lighting can interact synergistically with other hazards. For example, lights attract birds to other hazardous sites such as offshore petroleum platforms, wind turbines and buildings where they subsequently are at risk of colliding with glass.

Another synergistic consequence is the creation of polarised light by night lighting (Horváth *et al*., 2009). For example, mayflies are attracted to wet pavement at night because polarised light created by reflecting lights off the pavement is similar to the polarised light signal of water bodies.

The documented disruption of immune function by artificial lighting across a range of taxa has potentially synergistic adverse effects in combination with emerging pathogens and the spread of well-known pathogens under changed climates.

Mitigating Light Pollution

A comprehensive approach to mitigating the effects of light pollution on biological systems would include five considerations: need, spectrum, intensity, direction and duration (Longcore and Rich, 2016). In short, adverse impacts of artificial night lighting could be minimised if

- unnecessary lights are extinguished or not installed;
- spectrum of light is chosen to minimise impacts (especially not ultraviolet or blue, with a preference to reduce and avoid light less than 540 nm (Falchi *et al*., 2011));
- lights are only as bright as necessary for the purpose;
- light is directed only where it is needed, including shielding sensitive habitats from lights, even if those lights are directed downwards; and
- lights are only illuminated as long as necessary and are turned off when not needed (e.g. using timers, motion detectors or bilevel lighting systems that reduce light during low-use periods).

As an example of these considerations, duration and spectrum of lights are important for efforts to mitigate impacts on migrating birds. Attraction varies by wavelength of light (Poot *et al*., 2008) and much work remains to be done on the functioning of avian magnetoreception under different spectra and irradiances of artificial lighting and how these interact in the field. Both red and white solid lights attract birds in a way that flashing lights do not (Gehring *et al*., 2009). Attraction of birds to lights can be reduced by flashing (with a completely dark phase), regardless of spectrum (Gehring *et al*., 2009), so that changes to duration can mitigate spectrum. Where lights must be on all of the time, such as on offshore hydrocarbon platforms, green lights will apparently attract far fewer birds than full-spectrum (white) lights (Poot *et al*., 2008).

New technologies create both opportunities and challenges for mitigation of light pollution. LED (light-emitting diode) lamps have short warm-up time, are highly directional and can be dimmed easily to allow for a dynamic lighting system, but many also contain far more light in the blue spectrum than those lamps they might replace. These attributes provide the opportunity for better lighting control in terms of intensity and direction, but often also result in increased exposure to physiologically active short wavelengths that propagate more in the atmosphere. In 2016, the American Medical Association issued a statement warning against the use of blue-rich street lighting because of potential harmful effects on human health, public safety and the environment (see http://www.ama-assn.org/ama/pub/news/news/2016/2016-06-14-community-guidance-street-lighting.page). LEDs that are lower in blue content are reaching the market, and to reduce ecological and astronomical impacts, light and filter combinations are now being developed and installed.

Many approaches are available to mitigate the effects of light pollution on biological systems (Falchi *et al*., 2011), and unlike other forms of pollution, no costly clean-up is needed. Because other interest groups are involved in attempts to control lighting for the purpose of astronomical observation or energy conservation, full engagement by biologists and life scientists of all specialties is needed to ensure that measures proposed as solutions also reduce impacts to people, ecosystems and evolutionary processes. Testing and defining mitigation strategies for artificial night lighting will be an important research direction.

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