

Ecological light pollution

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Ecologists have long studied the critical role of natural light in regulating species interactions, but, with limited exceptions, have not investigated the consequences of artificial night lighting. In the past century, the extent and intensity of artificial night lighting has increased such that it has substantial effects on the biology and ecology of species in the wild. We distinguish “astronomical light pollution”, which obscures the view of the night sky, from “ecological light pollution”, which alters natural light regimes in terrestrial and aquatic ecosystems. Some of the catastrophic consequences of light for certain taxonomic groups are well known, such as the deaths of migratory birds around tall lighted structures, and those of hatchling sea turtles disoriented by lights on their natal beaches. The more subtle influences of artificial night lighting on the behavior and community ecology of species are less well recognized, and constitute a new focus for research in ecology and a pressing conservation challenge.

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As diurnal creatures, humans have long sought methods to illuminate the night. In pre-industrial times, artificial light was generated by burning various materials, including wood, oil, and even dried fish. While these methods of lighting certainly influenced animal behavior and ecology locally, such effects were limited. The relatively recent invention and rapid proliferation of electric lights, however, have transformed the nighttime environment over substantial portions of the Earth’s surface.

Ecologists have not entirely ignored the potential disruption of ecological systems by artificial night lighting. Several authors have written reviews of the potential effects on ecosystems or taxonomic groups, published in the “gray” literature (Health Council of the Netherlands 2000; Hill 1990), conference proceedings (Outen 2002; Schmiedel 2001), and journal articles (Frank 1988; Verheijen 1985; Salmon 2003). This review attempts to integrate the literature on the topic, and draws on a conference organized by the authors in 2002 titled *Ecological Consequences of Artificial Night Lighting*. We identify the roles that artificial night lighting plays in changing eco-

logical interactions across taxa, as opposed to reviewing these effects by taxonomic group. We first discuss the scale and extent of ecological light pollution and its relationship to astronomical light pollution, as well as the measurement of light for ecological research. We then address the recorded and potential influences of artificial night lighting within the nested hierarchy of behavioral and population ecology, community ecology, and ecosystem ecology. While this hierarchy is somewhat artificial and certainly mutable, it illustrates the breadth of potential consequences of ecological light pollution. The important effects of light on the physiology of organisms (see Health Council of the Netherlands 2000) are not discussed here.

■ Astronomical and ecological light pollution: scale and extent

The term “light pollution” has been in use for a number of years, but in most circumstances refers to the degradation of human views of the night sky. We want to clarify that this is “astronomical light pollution”, where stars and other celestial bodies are washed out by light that is either directed or reflected upward. This is a broad-scale phenomenon, with hundreds of thousands of light sources cumulatively contributing to increased nighttime illumination of the sky; the light reflected back from the sky is called “sky glow” (Figure 1). We describe artificial light that alters the natural patterns of light and dark in ecosystems as “ecological light pollution”. Verheijen (1985) proposed the term “photopollution” to mean “artificial light having adverse effects on wildlife”. Because photopollution literally means “light pollution” and because light pollution is so widely understood today to describe the degradation of the view of the night sky and the human experience of the night, we believe that a more descriptive term is now necessary. Ecological light pollution includes direct glare, chronically increased illumina-

In a nutshell:

- Ecological light pollution includes chronic or periodically increased illumination, unexpected changes in illumination, and direct glare
- Animals can experience increased orientation or disorientation from additional illumination and are attracted to or repulsed by glare, which affects foraging, reproduction, communication, and other critical behaviors
- Artificial light disrupts interspecific interactions evolved in natural patterns of light and dark, with serious implications for community ecology

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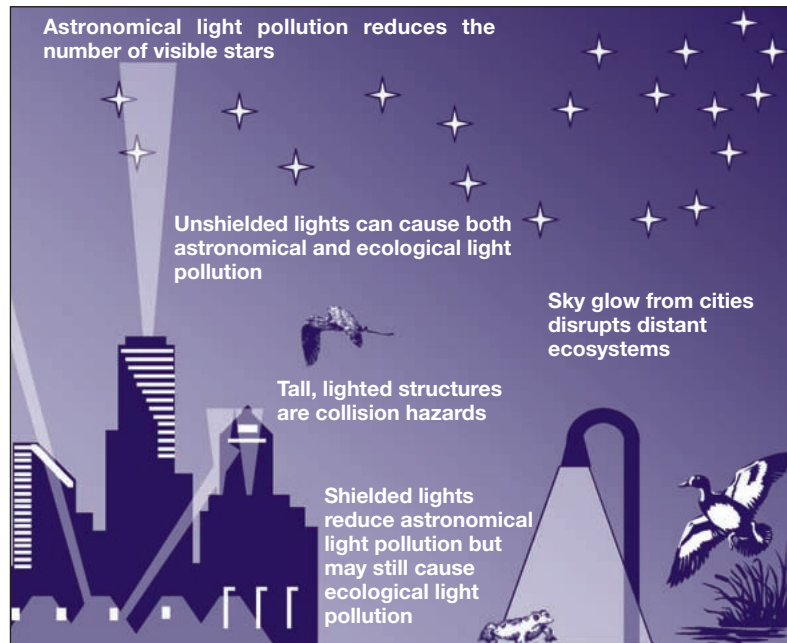


Figure 1. Diagram of ecological and astronomical light pollution.

tion, and temporary, unexpected fluctuations in lighting. Sources of ecological light pollution include sky glow, lighted buildings and towers, streetlights, fishing boats, security lights, lights on vehicles, flares on offshore oil platforms, and even lights on undersea research vessels, all of which can disrupt ecosystems to varying degrees. The phenomenon therefore involves potential effects across a range of spatial and temporal scales.

The extent of ecological light pollution is global (Elvidge *et al.* 1997; Figure 2). The first atlas of artificial night sky brightness illustrates that astronomical light pollution extends to every inhabited continent (Cinzano *et al.* 2001). Cinzano *et al.* (2001) calculate that only 40% of Americans live where it becomes sufficiently dark at night for the human eye to make a complete transition from cone to rod vision and that 18.7% of the terrestrial surface of the Earth is exposed to night sky brightness that is polluted by astronomical standards. Ecosystems may be affected by these levels of illumination and lights that do not contribute to sky glow may still have ecological consequences, ensuring that ecological light pollution afflicts an even greater proportion of the Earth. Lighted fishing fleets, offshore oil platforms, and cruise ships bring the disruption of artificial night lighting to the world's oceans.

The tropics may be especially sensitive to alterations in natural diel (ie over a 24-hour period) patterns of light and dark because of the year-round constancy of daily cycles (Gliwicz 1999). A shortened or brighter night is more likely to affect tropical species adapted to diel patterns with minimal seasonal variation than extratropical species adapted to substantial seasonal variation. Of course, temperate and polar zone species active only during a portion of the year would be excluded from this gen-

eralization. Species in temperate zones will also be susceptible to disruptions if they depend on seasonal day length cues to trigger critical behaviors.

■ Measurements and units

Measurement of ecological light pollution often involves determination of illumination at a given place. Illumination is the amount of light incident per unit area – not the only measurement relevant to ecological light pollution, but the most common. Light varies in intensity (the number of photons per unit area) and spectral content (expressed by wavelength). Ideally, ecologists should measure illumination in photons per square meter per second with associated measurements of the wavelengths of light present. More often, illumination is measured in lux (or footcandles, the non-SI unit), which expresses the brightness of light as perceived by the human

eye. The lux measurement places more emphasis on wavelengths of light that the human eye detects best and less on those that humans perceive poorly. Because other organisms perceive light differently – including wavelengths not visible to humans – future research on ecological light pollution should identify these responses and measure light accordingly. For example, Gal *et al.* (1999) calculated the response curve of mysid shrimp to light and reported illumination in lux adjusted for the spectral sensitivity of the species.

Ecologists are faced with a practical difficulty when communicating information about light conditions. Lux is the standard used by nearly all lighting designers, lighting engineers, and environmental regulators; communication with them requires reporting in this unit. Yet the use of lux ignores biologically relevant information. High-pressure sodium lights, for instance, will attract moths because of the presence of ultraviolet wavelengths, while low-pressure sodium lights of the same intensity, but not producing ultraviolet light, will not (Rydell 1992). Nevertheless, we use lux here, both because of the need to communicate with applied professionals, and because of its current and past widespread usage. As this research field develops, however, measurements of radiation and spectrum relevant to the organisms in question should be used, even though lux will probably continue to be the preferred unit for communication with professionals in other disciplines.

Ecologists also measure aspects of the light environment other than absolute illumination levels. A sudden change in illumination is disruptive for some species (Buchanan 1993), so percent change in illumination, rate, or similar measures may be relevant. Ecologists may also measure luminance (ie brightness) of light sources that are visible to organisms.

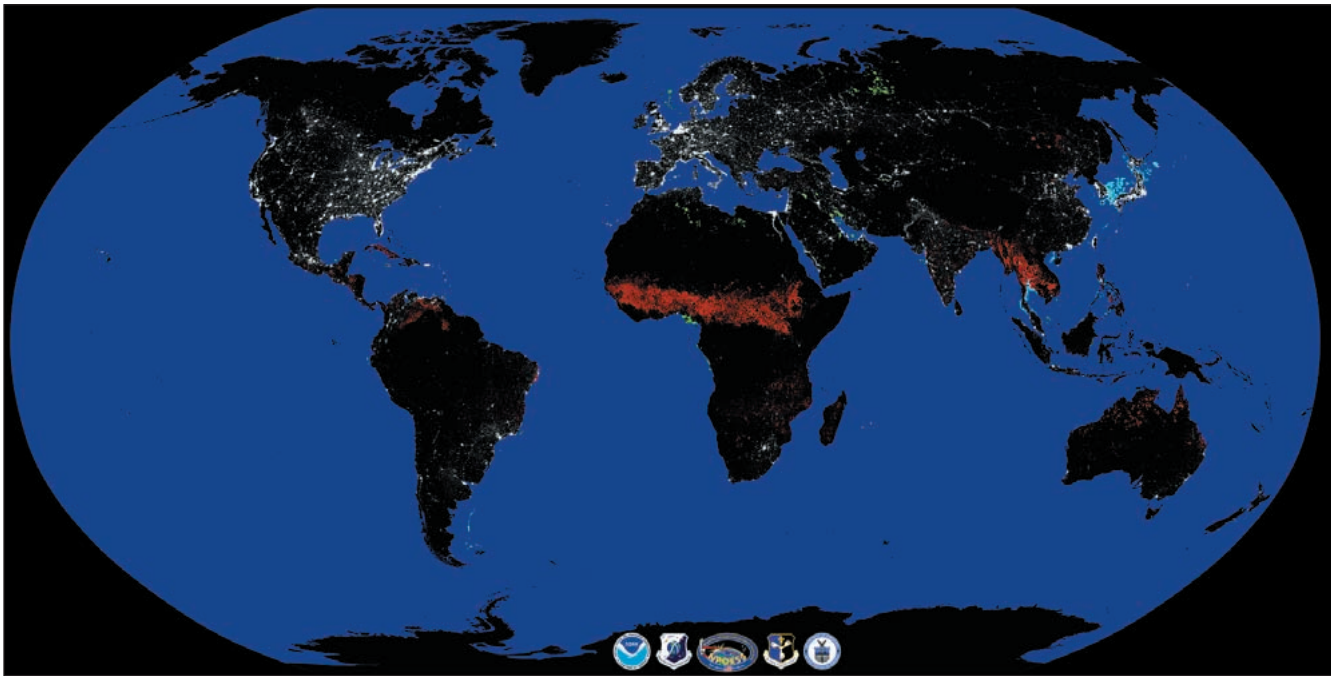


Figure 2. Distribution of artificial lights visible from space. Produced using cloud-free portions of low-light imaging data acquired by the US Air Force Defense Meteorological Satellite Program Operational Linescan System. Four types of lights are identified: (1) human settlements – cities, towns, and villages (white), (2) fires – defined as ephemeral lights on land (red), (3) gas flares (green), and (4) heavily lit fishing boats (blue). See Elvidge et al. (2001) for details. Image, data processing, and descriptive text by the National Oceanic and Atmospheric Administration's National Geophysical Data Center.

■ Behavioral and population ecology

Ecological light pollution has demonstrable effects on the behavioral and population ecology of organisms in natural settings. As a whole, these effects derive from changes in orientation, disorientation, or misorientation, and attraction or repulsion from the altered light environment, which in turn may affect foraging, reproduction, migration, and communication.

Orientation/disorientation and attraction/repulsion

Orientation and disorientation are responses to ambient illumination (ie the amount of light incident on objects in an environment). In contrast, attraction and repulsion occur in response to the light sources themselves and are therefore responses to luminance or the brightness of the source of light (Health Council of the Netherlands 2000).

Increased illumination may extend diurnal or crepuscular behaviors into the nighttime environment by improving an animal's ability to orient itself. Many usually diurnal birds (Hill 1990) and reptiles (Schwartz and Henderson 1991), for example, forage under artificial lights. This has been termed the "night light niche" for reptiles and seems beneficial for those species that can exploit it, but not for their prey (Schwartz and Henderson 1991).

In addition to foraging, orientation under artificial illumination may induce other behaviors, such as territorial singing in birds (Bergen and Abs 1997). For the northern mockingbird (*Mimus polyglottos*), males sing at night before mating, but once mated only sing at night in artificially

lighted areas (Derrickson 1988) or during the full moon. The effect of these light-induced behaviors on fitness is unknown.

Constant artificial night lighting may also disorient organisms accustomed to navigating in a dark environment. The best-known example of this is the disorientation of hatchling sea turtles emerging from nests on sandy beaches. Under normal circumstances, hatchlings move away from low, dark silhouettes (historically, those of dune vegetation), allowing them to crawl quickly to the ocean. With beachfront lighting, the silhouettes that would have cued movement are no longer perceived, resulting in disorientation (Salmon *et al.* 1995). Lighting also affects the egg-laying behavior of female sea turtles. (For reviews of effects on sea turtles, see Salmon 2003 and Witherington 1997).

Changes in light level may disrupt orientation in nocturnal animals. The range of anatomical adaptations to allow night vision is broad (Park 1940), and rapid increases in light can blind animals. For frogs, a quick increase in illumination causes a reduction in visual capability from which the recovery time may be minutes to hours (Buchanan 1993). After becoming adjusted to a light, frogs may be attracted to it as well (Jaeger and Hailman 1973; Figure 3).

Birds can be disoriented and entrapped by lights at night (Ogden 1996). Once a bird is within a lighted zone at night, it may become "trapped" and will not leave the lighted area. Large numbers of nocturnally migrating birds are therefore affected when meteorological conditions bring them close to lights, for instance, during inclement weather or late at night when they tend to fly lower.



Figure 3. Attraction of frogs to a candle set out on a small raft. Illustration by Charles Copeland of an experiment in northern Maine or Canada described by William J Long (1901). Twelve or fifteen bullfrogs (*Rana catesbeiana*) climbed on to the small raft before it flipped over.

Within the sphere of lights, birds may collide with each other or a structure, become exhausted, or be taken by predators. Birds that are waylaid by buildings in urban areas at night often die in collisions with windows as they try to escape during the day. Artificial lighting has attracted birds to smokestacks, lighthouses (Squires and Hanson 1918), broadcast towers (Ogden 1996), boats (Dick and Donaldson 1978), greenhouses, oil platforms (Wiese *et al.* 2001), and other structures at night, resulting in direct mortality, and thus interfering with migration routes.

Many groups of insects, of which moths are one well-known example (Frank 1988), are attracted to lights. Other taxa showing the same attraction include lacewings, beetles, bugs, caddisflies, crane flies, midges, hoverflies, wasps, and bush crickets (Eisenbeis and Hassel 2000; Kolligs 2000; Figure 4). Attraction depends on the spectrum of light – insect collectors use ultraviolet light because of its attractive qualities – and the characteristics of other lights in the vicinity.

Nonflying arthropods vary in their reaction to lights. Some nocturnal spiders are negatively phototactic (ie repelled by light), whereas others will exploit light if available (Nakamura and Yamashita 1997). Some insects are always positively phototactic as an adaptive behavior and others always photonegative (Summers 1997). In arthropods, these responses may also be influenced by the frequent correlations between light, humidity, and temperature.

Natural resource managers can exploit the responses of animals to lights. Lights are sometimes used to attract fish to ladders, allowing them to bypass dams and power plants (Haymes *et al.* 1984). Similarly, lights can attract larval fish to coral reefs (Munday *et al.* 1998). In the terrestrial realm, dispersing mountain lions avoid lighted areas to such a degree that Beier (1995) suggests installing lights to deter them from entering habitats dead-ending in areas where humans live.

Reproduction

Reproductive behaviors may be altered by artificial night lighting. Female *Physalaemus pustulosus* frogs, for example, are less selective about mate choice when light levels are increased, presumably preferring to mate quickly and avoid the increased predation risk of mating activity (Rand *et al.* 1997). Night lighting may also inhibit amphibian movement to and from breeding areas by stimulating phototactic behavior. Bryant Buchanan (pers comm) reports that frogs in an experimental enclosure stopped mating activity during night football games, when lights from a nearby stadium increased sky glow. Mating choruses resumed only when the enclosure was covered to shield the frogs from the light.

In birds, some evidence suggests that artificial night lighting affects the choice of nest site. De Molenaar *et al.*



Figure 4. Thousands of mayflies carpet the ground around a security light at Milleccoquins Point in Naubinway on the Upper Peninsula of Michigan.

(2000) investigated the effects of roadway lighting on black-tailed godwits (*Limosa l. limosa*) in wet grassland habitats. Breeding densities of godwits were recorded over 2 years, comparing lighted and unlighted conditions near a roadway and near light poles installed in a wet grassland away from the road influence. When all other habitat factors were taken into account, the density of nests was slightly but statistically lower up to 300 m away from the lighting at roadway and control sites. The researchers also noted that birds nesting earlier in the year chose sites farther away from the lighting, while those nesting later filled in sites closer to the lights.

Communication

Visual communication within and between species may be influenced by artificial night lighting. Some species use light to communicate, and are therefore especially susceptible to disruption. Female glow-worms attract males up to 45 m away with bioluminescent flashes; the presence of artificial lighting reduces the visibility of these communications. Similarly, the complex visual communication system of fireflies could be impaired by stray light (Lloyd 1994).

Artificial night lighting could also alter communication patterns as a secondary effect. Coyotes (*Canis latrans*) group howl and group yip-howl more during the new moon, when it is darkest. Communication is necessary either to reduce trespassing from other packs, or to assemble packs to hunt larger prey during dark conditions (Bender *et al.* 1996). Sky glow could increase ambient illumination to eliminate this pattern in affected areas.

Because of the central role of vision in orientation and behavior of most animals, it is not surprising that artificial lighting alters behavior. This causes an immediate conservation concern for some species, while for other species the influence may seem to be positive. Such “positive” effects, however, may have negative consequences within the context of community ecology.

■ Community ecology

The behaviors exhibited by individual animals in response to ambient illumination (orientation, disorientation) and to luminance (attraction, repulsion) influence community interactions, of which competition and predation are examples.

Competition

Artificial night lighting could disrupt the interactions of groups of species that show resource partitioning across illumination gradients. For example, in natural commu-



Figure 5. Crowned hornbill (*Tockus albotoerminatus*) hawking insects at a light at the Kibale Forest National Park, Uganda.

nities, some foraging times are partitioned among species that prefer different levels of lighting. The squirrel treefrog (*Hyla squirrela*) is able to orient and forage at lighting levels as low as 10^{-5} lux and under natural conditions typically will stop foraging at illuminations above 10^{-3} lux (Buchanan 1998). The western toad (*Bufo boreas*) forages only at illuminations between 10^{-1} and 10^{-5} lux, while the tailed frog (*Ascaphus truei*) forages only during the darkest part of the night at below 10^{-5} lux (Hailman 1984). While these three species are not necessarily sympatric (ie inhabiting the same area), and differ in other niche dimensions, they illustrate the division of the light gradient by foragers.

Many bat species are attracted to insects that congregate around light sources (Frank 1988). Although it may seem that this is a positive effect, the increased food concentration benefits only those species that exploit light sources and could therefore result in altered community structure. Faster-flying species of bats congregate around lights to feed on insects, but other, slower-flying species avoid lights (Blake *et al.* 1994; Rydell and Baagøe 1996).

Changes in competitive communities occur as diurnal species move into the “night light niche” (Schwartz and Henderson 1991). This concept, as originally described, applies to reptiles, but easily extends to other taxa, such as spiders (Frank pers comm) and birds (Hill 1990; Figure 5).

Predation

Although it may seem beneficial for diurnal species to be able to forage longer under artificial lights, any gains from increased activity time can be offset by increased predation risk (Gotthard 2000). The balance between gains from extended foraging time and risk of increased preda-

tion is a central topic for research on small mammals, reptiles, and birds (Kotler 1984; Lima 1998). Small rodents forage less at high illumination levels (Lima 1998), a tendency also exhibited by some lagomorphs (Gilbert and Boutin 1991), marsupials (Laferrier 1997), snakes (Klauber 1939), bats (Rydell 1992), fish (Gibson 1978), aquatic invertebrates (Moore *et al.* 2000), and other taxa.

Unexpected changes in light conditions may disrupt predator–prey relationships. Gliwicz (1986, 1999) describes high predation by fish on zooplankton during nights when the full moon rose hours after sunset. Zooplankton had migrated to the surface to forage under cover of darkness, only to be illuminated by the rising moon and subjected to intense predation. This “lunar light trap” (Gliwicz 1986) illustrates a natural occurrence, but unexpected illumination from human sources could disrupt predator–prey interactions in a similar manner, often to the benefit of the predator.

Available research shows that artificial night lighting disrupts predator–prey relationships, which is consistent with the documented importance of natural light regimes in mediating such interactions. In one example, harbor seals (*Phoca vitulina*) congregated under artificial lights to eat juvenile salmonids as they migrated downstream; turning the lights off reduced predation levels (Yurk and Trites 2000). Nighttime illumination at urban crow roosts was higher than at control sites, presumably because this helps the crows avoid predation from owls (Gorenzel and Salmon 1995). Desert rodents reduced foraging activity when exposed to the light of a single camp lantern (Kotler 1984). Frank (1988) reviews predation by bats, birds, skunks, toads, and spiders on moths attracted to artificial lights. Mercury vapor lights, in particular, disrupt the interaction between bats and tympanate moths by interfering with moth detection of ultrasonic chirps used by bats in echolocation, leaving moths unable to take their normal evasive action (Svensson and Rydell 1998).

From these examples, it follows that community structure will be altered where light affects interspecific interactions. A “perpetual full moon” from artificial lights will favor light-tolerant species and exclude others. If the darkest natural conditions never occur, those species that maximize foraging during the new moon could eventually be compromised, at risk of failing to meet monthly energy budgets. The resulting community structure would be simplified, and these changes could in turn affect ecosystem characteristics.

■ Ecosystem effects

The cumulative effects of behavioral changes induced by artificial night lighting on competition and predation have the potential to disrupt key ecosystem functions. The spillover effects from ecological light pollution on aquatic invertebrates illustrates this point. Many aquatic invertebrates, such as zooplankton, move up and down within the water column during a 24-hour period, in a

behavior known as “diel vertical migration”. Diel vertical migration presumably results from a need to avoid predation during lighted conditions, so many zooplankton forage near water surfaces only during dark conditions (Gliwicz 1986). Light dimmer than that of a half moon ($<10^{-1}$ lux) is sufficient to influence the vertical distribution of some aquatic invertebrates, and indeed patterns of diel vertical migration change with the lunar cycle (Dodson 1990).

Moore *et al.* (2000) documented the effect of artificial light on the diel migration of the zooplankton *Daphnia* in the wild. Artificial illumination decreased the magnitude of diel migrations, both in the range of vertical movement and the number of individuals migrating. The researchers hypothesize that this disruption of diel vertical migration may have substantial detrimental effects on ecosystem health. With fewer zooplankton migrating to the surface to graze, algae populations may increase. Such algal blooms would then have a series of adverse effects on water quality (Moore *et al.* 2000).

The reverberating effects of community changes caused by artificial night lighting could influence other ecosystem functions. Although the outcomes are not yet predictable, and redundancy will buffer changes, indications are that light-influenced ecosystems will suffer from important changes attributable to artificial light alone and in combination with other disturbances. Even remote areas may be exposed to increased illumination from sky glow, but the most noticeable effects will occur in those areas where lights are close to natural habitats. This may be in wilderness where summer getaways are built, along the expanding front of suburbanization, near the wetlands and estuaries that are often the last open spaces in cities, or on the open ocean, where cruise ships, squid boats, and oil derricks light the night.

■ Conclusions

Our understanding of the full range of ecological consequences of artificial night lighting is still limited, and the field holds many opportunities for basic and applied research. Studies of natural populations are necessary to investigate hypotheses generated in the laboratory, evidence of lunar cycles in wild populations, and natural history observations. If current trends continue, the influence of stray light on ecosystems will expand in geographic scope and intensity. Today, 20% of the area of the coterminous US lies within 125 m of a road (Riitters and Wickham 2003). Lights follow roads, and the proportion of ecosystems uninfluenced by altered light regimes is decreasing. We believe that many ecologists have neglected to consider artificial night lighting as a relevant environmental factor, while conservationists have certainly neglected to include the nighttime environment in reserve and corridor design.

Successful investigation of ecological light pollution will require collaboration with physical scientists and

engineers to improve equipment to measure light characteristics at ecologically relevant levels under diverse field conditions. Researchers should give special consideration to the tropics, where the constancy of day–night lighting patterns has probably resulted in narrow niche breadths relative to illumination. Aquatic ecosystems deserve increased attention as well, because despite the central importance of light to freshwater and marine ecology, consideration of artificial lighting has so far been limited. Research on the effects of artificial night lighting will enhance understanding of urban ecosystems – the two National Science Foundation (NSF) urban Long Term Ecological Research sites are ideal locations for such efforts.

Careful research focusing on artificial night lighting will probably reveal it to be a powerful force structuring local communities by disrupting competition and predator–prey interactions. Researchers will face the challenge of disentangling the confounding and cumulative effects of other facets of human disturbance with which artificial night lighting will often be correlated, such as roads, urban development, noise, exotic species, animal harvest, and resource extraction. To do so, measurements of light disturbance should be included routinely as part of environmental monitoring protocols, such as the NSF's National Ecological Observatory Network (NEON). Future research is likely to reveal artificial night lighting to be an important, independent, and cumulative factor in the disruption of natural ecosystems, and a major challenge for their preservation.

Ecologists have studied diel and lunar patterns in the behavior of organisms for the greater part of a century (see Park 1940 and references therein), and the deaths of birds from lights for nearly as long (Squires and Hanson 1918). Humans have now so altered the natural patterns of light and dark that these new conditions must be afforded a more central role in research on species and ecosystems beyond the instances that leave carcasses on the ground.

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