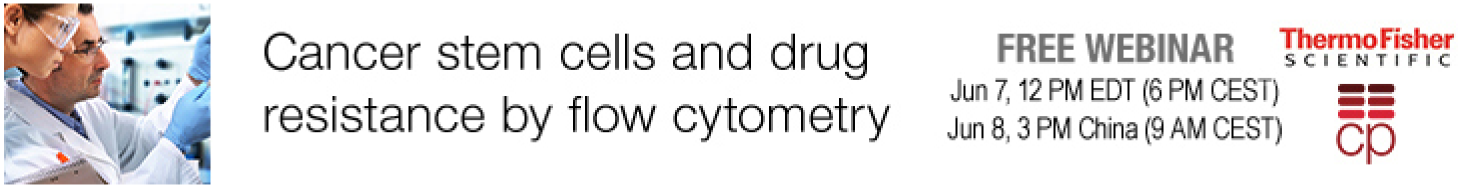

Original Article

# The ecological impacts of nighttime light pollution: a mechanistic appraisal

1. Kevin J. Gaston[1,*],
2. Jonathan Bennie[1],
3. Thomas W. Davies[1] and
4. John Hopkins[2]

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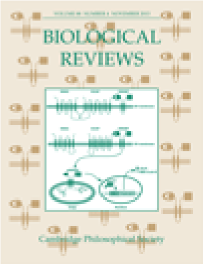
Issue



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## Author Information

[1]

Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, U.K.

[2]

Natural England, Peterborough, U.K.

*Author for correspondence (Tel: 01326 255810; E-mail: k.j.gaston@exeter.ac.uk).

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**Keywords:**

dark; information; light; moonlight; night; pollution; resources; rhythms; time

# ABSTRACT

The ecological impacts of nighttime light pollution have been a longstanding source of concern, accentuated by realized and projected growth in electrical lighting. As human communities and lighting technologies develop, artificial light increasingly modifies natural light regimes by encroaching on dark refuges in space, in time, and across wavelengths. A wide variety of ecological implications of artificial light have been identified. However, the primary research to date is largely focused on the disruptive influence of nighttime light on higher vertebrates, and while comprehensive reviews have been compiled along taxonomic lines and within specific research domains, the subject is in need of synthesis within a common mechanistic framework. Here we propose such a framework that focuses on the cross-factoring of the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the ways in which light influences biological systems, particularly the distinction between light as a resource and light as an information source. We review the evidence for each of the combinations of this cross-factoring. As artificial lighting alters natural patterns of light in space, time and across wavelengths, natural patterns of resource use and information flows may be disrupted, with downstream effects to the structure and function of ecosystems. This review highlights: (*i*) the potential influence of nighttime lighting at all levels of biological organisation (from cell to ecosystem); (*ii*) the significant impact that even low levels of nighttime light pollution can have; and (*iii*) the existence of major research gaps, particularly in terms of the impacts of light at population and ecosystem levels, identification of intensity thresholds, and the spatial extent of impacts in the vicinity of artificial lights.

# I. Introduction

It has been argued that the biological world is organized largely by light (Ragni & D'Alcalà, 2004; Foster & Roenneberg, 2008; Bradshaw & Holzapfel, 2010). The rotation of the Earth partitions time into a regular cycle of day and night (giving variation in light intensity of approximately 10 orders of magnitude; Table 1), while its orbital motion and the tilt of its axis cause seasonal variation in the length of time that is spent under conditions of light and darkness in each cycle. These major changes are overlain by more local variation caused by weather conditions, and the effect of the monthly lunar cycle on nighttime light. However, for any given latitude the light regime has been consistent for extremely long periods of geological time, providing a rather invariant context, and a very reliable set of potential environmental cues, against which ecological and evolutionary processes have played out.

**Table 1. Variation in levels of illuminance. Although widely used, note that lux measurement places emphasis on brightness as perceived by human vision**

| | Lux |
|---|---|
| Full sunlight | 103000 |
| Partly sunny | 50000 |
| Cloudy day | 1000–10000 |
| Full moon under clear conditions | 0.1–0.3 |
| Quarter moon | 0.01–0.03 |
| Clear starry night | 0.001 |
| Overcast night sky | 0.00003–0.0001 |
| Operating table | 18000 |
| Bright office | 400–600 |
| Most homes | 100–300 |

| | |
|---|---|
| Main road street lighting (average street level illuminance) | 15 |
| Lighted parking lot | 10 |
| Residential side street (average street level illuminance) | 5 |
| Urban skyglow | 0.15 |

From data in British Standards Institute (2003), Rich & Longcore (2006*b*), and Dick (2011).

Artificial lighting is a common characteristic of human settlement and transport networks (Boyce, 2003; Schreuder, 2010). The spread of electric lighting in particular has provided a major perturbation to natural light regimes, and in consequence arguably a rather novel environmental pressure, disrupting natural cycles of light and darkness (Verheijen, 1958, 1985; Outen, 1998; Health Council of the Netherlands, 2000; Longcore & Rich, 2004; Rich & Longcore, 2006*a*; Navara & Nelson, 2007; Hölker *et al.*, 2010*a*,*b*; Bruce-White & Shardlow, 2011; Perkin *et al.*, 2011). Changes in light regime can be characterized as changes in the spatial distribution, the timing and the spectral composition of artificial light sources. As human communities and lighting technologies develop, artificial light increasingly encroaches on dark refuges in space, in time, and across wavelengths.

# (1) Space

Urbanisation, population growth and economic development have led to rapid, and ongoing, increases in the density and distribution of artificial lighting over recent decades (Fig. 1A; Riegel, 1973; Holden, 1992; Cinzano, Falchi & Elvidge, 2001; Cinzano, 2003; Hölker *et al.*, 2010*a*). A wide variety of lighting devices contribute, including public street lighting, advertising lighting, architectural lighting, domestic lighting and vehicle lighting. The highest intensities of artificial light are experienced in the close vicinity (within metres to tens of metres) of light sources. Within illuminated urban and suburban areas, direct light from street lighting, domestic and commercial sources, and light reflected from the surrounding surfaces, can create a highly patchy light environment. Over much larger areas surrounding towns and cities, a somewhat lower intensity of diffuse background light derives from ‘sky glow’, artificial light scattered in the lower atmosphere. Under cloudy conditions in urban areas, the sky glow effect has been shown to be of an equivalent or greater magnitude than high-elevation summer moonlight (Kyba *et al.*, 2011*a*); it has been estimated that around 23% of the United States, 37% of the European Union, 54% of Japan and 5% of the land surface area of the world regularly exceeds a similar threshold (Cinzano *et al.*, 2001).

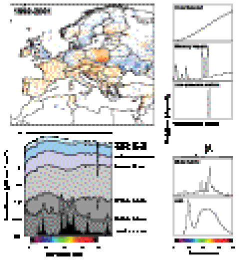

**Figure 1.** Artificial nighttime light varies in space, time and along electromagnetic spectrum. (A) Spatial variation in relative brightness trends of nighttime lights in Europe, using annual DMSP satellite data from 1992 to 2001 inclusive from NOAA National Geophysical Data Center http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html (http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html). As there is no onboard cross-calibration for this dataset between years and satellites, values are calibrated for sensor drift relative to a control area [the island of Sicily, following

Elvidge *et al*. (2009); red – rate of change in light significantly greater than the control region; blue – rate of change significantly lower than the control region]. Economic, technological and policy factors cause clear contrasts among countries and regions. (B) Temporal change in spectral irradiance of ambient light in grassland at Tremough, UK from day (blue) to night (black), 22.11.11; peaks at 19:30 h from indoor fluorescent lighting from nearby offices, and at 22:00 h from footpath lighting. (C) Spectral composition of main electric lighting types used since 1950, from data at http://www.ngdc.noaa.gov/dmsp/spectra.html (http://www.ngdc.noaa.gov/dmsp/spectra.html). In (A) all illustrated changes are relative to the net change in the control region, calculated from cross-calibrated annual images using sixth-order regression with Sicily's nighttime lights. While Sicily was selected as the most suitable calibration region among several candidates by Elvidge *et al*. (2009), changes in lighting have undoubtedly occurred during this period on the island, and hence blue regions do not necessarily indicate decreasing absolute brightness during this period. Only pixels with statistically significant relative change over time at $P < 0.05$ are shown, calculated from Spearman's rank correlation on annual values from 1992 to 2001 inclusive. No trends are detected for highly urban areas where satellite sensor values are saturated.

## (2) Time

Early municipal lighting systems often functioned only on moonless nights or prior to midnight (Jakle, 2001). Throughout the 20th century, the manufacture of cheaper lighting technologies led to more persistent street lighting in developed cities, typically from dusk until dawn, 365 days a year. Lights in commercial, industrial and residential premises may be kept permanently on or switched on intermittently during the hours of darkness for reasons of security or convenience, and amenity lighting, for example floodlighting of sports pitches, is often concentrated in the hours following sunset, leading to a varying light environment throughout the night (Fig. 1B). Economic pressures, limited energy supply and/or efforts to minimize energy consumption and carbon emissions have resulted in constraints on the timing of nighttime lighting in many regions of the world, and, led by developments in technology allowing automated timing and control, dimming or switching off of municipal lighting for periods during the night is being adopted in some developed countries (e.g. Lockwood, 2011).

## (3) Spectral composition

Different forms of artificial lighting have unique spectral signatures, each emitting light at varying intensities over a distinctive range of wavelengths (Fig. 1C; Thorington, 1985; Boyce, 2003; Elvidge *et al.*, 2010; van Langevelde *et al.*, 2011). These spectral signatures differ from those of natural direct and diffuse sunlight, twilight and moonlight, with certain types of lighting restricted to very narrow bandwidths, while others emit over a wide range of wavelengths. Early electric street lighting relied on incandescent bulbs (Jakle, 2001), emitting primarily in yellow wavelengths, while low-pressure sodium lighting, widely adopted in the 1960s and 1970s, emits a single narrow peak in the visible spectrum at 589.3 nm, giving objects a distinctive monochromatic orange hue. More recent light technologies emit over a broad range of wavelengths (high-pressure sodium lighting emits a yellow light allowing some colour discrimination; high-intensity discharge lamps emit a whiter light, with significant peaks in blue and ultra-violet wavelengths, and LED-based white street lighting typically emits at all wavelengths between around 400 and 700 nm, with peaks in the blue and green; Elvidge *et al.*, 2010). Over recent decades the spectral diversity of light sources has grown (Frank, 1988), and the trend towards adopting lighting technologies with a broader spectrum of 'white' light is likely to increase the potential for ecological impacts (including through changes in the colour of sky glow; Kyba *et al.*, 2012).

In combination, the increasing spatial, temporal and spectral distribution of nighttime light pollution provides the potential for major influences on ecological and evolutionary processes (Fig. 2; Navara & Nelson, 2007; van Langevelde *et al.*, 2011). Substantial attention has been paid to catastrophic events, such as the mortality that can follow from the disorientation of hatchling turtles and of birds by nighttime lighting (e.g. Howell, Laskey & Tanner, 1954; Verheijen, 1958, 1985; McFarlane, 1963; Reed, Sincock & Hailman, 1985; Witherington & Bjorndal, 1991; Peters & Verhoeven, 1994; Salmon *et al.*, 1995; Le Corre *et al.*, 2002; Jones & Francis, 2003; Black, 2005; Tuxbury & Salmon, 2005; Gauthreaux & Belser, 2006; Montevecchi, 2006; Evans *et al.*, 2007b; Lorne & Salmon, 2007; Gehring, Kerlinger & Manville, 2009; Tin *et al.*, 2009; Rodríguez, Rodríguez & Lucas, 2012). However, a much broader set of implications has been identified (Longcore & Rich, 2004; Hölker *et al.*, 2010*a*; Perkin *et al.*, 2011). In consequence, and echoing earlier statements (e.g. Verheijen, 1985), there have been several recent calls for a much improved understanding of these implications (e.g. Health Council of the Netherlands, 2000; Sutherland *et al.*, 2006; The Royal Commission on Environmental Pollution, 2009; Hölker *et al.*, 2010*a*,*b*; Perkin *et al.*, 2011; Fox, 2013).

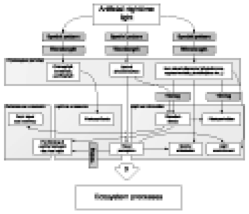

**Figure 2.** Potential pathways for ecosystem effects of light pollution. Light affects organisms *via* the visual system in animals, the photosynthetic system in plants, and through various non-visual pigments in both plants and animals. The effects of artificial light are mediated by the spatial pattern, wavelengths and/or timing of the light sources (here shaded bands represent filters through which effects are dependent on space, wavelength and/or timing). Ecological effects can be characterised as disruption of information flows and/or changes in resource use and availability. The extent to which these effects influence ecosystem processes is currently largely unknown.

Part of the challenge in providing this improved understanding lies in organizing the knowledge that already exists and in identifying the principal gaps. The literature that has developed to date is scattered, and largely lacks synthesis within a common mechanistic framework. Previous attempts to review this material have done so by taxonomic group (Rich & Longcore, 2006*b* – with sections on mammals, birds, reptiles and amphibians, fishes, invertebrates, plants), by different processes and/or levels of biological organization (Longcore & Rich, 2004 – with sections on behavioural and population ecology, community ecology, ecosystem effects; Longcore & Rich, 2006 – with sections on physiological ecology, behavioural and population ecology, community ecology, ecosystem ecology), and by research domain (Perkin *et al.*, 2011 – with sections on dispersal, evolution, ecosystem functioning, interactions with other stressors).

Here we propose a framework that focuses foremost on the cross-factoring (Table 2) of the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the ways in which light influences biological systems, particularly the distinction between light as a resource and light as an information source (Fig. 3). Reviews of the literature to date have highlighted examples of each of the different combinations of such a cross-factoring. However, many studies do not report, for example, the spectral properties, intensity, duration and/or spatial extent of the light regime, making it hard to draw general conclusions applicable outside their geographical and taxonomic limits. For this reason perhaps, despite the global nature of increases in artificial light, the ecological impacts of light pollution are often considered to be localised and restricted to a few vulnerable species or taxonomic groups. Considering these individual studies within our proposed framework: (*i*) helps to unify understanding of particular effects of light pollution across taxa, and to draw conclusions relevant to whole ecosystems; (*ii*) highlights the mechanisms behind the observed ecological effects of light pollution, and defines clear criteria for future ecological studies; and (*iii*) provides guidance in detecting, predicting and mitigating against current and future adverse effects of light pollution.

## Table 2. Cross-factoring of the effects of nighttime lighting on the spatial, temporal and spectral components of light regimes, and of the organismal effects of light as a resource and as an information source

| | | Space | Time | Spectra |
|---|---|---|---|---|
| Light as a resource | Photosynthesis | Very localized, close to lights, probably only ecologically significant in naturally dark habitats (e.g. caves). | Most effective when light is continuous throughout naturally dark period – effects will be reduced with duration of lighting. | Effective at broad range of wavelengths between 400 and 700 nm, overlapping lighting systems for human vision; peak sensitivities in red and blue. |
| | Partitioning of activity between day and night | Impacts could be widespread, as sky glow effects allow increased nocturnal activity, or highly localized, as direct light in the vicinity of lamps allows diurnal/crepuscular species to extend their period of activity into hours of natural darkness. Spatial heterogeneity in light and dark patches may lead to spatial partitioning of the light resource. | Probably most critical around dusk and dawn, but continuous lighting may extend effects throughout the night. | Effective wavelengths likely to vary among taxa. |
| | Dark repair and recovery | Could be widespread – few data available on physiological | Could be effective throughout night; | Emission in blue and UV-A may promote DNA repair |

| | | | | |
|---|---|---|---|---|
| | recovery | available on physiological mechanisms and required light intensities across species. | throughout night, short pulses of light may be sufficient to disrupt melatonin production. | may promote DNA repair through photoreactivation; blue light may disrupt melatonin production in higher vertebrates. |
| Light as an information source | Circadian clocks and photoperiodism | Effects could be widespread, but recorded instances usually in close proximity to light sources (e.g. retention of leaves in deciduous plants around street lighting). | Continuous and intermittent low lighting both shown to have effects; short pulses of light during night are sufficient to disrupt both circadian clocks and photoperiodism in some species. | Effects likely to vary among taxa; plants may be sensitive to the ratio of red to far-red light *via* the phytochrome pathway, rather than absolute intensity at a given wavelength. Plants and animals may also respond through to blue light through the cryptochrome pathway. |
| | Visual perception | Could be widespread over large areas; sky glow effects may be equal to or exceeding moonlight intensities. | Probably most effective around dawn and dusk, extending effective period of activity of normally diurnal and crepuscular species, but may also allow activity throughout night (e.g. wading birds). | Effective wavelengths will vary among species. Broader spectrum light sources will tend to give better colour definition and aid identification of objects from their background in most species. |

| | | | |
|---|---|---|---|
| Spatial orientation and light environment | Species are often highly sensitive to directional light even at low intensity, so isolated light sources can have a major disruptive effect on navigation across spatial scales. Diffuse sources, such as atmospheric sky glow, may mask natural light signals used for navigation, including moon position and polarized atmospheric light. | Intermittent light may have reduced impact – lighting during key periods of movement (e.g. during migration events) may be most significant. | Lights with high UV (e.g. mercury vapour lamps) shown to be disruptive in many insects; red light in some bird species. |

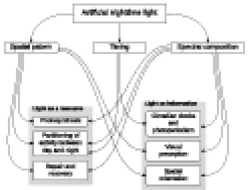

**Figure 3.** Cross-factoring of the effects of nighttime lighting on the spatial, temporal and spectral components of light regimes, and of the organismal effects of light as a resource and as an information source.

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In the sections below we review the evidence for each of the combinations of the cross-factoring. To avoid undue redundancy, and a bias towards certain well-studied systems, we have not attempted to provide an exhaustive list of studies on the ecological effects of light pollution, but rather in each section we aim to illustrate the key issues and identify progress and opportunities for further work.

# II. Light as a resource

Both light and darkness can act as a resource for organisms (Kronfeld-Schor & Dayan, 2003; Gerrish *et al.*, 2009). Through photosynthesis, energy is captured by autotrophs in the form of light and cycled through ecosystems; furthermore, many physiological processes and behavioural activities require either light or dark conditions to operate. The balance between hours of light and of darkness constrains the time available for these processes and so changes in the availability of both light and darkness as a resource can have positive or negative effects on an organism, dependent on whether it is the presence or absence of light that poses the greater constraint.

# (1) Photosynthesis

In green plants, light is absorbed for photosynthesis by chlorophylls and carotenoids at wavelengths between 400 and 700 nm. While this range encompasses much of the visible emissions by artificial lights, in most cases the levels of photosynthetically active radiation (PAR) associated with nighttime light pollution are extremely low relative to sunlit conditions (typically less than 0.5 µmol (Mole (unit)) m (Metre)$^{-2}$ s (Second)$^{-1}$ compared with between 100 and 2000 µmol (Mole (unit)) m (Metre)$^{-2}$ s (Second)$^{-1}$ for sunlit conditions) and the effect of light pollution on net carbon fixation is likely to be negligible in most cases. Although Raven & Cockell (2006) calculate that the combined PAR flux from sky glow in an urban area and moonlight from a full moon could theoretically exceed the lower limit for photosynthesis, in most cases only direct illumination in the close vicinity of light sources, for example the leaves of trees within a few centimeters of street lights, is likely to be sufficient to maintain net carbon fixation during nighttime and at lower light levels offset nocturnal respiratory losses. The consequences of this highly localized effect on individual plants and on ecosystems are largely unexplored.

One environment in which light pollution is known to have marked effects on ecosystems through photosynthesis is in artificially lit cave systems. The introduction of lighting into caves used as visitor attractions promotes highly localized growth of 'lampenflora' communities completely dependent on artificial light as a source of energy. These communities may include autotrophs such as photosynthetic algae, mosses and ferns growing in the vicinity of light fixtures, as well as fungi and other heterotrophs utilizing the input of organic matter (Johnson, 1979). These communities may displace or disrupt the trophic ecology of energy-limited cave ecosystems. Algal growth on the walls can also seriously damage and obscure geological and archaeological interest within caves (Lefèvre, 1974), and is an issue of some concern.

# (2) Partitioning of activity between day and night

Partitioning of time has been thought to be a major way in which the ecological separation of species is promoted (Kronfeld-Schor & Dayan, 2003). Temporal niche partitioning between diurnal, crepuscular and nocturnal species occurs as they avoid competition by specializing in a particular section along the light gradient (Gutman & Dayan, 2005). Indeed, whilst ecological and evolutionary studies have focused foremost on diurnal species, a substantial proportion of species is adapted to be active during low-light conditions (Lewis & Taylor, 1964; Hölker *et al.*, 2010*b*). Natural variation in nighttime lighting, particularly in moonlight due to the phase of the moon and cloud-cover conditions, has been shown to affect the timing of activity in a range of species (e.g. Imber, 1975; Morrison, 1978; Gliwicz, 1986; Kolb, 1992; Tarling, Buchholz & Matthews, 1999; Baker & Dekker, 2000; Fernandez-Duque, 2003; Kappeler & Erkert, 2003; Beier, 2006; Woods & Brigham, 2008; Gerrish *et al.*, 2009; Penteriani *et al.*, 2010, 2011; Smit *et al.*, 2011). Spatial gradients in the amount and seasonal distribution of biologically useful semi-darkness (including moonlight and twilight) have been proposed as drivers of patterns of behaviour (Mills, 2008). Visually orienting predators have a reduced ability to detect prey in dark conditions, and may increase their activity or achieve higher rates of predation success under lighter conditions; prey species may reduce activity in lighter conditions in response to a perceived increased risk of predation. Some shorebird species use visual foraging by day but tactile foraging during hours of darkness – nighttime light may allow them to use visual foraging throughout the night (Rojas *et al.*, 1999). Moonlight-driven cycles in predator–prey activity have been observed in such taxonomically diverse species as zooplankton and fish (Gliwicz, 1986), predaceous arthropods (Tigar & Osborne, 1999), blue petrels *Halobaena caerulea* and brown skuas *Catharacta skua* (Mougeot & Bretagnolle, 2000), owls and rodents (Clarke, 1983), and lions *Panthera leo* and humans (Packer *et al.*, 2011). Prey species may respond to the increased risk of predation at night by decreasing their activity (e.g. Kotler, 1984; Daly *et al.*, 1992; Vásquez, 1994; Skutelsky, 1996; Kramer & Birney, 2001) or changing their microhabitat to utilize dark spaces such as the shelter of bushes (e.g. Price, Waser & Bass, 1984; Kolb, 1992; Topping, Millar & Goddard, 1999), and may compensate by greater activity at dawn and/or dusk; Daly *et al.* (1992) have shown how such 'crepuscular compensation' in response to high nocturnal predation rates can lead to increasing rates of predation by diurnal predators as prey activity encroaches into daylight hours. Diurnal and crepuscular predators may become facultative nocturnal predators under suitable light conditions (e.g. Milson, 1984; Combreau & Launay, 1996; Perry &

Fisher, 2006). Conversely, nocturnal predators that rely on non-visual clues to hunt, such as snakes, may decrease activity during lighter nights in order to avoid detection by prey and their own predators (Bouskila, 1995; Clarke, Chopko & Mackessy, 1996). Behavioural changes are likely to induce changes in energetic costs; Smit *et al.* (2011) have shown that freckled nightjars *Caprimulgus tristigma* respond to dark nights by entering torpor, while moonlit nights allow foraging as food availability is sufficient to overcome the energetic costs of thermoregulation.

Despite the large number of studies that demonstrate the effect of moonlight in altering the behaviour of species, there have been relatively few that have formally examined the effect of artificial light in altering behaviour or restructuring temporal niche partitioning. Reports have long existed that some diurnal species exploit the 'night-light niche' and become facultatively nocturnal in urban environments, for example jumping spiders (Wolff, 1982; Frank, 2009), reptiles (Garber, 1978; Perry & Fisher, 2006), and birds (Martin, 1990; Negro *et al.*, 2000; Santos *et al.*, 2010). In rodents, Bird, Branch & Miller (2004) have shown that foraging behaviour in beach mice *Peromyscus polionotus* is restricted by artificial lighting, while Rotics, Dayan & Kronfeld-Schor (2011) have shown that while the nocturnal spiny mouse species *Acomys cahirinus* restricted activity under artificial light, its diurnal congener *Acomys cahirinus* did not expand its activity to compete during the hours of artificial illumination.

There are few known examples of artificial light as a resource directly mediating behaviour; although some species have been found to increase foraging activities and antipredator vigilance under such conditions (e.g. Biebouw & Blumstein, 2003), the vision of some nocturnal predators has been shown to be impaired by artificial lighting and their foraging success reduced (e.g. Buchanan, 1993). Reports of the effects of light in providing resources by attracting concentrations of prey are more frequent (e.g. Heiling, 1999; Buchanan, 2006). Increased foraging around street lights has been widely reported for some species of bats (e.g. Rydell, 1991, 1992, 2006; Blake *et al.*, 1994; Polak *et al.*, 2011), particularly around lamps which emit at low wavelengths, attract large numbers of insects, and which may interfere with prey defences (Svensson & Rydell, 1998); Rydell (2006) regards the habit of feeding around lights by bats as having become the norm for many species. Other bat species avoid lights (Kuijper *et al.*, 2008; Stone, Jones & Harris, 2009), possibly to minimise the risk of avian predation (Speakman, 1991; Rydell, Entwistle & Racey, 1996). Similarly, nocturnal orb-web spiders *Larinioides sclopetarius* preferentially build webs in areas which are well lit at night, where higher densities of insect prey are available; a behaviour that appears to be genetically predetermined rather than learnt (Heiling, 1999). This suggests the possibility of evolutionary responses to utilise novel niches created by artificial lighting.

The relative lengths of night and day can influence foraging opportunities, predation and/or competition costs and the trade-offs amongst these (e.g. Clarke, 1983; Falkenberg & Clarke, 1998; Berger & Gotthard, 2008). In turn this can influence the abundances of organisms (e.g. Carrascal, Santos & Tellería, 2012). Presumably nighttime lighting that served effectively to change perceived night and day lengths could amplify these effects.

## (3) Dark repair and recovery

It has been suggested that continuous periods of darkness are critical for certain processes controlling repair and recovery of physiological function in many species, and hence that darkness can be seen as a resource for physiological activity. Seeking an explanation for an observed increase in ozone injury in plants at high latitudes, Vollsnes *et al.* (2009) have shown that dim nocturnal light, simulating the northern Arctic summer, inhibits recovery from leaf damage caused by atmospheric ozone in subterranean clover *Trifolium subterraneum*. Futsaether *et al.* (2009) found a similar result in red clover *Trifolium pretense* but not in white clover *Trifolium repens*. In *Arabidopsis thaliana*, Queval *et al.* (2007) have shown links between day length and the rate of oxidative cell death. Since the patterns of anthropogenic light pollution and ozone pollution are spatially correlated on a global scale (see e.g. Cinzano *et al.*, 2001; Ashmore, 2005), the extent to which low-intensity nighttime light could affect repair and recovery from ozone damage requires further investigation.

Gerrish *et al.* (2009) argued that hours of darkness provide organisms with time for repair to DNA damage to cells caused by solar UV-B radiation (285–315 nm). However, light in the blue to UV-A portion of the spectrum is necessary for DNA repair through photoreactivation *via* the photolyase enzyme (with maximum absorption at 380 and 440 nm), while 'dark repair' through the excision repair pathways is independent of light (Sutherland, 1981; Britt, 1996; Sinha & Häder, 2002). The role of darkness here is presumably limited to the lack of damage due to solar UV-B radiation during the night. Since artificial lighting typically emits negligible amounts of UV-B radiation it is unlikely that light pollution either increases DNA damage or inhibits the processes of repair in this instance; indeed, light sources emitting in the blue and UV-A may have an effect in promoting DNA repair through photoreactivation.

# III. Light as an information source

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The direction, duration and spectral characteristics of natural light are widely used by organisms as sources of information about their location, the time of day and year, and the characteristics of their natural environment (Neff, Fankhauser & Chory, 2000; Ragni & D'Alcalà, 2004). Indeed, considerable energetic costs are often borne in order to maintain the necessary sensory systems (Niven & Laughlin, 2008). Artificial lighting can disrupt this flow of information and provide misleading cues. The wavelengths of light are critical to its efficacy as an information source due to the varying spectral sensitivity of organisms' receptors. In vascular plants, for example, the most well-studied photoreceptors are phytochromes, which exist in two photo-interconvertible forms – a biologically inactive red-light-absorbing form (Pr) which upon absorption of red light is converted to a biologically active form (Pfr). Pfr is converted back to Pr on absorbing far-red photons, so under steady light of a given red/far-red ratio the active form of phytochrome reaches equilibrium (Lin, 2000; Neff *et al*., 2000; Smith, 2000). The phytochrome system plays a key role in detecting shade and measuring day length, and has been shown to influence vegetative growth and architecture, the timing of germination, flowering, bud burst and dormancy and senescence, and the allocation of resources to roots, stems and leaves (Smith, 2000). In addition, blue and ultra-violet light receptors called cryptochromes influence light responses in many species of algae, higher plants, and animals (Cashmore *et al*., 1999), and have been shown to play a role in regulating circadian clocks in mammals (Thresher *et al*., 1998). In animals with vision, complex information on the spectral composition of light may be derived from several photoreceptors with varying spectral sensitivities (Kelber, Vorobyev & Osario, 2003), and in mammals retinal ganglion cells that are independent of the visual system may be involved in entraining circadian clocks (Berson, Dunn & Takao, 2002). In many cases organisms have been shown to be sensitive to extremely low levels of light at night, well within levels of anthropogenic light pollution (Kelber & Roth, 2006; Bachleitner *et al*., 2007; Evans *et al*., 2007a; Frank, Evans & Gorman, 2010).

## (1) Circadian clocks and photoperiodism

Three natural periodic cycles in the light regime are detected by organisms – the daily cycle of day and night, seasonal changes in day length, and the monthly lunar cycle. The daily and seasonal cycles in particular provide cues that can be used to anticipate regular changes in the environment such as temperature or humidity that also follow a daily or annual cycle. The lunar cycle has importance for activity and reproduction in some species, which may be responding directly to the availability of light as a resource (see section II) alternatively they may utilise the lunar light cycle to anticipate environmental changes connected with nighttime light or tidal conditions (Taylor *et al*., 1979), or purely as a regular cue to synchronise reproductive activity (e.g. Tanner, 1996; Baker & Dekker, 2000; Takemura *et al*., 2006).

Light may influence circadian patterns of behaviour in two ways, entrainment and masking, which may be difficult to distinguish in natural systems. Virtually all plants and animals possess a circadian clock, an endogenous system that regulates aspects of their activity and physiology on a cycle that approximates 24 h, but which in the absence of external cues may drift out of phase with day and night (Sweeney, 1963). In order for the clock accurately to track the diurnal cycle, it is regulated by ‘zeitgebers’, environmental cues that entrain or reset the clock. The light environment is critical in providing such cues in many species. Entrainment occurs when regular patterns of light and darkness regulate the phase and frequency of the endogenous clock (Menaker, 1968). Artificial light after dusk or prior to dawn can cause phase shifts in the circadian rhythm, delaying or advancing the cycle. Low levels of light at night may disrupt melatonin production in fish, birds and mammals, with a wide range of downstream physiological consequences (Navara & Nelson, 2007; for examples see Cos *et al*., 2006; Evans *et al*., 2007a; Reiter *et al*., 2007; Bedrosian *et al*., 2011*a,b*). Since light pollution typically occurs both before dawn and after dusk, it is difficult to predict the effect of any shift in the circadian clock. In laboratory experiments, entrainment has been shown to occur at both persistent levels of low light and with short pulses of relatively bright light (Table 3; Brainard *et al*., 1983; Haim *et al*., 2005; Zubidat, Ben-Shlomo & Haim, 2007; Shuboni & Yan, 2010). The duration and intensity of light required to disrupt circadian rhythms under field conditions is unknown, but these studies suggest potential for impacts on species affected by widespread low-level light such as urban sky glow or less often considered transient lighting sources such as vehicle lights (Lyytimäki, Tapio & Assmuth, 2012).

**Table 3. Examples of the levels at which nighttime lighting has been observed to have biological effects**

| Species | Setting | Effect | Nighttime lighting | Source |
|---|---|---|---|---|
| Barred owl<br>*Strix varia*<br>Long eared owl<br>*Asia wilsonianus*<br>Barn owl<br>*Tyto alba*<br>Burrowing owl<br>*Speotyto cunicaria* | Lab<br>…<br>…<br>… | Location of prey<br>…<br>…<br>… | $1.6 \times 10^{-6}$ lux*<br>$2.7 \times 10^{-6}$ lux*<br>$5.7 \times 10^{-6}$ lux*<br>$2.8 \times 10^{-4}$ lux* | Dice (1945)<br>…<br>…<br>… |
| Common toad *Bufo bufo* | Lab | Increased prey detection | $2.8 \times 10^{-4}$ lux (constant) | Larsen & Pedersen (1982) |
| Syrian hamster *Mesocricetus auratus* | Lab | Altered circadian rhythm | 0.01 lux (constant) | Evans *et al.* (2007a) |
| Salmon *Salmo salar* | Lab | Increased prey detection | 0.01–5 lux (constant) | Metcalfe *et al*. (1997) |
| Fruitfly *Drosophila melanogaster* | Lab | Increased activity levels and shifted typical morning and evening activity peaks into night | 0.03 lux (constant) | Bachleitner *et al*. (2007) |
| Brown rat *Rattus norvegicus* | Lab | Increased rates of tumor growth and metabolism | 0.2 lux (constant) | Dauchy *et al*. (1997) |
| Brown rat *Rattus norvegicus* | Lab | Increased rate of tumor growth | 0.21 lux (constant) | Cos *et al*. (2006) |
| Ringed plover<br>*Charadrius hiaticula*<br>Kentish plover<br>*Charadrius alexandrinus*<br>Grey plover | Field experiment | Higher prey intake<br>…<br>…<br>… | 0.74 lux (constant) | Santos *et al*. (2010) |

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|---|---|---|---|---|
| *Pluvialis squatarola*<br>Dunlin<br>*Calidris alpina*<br>Redshank<br>*Tringa totanus* | | … | | |
| Deer mouse *Peromyscus maniculatus* | Lab | Reduced nocturnal activity | 0.93 lux (constant) | Falkenberg & Clarke (1998) |
| Prairie Rattlesnake *Crotalus viridis* | Lab | Reduced activity | 1 lux | Clarke *et al*. (1996) |
| American robin *Turdus migratorius* | Field observations | Earlier initiation of singing | Mean 1.26 lux (range 0.05–3.06 lux; constant) | Miller (2006) |
| Leaf-eared mouse *Phyllotis xanthopygus* | Lab | Reduced nocturnal activity | 1.5 lux (constant) | Kramer & Birney (2001) |
| Leaf-eared mouse *Phyllotis darwini* | Lab | Predator avoidance and reduced food consumption | < 2.0 lux (constant) | Vasquez (1994) |
| Siberian hamster *Phodopus sungorus* | Lab | Suppressed immune response | 5 lux (constant) | Bedrosian *et al*. (2011*b*) |
| Green and blue-green algae | Field observations | Minimum artificial light required for continued photosynthetic growth in caves | 10–50 lux | Johnson (1979) |
| Mosses | … | | 50–180 lux | … |
| Ferns | … | | 250 lux | … |
| Atlantic salmon *Salmo salar* | Field experiment | Altered timing of nocturnal migration | 14 lux (constant; measured at stream surface) | Riley *et al*. (2012) |
| Pond bats *Myotis dasycneme* | Field observations | Reduced feeding rate, disturbed flight pattern | < 30 lux (constant) | Kuijper *et al*. (2008) |

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|---|---|---|---|---|
| Lesser horseshoe bats<br>*Rhinolophus hipposideros* | Field experiment | Reduced activity, onset of commuting delayed | 51.67 lux (average; constant) | Stone *et al*. (2009) |
| Social vole<br>*Microtus socialis* | Lab | Disruption of seasonal acclimatization of thermoregulation | 450 lux (15 min pulse) | Zubidat *et al*. (2007) |
| Field mouse<br>*Mus booduga* | Lab | Disruption of circadian rhythm | 1000 lux (15 min pulse) | Sharma *et al*. (1997) |

*Converted from reported values in foot candles.

Note that: (*i*) in many cases these represent levels of experimental treatments, and precisely where thresholds might lie remains unknown; and (*ii*) although widely used, lux measurement places emphasis on brightness at wavelengths perceived by human vision. Studies are ordered in increasing intensity of light.

Exposure to light at night has been shown to disrupt the circadian cycle of hormone production in humans, particularly melatonin, which has been linked to an increase in cancer risk in shift-workers (Stevens, 1987, 2009; Megdal *et al*., 2005; Reiter *et al*., 2011). Melatonin production is regulated by the circadian clock, which in mammals is entrained by retinal ganglion cells with a peak sensitivity in blue light at around 484 nm (Berson *et al*., 2002). Melatonin production is similarly reduced in rats under nighttime light levels of 0.2 lux (Dauchy *et al*., 1997), and in hamsters at levels above 1 lux (Brainard *et al*., 1982), and has been shown to suppress immune responses and increase the rate of tumour growth (Dauchy *et al*., 1997; Bedrosian *et al*., 2011*b*). Similar melatonin-mediated effects of nighttime light on immune function are seen in laboratory studies of birds (Moore & Siopes, 2000). The requirement for continuous periods of darkness to entrain the circadian clock and regulate hormone activity may be widespread amongst animals, yet the ecological effects of potential disruption of the circadian clock are unknown.

By contrast, masking occurs when a light stimulus overrides the endogenous clock; for example artificial light at night may increase activity in diurnal or crepuscular species (positive masking) or suppress it in others (negative masking; see e.g. Santos *et al*., 2010; Rotics *et al*., 2011). The ecological effects of direct entrainment of circadian clocks by artificial light may be difficult to distinguish from opportunistic changes in light-resource use or direct effects of light on behaviour through masking. For example, light pollution has been shown to advance the initiation of dawn singing considerably in some temperate bird species in urban areas (Miller, 2006), with implications for breeding success (Kempenaers *et al*., 2010). The extent to which this effect of light on behaviour is mediated by circadian rhythms, or whether light triggers this behaviour independently of an endogenous clock through masking is unknown.

In temperate and polar ecosystems, organisms frequently use day length as a cue to initiate such seasonal phenological events as germination, bud formation and burst, reproduction, senescence, eclosion, diapause, moult, embryonic development, and migration (e.g. Gwinner, 1977; Densmore, 1997; Dawson *et al*., 2001; Niva & Takeda, 2003; Heide, 2006; Cooper *et al*., 2011). By contrast, species whose ranges are restricted to lower latitudes are likely to be less dependent on day length to regulate annual cycles of activity (although in dry seasonal climates near the equator even very small differences in seasonal day length can be utilised by plants to trigger phenological events; see Rivera *et al*., 2002). Over evolutionary time species have adapted to wide variation in the range of day length that they encounter – in the Permian period deciduous forests existed in Antarctica at latitudes of 80–85°S, experiencing total darkness for months in the winter and 24 h daylight during summer, a light environment without analogue in modern forests and unlikely to be within the survivable range of extant tree phenotypes (Taylor, Taylor & Cúneo, 1992). Photoperiod, and therefore presumably changes in what is perceived as photoperiod as a result of artificial lighting, has consequences for a variety of physiological traits. It has long been observed that certain species of deciduous tree maintain their leaves for longer in autumn in the vicinity of street lights (Matzke, 1936), potentially leaving them exposed to higher rates of frost damage in late autumn and winter. Experiments in horticultural systems have shown a wide range of responses to artificial nighttime lighting, depending both on the species and the spectral composition of the light source, including delay and promotion of flowering, and enhanced vegetative growth (Cathey & Campbell, 1975; Kristiansen, 1988). Animal species, including lizards (*Sceloporus occidentalis*; Lashbrook & Livezey, 1970) and rodents (*Microtus socialis*; Zubidat *et al*., 2007) control their thermoregulatory activity in response to seasonal changes in photoperiod. Plant physiologists draw a distinction between 'long-day' responses, in which a long dark period suppresses an effect, and 'short day' responses, in which a long dark period promotes an effect. In animals, both day length and the relative change in day length may act as proximal triggers (Vepsäläinen, 1974). Species with a wide latitudinal range show local adaptation in their photoperiodic response (Bradshaw, 1976), and photoperiodic control allows species to coordinate key events in their life cycle with suitable weather conditions. Photoperiodic response has been shown to evolve rapidly in an invasive species expanding into different latitudes, reflecting changing relationships between the seasonal climate and the information given by day-length cues (Urbanski *et al*., 2012). Disruption of this control may lead to organisms becoming out of step with their climate, with the timing of other organisms (such as pollinators or food sources), or unable to adapt to climatic change (Bradshaw, Zani & Holzapfel, 2004; Bradshaw & Holzapfel, 2010).

The biological rhythms of organisms are known to be linked across different levels of food webs, with, for example, plant-herbivore-parasitoid rhythms being synchronized both as a consequence of bottom-up and top-down processes (Zhang *et al*., 2010). This raises the likelihood that disruptions to the rhythms of individual species by nighttime lighting can ramify widely.

# Visual perception

A wide range of adaptations exist throughout the animal kingdom to make use of reflected light at different levels and wavelengths, allowing the recognition of important features of the environment (Land & Nilsson, 2002; Warrant, 2004; Warrant & Dacke, 2011); discoveries about the breadth of the abilities of organisms in this regard continue to be made (e.g. Kelber, Balkenius & Warrant, 2002; Grémillet *et al*., 2005; Allen *et al*., 2010; Baird *et al*., 2011; Hogg *et al*., 2011). A substantial proportion of animal species are adapted to see at light levels well below those at which human vision is effective, in which they can often see colour and navigate well (Table 3; Warrant, 2004; Warrant & Dacke, 2010, 2011). The interaction between the intensity and spectral composition of artificial light and the adaptation of an organism's eyes will affect whether visual perception is enhanced, disrupted or unaffected by light pollution, and hence the potential downstream behavioural and ecological effects.

The intensity of light at which animals are able to identify objects varies considerably among species (Table 3). Many are able successfully to navigate visually and locate resources at light levels at which human vision is impossible (e.g. Dice, 1945; Larsen & Pedersen, 1982). A considerable proportion of nocturnal activity occurs during periods of 'biologically useful semi-darkness' (Mills, 2008), making use of the relatively low light intensities during twilight and moonlight; however, nocturnal species may also modify or reduce activity during such periods to avoid competition or predation (Clarke *et al*., 1996). Light intensities recorded from artificial sources, from both direct illumination a considerable distance from a source and diffuse sky glow, are well within the range shown to be effective in enhancing animal vision and triggering behavioural changes (Tables 1 and 3). Less well known is the extent to which artificial nighttime light may disrupt vision systems adapted to dark conditions.

The light-sensitive photoreceptor pigments of animal eyes vary in the wavelengths of light to which they are most absorbant. Colour is perceived as a representation in a limited number of dimensions of the multi-dimensional spectral reflectance of an illuminated surface, and the information content of colour perception varies as a function of the number and spectral sensitivity of different types of photoreceptor pigments. The human eye contains three photoreceptors (trichromatic) that are used in photopic (daytime) vision and maximally absorb light at wavelengths of 558 (red), 531 (green) or 419 nm (blue) (Dartnall, Bowmaker & Mollon, 1983). Reptiles and birds commonly possess four photoreceptor pigment types, increasing the information content of colour perception across much of the spectrum [including ultraviolet (UV) light] compared to the majority of mammals which possess two photoreceptor pigment types (Osorio & Vorobyev, 2008). The mantis shrimp *Odonatodactlyus* represents an extreme case of colour sensitivity, with 12 photoreceptor pigment types (Marshall & Oberwinkler, 1999). Large numbers of types potentially allow organisms better to discriminate between objects of contrasting spectral reflectance in their environment, and the relative distribution of photoreceptor sensitivities determines the portions of the electromagnetic spectrum in which colour vision is most sensitive.

Changing the spectral properties of artificial lights is therefore likely to alter the environment which individual organisms are able to see in different ways. Broader spectrum light sources such as light-emitting diodes (LEDs) are often likely to provide improved colour discrimination. This may allow animals better to navigate, forage for resources, locate and catch their prey, and identify or display for mating (such as in the plumage feathers of birds; Hart & Hunt, 2007). The trichromatic and tetrachromatic visual systems of many hymenopteran and lepidopteran insects allow them to recognize and compare between the nectar sources provided by flowering plants (Chittka & Menzel, 1992). The colour of a flowering plant as perceived by an insect, and the ease with which the insect can recognize different flowers, are likely to be improved under broad-spectrum compared to narrow-spectrum lighting conditions. Changing the spectral composition of artificial light could therefore affect the competitive fitness of animals in a variety of ways. Given the current shift in lighting technology towards broader spectrum light sources, future research into the impact of different artificial light sources on the recognition of important environmental signals by animal groups is clearly necessary.

# Spatial orientation and light environment

Many organisms use lightscapes as cues for directional movement (Tuxbury & Salmon, 2005; Ugolini *et al.*, 2005; Warrant & Dacke, 2011). The restructuring of these lightscapes by light pollution can thus result in these movements being disrupted. Examples of such disruption have been documented for moths and other insects (e.g. Frank, 1988), frogs (Baker & Richardson, 2006), reptiles (e.g. Salmon *et al.*, 1995), birds (e.g. Gauthreaux & Belser, 2006; Rodríguez *et al.*, 2012), and mammals (Beier, 1995; Rydell, 2006).

The widespread attraction of moth species to nighttime lights has long been exploited in the design of traps for their capture. The reasons for such disruption of their natural movement patterns remain to be fully determined, although interference with the use of moonlight for navigation is likely important (Warrant & Dacke, 2011). Many insects, including members of the Hymenoptera, Lepidoptera and Coleoptera, can navigate using the pattern of polarized celestial light in the sky (e.g. Dacke *et al.*, 2003). The use of UV light as opposed to other wavelengths to detect polarized light patterns has been postulated to be advantageous because the degree of polarized light scattered downwards from clouds and forest canopies is higher in the UV (Barta & Horváth, 2004). The natural signal is diminished by urban sky glow (Kyba *et al.*, 2011*b*), and through this effect variation in sky glow may potentially explain geographic differences in the response of moth-trap catches to phases of the moon (Nowinsky & Puskás, 2010). Whether flight-to-light behaviour is driven by the disruption of natural polarized light patterns alone seems unlikely as this behaviour occurs even with artificial lights which emit no UV component (van Langevelde *et al.*, 2011). However, the use of polarized UV light detection for navigation by insects may explain why flight-to-light behaviour is disproportionately associated with emissions at shorter wavelengths (van Langevelde *et al.*, 2011). Polarized light patterns reflected back from the ground can also be used to locate water bodies due to the polarizing nature of their surfaces. Indeed, a number of cases exist where insects have been attracted to sources of polarized light reflected back from anthropogenic structures such as wet asphalt roads, leading to increasing concern over the deleterious effects of these and other light polarizing anthropogenic structures (Horváth *et al.*, 2009). It seems likely that such effects may be exacerbated by the introduction of artificial lighting, although ecological case studies have not to our knowledge been documented.

Beetles of the family Lampyridae are notable for their use of bioluminescence in mate location. It is possible that artificial light is playing a significant role in the decline of these taxa, due to disruption of mate location (Lloyd, 2006).

Migrating birds utilize at least two mechanisms for navigation that may be disrupted by artificial lighting. Magnetoreception is considered to be the principal mode of orientation. The detection systems for magnetoreception include the magnetic-field-dependent orientation of paired radical molecules in the photopigment that forms during photon absorption, and the presence of magnetite within the beak (Wiltschko *et al.*, 2010). Migration direction has been demonstrated to be determined using the blue and green photoreceptors in European robins *Erithacus rubecula* (Wiltschko *et al.*, 2007), while red light disrupts migration direction in silvereyes *Zosterops l. lateralis* (Wiltschko *et al.*, 1993). This has led to calls for the spectral composition of artificial lighting to be managed to mitigate against disorientation of birds (Poot *et al.*, 2008), however the level of disorientation caused by particular wavelengths of light appears to vary according to intensity, and is not restricted to red lights alone (Wiltschko *et al.*, 2010).

In addition to possessing a magnetic compass for orientation, birds are also thought to calibrate this compass using celestial light during twilight or at night (Cochran, Mouritsen & Wikelski, 2004). In some species the mechanism of calibration has been demonstrated to be the detection of polarized light patterns during sunrise and sunset (e.g. Muheim, Phillips & Akesson, 2006). However, as is the case with insects, whether artificial lighting can affect these patterns, and the consequences this may have for navigation, are currently unknown.

In addition to the above examples of movement towards light, many motile organisms exhibit light-avoidance behaviours (e.g. Moore *et al.*, 2000; Buchanan, 2006; Boscarino *et al.*, 2009). It seems extremely likely that for many such taxa the avoidance of artificial illumination will result in reduction in the space and other resources available to them (e.g. Kuijper *et al.*, 2008). One of the ecologically most significant consequences of negative phototropic behaviour is the widespread diel migration of zooplankton in aquatic systems (e.g. Moore *et al.*, 2000) which would appear to be sensitive to levels of light oscillation well below those produced by artificial illumination (Berge *et al.*, 2009).

# IV. Conclusions

1. As human communities and lighting technologies develop, artificial light increasingly encroaches on dark refuges in space, in time, and across wavelengths. At a given latitude, natural light regimes have been relatively consistent through recent evolutionary time, and the global rapid growth in artificial light represents a potentially significant perturbation to the natural cycles of light and darkness. Natural light is utilized by organisms both as a resource and a source of information about their environment, and artificial light has the potential to disrupt the utilization of resources and flow of information in ecosystems.
2. A broad set of case studies of ecological implications of light pollution have been documented. Across a wide range of species, there is evidence that artificial light affects processes including primary productivity, partitioning of the temporal niche, repair and recovery of physiological function, measurement of time through interference with the detection of circadian, lunar and seasonal cycles, detection of resources and natural enemies and navigation. However, the effects on population- or ecosystem-level processes, such as mortality, fecundity, community productivity, species composition and trophic interactions are poorly known. Furthermore, the studies identifying these processes to date are scattered within literature from a wide range of disciplines, are strongly weighted towards higher vertebrates and ecosystems and largely lack synthesis within a common mechanistic framework.
3. We propose a framework that focuses foremost on the interactions between the ways in which artificial lighting alters natural light regimes (spatially, temporally, and spectrally), and the mechanisms by which light influences biological systems, particularly the distinction between light as a resource and light as an information source. Such a framework focusses attention on the need to identify general principles that apply across species and ecosystems, and integrates understanding of physiological mechanisms with their ecological consequences.
4. Reviewing the evidence for each of the combinations of this cross-factoring particularly highlights: (*i*) the potential influence of nighttime lighting at all levels of biological organisation (from cell to ecosystem); (*ii*) the significant impact that even low levels of nighttime light pollution can have; and (*iii*) the existence of major research gaps in understanding of the ecological impacts of light pollution.
5. Future research on the ecological impacts of light pollution needs to address several key issues: (*i*) to what extent does the disruption of natural light regimes by artificial light influence population and ecosystem processes, such as mortality and fecundity rates, species composition and trophic structure; (*ii*) what are the thresholds of light intensity and duration at different wavelengths above which artificial lighting has significant ecological impacts; and (*iii*) how large do ‘dark refuges’, where the intensity and/or duration of artificial light falls below such thresholds, need to be to maintain natural ecosystem processes?

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