

Demographic effects of artificial nighttime lighting on animal populations

Kevin J. Gaston and Jonathan Bennie

Abstract: Artificial lighting, especially but not exclusively through street lights, has transformed the nighttime environment in much of the world. Impacts have been identified across multiple levels of biological organization and process. The influences, however, on population dynamics, particularly through the combined effects on the key demographic rates (immigration, births, deaths, emigration) that determine where individual species occur and in what numbers, have not previously been well characterized. The majority of attention explicitly on demographic parameters to date has been placed on the attraction of organisms to lights, and thus effectively local immigration, the large numbers of individuals that can be involved, and then to some extent the mortality that can often result. Some of the most important influences of nighttime lighting, however, are likely more subtle and less immediately apparent to the human observer. Particularly significant are effects of nighttime lighting on demography that act through (i) circadian clocks and photoperiodism and thence on birth rates; (ii) time partitioning and thence on death rates; and (iii) immigration/emigration through constraining the movements of individuals amongst habitat networks, especially as a consequence of continuously lit linear features such as roads and footpaths. Good model organisms are required to enable the relative consequences of such effects to be effectively determined, and a wider consideration of the effects of artificial light at night is needed in demographic studies across a range of species.

Key words: diurnal, lighting, night, nocturnal, pollution.

Résumé : L'éclairage artificiel, surtout, mais non seulement via les lumières de rues, a transformé l'environnement nocturne sur une grande partie de la planète. On a identifié des impacts à plusieurs échelles sur l'organisation et les procédés biologiques. Cependant, les influences sur la dynamique des populations, surtout suite aux effets combinés sur les taux démographiques clés (immigration, naissances, morts, émigration) déterminant où les espèces individuelles se retrouvent et en quels nombres, n'ont jamais été caractérisées, jusqu'à ce jour. Jusqu'à maintenant, la majeure partie de l'attention explicite donnée aux paramètres démographiques a été appliquée sur l'attraction des organismes par les lumières, et ainsi effectivement sur la migration locale, les grands nombres d'individus impliqués, et jusqu'à un certain point la mortalité qui en résulte fréquemment. Cependant, certaines des influences les plus importantes de l'éclairage nocturne sont vraisemblablement plus subtiles et moins immédiatement apparentes pour l'observateur humain. D'importance particulière, on note les effets de l'illumination nocturne exercés sur la démographie, selon (i) les rythmes circadiens ainsi que le photopériodisme et conséquemment sur les taux de naissance; (ii) la répartition du temps et conséquemment les taux de mortalité; et (iii) l'immigration/émigration par les contraintes exercées sur les mouvements des individus dans les réseaux d'habitats, surtout comme conséquence des caractéristiques lumineuses linéaires, comme les routes et les trottoirs. Il faut identifier des organismes modèles afin de pouvoir déterminer efficacement les conséquences relatives de tels effets, et donner également une plus grande attention aux effets de l'éclairage artificiel nocturne dans les études démographiques pour un ensemble d'espèces. [Traduit par la Rédaction]

Mots-clés : diurne, éclairage, nuit, nocturne, pollution.

1. Introduction

The artificial lighting of nighttime has arguably been one of the most significant environmental perturbations exerted by humankind (Hölker et al. 2010a). It takes many forms, including public street lighting, and lighting from advertising, public and private buildings, and vehicles. Already widespread, its impact continues both to intensify and to spread, and it is likely to do so for many decades to come as the human population grows and the associated infrastructure develops (Cinzano et al. 2001; Cinzano 2003; Hölker et al. 2010b; Liu et al. 2012; Bennie et al. 2014). Moreover, unlike many other anthropogenic pressures, nighttime lighting constitutes a rather novel environmental change, without natural analogues, disrupting natural cycles of light and darkness that have otherwise provided rather consistent resources and sources of information for organisms for long periods of geological and evolutionary time (Gaston et al. 2013).

An extensive literature has developed on the biological implications of artificial nighttime lighting (for reviews see, e.g., Longcore and Rich 2004; Rich and Longcore 2006; Depledge et al. 2010; Hölker et al. 2010a; Perkin et al. 2011; Gaston et al. 2013; Davies et al., *In press*). This has highlighted three key points. First, it has shown the wide breadth of the effects, including on physiology, behaviour, reproduction, movements, and community structure (e.g., Bird et al. 2004; Navara and Nelson 2007; Stone et al. 2009; Kempnaers et al. 2010; Brüning et al. 2011; Davies et al. 2012; Rodríguez et al. 2012). Second, it has demonstrated the wide diversity of organisms that can be influenced, including plants (e.g., Cathey and Campbell 1975; Roman et al. 2000), crustaceans (e.g., Ugolini et al. 2005), arachnids (e.g., Heiling 1999), insects (e.g., Frank 1988, 2006; Eisenbeis 2006), fish (e.g., Brüning et al. 2011; Riley et al. 2012, 2013), amphibians (e.g., Baker and Richardson 2006; Buchanan

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2006), reptiles (e.g., Peters and Verhoeven 1994; Perry and Fisher 2006; Lorne and Salmon 2007), birds (e.g., Le Corre et al. 2002; Gauthreaux and Belser 2006; Miller 2006; Montevecchi 2006), and mammals (e.g., Beier 1995, 2006; Bird et al. 2004; Stone et al. 2012). Third, it has emphasized the pressing importance of determining the most appropriate methods of managing and mitigating the effects of artificial nighttime lighting, and of implementing these (e.g., Health Council of the Netherlands 2000; Sutherland et al. 2006; The Royal Commission on Environmental Pollution 2009; Hölker et al. 2010a, 2010b; Falchi et al. 2011; Perkin et al. 2011; Fox 2013).

There have been a number of attempts at synthesising the evidence for the biological effects of artificial nighttime lighting, and at producing frameworks by which to organize it (e.g., Frank 1988; Longcore and Rich 2004; Rich and Longcore 2006; Perkin et al. 2011; Gaston et al. 2012, 2013). Valuable as these contributions have been, substantial gaps in understanding remain. One such is a synthetic consideration of how artificial nighttime lighting can influence population dynamics, and particularly each of the key demographic parameters of a local population of a species, namely immigration, births, deaths, and emigration. In other words, ascertaining the influence on the factors that determine where individual species occur and in what numbers, and hence ultimately the spatial patterns of species richness and composition. Whilst multiple studies have been conducted that are relevant to understanding the effect of artificial nighttime lighting on each demographic parameter in isolation (see later references), this more all-encompassing viewpoint of considering all four parameters has seldom been adopted. Here, focusing on animals, we consider how artificial nighttime lighting can affect each demographic parameter in turn. Because of the potential for laboratory and field studies to reach different findings on some of the impacts of artificial nighttime lighting (Calisi and Bentley 2009), where pertinent we differentiate carefully between the two.

2. Immigration

The presence of artificial nighttime lights in a locality can serve to draw in individuals of a species from beyond its bounds, sometimes over substantial distances. Indeed, such effects have been well documented. The different responses of organisms to light have been much discussed (e.g., Rich and Longcore 2006) and, albeit crude, one might usefully distinguish between two broad groups of species that are drawn to nighttime lights. First, there are what we shall term for present purposes light-distracted species, which respond directly to artificial nighttime lighting itself, usually through some form of disorientation to movements that are otherwise normally conducted in dark environments (e.g., Witherington and Bjørndal 1991; Ugolini et al. 2005; Lorne and Salmon 2007; Warrant and Dacke 2010); in the context of insects this is often referred to as flight to light (Hsiao 1973). These organisms are most obvious when they arrive at artificial lights in very large numbers. The phenomenon is, however, more widespread. These responses are often not well understood, although commonly argued to result from confusion of artificial nighttime lights with natural light sources used for orientation (other hypotheses have also been suggested; Verheijen 1958; Imber 1975; Poot et al. 2008).

Second, there are those we might term light-exploiter species, which are responding not foremost to the artificial nighttime lighting itself, but to the opportunities provided by that light; the term night light niche has been coined to describe the opportunities for extended activity that artificial light may provide (Garber 1978). Usually these are improved opportunities to forage. In some cases, this foraging occurs on organisms that are simply made more detectable in the presence of lights, for example, some otherwise diurnal predators extend their foraging hours under artificial nighttime lights (Garber 1978; Frank 2009). In other cases,

this foraging occurs on organisms that are themselves light distracted (e.g., Heiling 1999; Rydell 1991, 1992; Negro et al. 2000; Canário et al. 2012).

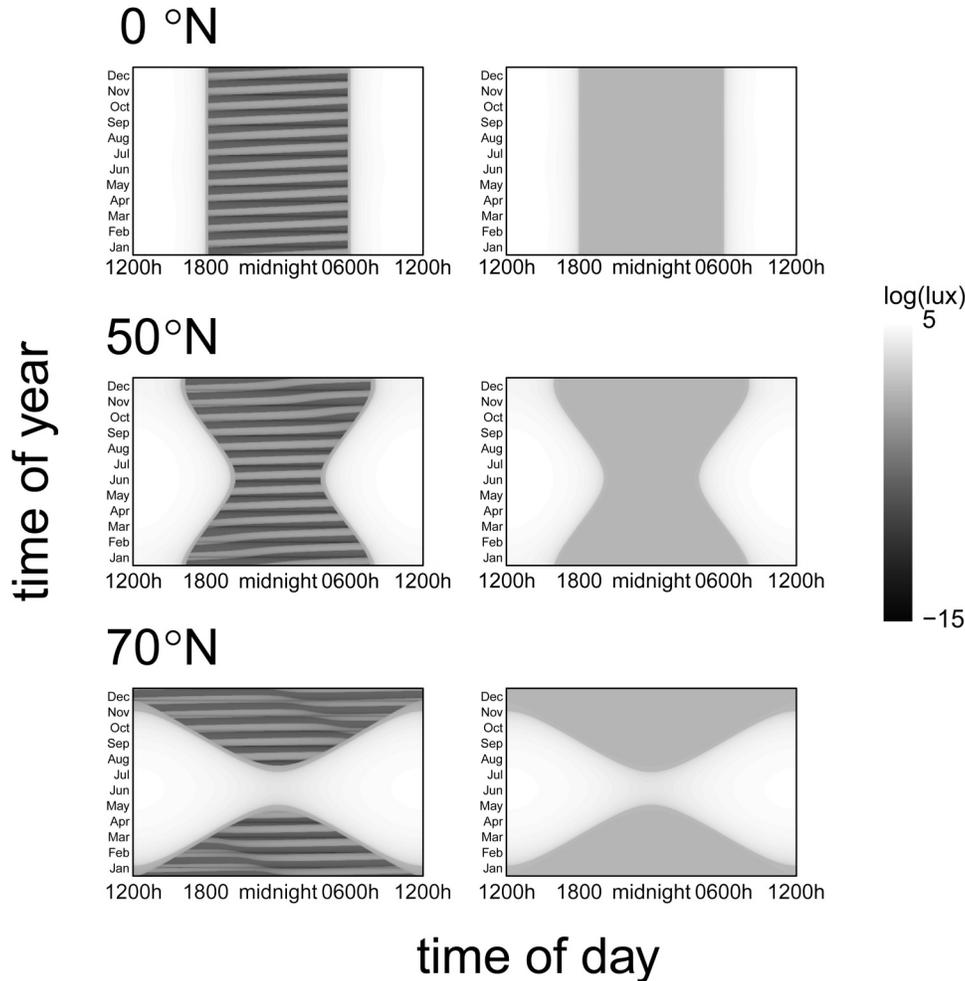
In the main, the effects of artificial nighttime lighting on the dynamics of the recipient population (rather than the source) through immigration seem likely to be transitory. Whilst large numbers of individuals of light-distracted species may be attracted, these tend rapidly to dissipate (often at or before dawn), either as a consequence of mortality or from subsequent emigration. There is the potential, however, for marked population sink effects (*sensu* Pulliam 1988), with artificial nighttime lights attracting then trapping or fixating individuals from the surroundings. The degree to which this occurs and the extent of the areas affected remain poorly understood (Eisenbeis 2006).

For light-exploiter species the importance of immigration due to the presence of artificial nighttime lights may be very significant when these lights are first established, but may subsequently settle to some steady state, reflective of the general movement patterns of the species. If such dynamics do exist this is not, however, trivial. The local distributions of some species may have been reshaped dramatically across much of their geographic ranges by the opportunities provided for foraging at artificial nighttime lights (e.g., some bat species; Arlettaz et al. 2000). In turn, this is likely to influence their role in ecological function and process.

Both for light-distracted and light-exploiter species it is possible that immigration may also have population dynamic effects through gene swamping. Here, immigrants from local populations existing under different environmental conditions restrict possible local adaptation by introducing alleles adapted to those other conditions. For example, the continual influx of individuals from unlit environments, if they stayed in the vicinity, could limit the rate of adaptation of a local population to living under artificially lit conditions. To our knowledge, such potential effects remain unexplored.

The focus of this discussion of the effects of artificial nighttime lights on immigration thus far has been on how they serve to increase the influx of individuals into a local population. Equally, and perhaps more significantly, artificial nighttime light could serve to reduce immigration by repelling individuals that otherwise would have moved in, due to negative phototaxis. The extent of such effects is extremely difficult to quantify (especially when distinguished from the effects of artificial nighttime lighting on emigration from a local population; see below). Nevertheless, undoubtedly, some, and likely many, species avoid artificially lit areas or alter their movements in response to the presence of artificial lights (e.g., Kuijper et al. 2008; Stone et al. 2009, 2012; Polak et al. 2011; Riley et al. 2012, 2013); one might usefully recognize these as a third group comprising light-repelled species. Indeed, for some species artificial nighttime lights serve to fragment landscapes in rather different ways than are apparent from patch structures based on other, and more commonly measured, habitat and environmental variables (e.g., Beier 1995; Eisenbeis 2006; Frank 2006; Stone et al. 2009, 2012). This can include the severance of corridors of movement and the creation of otherwise suitable "island" but unoccupied habitat patches. In particular, artificial lighting along roads and footpaths often forms continuously lit linear features that may act as a "crash barrier" that may limit effective dispersal of species that are deterred by light, become fixated and trapped within the lit area or suffer mortality (Eisenbeis 2006). Illuminated road networks may, therefore, be effective barriers isolating habitat patches and populations from immigration and reducing the connectivity of habitat within the landscape (Beier 1995, 2006; Eisenbeis 2006; Frank 2006).

Fig. 1. Estimated diurnal and annual light regimes under clear sky conditions with natural (left) and artificial (right) nighttime lighting at three latitudes. Shading represents light levels in lux on a logarithmic scale. Natural light regime incorporates estimated clear-sky light levels on a horizontal surface from sunlight, moonlight, and starlight, and shows both annual variation in daylight and variation in moonlight over the lunar cycle. Artificial nighttime light regime incorporates sunlight, moonlight, and starlight, and an additional 15 lx light source, typical of average levels of lighting at ground-level in areas lit by municipal street lighting, triggered whenever natural light levels fall below 50 lx. The artificial light source masks the monthly lunar cycle and decreases the contrast between night and day light levels, potentially reducing the ability of organisms to sense daylength as a cue.



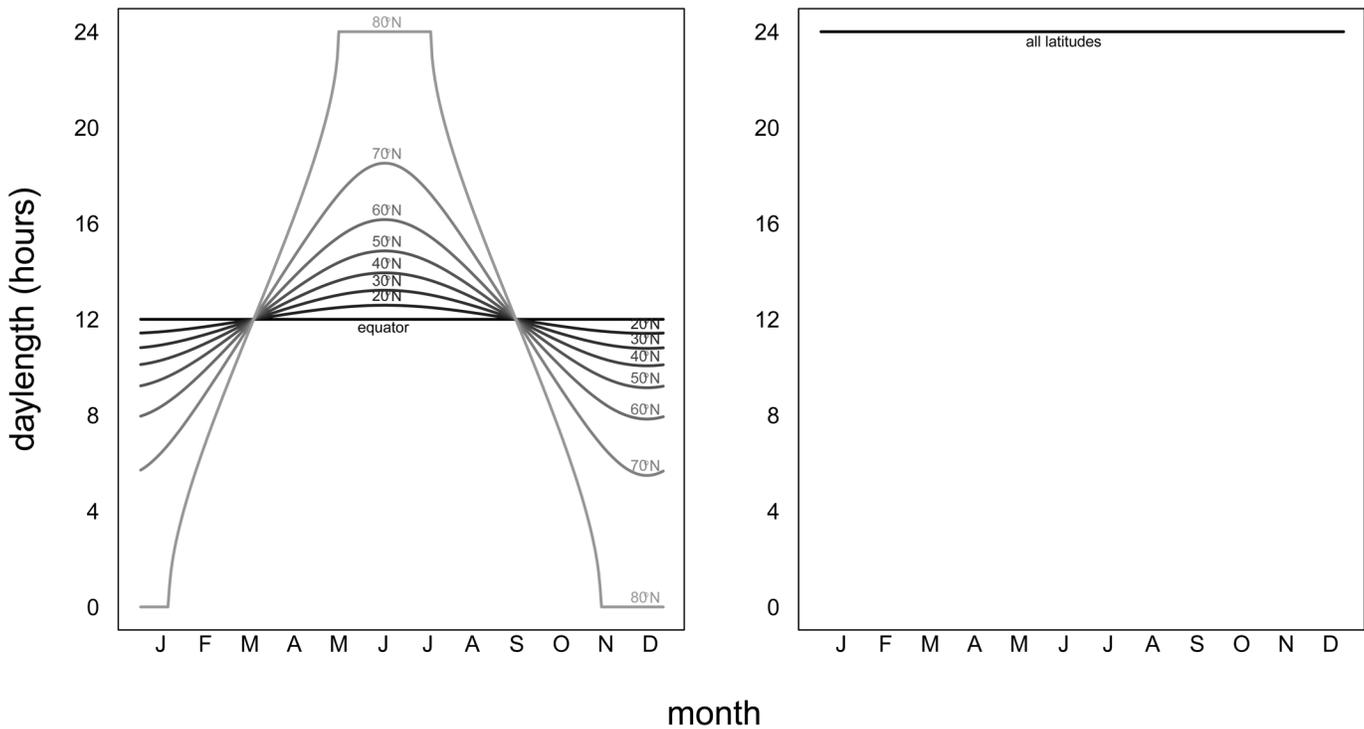
3. Births

It is quite plausible that the reproductive patterns of light-distracted species may be changed as a consequence of artificial nighttime lights. Frank (1988) reports that some moth species lay higher egg densities in the vicinity of lamps, which may lead to poor site selection and low survival to the larval stage. Disorientation and entrapment of individuals around light sources may reduce the opportunities for successful mating and decrease reproductive rates, or may aggregate fertile individuals and increase mating success in some species. Certainly, artificial nighttime light has been shown to affect breeding behaviour in both nocturnal and diurnal species (de Molenaar et al. 2000; Baker and Richardson 2006), which has the potential to influence reproductive success. Likewise, changes in resource availability as a consequence of artificial nighttime lighting, particularly for light-exploiter species, might influence levels of successful reproduction. A major increased flow of prey individuals at the right time of the season, for example, might enable greater numbers of offspring to be produced, greater investment in offspring, and (or) their faster development.

This said, a far more pervasive effect on reproduction seems likely to result from influences of artificial nighttime lighting on

circadian clocks and photoperiodism. Animals variously anticipate environmental changes using as cues the daily cycle of day and night, seasonal changes in daylength, and the monthly lunar cycle. Thus, in many species, the light environment is critical in providing the “zeitgebers” that entrain or reset a circadian clock (the 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). Artificial nighttime lighting alters these cues (Fig. 1). First, this may modify the entrainment of the circadian clock, delaying or advancing the cycle (i.e., altering the phase angle). Second, it may mask the clock, overriding the endogenous signal that it provides. Light no brighter than moonlight has been determined to have circadian effects (lab study — Evans et al. 2007). Indeed, influences of artificial nighttime lighting have been associated with (i) changes in early stage development in freshwater fish (lab study — Brüning et al. 2011); (ii) advances in the initiation of dawn singing in temperate birds (field studies — Miller 2006; Kempenaers et al. 2010); and (iii) advances in egg laying and increased extra-pair siring success in temperate birds (field study — Kempenaers et al. 2010).

Fig. 2. Daylength at different latitudes under natural (left) and artificial (right) nighttime light regimes. The artificial light source masks the daily cycle, potentially reducing the ability of organisms to sense daylength as a cue.



Animals at mid to high latitudes use seasonal changes in day length as a cue to initiate such events as reproduction, eclosion, diapause, moult, embryonic development, and migration (lab studies — Gwinner 1977; Niva and Takeda 2003; review - Dawson et al. 2001). Again, artificial nighttime lighting can serve to mask the natural light cycle (Fig. 2), providing misleading information on which to base these timings. Indeed, artificial photoperiods are used to postpone sexual maturity in some animal farming systems (e.g., Juell et al. 2003). The effects of nighttime lighting on photoperiod have been associated with changes to food provisioning of chicks by adult birds (field study — Titulaer et al. 2012).

Photoperiodic responses have been shown to exhibit local adaptation (Bradshaw 1976) and to be capable of evolving rapidly (Urbanski et al. 2012). This raises the potential of quick responses to changes in nighttime lighting conditions. Such effects could interact with photoperiodic responses to climate change.

4. Deaths

Much attention has been placed on the, sometimes high, levels of mortality of individuals of light-distracted species around artificial nighttime lights. This occurs both through their disorientation and resultant collisions with obstacles (e.g., Le Corre et al. 2002; Jones and Francis 2003; Longcore et al. 2012), and through their predation by light-exploiter species (Garber 1978; Frank 2009). In addition, light-distracted species may suffer mortality due to distraction from normal behaviour such as feeding or foraging. These effects are sometimes dramatic, and with potentially significant consequences for rarer species or small or fragmented populations in the vicinity of illuminated areas. Given the limited mobility of most animal species, they are, however, typically quite localized (albeit the individual organisms concerned may in some cases be drawn from potentially large areas, as with, for example, mortality of birds at communication towers; Longcore et al. 2012).

Given the much greater range of organisms potentially involved (not just those with the mobility to be drawn to lights), it seems likely that more widespread consequences of nighttime

lighting for mortality result from changes in the ways in which organisms can partition time. Dunbar et al. (2009) observe that, for most practical purposes, an animal's time must be allocated to one of four major categories of activity: feeding, moving, social interaction, and resting (including resting time that is enforced by thermoregulatory and digestive constraints, and resting time that can be converted into time for feeding, moving, and social interaction). Because the failure to meet nutritional requirements will lead to starvation and death, fulfilling feeding time is assumed to take precedence over the other categories. Indeed, it is well established that the distribution and abundance of many species are constrained by the amount of time available for foraging (e.g., Sanz et al. 2000; Dunbar et al. 2009; Carrascal et al. 2012; Zárýbnická et al. 2012; Dunbar and Shi 2013). This is particularly the case when temperatures are low and thus metabolic demands are high, when individual resource units are nutritionally poor, and when foraging at particular times carries high risks of predation. The light cycle may pose marked constraints on feeding time. Thus, when predominantly diurnal organisms forage at night, or predominantly nocturnal organisms forage during the day, they can experience increased predation pressure (Fenn and MacDonald 1995; Zavalaga et al. 2012); predation pressure often shapes activity patterns of night feeding species in response to changes in the lunar cycle (e.g., Daly et al. 1992; Skutelsky 1996; Kramer and Birney 2001); and when predation pressure is alleviated some organisms expand or change their temporal niches (e.g., Fraser et al. 2004; McCauley et al. 2012).

For diurnal organisms, artificial nighttime lighting may increase the amount of time available for feeding, whilst for nocturnal organisms the reverse is likely to occur (e.g., Santos et al. 2010; Dwyer et al. 2013). For the former this may bring tangible benefits, arguably particularly for herbivores for which available foraging time is closely linked to body condition. Artificial nighttime lighting can also change the foraging behaviour of organisms that do feed in the dark (e.g., Heiling 1999; Santos et al. 2010). In much of the world, the duration of artificial nighttime lighting is clearly

such that the effects on time partitioning, and particularly on feeding time if this is heavily constrained, could be marked (Fig. 1). In principle, these pressures could simply be ameliorated if individuals moved elsewhere (i.e., emigrated from their local populations), but this will often not be possible, because of shortages of alternative options, barriers to movements, and costs of movements (including reductions in time for feeding and increased risks of predation). Thus marked mortality could result.

Given lower nighttime temperatures, and hence potentially greater metabolic demands, the pressure on feeding time for nocturnal species may be disproportionately acute, and hence the consequences (including mortality) of that time being further curtailed by artificial nighttime lighting. Amongst some ectotherms this may be further exacerbated if at a given temperature nocturnal species have higher metabolic rates than do diurnal ones, as has been shown in some cases (e.g., Hare et al. 2010). Amongst endotherms this may be less likely to be a concern, as nocturnal species often have lower metabolic rates than do diurnal ones (e.g., Bennett and Harvey 1987; Duriez et al. 2010).

An influence of artificial nighttime lighting that is mediated through effects on time partitioning and metabolic demand raises the potential for interactions amongst artificial nighttime lighting and anthropogenic climate change pressures on organisms. The expansion of artificial nighttime lighting is one contributor to the rise in CO₂ levels that has driven increases in global temperatures (worldwide, the energy consumed to supply grid-based electric lighting has been estimated to generate 1900 Mt of CO₂ per year; International Energy Agency 2006). Those rising temperatures may, however, lower the metabolic demands of many species (particularly those in temperate regions and needing actively to feed during winter periods), reducing the requirement for feeding time, and the consequences of changes to that time resulting from artificial nighttime lighting. Some diurnal species can extend activity into the nocturnal niche under warmer conditions (Hoogenboom et al. 1984; Maloney et al. 2005; Jayatilaka et al. 2011; Hetem et al. 2012), and interactions between the anthropogenic forcing of increasing nighttime temperatures and of increased ambient light may favour species that are able to increase activity during the night.

Various studies on laboratory animals and humans have shown that artificial nighttime lighting increases cancer risk and suppresses immune function (linked to disruption to normal cycles of melatonin production and diverse metabolic consequences), including prolonged exposure to low light levels and brief exposure to intense ones (e.g., lab studies — Dauchy et al. 1997; Moore and Siopes 2000; Cos et al. 2006; Zubidat et al. 2007; Bedrosian et al. 2011; field study — Kloog et al. 2012). This raises the potential for artificial nighttime lighting to have health effects on wild animals, and thence potentially on death rates; there may also be sublethal effects on other components of fitness. To our knowledge, studies of this topic remain wanting.

5. Emigration

The role of artificial nighttime lighting in influencing levels of emigration of individuals from an area has not been well documented. It seems likely, however, that at least in the initial introduction of such lighting the individuals of some species will depart elsewhere. Distinguishing these effects from others associated with such introduction (e.g., other components of urbanization, such as land use change and disturbance) will often be difficult. The population effects of emigration are likely to be most evident when the illumination of an area of habitat is temporary, or intermittent, or where populations are monitored during a rapid increase in artificial nighttime light (e.g., introduction of street lights to a previously unlit area, without additional infrastructural changes). In this case, population decline may be rapid as individuals leave illuminated areas for darker refuges;

however, despite the apparent likelihood of this process we know of no clear evidence of such effects on emigration, or the relative importance of emigration and mortality due to loss of suitable habitat.

6. Discussion

The influence of artificial nighttime lighting on the balance of immigration, births, deaths, and emigration in local populations is doubtless highly variable both between and within animal species, as is the net effect on population numbers. This variability has at least two major sources. First, it will arise from differences in the lighting and its environmental circumstances. Artificial nighttime lighting can take many different forms (both public and private), vary in spatial distribution, intensity, and timing, and be provided through a diversity of lamps with different spectral properties (e.g., incandescent, quartz halogen, fluorescent, metal halide, high- and low-pressure sodium, light-emitting diode). Moreover, in any one location changes can take place in one or more of these, with some of these changes currently being widespread (e.g., in timing and type of illumination to reduce energy consumption and hence costs; Gaston et al. 2012).

Second, variability in the influence of artificial nighttime lighting on demographic parameters will arise from differences in the fundamental biology of populations and species, including basic time partitioning behaviour, spectral sensitivities of vision systems, movement patterns, navigation, photoperiodism, and circadian rhythms (e.g., Davies et al. 2013). Considerable gaps exist in understanding of the physiological and ecological effects of nighttime light on animals, and how these may map onto demographic processes.

At this stage it is difficult to provide broad generalizations as to the relative importance of artificial nighttime lighting on immigration, births, deaths, and emigration. The majority of attention on demographic rates to date has been placed on effects on immigration to localities, and to some extent the mortality that can result. It seems likely, however, that some of the most important influences of artificial nighttime lighting are more subtle and less immediately apparent to the observer, operating through birth and death rates. Indeed, suites of fitness characteristics may be impacted simultaneously (e.g., changed apparency to predators, mates and other conspecifics, modified foraging ability, increased susceptibility to disease). Constraints on migration between habitat patches due to the presence of illuminated urban development and road networks may also affect the long-term viability of metapopulations of nocturnal species reluctant or unable to pass through lit areas.

Good model organisms for the study of the impacts of artificial nighttime lighting on demographic parameters have yet to emerge. What are ideally required are organisms for which all four of the key parameters can readily be measured. As is often the case in population biology (Gaston 2009), a major challenge lies in the fact that different kinds of species are typically most suited to the measurement of different parameters. However, some broad guidelines may be outlined here. The extent of exposure to artificial light can be difficult to assess for mobile species, and cumulative, nonlethal effects hard to quantify in realistic, complex environments. Less mobile species, for which demographic parameters can be compared between lit and unlit environments, or those for which dispersal between light environments is limited to movement between discrete patches of habitat or along discrete pathways (for example, river or other habitat corridors) may be more tractable model organisms. Birth and death rates are more easily measured in species with short life-spans, and experimental studies in the laboratory are more suited to small organisms, while tracking movements in the field is more easily carried out on relatively large, long-lived animals. Compromises between the different constraints imposed by field observations and experi-

mental studies, between the simplicity of experimental light treatments and the spectral and spatial complexity of urban light-scapes, and between the measurement of survival and fecundity on the one hand and movement on the other, will inform choices of model organisms.

All this said, there is no doubt that the variable responses to artificial nighttime lighting exhibited by species and populations can change the abundance and species composition of assemblages (e.g., Polak et al. 2011; Rotics et al. 2011; Davies et al. 2012). In turn this will almost inevitably shape many ecological processes. In parallel with more detailed demographic studies of selected species, a wider consideration of the effects of artificial light on demographic processes across a range of taxa is needed.

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