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Introduction

Cite this article: Gaston KJ, Visser ME, Hölker F. 2015 The biological impacts of artificial light at night: the research challenge. *Phil. Trans. R. Soc. B* **370**: 20140133.

Phil. Trans. R. Soc. B **370**: 20140133.

<http://dx.doi.org/10.1098/rstb.2014.0133>

One contribution of 14 to a theme issue 'The biological impacts of artificial light at night: from molecules to communities'.

Subject Areas:

environmental science

Keywords:

communities, dose-response, individuals, light spectrum, night-time

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The biological impacts of artificial light at night: the research challenge

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1. The challenge

Daily, lunar and seasonal cycles of natural light have been key forms of environmental variation across the Earth's surface since the first emergence of life. They have driven the development of biological phenomena from the molecule to the ecosystem, including metabolic and physiological pathways, the behaviour of individuals, geographical patterns of adaptation and species richness, and ecosystem cycles (e.g. [1–4]). Indeed, biological systems are arguably organized foremost by light [5–7].

The natural patterns of light have over the last 100 years come to be greatly disrupted through the introduction of artificial light into the night-time environment: artificial light at night (ALAN). This derives from a diversity of sources, including street lighting, advertising lighting, architectural lighting, security lighting, domestic lighting and vehicle lighting. ALAN disrupts natural patterns of light both via direct effects of illumination from these sources as well as via skyglow (the scattering by atmospheric molecules or aerosols in the atmosphere of ALAN that is emitted or reflected upwards; [8–10]).

On the ground this disruption of natural patterns of light takes two principal forms [11]. First, light has been introduced in places, times and at intensities at which it does not naturally occur. This has been firmly fixed in the public imagination through the creation from satellite and astronaut acquired night-time imagery of pictures of the Earth which illustrate the extent of ALAN, of urbanization and of major centres of human population (figure 1; e.g. [12,13]). Given the nature of such images, it is challenging to use these to make some categorical quantification of the extent of ALAN, although it is plainly much more widespread than urban infrastructure alone, mainly because of the skyglow effect. One estimate that accounted explicitly for the effects of skyglow was that 18.7% of the global land area experienced ALAN [12], another based more directly on satellite imagery that 11.4% of terrestrial and 0.2% of marine areas of the globe experienced ALAN [11], and another that ALAN is increasing at around 6% per annum with huge geographical variation (0–20%; [14]).

Second, ALAN is introducing light with a spectrum that is different from those of sunlight, moonlight or starlight [11]. The spectrum of ALAN depends fundamentally on the kind of lighting device that is being used, ranging from narrow (e.g. low pressure sodium) to broad bandwidths (e.g. high intensity discharge and light-emitting diode—LED, [15]). The dominant technology tends to vary geographically, but can be locally quite heterogeneous. However, there is a general trend towards the use of 'whiter lighting' sources, often with a strong component in the blue portion of the spectrum (especially using LEDs; e.g. [16]).

Unlike many other anthropogenic changes that have been wrought on the environment (e.g. in CO₂, temperature, habitat change), those resulting from ALAN are entirely unprecedented. There have been no natural analogues, at any time scale, to the nature, extent, distribution, timing or rate of spread of ALAN [11,17].

The introduction of ALAN has provided significant and substantial benefits to humankind [18,19]. However, if biological systems are fundamentally shaped by light, and ALAN has changed the patterns of light in novel and extensive ways, it seems logical to predict that ALAN will have numerous biological impacts.



Figure 1. Remote imagery of artificial light at night. (a) Monthly composite satellite image of night-time light from the Visible Infrared Imaging Radiometer Suite (VIIRS) day/night band (DNB). NASA Earth Observatory image, using Suomi NPP VIIRS data provided by NOAA National Geophysical Data Center. (b) Photograph of the Iberian Peninsula at night from the International Space Station showing Spain and Portugal. Image courtesy of the Earth Science and Remote Sensing Unit, NASA Johnson Space Center (<http://eol.jsc.nasa.gov>).

This is not a new argument. Concerns as to the biological impacts of ALAN have been expressed for a long time (e.g. [20–23]). Numerous studies have also been published that demonstrate such impacts (for recent examples, see [24–31]). However, understanding the genuine severity of the problem is both challenging and timely: with the large scale and rapid introduction of LED lights and the use of ‘smart illumination’ [16], we now have the opportunity to adjust ALAN to reduce any negative environmental impacts provided that there is a good understanding of the effects of both intensity and spectral composition of ALAN. This special issue is a step toward

addressing that research challenge, which takes several key forms. In this introductory paper, we distinguish those associated with light, with individual organisms and with populations, communities and ecosystems.

2. Light

In the main, understanding of the patterns of ALAN has come from analyses of satellite imagery (e.g. [12,32]), aerial surveys (e.g. [33,34]) and ground-based measurements of

direct illumination and skyglow ([8,35]; some produced from citizen science data, e.g. [36]). These have proven invaluable and will continue to provide significant insights. However, to improve understanding of the biological impacts of ALAN, such an approach has to be enriched in a number of ways.

First, more attention needs to be paid to differences in the nature and relative importance of the three main sources of ALAN, namely direct illumination, light scattered by cloud cover and light scattered from a clear sky [37]. While ALAN is perhaps most commonly envisaged in terms of direct illumination (e.g. typical diagrammatic representations of ALAN focus on the immediate illumination from one or more streetlights), the atmospheric scattering of light, and the resultant skyglow, is likely also to be very important. This is particularly so because while direct illumination may extend metres to hundreds of metres and is readily blocked by obstacles, skyglow may extend kilometres to hundreds of kilometres [17] and is little influenced even by terrain blocking [37]. Indeed, much more needs to be known about the nature of skyglow, exploiting the computational tools that are now available [37].

Second, more attention needs to be paid to the spectra of ALAN. ALAN tends to be mapped in terms of the intensity of illumination, commonly with respect to human vision. However, biological processes (e.g. photosynthesis, circadian clocks, vision) vary markedly in the components of spectra to which they are most sensitive. Of concern here is not simply the spectrum of direct illumination but also of skyglow, and how the two interact. For example, in urban areas clouds have a much bigger impact on the proportion of red than blue light redirected towards the surface [38]. Relative to white or blue light sources, reddened sources are believed to reduce skyglow owing to the stronger Rayleigh scattering at short wavelengths [10,39].

Third, and perhaps most critically, too little is presently known about what ALAN is actually experienced by organisms, and how this varies. In the absence of better information, it has commonly to be assumed that the average levels of ALAN in an area are those experienced by the organisms that occur there. However, particularly given the spatial resolutions at which it is mapped, animals can often behaviourally avoid the typically more heterogeneous patterns of ALAN through the spatial and temporal habitat and movement choices that they make. In one of the few examples we are aware of to date, Dominoni & Partecke [40] show that urban blackbirds do actually experience longer subjective day lengths as a consequence of ALAN.

3. Individual organisms

The vast majority of studies of the biological impacts of ALAN concern the effects on individual organisms. These span studies of gene expression (e.g. [41,42]), physiology (e.g. [43–46]), foraging [24,47–50], daily movements [51–55], migratory behaviour (e.g. [56,57]), reproductive behaviour (e.g. [58–62]) and mortality (e.g. [63,64]). There is almost a complete lack of published examples in which no effect was documented (but see [35]), suggesting either that biological impacts are quite pervasive or the potential for a severe ‘file drawer’ problem (see [65]) in the literature. Although a file drawer problem of some degree would not be surprising, the truth most probably lies somewhere in between.

What is lacking at this point is a well-developed understanding of how the biological impacts of ALAN change with variation among individual organisms, life stages, spatial-temporal contexts and with the form of the ALAN. With respect to the organisms, key challenges are to determine: (i) how intraspecific responses to ALAN vary among and within classes of individuals (e.g. sex, age, body size); (ii) how responses to ALAN vary among a wide array of different species—much reliance is presently placed on studies of birds and mammals [66], with almost no knowledge about effects on microorganisms (but see [67]) and plants (but see [68]), and little known about invertebrates (with the exception of moths; but see [69] for a review, and [68,70,71]); (iii) how responses to ALAN by laboratory organisms or humans extrapolate to organisms in the wild—particularly notable is the evidence of significant stress and disease impacts in laboratory or domestic situations [72], and the limited studies of these effects in wild organisms; and (iv) how metabolic, physiological and behavioural responses to ALAN influence organismal fitness—studies are beginning to uncover such fitness consequences [62].

With respect to the ALAN itself, the challenges are to determine: (i) the form of dose (intensity)-response relationships for a range of biological impacts of ALAN—almost exclusively, studies to date have contrasted predominantly two ALAN treatments (ALAN versus no ALAN), preventing determination of thresholds and the overall shapes of dose-response functions; and (ii) the form of spectral-response relationships for a range of biological impacts of ALAN—again, as with dose-response relationships, the state-of-the-art experiments are employing just a few spectral treatments [68,71,73] or typical light sources for outdoor lighting with different colour spectra (see [74,75]). Understanding of both dose-response and spectral-response relationships, and their interaction, will be critical to providing the best advice on how to limit the negative biological impacts of ALAN.

4. Populations, communities and ecosystems

While ALAN has been widely documented to have effects on the physiology and behaviour of individual organisms, the extent to which this translates into impacts on populations, communities and ecosystems remains poorly understood. The principal problem here is simply that the number of studies that have been conducted is extremely small (see [27,67,68,71,76,77]).

A challenge in determining the influence of ALAN on populations is that while it can potentially influence each of the key demographic parameters (births, deaths, immigration, emigration), it is difficult to study each of these effects for a single study species [78]. Those species for which births and deaths are relatively easy to measure are commonly those for which immigration and emigration are hard to determine, and vice versa.

Although there are documented examples of the impacts of ALAN on prey influencing their predators, and of impacts on predators influencing their prey (e.g. [50,79,80]), the manner in which such influences ramify through communities remains poorly understood [11]. Bennie *et al.* [68] report experimental evidence of bottom-up, but not top-down, effects in simple plant–herbivore–predator communities.

To predict the ecological consequences of ALAN in natural systems reliably, it is critical to have a better understanding of

longer term processes that moderate the susceptibility of populations, communities and ecosystems to an illuminated environment. Much of the available knowledge is based on short-term experiments within one generation time (often days to weeks) that do not allow the consideration of response mechanisms, such as acclimation, adaptation, physiological, behavioural and even evolutionary compensatory mechanisms linked to environmental context and seasonal timing. For example, an illumination period of more than 1 year was necessary to cause a clear change in an ALAN-naive freshwater microbial community [67].

Although largely unknown, it has to be expected that effects on ecosystem functions and services do occur [7,11]. In the tropics, for example, nocturnal seed dispersers such as bats are crucial for ecosystem functioning. It was found that natural forest succession and connectivity of forest patches may suffer owing to ALAN through a reduction in nocturnal seed disperser activity in illuminated areas [29]. Another example is microbial communities living in aquatic sediments. These are highly diverse and play an important role in the global carbon cycle. Hölker *et al.* [67] report ALAN-induced changes in the species composition of such sediment communities. This has implications for ecosystem functions (here carbon mineralization) and could even shift the system from negative to positive net ecosystem production at night.

To determine the effects of ALAN on populations, communities and ecosystems most effectively, it is necessary to establish replicated field experiments. The first such experiments report findings in this special issue—the ECOLIGHT experiment [68], the 'Verlust der Nacht' experiment [67] and the LightOnNature experiment [71]. Early evidence is suggesting that there may be marked between-year variation in the influences of ALAN, emphasizing the importance of developing or maintaining long-term experiments including several generations of key species.

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5. Conclusion

Over just the last few years there has been an explosion of research interest in the biological impacts of ALAN (albeit the topic has deep historical roots; for reviews see [69,81–83]). This has been fuelled by (i) several policy reports that have highlighted its likely importance among the plethora of anthropogenic influences on the environment (e.g. [84–86]); (ii) the need to cut energy costs by altering public lighting systems and the associated potential for environmental gains [87,88]; (iii) the wide-scale change to LED lighting and calls for the design of eco-friendly spectral composition of lamps [14,66,89] and arguably, (iv) the serendipitous contemporaneous emergence both of major independent funded research programs experimentally addressing ecological impacts of ALAN [67,68,71] and of the interdisciplinary 'Loss of the Night Network' funded by the EU COST program. The resultant body of research work has mapped out the potential breadth of biological impacts of ALAN, has highlighted many important targets for future work and has begun to identify ways in which practical steps can be taken to reduce environmental concerns. This special issue contributes further to that trajectory.

Acknowledgements. We are grateful to the authors who kindly agreed to contribute to this special issue, to the reviewers who provided valuable comments on the manuscripts, and to H. Eaton and other members of the editorial and production staff of *Philosophical Transactions of the Royal Society B* who have as ever been a delight to work with. We thank J. Bennie and S. Gaston for comments on the manuscript.

Funding statement. The research leading to this paper has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC grant agreement no. 268504 to K.J.G.; from the Verlust der Nacht project, funded by the Federal Ministry of Education and Research, Germany to F.H. (BMBF-033L038A); and from the Dutch Technology Foundation STW, which is part of the Netherlands Organisation for Scientific Research (NWO), and which is partly funded by the Ministry of Economic Affairs, to M.E.V.

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