Review

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Review

Biological Spectral Sensitivity Functions for Measuring and Managing Light at Night

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Abstract

Anthropogenic/artificial light at night (ALAN) may have detrimental effects on individual organisms, ecosystem structure and integrity, and human sleep and circadian rhythms. The wavelength dependence of diverse biological photosensory systems is thus an appropriate consideration when quantifying ALAN. We propose spectral weighting functions for biological detection in animals ($B_A(\lambda)$) and all organisms ($B_E(\lambda)$) based on established features of biological spectral sensitivity. Light metrics employing $B(\lambda)$ provide a biologically relevant way to measure ALAN and evaluate solutions to reduce it through spectral tuning.

Keywords: light; light at night; ALAN; light pollution; anthropogenic light; artificial light; photoreceptor; photopigment; phototaxis; biological rhythms; chronobiology

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Access to electricity has spread anthropogenic/artificial light at night (ALAN) worldwide, raising concerns about harm to ecosystems and human health[1]. This has created a need to consider

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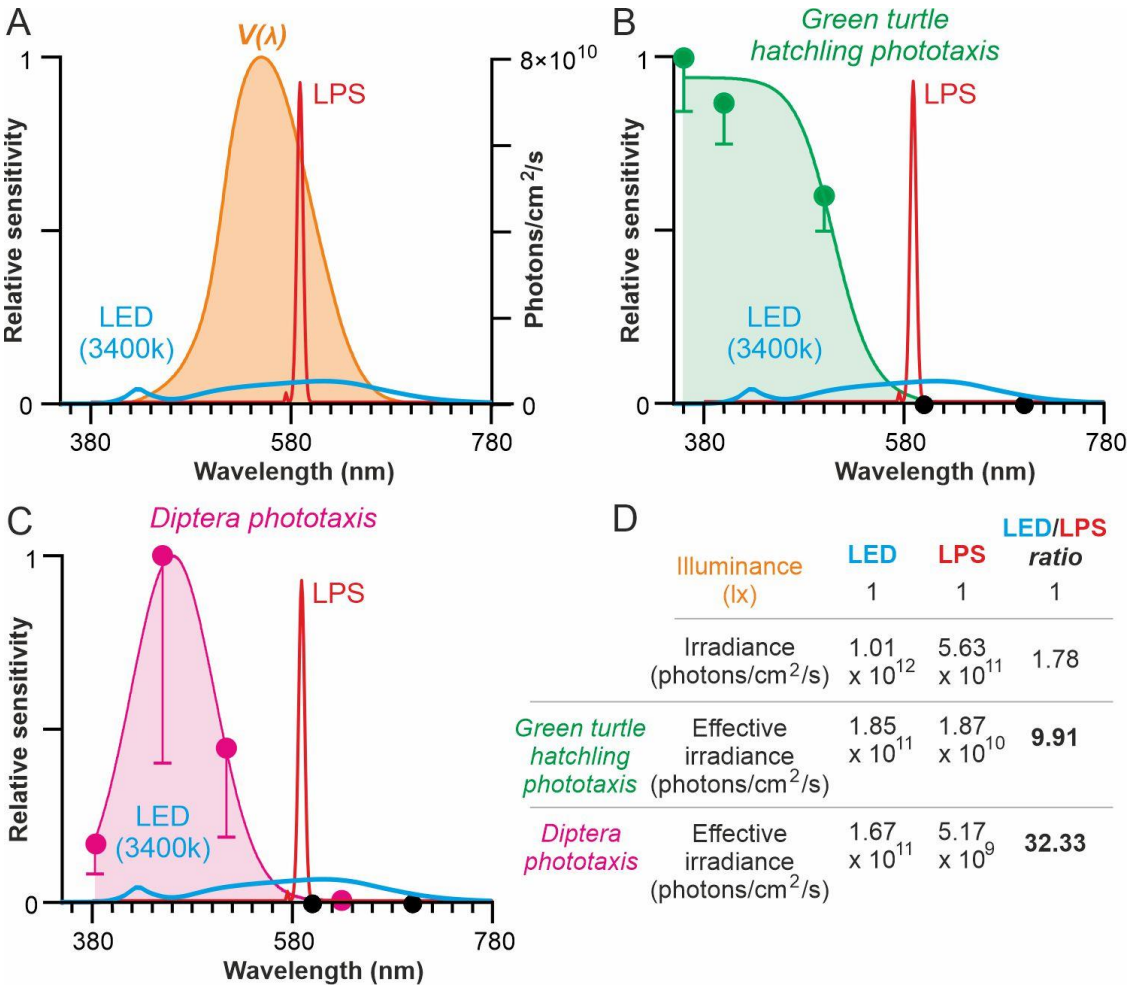
ALAN as a pollutant, monitor its distribution, and ameliorate its impact by decreasing light output, restricting light to places and times at which it is required, and by spectral tuning away from wavelengths with highest potential for damage[2,3]. To measure and reduce ALAN's impact most effectively, we need methods of quantification that account for how light varies in both intensity and wavelength composition. Since biological systems are not equally responsive to all wavelengths, predicting biological effects requires weighting functions that match the spectral sensitivity of the organisms or processes under consideration.

ALAN is often quantified in terms of its illuminance (unit: lux), a standard lighting metric familiar to lighting professionals, decision makers and the public. Illuminance, and related photometric quantities of luminous intensity (unit: candela) and luminous flux (unit: lumen), use a wavelength weighting function $V(s)$ (Figure 1) peaking at 555 nm. Now 100 years old, $V(\lambda)$ is an idealized efficiency curve for perceived brightness in a 'standard' human adult observer in bright light. As the myriad effects of ALAN on the living world do not reliably follow the wavelength sensitivity of $V(\lambda)$, measuring light this way can underestimate biological sensitivity to sources with strong output outside the green-yellow range (~555 nm), and wrongly treat different lights as equivalent when they have different biological potency (Figure 1). In this paper, we present an attempt by experts in light measurement, photobiology, and ecological light pollution to agree an alternative to V(λ) more relevant for ALAN's effects on human health and ecosystems.



		LED	LPS	LED/LPS ratio
	Illuminance (lx)	1	1	1
	Irradiance (photons/cm²/s)	1.01 x 10¹²	5.63 x 10¹¹	1.78
Green turtle hatchling phototaxis	Effective irradiance (photons/cm²/s)	1.85 x 10¹¹	1.87 x 10¹⁰	**9.91**
Diptera phototaxis	Effective irradiance (photons/cm²/s)	1.67 x 10¹¹	5.17 x 10⁹	**32.33**

Figure 1. Transition from low pressure sodium (LPS) to warm white LED (Correlated Colour Temperature=3400K) lighting could change light pollution potential even if illuminance is matched. **A**. The wavelength weighting function $V(\lambda)$ (orange) plotted against spectral photon flux distributions for LPS (red) and LED (blue) sources producing illuminance of 1 lx. **B, C.** The same spectral photon flux distributions plotted alongside the spectral sensitivity of green turtle hatchling (**B**; from[34]) or Diptera (e.g. flies, mosquitos, midges)

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(**C**; from[112]) phototaxis. **D**. Despite equal illuminance and similar total photon flux, the two sources differ ~10-fold in effective irradiance for hatchling and >30-fold for Diptera phototaxis (calculated by applying phototaxis action spectrum (**B**) as a normalization function prior to integrating across wavelength).

Biological Wavelength Sensitivity

Any spectral weighting function for unwanted biological effects of ALAN should build upon what is already known about the consequences of light pollution and their photosensory origins. Defining wavelength sensitivity for the damaging effects of ALAN on the living world is inherently challenging. Photosensitivity is widespread among the estimated ~8.7 million eukaryotic species worldwide[4]. Moreover, it is common for organisms to have multiple, spectrally distinct, photoreceptive mechanisms and to combine their output in complex ways to allow responses over a wide range of intensities/wavelengths or to extract higher level features such as colour. Accordingly, different phenotypic (behavioural or physiological) responses to light even within a single organism often have divergent spectral sensitivity[5]. Furthermore, the ultimate impacts of light pollution will be defined by the complex inter-relationships between species, with damaging effects on one species likely often having secondary or tertiary effects on others (see for example [6–9]).

The most valuable information about wildlife spectral sensitivity would be for ecosystem level impacts. While a number of papers have demonstrated consequences of light pollution on interactions between species (e.g.[10–16]), few have specifically examined how light spectrum impacts these interactions[17–23]. Given the paucity of ecosystem level assessments of wavelength sensitivity, several authors have assembled compilations of spectral sensitivities and phenotypic responses in multiple species in order to examine and draw conclusions about the general likelihood of different parts of the electromagnetic spectrum to elicit biological impact[24–29]. Following that lead we here consider the general features of spectral sensitivity in the living world.

Unwanted effects of ALAN in animals include disruptions to: daily, lunar, tidal and seasonal rhythmicity; navigation; food web interactions; reproductive behaviour; recognition of conspecifics; and species community composition[30,31]. Action spectra for light pollution-relevant phenotypic responses in animals reveal great variation in wavelength sensitivity[32–34] reflecting diversity in this aspect of animal photoreception. Responses to ALAN in animals will be produced primarily by the opsin family of light activated G-protein coupled receptors, which support both vision and accessory neurophysiological responses to light. Cryptochrome photopigments, however, also contribute to circadian and other timing functions and magneto-orientation in some species[35,36]. Cryptochromes show maximal sensitivity in blue/UV-A portions of the spectrum. Opsin-based visual pigments have spectral sensitivities composed of two broad superimposed curves, creating a main bell-shaped curve with a short wavelength shoulder[33]. The position of the main peak shows great variability from below 340 nm to above 600 nm[23]. Spectral filtering can meanwhile shift functional peak sensitivity to much longer wavelengths than implied by their pigment (λmax)[37–39]often to >600 nm. In addition, many freshwater fish have visual pigments based on vitamin A2, which may also shift peak sensitivity to above 600 nm[40]. At the extreme, there are rare examples of photoreceptors peaking as far up as 640 nm[41,42]. Additional diversity in wavelength sensitivity for animals is provided by the tendency of visual systems to combine photoreceptor outputs in complex ways, including spectral opponency.

Humans represent a particular case among animals, both because human health receives special attention, and because so much is known about our photosensitivity. While the specific impact of outdoor ALAN on human health is hard to quantify[43–47], there is reason for concern. Epidemiological data correlate exposure to light at night (including in some cases outdoor ALAN) with poor health, including increased incidence of various cancers[44,45], cardiometabolic disease[46–51], neuropsychiatric disorders[43,52], disrupted sleep[53] and all-cause mortality[54,55]. One accepted origin of such effects is disruption of sleep and circadian systems and associated alterations in neuroendocrine, autonomic and other homeostatic processes[56–60]. Levels of

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nocturnal illumination in the range of those commonly encountered on residential streets, while typically lower than indoors, can engage these effects[61,62]. Such circadian and related physiological effects of light in humans primarily arise via a specialised class of intrinsically photosensitive retinal ganglion cells (ipRGCs) that express the photopigment melanopsin[63,64]. Expert consensus frameworks[62,65] and an international measurement standard (CIE S026[66]) have addressed the problem of wavelength weighting for ipRGC-influenced responses. Those concluded that melanopic irradiance, calculated by applying a wavelength weighting function peaking in the blue part of the spectrum (around 490 nm), is the best currently available predictor for effects of light on these aspects of human biology.

The impact of light pollution on plants and microorganisms has been less studied[6,67–69]. Nevertheless, ALAN has been reported to alter the timing of germination, flowering and bud burst, impact biomass, pollination and fruit set, and alter phyllosphere microbial diversity [6,10,70–73]. Adverse effects of ALAN can impact plant and microorganism communities by disrupting circadian and seasonal control, with knock-on effects on rhythms in processes such as water loss and carbon partitioning[14,74,75], vertical migration in aquatic microorganisms[76], cold acclimation[77], and reproductive timing[78]. Temporal shifts in floral development may misalign flower and pollinator availability and expose reproductive structures to adverse temperatures. Both plants and microorganisms possess arrays of photopigments absorbing light across a broad spectrum from <300 nm to >900 nm to produce these effects[79–81]. At shorter wavelengths the UV RESISTANCE LOCUS 8 (UVR8) protein provides UV-B sensitivity, while cryptochromes, phototropins, and other light-oxygen-voltage sensing (LOV) domain proteins are sensitive across blue/UVA. Phytochromes show red/far-red photo-reversibility and in some species extended long-wavelength[82,83] or broader spectral[84] sensitivity. In archaea, bacteria, fungi and algae, sensory rhodopsins are used for orientation, light-regulated development and photoprotection. These light sensors generally show maximal absorbance below 600 nm, although some may have high sensitivity to longer wavelengths[85,86].

In the aquatic environment, the optical properties of the water and its constituents are an additional determinant of spectral sensitivity for all forms of life. Incident light, measured at the surface, is scattered and absorbed as it passes through the water column. Water itself optimally transmits wavelengths between 400 and 500 nm[87], but dissolved/suspended matter can apply strong additional filtration, as can phytoplankton and algae[88]. Dissolved organic matter, such as humic substances, for example, can shift freshwater peak transparency to longer wavelengths above 550 nm[86]. The water constituents, and therefore the spectral properties of water, can vary according to weather, season, climate and time of day (e.g. algal blooms) and be impacted by anthropogenic activities and climate change[89,90]. Species wavelength sensitivity often reflects optical properties of their environment. For example, fish or turtles in clear marine waters are often more responsive to shorter wavelengths than species living in freshwater stained by humic substances[91,92]. In turbid waters, more broad-spectrum responsiveness has been reported e.g.[27,93]. Spectral sensitivity can also change during ontogeny, particularly in amphibiotic species transitioning from aquatic to terrestrial habitats or when this involves transitions between fresh and oceanic water[94,95].

Spectral Weighting Function for Biological Light Detection

Faced with the abundance of biological responses to light and the diversity in photoreceptor wavelength sensitivity, one might question the purpose of any ‘catch all’ spectral weighting function. Each damaging effect of ALAN will have its own wavelength dependence that will, by necessity, be imperfectly approximated by a spectral sensitivity function hoping to also encompass other phenotypic responses with their own distinct wavelength dependence. However, the case for ‘least-worst’ generic measures of light pollution is strong. Firstly, a spectral weighting function is a powerful tool in the armoury of those charged with measuring and manipulating light. Such a function allows light to be quantified in a single dimension - effective light dose – that allows ‘apples

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and apples' comparisons between divergent light spectra. As such, it facilitates simple quantification of ALAN and the appearance of quantitative engineering standards. By encompassing differences in spectral power distributions within a single measure of effective light dose it also allows appropriate emphasis on spectral engineering as a component of mitigation methods. With these advantages in mind, what are the options for defining a spectral weighting function for unwanted biological impacts of ALAN?

We have seen that the most commonly applied wavelength weighting in light quantification ($V(\lambda)$) imposes bias in favour of light close to its peak at 555 nm (Figure 1). Given the abundance of photoreceptive mechanisms and diversity of responses to ALAN, it is tempting to address this inadvertent bias by replacing V(λ) with a solution imposing no bias whatsoever, by employing a flat response setting sensitivity equal to 1 across the extent of visible light (360-800 nm). That approach would capture the important concept that all ALAN is potentially detectable by living organisms and that no wavelengths are 'safe'. The implicit assumption that all portions of the visible spectrum are equally damaging, however, does not accord with what is known for biological photosensitivity where, for instance, it is much more common to encounter photoreceptors with high sensitivity to 500 than 800 nm [23].

The best approach to encompassing biases in wavelength sensitivity across the living world would be to start from descriptions of spectral sensitivity for damaging impacts of ALAN. Unfortunately, the number of defined action spectra for pollution effects is small when viewed against the range and complexity of potential impacts. Furthermore, because constructing such action spectra in the wild is challenging, such an action spectrum database will always be incomplete and biased towards those responses that are easier to measure. Single phenotypic action spectra are also an imperfect substitute for ecosystem-level impacts. Welfare of a single species may be impacted by multiple phenotypic effects on that species as well as ALAN impacts on other species, including its symbiotic micro-organisms (holobiont). Within any environment, unwanted effects of ALAN will then encompass multiple phenotypic responses across numerous species whose relative importance may vary over space and time. As a result, the prevailing light pollution wavelength sensitivity in an environment will be a composite of spectral sensitivity functions for individual effects whose relative importance is hard to discern and likely inherently labile. Such circumstances require an alternative 'least-worst' approach to approximating biological wavelength sensitivity.

A pragmatic solution is to replace V(λ) with a curve defined according to the wavelength biases of biological photoreceptors. We already know much about photoreceptor wavelength sensitivity across organisms (see above) and the quality of that information will grow over time. Strictly speaking such a curve is a tool aiming to quantify light in terms of its biological detection potential, rather than its polluting impact. Using that curve as an achievable solution to measuring ALAN in a manner relevant for biological impacts requires the assumption that detection is the first step in damage. That seems reasonable, but it is important to acknowledge that it is a compromise. Not all aspects of detection are equally likely to result in damage and downstream processing of photoreceptor outputs could impact phenotypic wavelength sensitivity. Keeping these caveats in mind, we nonetheless consider a biological wavelength weighting function $B(\lambda)$ designed according to the known spectral sensitivity of photoreceptors in organisms that may be adversely affected by ALAN as the most viable approach.

Building B(l) from photopigment spectral sensitivity faces the challenge of accounting for the substantial diversity in this parameter within and between species. As outlined above, plants and microorganisms share photopigment classes that are distinct from those of animals. We therefore first consider animals separate from plants+microorganisms. In animals, while cryptochromes likely always respond primarily to light below 500 nm [96], opsin-based visual pigments show substantial diversity in wavelength sensitivity. The most complete currently available dataset of opsin visual pigments for terrestrial animals[24] reveals that maximum sensitivity (lmax) of individual pigments covers a wide spectral range, from UV to>600 nm (Figure 2A). That dataset has been summarised as a global mean spectral sensitivity profile, which represents a potential extension of a previously

 doi:10.20944/preprints202604.1368.v1

proposed 'actinic power' spectral response function for individual light pollution effects [25]. The corresponding profile shows peak sensitivity at 520 nm and has higher sensitivity across shorter wavelengths. The underlying dataset[24], by necessity, reflects those species and aspects of photosensitivity that have been subject to scientific investigation rather than an unbiased survey of animal photoreception. Moreover, vertebrate rod opsins (responsible for dim light vision) are under-represented, and it excludes aquatic species and 'non-visual' photopigments including melanopsins and cryptochromes. As several of those known omissions tend to have shorter wavelength sensitivity, we propose adopting a precautionary assumption that shorter wavelengths have generally high capacity for animal detection. Conversely, we accept the relative rarity of very long wavelength sensitivity in the database as being broadly representative of the situation across animals. A wavelength weighting function capturing these concepts would have maximum sensitivity across middle and shorter wavelengths and fall away at longer wavelengths. In defining the decay in sensitivity over longer wavelengths we work from the observations that this portion of the global mean wavelength sensitivity plot[24] resembles the long wavelength limb of a standard opsin-based pigment nomogram[97], and that >95% of invertebrate (and 99% of vertebrate) opsin pigments in the dataset [24] have lmax <590nm. For simplicity we capture these features using a logistic function describing the relationship between relative sensitivity to photon flux (y) and wavelength (x) of animals (y=1/(1+10^(0.026*(x-590))); Figure 2B whose slope recreates the long wavelength limb of an opsin photopigment nomogram and has 50% sensitivity at 590nm. Because it does not approach zero until very long wavelengths (Supplementary Figure 1) this function accounts for the fact that some animals are highly sensitivity to longer wavelengths.

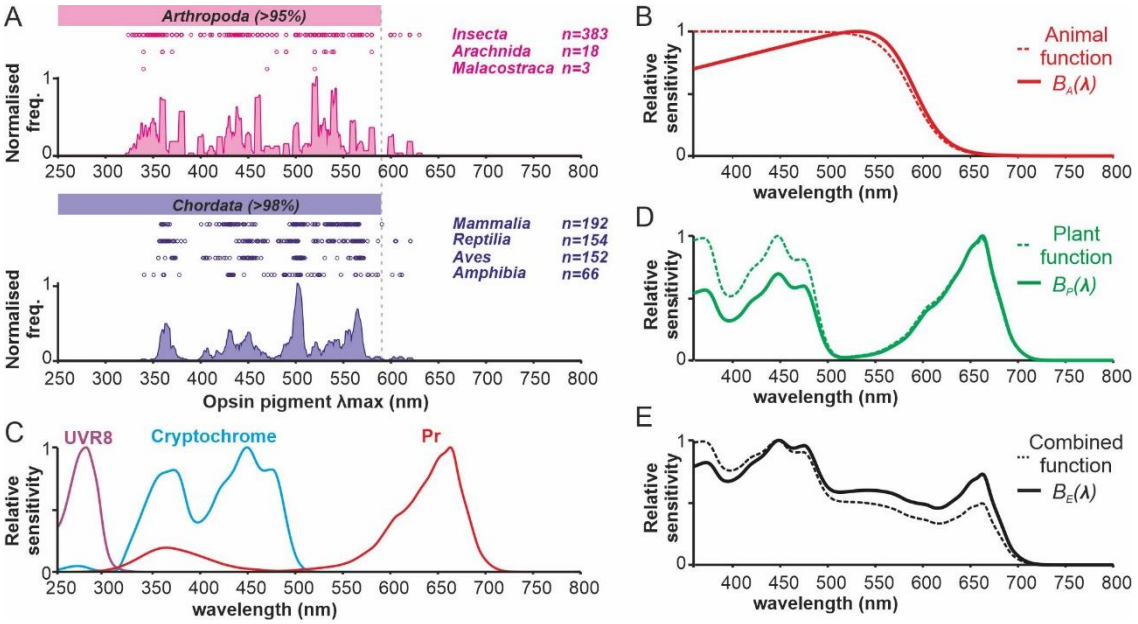

Figure 2. Wavelength normalisation functions ($B(\lambda)$) for biological photosensory responses. **A**. Opsin photopigments in a large collated dataset[24] from Arthropoda (top) and Chordata (bottom) plotted according to their wavelength of peak sensitivity to photon flux (λ_{max}) represented as individual datapoints above normalised frequency distributions. Dotted vertical line marks the wavelength (590nm) encompassing >95% of arthropod opsin λ_{max}. **B.** Relative sensitivity of animals to photons as a function of wavelength (thin dashed line) as defined by a logistic function $y = \frac{1}{1+10^{(0.026*(x-590))}}$ Correction for photon energy provides a final $B_A(\lambda)$ function (thick solid line) expressing sensitivity as a function of radiant flux (energy) as a function of wavelength. **C.** Normalised sensitivity to photon flux across wavelength for the three major types of plant photoreceptors; UVR8 (magenta), cryptochrome (as representative of flavoproteins, blue) and red-sensitive phytochrome (Pr, red). **D.** An integrated plant wavelength sensitivity function produced by adding sensitivity profiles in (A) across the visible range (thin dashed line) and final weighting for radiant flux as a function of wavelength, following correction for photon energy ($B_P(\lambda)$, thick solid line). **E**. Environmental sensitivity weighting function for all

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classes of organism produced by summing the sensitivity estimates for plants and animals (thin dashed line, sum of curves in **B** and **D** respectively) and correcting for photon energy to derive the final weighting for radiant flux as a function of wavelength ($B_E(\lambda)$, thick solid line).

The logistic function in Figure 2B aims to approximate the relative sensitivity of animals to photon flux (photons/s) as a function of wavelength. As physical light measurement technologies commonly measure radiant flux (units W), we present a final function (termed $B_A(\lambda)$) expressing spectral sensitivity as a function of radiant flux corrected to the wavelength-dependent photon energy (Figure 2B solid line; Supplementary Table 1).

Beyond animals, physiology of light detection become more diverse and there is at least as much difference across plants and micro-organisms as between these groups and animals. Although photosynthetic processes are common in these groups, the major detrimental light pollution impacts are likely photosensory in origin. It follows that these will originate from sensory photoreceptors (UVR8; blue-light receptive cryptochromes, phototropins, and related LOV and blue-light-utilising FAD domain receptors; and the biological inactive, Pr, form of phytochrome)[96,98–100]. These pigments show rather stable spectral dependent activation across many species (Figure 2C). Given how little is known about the relative importance of these diverse photoreceptor mechanisms as an origin for damaging effects of ALAN, attempts to account for them in light measurement carry a high level of uncertainty. Assuming equal weighting produces a function that defines the wavelengths of light that these groups of organisms may show high sensitivity to ($B_P(\lambda)$; Figure 2D).

The final, most difficult, challenge is to produce a single curve suitable for all organisms. In principle, this would be based upon a combination of $B_A(\lambda)$ and $B_p(\lambda)$. Simply summing them provides a function representing one approach to the biological sensitivity to light environment ($B_E(\lambda)$; Figure 2E). This definition of B_E provides responsiveness across the spectrum with bias towards shorter wavelengths, matching a reasonable qualitative summary of biological photodetection mechanisms. The implicit assumption, however, that each of the input photoreceptive mechanisms makes, on average, an equal contribution to damaging effects of ALAN is not based upon empirical evidence and may be regarded as unlikely. Applying different weightings to the four constituent curves (animal, UVR8, phytochrome and cryptochrome) reveals the extent to which such a composite curve is sensitive to assumptions regarding the relative importance of these photoreceptor classes to estimates of aggregate biological spectral sensitivity (Supplementary Figure 2). Thus, while $B_E(\lambda)$ may be regarded as a first attempt to encompass all biological photosensitivity, the degree of uncertainty in its derivation should be acknowledged.

Features and Applications

In principle, either of the functions $\underline{B_A(\lambda)}$ or $B_E(\lambda)$ presented above (or future modifications of them) can be applied to provide biologically relevant measures of light. For simplicity we show here how this may be achieved for the animal function, $B_A(\lambda)$, as this is probably of greatest relevance for current light pollution considerations. Applying $B_A(\lambda)$ as a weighting function to spectral power density measures and integrating across wavelength will return a quantity that may be termed 'Biological Irradiance' for animals ($E_{e,BA}$= W/ m^2; Figure 3A (Equation 1)). Thus, $E_{e,BA}$ represents an estimate of the effective irradiance for animals.

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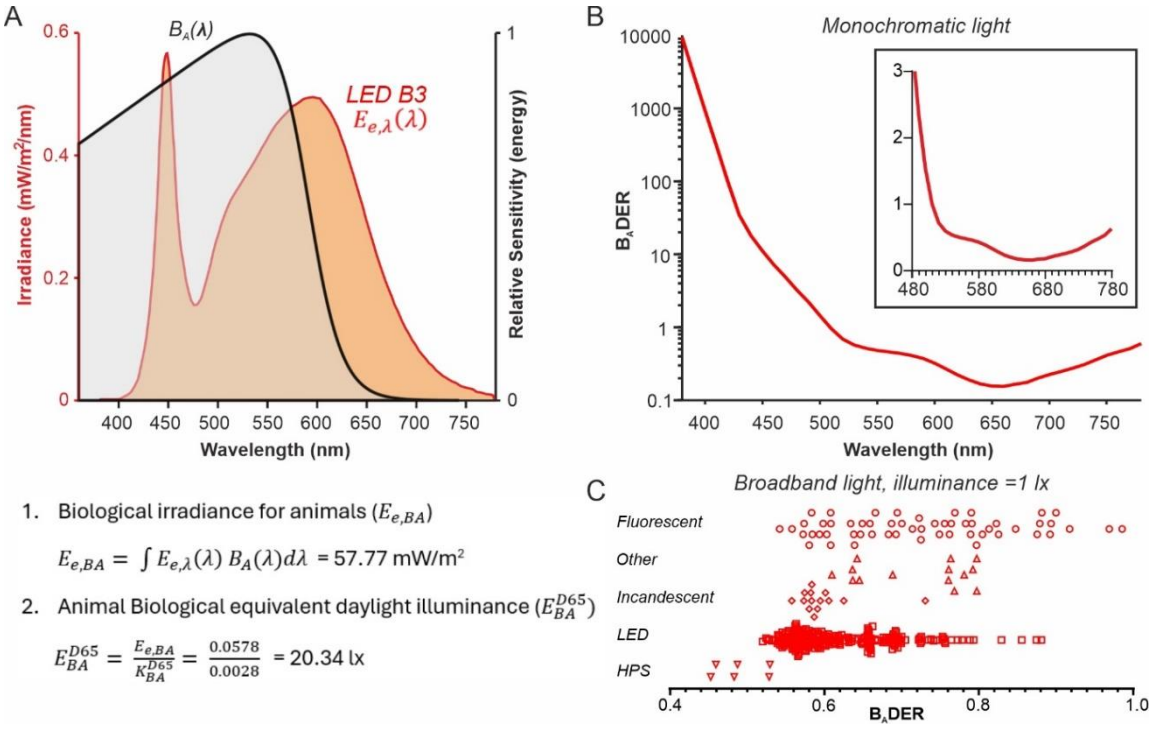

Figure 3. Calculating and applying biological irradiance. **A.** Spectral power distribution for a white LED source at 30 lx illuminance (orange curve) against $B_A(\lambda)$ (grey). Animal-specific biological irradiance for this light ($E_{e,BA}$: W/m²) can be calculated according to equation 1 by weighting spectral power distribution ($E_{e,\lambda}(\lambda)$) with $B_A(\lambda)$, and expressed as an equivalent daylight illuminance (E_{BA}^{D65}: lx) by correcting according to the polluting efficacy of luminous radiation for daylight (K_{BA}^{D65}; which is a constant equal to 2.8401 mW/lm, derived by weighting 1 lumen of daylight (D65) by $B_A(\lambda)$ and integrating across wavelengths) following equation 2. **B.** Animal-specific biological irradiance daylight efficacy ratio (B_ADER; the ratio of E_{BA}^{D65} to photopic illuminance) as a function of wavelength for monochromatic light plotted on a log scale (inset shows middle to long wavelength region on a linear scale). **C.** B_ADER for a range of standard incandescent (diamonds), broadband LED (squares), fluorescent (circles), high pressure sodium (HPS; inverted triangles) and other (triangles) sources[113] illustrates the scope for reducing biological irradiance by choosing the right source.

The CIE standard S026[66] introduced the concept of equivalent daylight illuminance (EDI) as a method of describing such irradiance measures in units that are more intuitive for many people. In brief, EDI quantifies light in terms of the illuminance of 'daylight' (in practice a CIE defined spectral power distribution called D65[101]) required to produce the target irradiance. A similar approach has been proposed for wildlife [24]. Equation 2 applies this to 'biological irradiance' to calculate biological EDI (E_{BA}^{D65} units = lx). In this way, a biological EDI of 1 lx signifies that the light being measured has the same 'biological irradiance' as daylight at illuminance of 1 lx.

A further application of such a spectral weighting function is to rank light sources according to their relative biological potency. Faced with a stipulation to achieve a particular (il)luminance, which light source can achieve this with lowest biological irradiance? The biological daylight equivalent methodology described above can be extended to any photometric unit (lux, lumens, candela, and the like). Dividing such measures by their corresponding photometric quantities then provides a straightforward measure of relative efficacy for biological detection (Biological (Animal) daylight efficacy ratio, B_ADER). High B_ADER is thus a feature of light sources producing high biological EDI for a given illuminance. The biological efficacy for nominal monochromatic sources (Figure 3B) confirms that longer wavelengths are favoured for minimising biological impact. This outcome is consistent with current pollution reduction advice to choose longer wavelength lights where possible [102–105].

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Metrics applying $B_A(\lambda)$ thus provide an opportunity to compare light environments and light sources quantitatively. From a lighting design perspective, by quantifying the potential benefits of spectrum engineering, it also reveals the limitations of that approach. Light across the visible spectrum contributes to biological irradiance, highlighting that there is no part of the spectrum that does not have the potential for biological impact. Across a range of standard 'white' light sources, biological efficacy for animals varies between 0.45 and 1 (Figure 3C), highlighting the benefits to be gained by choosing the right source but also the importance of minimising light irrespective of the source used.

We provide an online resource to calculate biological irradiance, biological EDI and biological daylight efficacy ratio from spectral power measurements (https://alphaopics.shinyapps.io/ecological_light_toolbox/). In due course it would be helpful to have devices that measure Biological Irradiance directly. $B_A(\lambda)$ is qualitatively consistent with the current advice for mitigating light pollution *viz* that light of any wavelength should be regarded as polluting but that light sources with less short wavelength are preferred[102–105] (but see also[106,107]). $B_A(\lambda)$ also produces values that are qualitatively consistent with other proposed metrics relevant for light pollution. Thus, across a bank of standard 'white' light sources, biological efficacy is strongly correlated with colour temperature, melanopic efficacy and starlight index[108] (Supplementary Figure 3A-C).

Concerns and Considerations

$B_A(\lambda)$ and $B_E(\lambda)$ represent attempts to provide evidence-based weighting functions for sensory detection of ALAN. Both the logic applied to producing these functions and the information upon which they are based are available for challenge and improvement. Nonetheless, any version of $B(\lambda)$ will be a catch-all and, as such, will provide an imperfect prediction of effective light dose for any single effect of ALAN. It follows that, where there are particular light pollution impacts to avoid, quantification should ideally employ a more specific wavelength sensitivity function matched to the relevant phenotypic action spectrum[25]. This could include cases in which a more precise description of light pollution spectral sensitivity is available (e.g. circadian and sleep disruption in humans) or where portions of the spectrum are known to have specific relevance (e.g. firefly courtship). Similarly, where empirical data exist regarding the best light sources for mitigating particular unwanted effects it may be sensible to apply that knowledge in lighting design even if it produces higher biological irradiance. These caveats notwithstanding, the principles underlying generation of $B(\lambda)$ should ensure reasonable outcomes for many polluting responses whose action spectrum is not exactly matched by that function. Thus, for example, although neither the green turtle nor dipteran attraction action spectra reproduced in Figure 1 are closely aligned to $B_A(\lambda)$, ranking light according to B_ADER represents a reasonable prediction of efficacy for eliciting either of these effects of pollution (Supplementary Figure 3E&F).

It may be appropriate to generate variants of $B(\lambda)$ functions according to the specific context of light exposure. That strategy has been adopted for $V(\lambda)$ where e.g. age-dependent corrections account for predictable changes in human spectral sensitivity. Similar wavelength-dependent correction factors may be applied to $B(\lambda)$ where concern is focussed on a particular group of species or to account for known biases in light propagation. In aquatic environments these could approximate filtering properties of the water column[109] and, on land, the wavelength dependence of skyglow[110]. There may be systematic differences in photosensory spectral sensitivity for animals in marine, freshwater, arid, arctic, tropical, alpine, rural, and suburban ecosystems, and according to season or other conditions. Higher light intensities engage different response systems, meaning that wavelength sensitivity may also differ depending on absolute light intensity. To ensure compatibility with any such refined versions of $B(\lambda)$ to appear in future, and allow ready conversion to photometric and radiometric measures, we recommend recording spectral power distribution whenever possible.

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Defining biological wavelength sensitivity from the properties of individual photoreceptors does not account for the possibility of spectral opponency ('colour vision') produced by antagonistic interactions downstream[111]. Provided that light levels fall between threshold and saturation points for the photoreceptors involved, the outcome of such spectral opponency is a product of spectrum but not intensity. Consequently, it does not fall within the scope of metrics such as Biological EDI that are designed to quantify effective intensity. Nevertheless, it is worth considering the extent to which such colour vision mechanisms may produce especial sensitivity to parts of the spectrum assigned low sensitivity in $B_A(\lambda)$. Lack of broad comparative quantifications makes it difficult to determine the degree to which colour vision would conflict with the $B_A(\lambda)$ function. Colour-opponent chromatic processing can roughly be described as the difference between two spectral inputs, and the range of hues depends on the total spectral range and the overlap between opponent channels. For human colour vision this means that we experience red between 620 and 750 nm although our red sensitive cones peak at 564 nm. For most other animals, this long wave shift is much smaller because the opponent overlap is smaller. It follows that most colour vision would produce sensitivity to parts of the spectrum already covered by the animal curve (Figure 2B) and further extension towards longer wavelengths would not change $B_A(\lambda)$ by very much.

The $B(\lambda)$ curves describe sensitivity to visible light (360nm to 800nm). Importantly, this does not imply that electromagnetic radiation outside this range is biologically inert. The DNA and protein damage potential of shorter wavelengths is reason enough to argue against their inadvertent release. Meanwhile as plants, microorganisms and animals can all display sensitivity to near and far infra-red radiation[82,83], the potential biological impact of longer wavelengths should receive separate consideration.

Conclusions

$B(\lambda)$ curves represent a best attempt to describe biological wavelength sensitivity. While certainly imperfect for any single damaging effect of ALAN they avoid the bias towards 555nm of $V(\lambda)$ and are based on the best currently available knowledge of biological photosensitivity. We argue therefore that they represent a useful spectral weighting function for measurement applications considering the biological impacts of ALAN. The biological irradiance metric can facilitate descriptions of the intensity dependence of responses to ALAN and be used to normalise intensity when exploring the effects of changing spectra. Data collected in such a way will be available for subsequent meta-analyses aimed at defining acceptable thresholds for ALAN and refining the $B(\lambda)$ functions.

Given the current focus of concern and regulation towards minimising effects on animals we anticipate that $B_A(\lambda)$ will be of greater immediate utility than $B_E(\lambda)$. $B_A(\lambda)$ also has the advantage of incorporating fewer extrapolations from known properties of biological photosensitivity than $B_E(\lambda)$ (in which the relative contribution of different photoreceptor classes to the combined function is arbitrarily defined). Nonetheless, we hope that our description of $B_E(\lambda)$ is a useful step in the process of also considering the contribution of plants and micro-organisms to detrimental effects of ALAN. Across a basket of 'white' light sources the biological daylight efficacy ratio for $B_E(\lambda)$ is positively correlated with that $B_A(\lambda)$ (Supplementary Figure 3D), highlighting that much of the wavelength bias of plants+microorganisms is accounted for by the animal function. The exception is at very long wavelengths in which the inclusion of phytochromes boosts sensitivity for $B_E(\lambda)$. Accordingly, accounting for plants and microorganisms in lighting designs aiming to minimise unwanted effects of ALAN may require applying an additional penalty to light sources with strong long wavelength output (Supp Figure 3). Further observational and interventional studies on all aspects of biological light pollution are required, but there is a particular need for more community ecology studies of all types, and particularly ones encompassing cross-species interactions considering plant-animal interactions, the role of ecosystem engineers/habitat formers, and the holobiont. We hope that those

 doi:10.20944/preprints202604.1368.v1

will be able to inform refinements to $B_E(\lambda)$ to the extent that it provides best possible predictions for ecosystem level impacts of ALAN and could eventually supercede $B_A(\lambda)$ as a tool for quantification.

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Conflicts of interest: RJL – none. TMB –none. GCB- has a current unlicensed patent (USPTO 7678140 B2). He has received research grant funding and equipment donations from PhotoPharmics Inc. and is a paid member of the PhotoPharmics Scientific Advisory Board. He is a Scholar and Consultant for the Nova Institute. AD-declares the following potential conflicts of interest in the past five years (2022–2026). Academic roles: Member of Joint Technical Committee 20 (JTC20) of the International Commission on Illumination (CIE); Division Reporter (DR6-50) of the International Commission on Illumination (CIE). DMD – none. KAF – none. KJG - serves as an uncompensated member of the board of directors of DarkSky International. PH – none. FH – none. AJ – none. EK – none. CK – dues paying member of DarkSky International, uncompensated member of CIE TC4-48 until 2021. TL – none. EM – none. D-EN – none. GO – none. NWR- none. BS – none. KS – serves as an uncompensated member of the expert team obtrusive lighting of the Dutch Light Science Foundation (NSVV). PT-is an employee of Thorn Lighting. RAH – none.

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