Ecological Aspects and Measurement of Anthropogenic Light at Night

Eric Abelson[1], Brett Seymoure[2], Andreas Jechow[3], Elizabeth K. Perkin[4], Hannah Moon[5], Christopher C. M. Kyba[6], Franz Hölker[7], Jeremy White[8], Travis Longcore[9]

Affiliations:

1 Department of Integrative Biology, University of Texas at Austin. Austin, TX 78712 USA
2 Department of Biological Sciences, University of Texas at El Paso. El Paso, TX 79968 USA
3 Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), 12587. Berlin, Germany
4 Native Fish Society. Oregon City, OR 97045 USA
5 Department of Biology, University of Hawaiʻi at Mānoa. Honolulu, HI 96822 USA
6 GFZ German Research Centre for Geosciences, Potsdam, 14473 Germany & Ruhr Universität Bochum, Bochum, 44780, Germany
7 Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany & Institute of Biology, Freie Universität Berlin, Berlin, Germany
8 U.S. National Park Service, Fort Collins, CO 80525 USA
9 UCLA Institute of the Environment and Sustainability. Los Angeles, CA 90095 USA

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Correspondence: Eric Abelson. abelson@alumni.stanford.edu. 2415 Speedway, stop C0930, Austin, TX 78712.

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Abstract

Anthropogenic light at night (ALAN) has pervasive ecological effects on species, habitats, and ecosystems. Research into the impact of ALAN has increased dramatically in the past decade, however, we find (through a literature review of 341 publications) a troubling lack of consistency and conceptual organization in the measurement of night-time light and related organismal responses. To address this, we propose a holistic framework that considers space, time, taxonomic uniqueness, and the physics of light. Principally, we suggest that light measurements should both match the mechanism of influence and the unique photoreceptor system of the organism being studied. Anthropogenic light at night is continuing to increase globally, as are its impacts on organisms and biodiversity (from genes to ecosystems). A measurement framework for disentangling the loss of natural night-time darkness and disruption of ecological systems provides a deeper insight into the nature of these relationships and is important for establishing paths forward in the face of intensifying global change.

Introduction: Anthropogenic light at night (ALAN) disrupts natural systems

Human created lighting technologies have vastly changed when and where **light**[1] is found, resulting in increasingly prevalent light at night. Anthropogenic light at night (ALAN) is an environmental pollutant with wide-ranging impacts on organismal physiology, behavior, and interactions. (Longcore & Rich 2004; Sanders *et al.* 2021). In the face of increasing ALAN and global loss of night-time darkness (Falchi *et al.* 2016; Kyba *et al.* 2017), additional understanding of the effects of ALAN are needed (Gaston *et al.* 2015). Interest in the emergent ecological effects of ALAN on species, habitats, and ecosystems has increased dramatically in the past decade. However, rapid growth in this interdisciplinary field has resulted in uncoordinated methods and metrics for studying light in ecological contexts (Hölker *et al.* 2021).

Research into organismal response to ALAN ideally starts by measuring the biochemical or physiological response of an organism to light directly (e.g., using in vivo electrodes that record nerve responses to highly controlled light stimuli). However, this is generally not possible in the scope of most ecological studies. Instead, ALAN research often uses measurements of environmental light in areas surrounding study

[1] We use the term *light* here to refer to the portion of the electromagnetic spectrum with wavelengths ranging from ultraviolet to infrared. There are many fields with specific terms describing light (e.g., lighting engineers use “intensity” to refer to radiant intensity, W/sr, while for the layperson “intensity” is a general unitless term indicating a range from dim to bright). We aim to strike a balance of using terms that will be understood by a broad, non-technical, audience – for example, we use *amount* to approximate what may colloquially be called *intensity* or *brightness*. Additionally, this manuscript is written with the perspective that *light* is sensed by *photoreceptors* that are stimulated by photons with a distinction being made between the perception of light vs heat receptors as exemplified by pit vipers (Crotalinae), boas (Boidae), pythons (Pythonidae) and ticks (Acari).

organisms as a proxy for organism-level physiological responses. Proxy measurements are then used to address ecological questions in diverse disciplines ranging from cellular to behavioral biology. Characterizing the amount of light, its temporal variation, spatial distribution, and spectral composition are important and influence species differently (Jechow *et al.* 2019; Dominoni *et al.* 2020a; Kalinkat *et al.* 2021). Unfortunately, selecting appropriate metrics for light measurement is not simple, either conceptually or methodologically. With increasing levels of ALAN worldwide, and concomitant increases in research on the effects of ALAN on ecological systems, it is urgent to unify the discipline under a conceptual umbrella.

After a review of literature investigating the impacts of ALAN on organisms, we find a concerning use of ill-suited metrics and a lack of consistency in the measurement and reporting of night-time light conditions. These methodological choices, in turn, reduce the ability to directly tie light measurements to organismal behavior and physiology. We aim to provide guidance on best practices and advocate for increased standardization of light measurement and reporting in ALAN research.

Organisms rely on their sensory organs to develop an awareness of their surroundings (Dominoni *et al.* 2020a). Studies examining response to environmental characteristics should therefore consider taxa-specific sensory abilities. Unfortunately, the diversity of species' sensory perception has been poorly represented in prior ALAN research as evidenced by the abundance of studies using light metrics tuned to human visual systems. Because the human visual system differs greatly from many non-human organisms, human-centric metrics alone may not be appropriate to measure light that drives physiological and behavioral responses of other organisms (Seymoure *et al.* 2019b). For example, moths exhibit behaviors in response to ultraviolet light which are **wavelengths** of light that humans cannot see (van Langevelde *et al.* 2011; Donners *et al.* 2018; Seymoure *et al.* 2019b). We suggest using metrics that are inclusive of the full diversity of life and not limited to light as perceived by human visual systems[2].

We propose that it is critical to consider multiple characteristics of light environments, (e.g., those discussed in this manuscript) when examining light's ecological, behavioral, or physiological effects on organisms. Prior research has provided important insights into the serious effects of ALAN on organisms (Grubisic *et al.* 2019; Falcón *et al.* 2020; Sanders *et al.* 2021). Future research can build upon past work by employing well considered study design, implementation, interpretation, and reporting (informed by the physics of light and taxonomically appropriate lightscape characteristics) to provide additional clarity in understanding the effects of ALAN on organisms. Using standardized and rigorous metrics will additionally yield research that is well suited for future meta-analyses, reviews, and other work that synthesizes studies to inform policy and conservation efforts.

We aim to establish a conceptual framework that clearly delineates the main aspects of light ecological systems. We hope future manuscripts will address related

[2] That said, we find value in concurrently reporting data in human-centric metrics (i.e., photometric units) to communicate results to the broadest audience possible (e.g., lighting engineers, decision makers) as well as to compare across previous studies (Pérez Vega *et al.* 2022).

methodological considerations including the myriad of light measurement units and the equipment best suited to quantifying light in ecological settings. We first establish the tremendous variation in how light has been measured in past research as a tangible example of the need for a unifying conceptual framework. We then identify four main topics that should be considered in understanding the effects of ALAN on organisms. Finally, we present real-world examples and guidance for implementing ALAN research in, and addressing the unique challenges posed by, ecological systems.

Inconsistent light metrics and reporting: a review.

In prior ALAN research, a highly variable set of light metrics have been applied to understanding ecological systems. This is not surprising because there are many different aspects of light relevant to organisms and numerous different light metrics. Adding additional complexity is that correctly choosing and taking light measurements can require an advanced understanding of physics. It is commonplace for suboptimal metrics of light to be employed – worse still, many studies do not provide any quantifiable metric of light in the study system at all.

We reviewed 341 publications examining the effects of light pollution on organisms to assess light metrics used in ALAN studies (additional details, methodology, and data, can be found in Supplemental Information 1 & 2). Through reviewing these research manuscripts, we found troubling trends in methods in which light is measured, reported, and linked to species' responses. Commonly used approaches reflect deficiencies in study design, which could lead to challenges with replication, and the possibility of missing significant ecological effects. We discuss three important trends below.

First, 29% of studies (n=98) did not report *any* metric of light; employing vague descriptions such as “lights were present” (Figure 1). This is problematic because there is tremendous variability in light sources which differ in amount of light and its spatial distribution, wavelength and **flicker** (Kalinkat *et al.* 2021). Important ecological effects can be linked to one light source but not to another (Witherington & Bjorndal 1991; Cruz *et al.* 2018) and different organisms may have unique responses to the same light source (Lewanzik & Voigt 2017; van Grunsven *et al.* 2019) (Figure 2). If light is not sufficiently quantified in a study system, it is difficult to interpret results across systems, and the resulting study may not be reproducible.

Second, of those studies that reported quantitative metrics of light, most used human-centric metrics that do not match the study species’ unique responsivity to light. For example, 61% (208) of studies reported only **illuminance**, a human-centric metric of **irradiance**.

Finally, in our review, we find that data from readily available light measuring devices (i.e., inexpensive **lux** meters designed for testing light levels in human industrial work settings) are often inappropriately interpreted in ecological studies (Longcore & Rich 2004; Aulsebrook *et al.* 2022). Aside from reporting human-centric light metrics (e.g., illuminance), these devices frequently have poor sensitivity (e.g., minimum reported value of 0.1 lx) below which light levels are not measured, but simply reported as 0 lx; unfortunately, these 0 lx values have been mistakenly interpreted as meaning "no light". This is especially problematic because, in many cases, light levels below 0.1 lx are biologically relevant across biological and ecological systems (Biberman *et al.* 1966; Duriscoe 2016; Grubisic *et al.* 2019; Seymoure *et al.* 2019a). For example, there are critical ecological differences between nighttime light levels of under 0.001 lux from a clear starry sky and 0.05 lx from a gibbous moon, yet these differences are indistinguishable to many commercial lux meters, and both might incorrectly be reported as 0 lx.

Ecologically relevant aspects of light

A complete review of the relevant physics of light is beyond the scope of this manuscript (see Johnsen 2012 for an excellent introduction to the study of light for biologists). Here, we focus on key aspects of light that are essential for performing ecological studies. Unlike other familiar measures (e.g., temperature, mass, distance), humans are not able to accurately estimate light exposure. This is because 1) our visual system is non-linear and allows for vision over many orders of magnitude in amount of light, 2) the perception of light wavelengths (e.g., colors) is limited by human physiology, and 3) the brightness perception is not constant across the **spectrum** (such that it may require far more photons of one color to appear as "bright" as a different color). Perhaps because measuring light is often not intuitive, many light quantification approaches are misused and/or misinterpreted (Johnsen 2012; Aulsebrook *et al.* 2022); to address this, we aim to provide a broad overview of light aspects especially relevant to ALAN impacts on ecological systems.

Because it is generally impractical to directly measure physiological response to light or to collect all light information from a setting in a profoundly granular way, proxies must be sought that balance necessary trade-offs due to cost, time, and available technology. Some ecological research questions addressing ALAN can be achieved by broad/general metrics while others require more nuanced techniques. Regardless, compromises are often made when selecting metrics of light in ecological studies (e.g., greater spatial coverage over accuracy) with the goal of serving as a proxy for what organisms perceive. Each light source (e.g., light from a streetlight) and environment (e.g., the night-time environment of a mountain lion with **skyglow** from a nearby city) has unique attributes that include its spectrum, spatial distribution, temporal dynamics (e.g., seasonal variation), and **polarization**. After identifying the aspects of light that are appropriate to the visual system of the study organism, measurable proxies can be selected.

Identifying optimal proxies of light is difficult. Making the process more difficult is that light metrics are not familiar to many people; for example, the use of spectrally resolved versus spectrally **integrated light metrics** has been ill defined in the existing body of ALAN literature. We aim to clarify many of these topic areas; in the following sections we address four axes of interest for biological research: measurement of radiation, taxonomically relevant light metrics, temporal variation, and spatial considerations.

Measurement of radiation (polarization, radiance, and irradiance)

Polarization

Though the polarization of light is not generally visible to humans, and therefore is a light property that can be hard to grasp for humans, many other animals can perceive it (Horváth 2014). Unpolarized light oscillates in all possible planes equally, while linearly polarized light only oscillates on one plane (Figure 4). Most light sources, including the sun and incandescent lights, produce light that is not polarized. However, light can become polarized by scattering from molecules or when being reflected at some surfaces (for example the air-water interface). The ability to perceive polarized light has been documented in zooplankton, arthropods and fish (Cronin *et al.* 2014) and, for these species, polarized light provides important information. Not all surfaces polarize light, and those that do, such as water, provide information that alter and guide organism behavior. Therefore, polarization can be an important aspect of light for ecological research (see Horváth *et al.* 2009; Johnsen 2012 for full reviews).

In anthropogenic landscapes, polarized light pollution from reflection from human-made structures (e.g., asphalt, plastic, photovoltaic panels) can alter the landscape as it is perceived by organisms and result in the disruption of responses and natural processes (Horváth *et al.* 2009). For example, in natural environments, mayflies (Ephemeroptera) identify and lay eggs on the surface of waterbodies which are unique in the way they polarize reflected light. However, in anthropogenic landscapes, mayflies lay eggs on an asphalt roads which are perceived to be similar to water in the way they polarize reflected light (Horváth *et al.* 2014) (Figure 4).

Additionally, polarized light in the night sky is washed out and disappears as night-time light pollution (i.e., skyglow) increases (Kyba *et al.* 2011). Polarized light has been shown to influence zooplankton movement (Horváth & Varjú 2004), and arthropods, birds, and bats can use polarized light as a cue for flight orientation (Horváth & Varjú 2004; Horváth *et al.* 2009; Greif *et al.* 2014) and navigation during foraging (Dacke *et al.* 1999). Although humans cannot perceive the polarization of light, it is a critical aspect of light to consider when designing ALAN studies.

Radiance and irradiance

Spatially, light sensors range from devices that measure light from every direction around the sensor to being restricted to a small part of a field of view. In practice, three principal cases are most often used: 1) **scalar irradiance** (also called spherical irradiance) is the amount of light hitting the sensor, with light from all directions weighted equally[3]. 2) **Planar irradiance** (also called vector irradiance) is the amount of light across an entire hemisphere detected by a flat sensor[4] (SI1, Figure S1). While the term "vector" irradiance has a long history in ecological literature, it has different meanings in physics; to avoid potential confusion we use planar irradiance when referencing to irradiance that is measured with a planar instrument. 3) **radiance** usually (but not

[3] Scalar irradiance is almost impossible to measure perfectly as spherical scalar irradiance sensors have a blind spot that results from an optical fiber transmitting the signal to a spectroradiometer (picture a ping pong ball like sensor that has a small cable attached to it).

[4] Flat sensors that measure planar irradiance weight light according to a cosine: light shining directly on to them is weighted most strongly, and light shining horizontally does not contribute at all. Additionally, the study of light involves many disciplines (e.g., physics, astronomy, biology) and each have their own norms and definitions of terms. Here we use the norms of biological and ecological approaches in defining spherical/scalar and planar/vector irradiance.

necessarily) measures light arriving from a small field of view[5] (see Supplemental Information 1 for more details).

To give an intuitive picture of the difference between planar irradiance, scalar irradiance, and radiance, imagine standing in a field on a clear night with a full moon well above the horizon and stars visible. The stars and moon are visible to you because they have a different radiance from that of the night sky. Radiance is the light passing through (or falling on) a defined area (e.g., an observer's pupil) from a specific range of directions (e.g., the part of the sky where you see the moon). The total amount of light falling on a flat surface is called planar irradiance. As the moon rises even higher in the sky, its brightness (radiance) will appear almost the same to you, but the amount of light falling on the ground (planar irradiance) will increase. The brightness (radiance) of reflected light from the ground will increase in the same proportion. The distinction between these metrics is important, as biological processes may be more influenced by one than the other and they are not always correlated (Figure 3).

In biology, planar irradiance is usually measured with a flat or near-flat detector. Such a detector is most sensitive to light that arrives at an angle perpendicular to its surface. This can occasionally be problematic for biological measurements, since in some cases a large fraction of the overall light can come from sidewards directions (e.g., underwater, especially in turbid environments). For this reason, sensors that measure

[5] Technically, radiance is the radiant flux (given in number of photons per second or in W) per unit area and unit solid angle (steradians). The unit of radiance is W/m^2sr. Both scalar and planar irradiance is the radiant flux incident on an area with the unit W/m^2. Also, please note that angle of incidence is critically important for planar irradiance (SI 1).

scalar irradiance have been developed. Scalar irradiance detectors differ from planar irradiance detectors in that they have equal sensitivity to light coming from all directions.

Pragmatically, radiance reports the amount of light that shines on an object from a particular direction while scalar irradiance ignores direction altogether. Planar irradiance strikes a balance between radiance and scalar irradiance by considering light broadly across an entire hemisphere. The decision between whether to use irradiance or radiance is based on the unique goals of a given research project. Radiance measures a specific light source or how lights are distributed. For example, radiance can provide information on **glare** in a scene or **contrast** of a butterfly wing. If all light in the environment (regardless of orientation or perspective) is to be considered, then scalar irradiance is likely the best metric. For example, scalar irradiance can provide insights into the amount of light falling on all the **photoreceptors** of a baby bird in its nest that are relevant to its circadian rhythms. Finally, if light from a hemispherical area (and the corresponding orientation or perspective) is important, then planar irradiance is generally most appropriate (Table 1-2).

Measurements of planar irradiance can be taken in any orientation, but there are two commonly used cases: 1) **horizontal irradiance** (sometimes also **downwelling irradiance**); and 2) vertical planar irradiance (sometimes referred to as sidewelling irradiance). The difference between the two depends on the orientation of the flat sensor. Horizontal planar irradiance measures light falling onto a horizontal surface (i.e., the ground) whereas vertical planar irradiance is light falling onto a vertical surface (e.g., the side of a tree trunk). Often, the term “irradiance” is used ambiguously when horizontal planar irradiance is meant. Ultimately, planar irradiance, scalar irradiance, and radiance each measure distinct aspects of the light environment and are useful depending on the ecological question (see Figure 3).

Photometric units: radiance and irradiance vs. luminance and illuminance

Light is a small subset of electromagnetic radiation and is most commonly defined based on the daytime vision of humans to include wavelengths between ~390 nm (seen by humans as the color violet), and ~750 nm (seen by humans as the color red), with a spectral weighting that peaks at 555 nm (seen as green to humans) (Figure 2) (Taylor 2001; Bureau International des Poids et Mesures 2019). Metrics of measuring the amount of light, as perceived by a human observer, are called **photometric**.

While, in theory, radiance and irradiance consider all measured wavelengths of light equally, their photometric analogues, **luminance** and illuminance, use wavelength weighting based on human vision (Figure 2)[6]. For example, a 650 nm light source would have a lower luminance value compared to the luminance of a 550 nm light source with the same radiance (650 nm is downweighted since the human eye doesn't respond strongly at 650 nm compared to 550 nm). Similarly, an ultraviolet light source emitting at near 300 nm has a luminance of zero, regardless of how radiant it is (because 300 nm ultraviolet radiation is not perceived by the human visual system).

[6] For both luminance and illuminance, radiant flux (in W or photons/s) is substituted by the luminous flux (given in lm – lumen), which is simply radiant flux referenced to what is perceived by the human visual system. Luminance is the luminous flux per unit solid angle and unit area, given in lm/m^2sr (instead of W/m^2sr), which is rewritten to cd/m^2 (because 1cd = 1 lm/sr). Illuminance is the luminous flux per unit area, given in lm/m^2 (instead of W/m^2), which is rewritten to lux (lx).

The geometric variations of irradiance (i.e., planar, scalar) can be applied to illuminance.

Despite the prevalence of photometric tools and the widespread use of photometric quantities in the existing literature, we urge researchers to not solely employ and report human-centric definitions and metrics of light to address ecological impacts of ALAN. Light that is relevant to non-human species 1) may include a different set of wavelengths (Hárosi 1994; Rai *et al.* 2020; Musilova *et al.* 2021), 2) may have different brightness (the same amount of light at a particular wavelength may appear dim to an individual of one species while appearing bright to an individual of a different species), and 3) is not limited to visual systems (e.g., circadian photoentrainment and plant physiology). See *taxonomically relevant light metrics* section for ways in which human-biased definitions lead ecological studies astray).

Converting between light metrics

Generally, converting between spatially different light metrics like radiance, scalar irradiance, and planar irradiance is impossible because the three-dimensional light field is not spatially homogeneous (see Supplemental Information 1 for more detail). Similarly, while sometimes correlated (e.g., the radiance of an overcast sky and the resulting downwelling planar irradiance on the ground; Figure 2), it is not functionally possible in ecological contexts to convert between scalar and planar irradiance nor between horizontal and vertical irradiance. Adding complexity is that the distance and medium (e.g., air with fog, turbid water) between a light source and a light meter can influence different metrics in unique ways and compounds difficulty in converting between metrics. We recommend collecting light data that is generalized rather than specialized; for example, converting spectrally-resolved radiance to the human-specific luminance is straightforward (while the reverse is generally not possible).

Taxonomically relevant light metrics

Most animals possess photoreceptors with varying sensitivities at different wavelengths. In existing ALAN literature, the relationship between spectral composition of a light environment and the spectral sensitivity of an organism's photoreceptors is often neglected, and there is a corresponding lack of spectrally resolved (i.e., amount of light per wavelength) light measurements. In this section we encourage collecting light data that matches the unique photoreceptors of study organisms.

Assessing light in energy flux (watts) or photon flux (photon quantity)

Light can be described as electromagnetic waves (e.g., measured as energy flux in Watts (W)) and/or as a stream of photons (photon flux in photons per second)[7]. Photon energy is inversely proportional to its wavelength; for example, 1 W (**watt)** of 390 nm light will have *half* the number of photons as 1 W of 780 nm light. As a result, metrics of energy flux do not intuitively correlate to metrics of photon flux, particularly for a specific spectrum of light. This complicates measuring the effects of ALAN on ecological systems because photoreceptors (e.g., eyes) detect photons (i.e., photon flux), not energy. Thus, we suggest converting light measurements from energy flux (the likely output of a spectroradiometer) to photon flux to be consistent with units that are central

[7] Each photon carries a specific energy tied to its wavelength ($E=hc/\lambda$, where is h is Planck's constant, c is the speed of light, and λ is wavelength). It is possible to convert all energy units in photons if the wavelength is known. For example, 1 W of photons at 500 nm is approximately 2.5 x 10^18 photons per second.

to visual processing (see Johnsen 2012 for details). We also suggest that reporting measurements in both energy flux and photon flux can make results accessible to all disciplines interested in light at night (e.g., both lighting engineers and ecologists).

Characterizing the range of perceptible wavelengths

Though "light" is often defined as electromagnetic radiation visible to *humans*, (wavelengths from ~400 nm to ~700 nm), each species can perceive its own unique range of wavelengths that may include ultraviolet radiation (UV; < 390 nm) and infrared radiation (IR; >780 nm) (Cronin *et al.* 2014). Consequently, light measurements for ecology should not be restricted to the spectrum visible to *Homo sapiens* and instead should include all wavelengths relevant to the target species' sensory capacity. Furthermore, not all wavelengths perceived by an organism are processed equally. For example, humans are considerably more sensitive to wavelengths near 555nm than to wavelengths around 650 nm (Figure 2). As a result, many common metrics of light are not only biased toward human vision in terms of the range of wavelengths, but also in the weighting of the wavelengths that fall within that range (i.e., following a human-specific **spectral response curve**). Ideal light measurements include wavelengths, and corresponding sensitivities to those wavelengths, which are relevant to a given study species. Where possible, taxon-specific spectral response curves should be used to transform available light into a metric representing what target organisms perceive (see e.g., Longcore et al. 2018). This means that measuring light as spectrally resolved radiance or irradiance, which can be later converted to one or more species-specific metrics, is preferred over measuring light with tools that have built-in taxon-specific weightings (e.g., lux for humans, clux for chickens (Prescott & Wathes 1999) or PAR (photosynthetically active radiation) for plants.

Wavelength weighting and integrated metrics

Thorough quantification of light requires measuring the number of photons per wavelength. One approach is to measure the number of photos across one nanometer wide bands; however, this is more precise than needed for most biological questions. Another approach is the use of *integrated* and *weighted* units, which sum all photons within a specific spectrum (e.g., 400 through 700 nm) and thus have little wavelength information. Integrated units are aptly named as they result from taking the integral of the spectral curve across a range of wavelengths. However, most integrated units have the spectral curve weighted by a species-specific spectral sensitivity (e.g., human photopic visual system for lux) (Figure 2; spectral response curve; Supplemental Information 1). Although there are rare cases where collected light data will *only* be used for the species the integrated metric was designed for, we suggest that spectral measurements should be preferentially used over integrated metrics because spectrally resolved data can be converted to (one or many) integrated metrics and can be expanded upon in future studies. However, we do realize that currently the technology for automated measurements of full **spectra** in dim light is lacking, and to measure light at night across time, one is likely forced to use equipment that integrates the spectrum (i.e., luxmeters). In this scenario, we highly encourage researchers to also measure spectral samples across time to complement the numerous integrated measurements.

(Mis)use of human-based, photometric, light metrics

Given the complexity of visual systems held by life on earth, a single metric for all taxa doesn't exist and recording only integrated measurements has several serious disadvantages. The first problem is that, although spectral metrics can be converted into integrated metrics, integrated metrics themselves cannot be converted to other integrated metrics (unless spectral information was also collected), nor can underlying spectra be identified.

A related concern in ALAN research is the prevalent use of (inexpensive) photometric measurement tools that do not report spectrum or represent the visual capacity of studied species. For example, the ultraviolet "bull's-eye" pattern on some flowers may communicate the presence of pollen to some species (e.g., pollinators) while being completely invisible to other species (Papiorek *et al.* 2016). In the same way that photometric tools cannot capture the ultraviolet world of bees, research that relies on photometric tools could easily result in misinterpreting a light-scape or the wholesale exclusion of salient environmental characteristics.

It is worth repeating that many (often inexpensive) photometric (wavelength weighting and integrating) measurement tools have insufficient intensity sensitivity and measurement thresholds (e.g., values below 0.1 lux are reported as 0 lux) for measuring ALAN. Unfortunately, most light meters report values of zero when the light values are less than the equipment's lowest threshold (e.g., values below 0.1 lux are reported as 0 lux). Many nocturnal species can see in conditions with many orders of magnitude less light than these devices are capable of recording (see Aulsebrook et al. 2022), and thus stating that the environmental light condition is 0 is not only wrong, but it is misleading with regards to the biological effects of low light levels.

Temporal variation

Variability of light over time is ecologically important and occurs at a range of temporal scales. While the most intuitive, ecologically relevant, temporal change in light occurs between day and night, there are other changes in the lightscape ranging from milliseconds (e.g., the flicker of a light source) to years (e.g., increasing ALAN from expanding urban areas). Further, as variation in light amount changes over time, there is often a concomitant change in spectral composition (e.g., twilight vs. starlight, ALAN as human-made lights switch on or off over time).

Short (sub-second) temporal variation - flicker

Some ALAN sources flicker: they quickly turn on and off, or dim and brighten, many times per second. While humans are intuitively familiar with light changes across days and seasons, we typically do not have regular experiences with flicker because lamps are designed to flicker at a frequency that is imperceptible to most humans. Flicker that is faster than a species-specific frequency, called the critical fusion frequency (CFF; measured in Hz – the number of times per second a light flickers) cannot be resolved by the visual system and appears constant (Rider *et al.* 2021). While the CFF for humans is typically 50-70 Hz (Rider *et al.* 2021), CFFs across Animalia range from less than 10 Hz in some amphibians to 400 Hz in some insects (Inger *et al.* 2014). It is also important to note that CFF may also be wavelength dependent (Hecht & Shlaer 1936; Rubene *et al.* 2010; Skorupski & Chittka 2010).

To explore the perception of flicker, imagine a bird and a human watching a 60 FPS (frames per second) video; the human (with a CFF of ~50 Hz) would observe continuous motion while a pigeon (CFF of ~100) would see flashes of individual images with periods of darkness in between. The importance of flicker depends on phenomena of interest, the CFF of the organism being studied, and the light sources in the study area (Figure 5). For example, organisms have been found to alter movement behavior not only based on flicker rates but also simply on the very presence of flicker (Barroso *et al.* 2017). Flicker can also have non-visual physiological effects including increased stress, eyestrain, and headaches (Berman *et al.* 1991; Morgan & Tromborg 2007; Wilkins *et al.* 2010).

Intermediate temporal variation – minutes to days

Light in nature may vary by many orders of magnitude throughout a 24-hour period ranging from bright sunny days (approximately 100,000 lx in photometric units) to dark cloudy nights without anthropogenic light (approximately 0.0001 lx in photometric units) (Hänel *et al.* 2018). While variation through daylight hours influences diurnal organisms (e.g., plant photosynthesis), variation in the timing of light ranging from minutes (e.g., changing cloud cover) to weeks also plays a pivotal role in the physiology and ecology of organisms.

ALAN extends the timing of light beyond dusk and, concomitantly, studies find diurnal wildlife extending their hours of activity (Sanders *et al.* 2021). For example, diurnal geckos have been observed foraging into night-time hours near electric lights (Baxter-Gilbert *et al.* 2021). By staying active "past their bedtime," these geckos exploit a rich nocturnal insect fauna attracted to lights with the potential effects of decimating populations of insects and increased competition for nocturnal insectivores. Natural sources of nocturnal light also vary across intermediate time scales. Differences in moon elevation and moon phases have been found to alter wildlife behavior including the alteration of hunting behavior (Palmer *et al.* 2017), correlated mate finding with moon elevation (Storms *et al.* 2022), the triggering of mass spawning events (Kaniewska *et al.* 2015) and fluctuations in movement activities across roads (and related wildlife-vehicle collisions) (Mestre *et al.* 2019).

Long temporal variation - monthly, seasonally, and annually

In addition to sub-second and sub-month light variation, light also changes across months, seasons, and years (both naturally and due to anthropogenic activities). Due to ALAN, night-time environments are increasingly getting brighter and lit areas are growing globally (Kyba *et al.* 2017). One important, naturally occurring, and well-studied example of longer-term temporal variation is photoperiod (i.e., the ratio of light to dark throughout the 24-hour day). Photoperiod changes naturally across the year, varies strongly by latitude, and serves as an indication of the season for an organism's timing of activities including mating, migration, and senescence; ALAN has potential to interfere with the timing of these behaviors (Bradshaw & Holzapfel 2007; Robert *et al.*

2015). Because ALAN has been both spatially and temporally variable, researchers may need to consider how night-time light levels have changed over years and/or decades.

Spatial considerations

Spatial arrangement of light sources across a landscape can be considered in four main ways:

1) *Locations of light sources across three-dimensional space*: light sources, and their arrangement across space, impact the lightscape both directly as point-like sources (e.g., streetlights, gas flares, full moon) and indirectly (e.g., skyglow). For example, individual, or clusters, of light sources can be used to aid navigation (Dacke *et al.* 2013) acting as a reference or beacon.

2) *Distance between an observer and each light source*: The distance between light sources and an organism influences the role they play on the perceived lightscape (Land & Nilsson 2012). For example, while light from distant sources can serve as a spatial reference, light from nearby sources can be more important for influencing contrast and the ability of an organism to detect objects (e.g., prey, predators).

3) *Medium between observer and light source(s)*: The medium in which light is propagating (e.g., air, water) and conditions (e.g., fog, atmospheric dust), between the light source and observer further modifies the light field (e.g., via absorption, scattering).

Each medium inherently has unique characteristics to consider such that, when measuring ALAN, one must also account for prevailing conditions (e.g., turbid vs. clear water) (Hänel *et al.* 2018; Grubisic *et al.* 2019; Jechow & Hölker 2019).

4) *Relative movement of the observer over time*: the prior three characteristics change over time due to the movement of an observer and/or light sources. For example, the movement of an organism using distant light clusters to aid in navigation (Warrant & Dacke 2010) will experience shifts in the prior three light attributes; appropriate study design in such cases likely require spatial light aspects to be measured at multiple locations along the path of travel for the organism of interest.

Emergent effects of light distribution include glare and contrast. Glare causes a reduction in visual capacity in the presence of an intense light source against a comparatively dark background, like the passing headlights of an oncoming vehicle at night (Reeves *et al.* 2018). When contrast is too large, it can become difficult or impossible to distinguish between objects, once easily visible, in the dimmer parts of the **viewshed**. Further, animals with low acuity and/or slow flicker fusion may take longer to recover from blinding by a light point source (Kimlin *et al.* 2017). Unsurprisingly, ALAN affects visual contrast in many ecological important ways including, for example, the inability to orient or being unable identify a nearby predator (Tuxbury & Salmon 2005).

Ecologically relevant metrics for light at night

Ideally, direct neurological or physiological measurements would be taken to assess organismal response to ALAN. Given that this is nearly impossible in all but the rarest of study designs, researchers are left with identifying light measurements that best serve as proxies. Optimally, full spectral radiance from every direction would be recorded at high spatial and temporal resolution, along with the orientation of study organism receptors; however, this is impractical. Instead, there are necessary tradeoffs and (often difficult) decisions must be made to identify the most appropriate light metric that can serve as a proxy. In this section we transition from conceptual aspects of light measurement to a discussion of implementation, providing pragmatic examples of how light measuring approaches and metrics can be applied to assessing the effects of light on ecological systems (detailed questions, example mechanisms, and example measurement approaches can be found in Table 2).

Impacts of ALAN on organisms often fall in two general categories: physiological and behavioral. It is important to re-emphasize that research examining the ecological effects of ALAN is best served when considering possible mechanisms of behavioral and physiological responses of interest. For example, comprehensive metrics of light may be appropriate for gross primary production of a grassy field while behaviors such as mate choice, relying on multiple photoreceptors that are context dependent, require more sophisticated light assessments. Any measurement approach short of measuring the spectral radiance of all light in all directions at all times (along with the orientation of the study organism) is a compromise; correspondingly, different questions will have different appropriate compromises.

Measuring irradiance at the location of a subject is usually sufficient to evaluate physiological responses. It is generally impossible to know what direction organismal photoreceptors will be facing except in the most general sense, so resolving detailed radiance maps is unnecessary and the use of planar or scalar irradiance can approximate exposure. Most physiological responses such as melatonin suppression, gene expression, and phenology involve systems that have specific spectral sensitivity and therefore spectrally resolved metrics are important.

Positive and negative phototaxis and wayfinding are most likely to be associated with radiance. Movements involving either instinctual attraction/repulsion, deliberate wayfinding, or orientation are often in response to the brightness and contrast of light points in the field-of-view. Radiance maps (i.e., photographs) documenting the spatial distribution, contrast, and spectral distribution of light sources are more likely to be explanatory than measures of irradiance in these situations. Because irradiance metrics integrate light across a large area, they are not well suited for many questions addressing behaviors such as orientation or wayfinding. However, some taxonomic groups lack the visual resolution to resolve individual light sources and, for these taxa, measuring spectral irradiance is reasonable. For example, planar irradiance, taken at different orientations, may be informative if the study species moves along light gradients as opposed to in response to a visual field.

Activity associated with visual discrimination in the local environment is often associated with scene brightness. Activity is often dependent on threshold light levels in areas surrounding organisms. Therefore, irradiance is often appropriate when assessing the role of ALAN on activities that rely on vision to detect items in the environment, such as foraging, pollination, hunting, and the initiation of vigilance behavior. Spectrum is also important as the ability to discriminate between items in the environment differs substantially depending on availability of different wavelengths of light (McMahon *et al.* 2022), again demonstrating the importance of irradiance over illuminance.

General guidance

There is not a simple or single way to measure ALAN that will suit all biological questions. The nightscape is littered with anthropogenic light sources that vary in intensity, spatial distribution, and spectra; radiance and irradiance vary across a landscape and over the course of the night. With global distribution and intensities of light shifting, measuring and monitoring light across many scales is increasingly important (Keitt & Abelson 2021). The first critical step in understanding the effects of ALAN on organisms is to identify lightscape features that can address specific biological questions of interest (Table 2). Umbrella factors important for consideration include:

- *Amount of light is different than the visual effects of light*: The *effect* of light is highly contextual; the amount, wavelength, and distribution of lights can have different effects on organisms depending on, for example, behavior (e.g., mating vs. foraging), timing, or developmental stage (e.g., Kühne *et al.* 2021). Additionally, prior lighting exposure can also vastly change the perception of subsequent light changes. A human example: dim light in a bedroom might be uncomfortable to a visual system acclimated to darkness after being awoken in the middle of the night while the same amount of light would be unnoticeable mid-day with full sunlight streaming into the room. Understanding the visual effects of the amount of light, as measured in an environment, can also be complex because light perception is dependent on the visual field rather than the entirety of the lightscape itself; each species is unique in how much of the world around it that it can see at any given moment.

- *The distinction between radiance and irradiance is important*: A streetlight observed at a great distance may appear bright (i.e., high radiance value) while it may not contribute appreciably to the amount of light falling at the observer's feet (i.e., contributing little to horizontal planar irradiance). In this instance, radiance from this streetlight may impact spatial orientation with little effect on predator detection (driven by local irradiance) (Figure 3). If directionality of the light source and contrast in the visual field are likely to be important, then radiance is more appropriate than irradiance.

- *Tailoring measurements to study organisms and lightscapes*. Each species has a unique response to light of different wavelengths, amounts, polarization, spatial orientation, and temporal characteristics; similarly, each lightscape has a unique combination of these same characteristics. Research should attempt to measure light that is relevant to the sensitivities of their target species. That said, there is considerable overlap in visual systems among closely related organisms (Donners et al. 2018); these similarities can be used to parameterize metrics in cases where data are lacking for a species of interest but are available for a related species. However, similarities are not guaranteed, and generalization may ignore important variation within taxonomic groups, or even between different life stages of the same organism (e.g., coho salmon; Alexander *et al.* 1994).

- *Photoreceptors, both between organisms and within a given organism, are highly variable*: photoreceptors range from ocular photoreceptors (i.e., light detection that occurs in the eye) to extraocular photoreceptors such as organs deep within a juvenile bird's diaphanous skull or on the genitalia of butterflies (Arikawa *et al.* 1980; Grubisic *et al.* 2019). Each photoreceptor is unique and, while there are many metrics available to measure light in an environment, these tools/metrics are approximations of lighting conditions as perceived by the photoreceptor in question. As a result, appropriate light metrics are both study species and photoreceptor specific.

- *Use equipment to record general metrics when possible*: it is preferable to use comprehensive metrics (e.g., radiance instead of luminance, spectrally resolved instead of integrated) and later apply species-specific weightings for taxa of interest. This is important, as there is much unknown about the perception systems of many organisms alive today. Especially for species for which there is little known about wavelength sensitivity, we suggest that researchers employ general light measurements so that they can later be converted if/when more information is available; this is especially important because, most often, specialized metrics cannot be converted to general metrics.

- *When using only human-centric photometric metrics (e.g., lux) is unavoidable*: reporting the **spectral power distribution** of the relevant light sources is important for interpreting resulting data and future re-analysis; by coupling photometric units with spectral response curves of target organisms it is possible to calculate measures of exposure that are tailored to an organism's visual system (Gal et al. 1999). We also encourage researchers to report the spectral sensitivity of their equipment and exercise caution in conclusions so that they do not reach beyond data collected.

- *Reporting photometric metrics has value*: reporting human-centric metrics has value insofar as it can help translate works intended for ecological audiences to research that is accessible/actionable by those interested in light outside of ecological contexts. For example, reporting human-centric illuminance in lx may be necessary to effectively communicate important ecological findings to policy makers, lighting professionals, and managers with the goal of reducing deleterious impacts of ALAN (Pérez Vega *et al.* 2022).

- *Reporting should be thorough*: Reporting a description of measured aspects of light, clearly and explicitly, for each study lightscape is critical for interpretation of any manuscript on its own as well and in the context of past (and future) work. It is important to consider all aspects of the light environment that might impact study organisms, for example moon phase and elevation angle should be recorded and reported (Kyba *et al.* 2020) as this might have implications for behavior (Storms *et al.* 2022). Reporting the light environment is equally important for lab settings as it is in field settings – for example, if lighting a terrarium or aquarium, the study design description should include if a single large light panel was used versus an array of LED lights (detailed descriptions of the lighting environment can be done either via words, photographs, or both). Without lightscape details, the study design would be difficult or impossible to recreate and hinders interpretation of results. To reiterate, it is essential to report 1) the dynamic range of light meters used, 2) include spectral distribution, and 3) never report zero values for light (Aulsebrook *et al.* 2022), but rather report that light levels were below the minimum sensitivity of the instrument used.

Concluding considerations

The breadth of ways to measure light is often overlooked in ecology and conservation literature, and this is problematic as interest in effects of ecological light pollution has increased and brought additional research attention to the field. Failure to recognize the differences in measurement techniques and their applicability to biological responses can lead to poor study design and findings that are difficult to interpret.

There are complexities and subtleties associated with measuring light, and these coupled with the realities of field work result in an unavoidable gap between ideal measurements and the metrics employed in real-world situations. However, ensuring that future work systematically considers that light has ecologically relevant characteristics other than the intuitive amount of light (other important characteristics include polarization, critical fusion frequency, wavelength bias, etc.), and thoroughly reports these data, will provide tremendous benefits to those working to mitigate the ecological impacts of ALAN.

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Literature cited

ALAN database Zotero group library. (2022). . Available at: https://www.zotero.org/groups/2913367/alan_db. Last accessed 9 February 2022.

Alexander, G., Sweeting, R. & Mckeown, B. (1994). The shift in visual pigment dominance in the retinae of juvenile coho salmon (oncorhynchus kisutch): an indicator of smolt status. *Journal of Experimental Biology*, 195, 185–197.

Arikawa, K., Eguchi, E., Yoshida, A. & Aoki, K. (1980). Multiple extraocular photoreceptive areas on genitalia of butterfly Papilio xuthus. *Nature*, 288, 700–702.

Aulsebrook, A.E., Jechow, A., Krop-Benesch, A., Kyba, C.C.M., Longcore, T., Perkin, E.K., *et al.* (2022). Nocturnal lighting in animal research should be replicable and reflect relevant ecological conditions. *Biology Letters*, 18, 20220035.

Bará, S., Pérez-Couto, X., Falchi, F., Kocifaj, M. & Masana, E. (2022). Estimating linear radiance indicators from the zenith night-sky brightness: on the Posch ratio for natural and light-polluted skies. *Monthly Notices of the Royal Astronomical Society*, 512, 2125–2134.

Barroso, A., Haifig, I., Janei, V., da Silva, I., Dietrich, C. & Costa-Leonardo, A. (2017). Effects of flickering light on the attraction of nocturnal insects. *Lighting Research & Technology*, 49, 100–110.

Baumhardt, P.E., Moore, B.A., Doppler, M. & Fernández-Juricic, E. (2014). Do American goldfinches see their world like passive prey foragers? A study on visual fields, retinal topography, and sensitivity of photoreceptors. *Brain Behav Evol*, 83, 181–198.

Baxter-Gilbert, J., Baider, C., Florens, F.B.V., Hawlitschek, O., Mohan, A.V., Mohanty, N.P., *et al.* (2021). Nocturnal foraging and activity by diurnal lizards: Six species of day geckos (Phelsuma spp.) using the night-light niche. *Austral Ecology*, 46, 501–506.

Bennie, J., Davies, T.W., Cruse, D., Bell, F. & Gaston, K.J. (2018). Artificial light at night alters grassland vegetation species composition and phenology. *Journal of Applied Ecology*, 55, 442–450.

Bennie, J., Davies, T.W., Cruse, D. & Gaston, K.J. (2016). Ecological effects of artificial light at night on wild plants. *Journal of Ecology*, 104, 611–620.

Berman, S.M., Greenhouse, D.S., Bailey, I.L., Clear, R.D. & Raasch, T.W. (1991). Human electroretinogram responses to video displays, fluorescent lighting, and other high frequency sources. *Optom Vis Sci*, 68, 645–662.

Biberman, L.M., Dunkelman, L., Fickett, M.L. & Finke, R.G. (1966). *Levels of nocturnal illumination*. Defense Technical Information Center, Institute for Defense Analyses, Research and Engineering Suport Division, Fort Belvoir, VA.

Bradshaw, W.E. & Holzapfel, C.M. (2007). Evolution of Animal Photoperiodism. *Annu. Rev. Ecol. Evol. Syst.*, 38, 1–25.

Brüning, A., Hölker, F., Franke, S., Kleiner, W. & Kloas, W. (2016). Impact of different colours of artificial light at night on melatonin rhythm and gene expression of gonadotropins in European perch. *Science of The Total Environment*, 543, 214–222.

Bureau International des Poids et Mesures. (2019). The international system of units (SI).

Cronin, T.W., Johnsen, S., Marshall, N.J. & Warrant, E.J. (2014). *Visual Ecology*. *Visual Ecology*. Princeton University Press.

Cruz, L.M., Shillinger, G.L., Robinson, N.J., Tomillo, P.S. & Paladino, F.V. (2018). Effect of light intensity and wavelength on the in-water orientation of olive ridley turtle hatchlings. *Journal of Experimental Marine Biology and Ecology*, 505, 52–56.

Da Silva, A., Valcu, M. & Kempenaers, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140126.

Dacke, M., Baird, E., Byrne, M., Scholtz, C.H. & Warrant, E.J. (2013). Dung Beetles Use the Milky Way for Orientation. *Current Biology*, 23, 298–300.

Dacke, M., Nilsson, D.-E., Warrant, E.J., Blest, A.D., Land, M.F. & O'Carroll, D.C. (1999). Built-in polarizers form part of a compass organ in spiders. *Nature*, 401, 470–473.

Dominoni, D.M., Halfwerk, W., Baird, E., Buxton, R.T., Fernández-Juricic, E., Fristrup, K.M., *et al.* (2020a). Why conservation biology can benefit from sensory ecology. *Nat Ecol Evol*, 4, 502–511.

Dominoni, D.M., Jensen, J.K., Jong, M. de, Visser, M.E. & Spoelstra, K. (2020b). Artificial light at night, in interaction with spring temperature, modulates timing of reproduction in a passerine bird. *Ecological Applications*, 30, e02062.

Donners, M., Grunsven, R.H.A. van, Groenendijk, D., Langevelde, F. van, Bikker, J.W., Longcore, T., *et al.* (2018). Colors of attraction: Modeling insect flight to light behavior. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329, 434–440.

Duriscoe, D.M. (2016). Photometric indicators of visual night sky quality derived from all-sky brightness maps. *Journal of Quantitative Spectroscopy and Radiative Transfer*, Using remote sensing to better understand light pollution (Light Pollution Theory Modelling and Measurements 2015), 181, 33–45.

Durrant, J., Botha, L.M., Green, M.P. & Jones, T.M. (2018). Artificial light at night prolongs juvenile development time in the black field cricket, Teleogryllus commodus. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 330, 225–233.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., *et al.* (2016). The new world atlas of artificial night sky brightness. *Science Advances*, 2, e1600377.

Falcón, J., Torriglia, A., Attia, D., Viénot, F., Gronfier, C., Behar-Cohen, F., *et al.* (2020). Exposure to Artificial Light at Night and the Consequences for Flora, Fauna, and Ecosystems. *Frontiers in Neuroscience*, 14.

Fernández-Juricic, E., Baumhardt, P.E., Tyrrell, L.P., Elmore, A., DeLiberto, S.T. & Werner, S.J. (2019). Vision in an abundant North American bird: The Red-winged Blackbird. *The Auk*, 136.

Fernández-Juricic, E., Ojeda, A., Deisher, M., Burry, B., Baumhardt, P., Stark, A., *et al.* (2013). Do Male and Female Cowbirds See Their World Differently? Implications for Sex Differences in the Sensory System of an Avian Brood Parasite. *PLOS ONE*, 8, e58985.

Franke, S., Brüning, A., Hölker, F. & Kloas, W. (2013). Study of Biological Action of Light on Fish. *Journal of Light & Visual Environment*, 37, 194–204.

Gaston, K.J., Visser, M.E. & Hölker, F. (2015). The biological impacts of artificial light at night: the research challenge. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140133.

van Geffen, K.G., van Grunsven, R.H.A., van Ruijven, J., Berendse, F. & Veenendaal, E.M. (2014). Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution*, 4, 2082–2089.

Greif, S., Borissov, I., Yovel, Y. & Holland, R.A. (2014). A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. *Nat Commun*, 5, 4488.

Grubisic, M., Haim, A., Bhusal, P., Dominoni, D.M., Gabriel, K.M.A., Jechow, A., *et al.* (2019). Light Pollution, Circadian Photoreception, and Melatonin in Vertebrates. *Sustainability*, 11, 6400.

van Grunsven, R.H.A., Becker, J., Peter, S., Heller, S. & Hölker, F. (2019). Long-Term Comparison of Attraction of Flying Insects to Streetlights after the Transition from Traditional Light Sources to Light-Emitting Diodes in Urban and Peri-Urban Settings. *Sustainability*, 11, 6198.

Hänel, A., Posch, T., Ribas, S.J., Aubé, M., Duriscoe, D., Jechow, A., *et al.* (2018). Measuring night sky brightness: methods and challenges. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 205, 278–290.

Hárosi, F.I. (1994). An analysis of two spectral properties of vertebrate visual pigments. *Vision Research*, The Biology of Ultraviolet Reception, 34, 1359–1367.

Hecht, S. & Shlaer, S. (1936). Intermittent stimulation by light: v. the relation between intensity and critical frequency for different parts of the spectrum. *Journal of General Physiology*, 19, 965–977.

Hölker, F., Bolliger, J., Davies, T.W., Giavi, S., Jechow, A., Kalinkat, G., *et al.* (2021). 11 Pressing Research Questions on How Light Pollution Affects Biodiversity. *Frontiers in Ecology and Evolution*, 9.

Horváth, G. (Ed.). (2014). *Polarized Light and Polarization Vision in Animal Sciences*. Springer Berlin Heidelberg, Berlin, Heidelberg.

Horváth, G., Kriska, G., Malik, P. & Robertson, B. (2009). Polarized light pollution: a new kind of ecological photopollution. *Frontiers in Ecology and the Environment*, 7, 317–325.

Horváth, G., Kriska, G. & Robertson, B. (2014). Anthropogenic Polarization and Polarized Light Pollution Inducing Polarized Ecological Traps. In: *Polarized Light and Polarization Vision in Animal Sciences*, Springer Series in Vision Research (ed. Horváth, G.). Springer, Berlin, Heidelberg, pp. 443–513.

Horváth, G. & Varjú, D. (2004). *Polarized light in animal vision: polarization patterns in nature*. Springer, Berlin ;

Jechow, A. & Hölker, F. (2019). How dark is a river? Artificial light at night in aquatic systems and the need for comprehensive night-time light measurements. *WIREs Water*, 6, e1388.

Jechow, A., Kyba, C.C.M. & Hölker, F. (2019). Beyond All-Sky: Assessing Ecological Light Pollution Using Multi-Spectral Full-Sphere Fisheye Lens Imaging. *Journal of Imaging*, 5, 46.

Jechow, A., Kyba, C.C.M. & Hölker, F. (2020). Mapping the brightness and color of urban to rural skyglow with all-sky photometry. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 250, 106988.

Johnsen, S. (2012). *The Optics of Life: A Biologist's Guide to Light in Nature*. Princeton University Press.

Johnsen, S. (2016). How to measure color using spectrometers and calibrated photographs. *Journal of Experimental Biology*, 219, 772–778.

Kalinkat, G., Grubisic, M., Jechow, A., Grunsven, R.H.A. van, Schroer, S. & Hölker, F. (2021). Assessing long-term effects of artificial light at night on insects: what is missing and how to get there. *Insect Conservation and Diversity*, 14, 260–270.

Kaniewska, P., Alon, S., Karako-Lampert, S., Hoegh-Guldberg, O. & Levy, O. (2015). Signaling cascades and the importance of moonlight in coral broadcast mass spawning. *eLife*, 4, e09991.

Keitt, T.H. & Abelson, E.S. (2021). Ecology in the age of automation. *Science*, 373, 858–859.

Kernbach, M.E., Newhouse, D.J., Miller, J.M., Hall, R.J., Gibbons, J., Oberstaller, J., *et al.* (2019). Light pollution increases West Nile virus competence of a ubiquitous passerine reservoir species. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191051.

Kimlin, J.A., Black, A.A. & Wood, J.M. (2017). Nighttime Driving in Older Adults: Effects of Glare and Association With Mesopic Visual Function. *Investigative Ophthalmology & Visual Science*, 58, 2796–2803.

Kocifaj, M., Posch, Th. & Solano Lamphar, H.A. (2015). On the relation between zenith sky brightness and horizontal illuminance. *Monthly Notices of the Royal Astronomical Society*, 446, 2895–2901.

Kühne, J.L., van Grunsven, R.H.A., Jechow, A. & Hölker, F. (2021). Impact of Different Wavelengths of Artificial Light at Night on Phototaxis in Aquatic Insects. *Integrative and Comparative Biology*, 61, 1182–1190.

Kyba, C.C.M., Conrad, J. & Shatwell, T. (2020). Lunar illuminated fraction is a poor proxy for moonlight exposure. *Nat Ecol Evol*, 4, 318–319.

Kyba, C.C.M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., *et al.* (2017). Artificially lit surface of Earth at night increasing in radiance and extent. *Sci Adv*, 3, e1701528.

Kyba, C.C.M., Ruhtz, T., Fischer, J. & Hölker, F. (2011). Lunar skylight polarization signal polluted by urban lighting. *Journal of Geophysical Research: Atmospheres*, 116.

Land, M. & Nilsson, D. (2012). Animal eyes: Oxford Univ Press.

van Langevelde, F., Ettema, J.A., Donners, M., WallisDeVries, M.F. & Groenendijk, D. (2011). Effect of spectral composition of artificial light on the attraction of moths. *Biological Conservation*, 144, 2274–2281.

Lewanzik, D. & Voigt, C.C. (2017). Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology*, 54, 264–271.

Longcore, T. & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, 2, 191–198.

Longcore, T., Rodríguez, A., Witherington, B., Penniman, J.F., Herf, L. & Herf, M. (2018). Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329, 511–521.

Massetti, L. (2018). Assessing the impact of street lighting on Platanus x acerifolia phenology. *Urban Forestry & Urban Greening*, 34, 71–77.

McLaren, J.D., Buler, J.J., Schreckengost, T., Smolinsky, J.A., Boone, M., Emiel van Loon, E., *et al.* (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters*, 21, 356–364.

McMahon, O., Smyth, T. & Davies, T.W. (2022). Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey. *Journal of Applied Ecology*, 59, 1324–1333.

Mestre, F., Lopes, H., Pinto, T., Sousa, L.G., Mira, A. & Santos, S.M. (2019). Bad moon rising? The influence of the lunar cycle on amphibian roadkills. *Eur J Wildl Res*, 65, 58.

Morgan, K.N. & Tromborg, C.T. (2007). Sources of stress in captivity. *Applied Animal Behaviour Science*, Conservation, Enrichment and Animal Behaviour, 102, 262–302.

Musilova, Z., Salzburger, W. & Cortesi, F. (2021). The Visual Opsin Gene Repertoires of Teleost Fishes: Evolution, Ecology, and Function. *Annu. Rev. Cell Dev. Biol.*, 37, 441–468.

Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M. & Packer, C. (2017). A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecology Letters*, 20, 1364–1373.

Papiorek, S., Junker, R.R., Alves-dos-Santos, I., Melo, G. a. R., Amaral-Neto, L.P., Sazima, M., *et al.* (2016). Bees, birds and yellow flowers: pollinator-dependent convergent evolution of UV patterns. *Plant Biology*, 18, 46–55.

Pérez Vega, C., Zielinska-Dabkowska, K.M., Schroer, S., Jechow, A. & Hölker, F. (2022). A Systematic Review for Establishing Relevant Environmental Parameters for Urban Lighting: Translating Research into Practice. *Sustainability*, 14, 1107.

Perkin, E.K., Hölker, F., Richardson, J.S., Sadler, J.P., Wolter, C. & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere*, 2, art122.

Porter, M.L., Blasic, J.R., Bok, M.J., Cameron, E.G., Pringle, T., Cronin, T.W., *et al.* (2012). Shedding new light on opsin evolution. *Proc Biol Sci*, 279, 3–14.

Prescott, N.B. & Wathes, C.M. (1999). Spectral sensitivity of the domestic fowl (Gallus g. domesticus). *British Poultry Science*, 40, 332–339.

Rai, N., O'Hara, A., Farkas, D., Safronov, O., Ratanasopa, K., Wang, F., *et al.* (2020). The photoreceptor UVR8 mediates the perception of both UV-B and UV-A wavelengths up to 350 nm of sunlight with responsivity moderated by cryptochromes. *Plant, Cell & Environment*, 43, 1513–1527.
Reeves, A., Grayhem, R. & Hwang, A.D. (2018). Rapid Adaptation of Night Vision. *Frontiers in Psychology*, 9, 8.
Renoult, J.P., Kelber, A. & Schaefer, H.M. (2017). Colour spaces in ecology and evolutionary biology. *Biological Reviews*, 92, 292–315.
Rider, A.T., Henning, G.B. & Stockman, A. (2021). A reinterpretation of critical flicker-frequency (CFF) data reveals key details about light adaptation and normal and abnormal visual processing. *Progress in Retinal and Eye Research*, 101001.
Robert, K.A., Lesku, J.A., Partecke, J. & Chambers, B. (2015). Artificial light at night desynchronizes strictly seasonal reproduction in a wild mammal. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151745.
Rosenberg, Y., Doniger, T. & Levy, O. (2019). Sustainability of coral reefs are affected by ecological light pollution in the Gulf of Aqaba/Eilat. *Commun Biol*, 2, 1–9.
Rubene, D., Håstad, O., Tauson, R., Wall, H. & Ödeen, A. (2010). The presence of UV wavelengths improves the temporal resolution of the avian visual system. *Journal of Experimental Biology*, 213, 3357–3363.
Sanders, D., Frago, E., Kehoe, R., Patterson, C. & Gaston, K.J. (2021). A meta-analysis of biological impacts of artificial light at night. *Nat Ecol Evol*, 5, 74–81.
Seymoure, B., Buxton, R., White, J., Linares, C., Fristrup, K., Crooks, K., *et al.* (2019a). Anthropogenic Light Disrupts Natural Light Cycles in Critical Conservation Areas. *SSRN Electronic Journal*.
Seymoure, B.M., Linares, C. & White, J. (2019b). Connecting spectral radiometry of anthropogenic light sources to the visual ecology of organisms. *Journal of Zoology*, 308, 93–110.
Skorupski, P. & Chittka, L. (2010). Differences in Photoreceptor Processing Speed for Chromatic and Achromatic Vision in the Bumblebee, Bombus terrestris. *J. Neurosci.*, 30, 3896–3903.
Storms, M., Jakhar, A., Mitesser, O., Jechow, A., Hölker, F., Degen, T., *et al.* (2022). The rising moon promotes mate finding in moths. *Commun Biol*, 5, 1–6.
Taylor, B.N. (Ed.). (2001). United States version of the English text of the seventh edition (1998) of the International Bureau of Weights and Measures publication. NIST Special Publication 330, 2001 Edition. *National Institute of Standards and Technology*.
Tuxbury, S.M. & Salmon, M. (2005). Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. *Biological Conservation*, 121, 311–316.
Vásquez, R.A. (1994). Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent Phyllotis darwini. *Behav Ecol Sociobiol*, 34, 375–381.
Warrant, E. & Dacke, M. (2010). Visual Orientation and Navigation in Nocturnal Arthropods. *BBE*, 75, 156–173.
Wilkins, A., Veitch, J. & Lehman, B. (2010). LED lighting flicker and potential health concerns: IEEE standard PAR1789 update. In: *2010 IEEE Energy Conversion Congress and Exposition*. Presented at the 2010 IEEE Energy Conversion Congress and Exposition, pp. 171–178.
Witherington, B.E. & Bjorndal, K.A. (1991). Influences of Wavelength and Intensity on Hatchling Sea Turtle Phototaxis: Implications for Sea-Finding Behavior. *Copeia*, 1991, 1060–1069.

Tables:

Table 1: Use cases of radiance and irradiance

	Description	Benefits/use cases	Considerations
Radiance	Directional light, ideally with spectral information (photons measured in individual wavelength bins) from a specific area (e.g., a lizard's dewlap or a light source)	Measures light, from an organism's perspective, of a small and specific area of interest (e.g., a showy decorative trait of a potential mate)	Many radiance measurements in different directions may be helpful to better understand light coming from different sources; for example, to differentiate ALAN from the night sky background (see radiance map below)
Planar irradiance	Amount of light incident on a flat surface. (While planar irradiance can be taken at any orientation, two common orientations are: 1) downwelling or horizontal planar irradiance, to collect light incident on the ground and 2) vertical planar irradiance.)	Light in an organism's habitat with some restrictions in direction. E.g., vertical planar irradiance approximates all light across an entire viewshed of an organism.	Must consider alignment of sensor so that it is perpendicular to the area of interest.
Scalar irradiance	General illumination in an animal's entire	This metric is not limited to a geometry or orientation as is planar	Orientation of sensor is less important since light from every angle is accounted for. While

	environment – for example a nest or foraging area.	irradiance (e.g., only light entering from a hemisphere) but rather accounts for all light in an area (e.g., light originating from every direction that may fall on a leaf)	sometimes correlated, prior studies often used downwelling planar irradiance instead of scalar irradiance. If comparisons are to be made with prior work, it may be necessary to measure both scalar and downwelling planar irradiance.
Radiance map (mostly using imaging devices)	Many radiance measures equally distributed across an area (e.g., across an entire hemisphere or matched to a species' viewshed)	Spectrally resolved radiance maps are powerful and can be used to 1) identify spatial distribution and variability of light, 2) converted to irradiance if obtained over a hemisphere or sphere, and 3) can be used to calculate species-specific metrics	If spectral information is not available or limited (e.g., using an RGB camera), reporting should also include full spectral power distribution of major light sources.

977 Table 2. Light metrics appropriate for a range of ecological questions

Level of analysis	Question	Example mechanism	Measurement	Citation
Physiological	Gene expression (e.g., *vis a vis* signaling pathways)	Detection of light by photoreceptors. Influenced by species specific opsin diversity and expression patterns.	Scalar irradiance or planar irradiance if only a particular orientation is important (e.g., horizontal or in direction of sight). Spectrum is important.	(Porter *et al.* 2012; Brüning *et al.* 2016; Kernbach *et al.* 2019; Rosenberg *et al.* 2019)
	Growth rate and timing (e.g., metamorphosis, eclosion)	Detection of light by photoreceptors. Influenced by species specific opsin diversity and expression patterns.	Scalar irradiance or planar irradiance if only a particular orientation is important (e.g., horizontal or in direction of sight). Spectrum is important.	(Durrant *et al.* 2018)
	Phenology (e.g., germination, leaf out, egg production, nest building, metamorphosis, eclosion, migration)	Detection of light by photoreceptors. Influenced by species specific opsin diversity and expression patterns.	Scalar irradiance or planar irradiance if only a particular orientation is important (e.g., horizontal or in direction of sight). Spectrum is important.	Illuminance: (van Geffen *et al.* 2014; Bennie *et al.* 2018; Dominoni *et al.* 2020b). Surface brightness/irradiance: (Massetti 2018). No light measurement:

				(Da Silva *et al.* 2015)
	Photophysiology and Photosynthesis	Detection of light by photoreceptors (e.g., cryptochrome, phototropins, phytochrome) influencing plant signaling pathways.	Scalar irradiance or planar irradiance if only a particular orientation is important (e.g., horizontal or in direction of sight). Spectrum is important.	(Bennie *et al.* 2016) Note: we emphasize their suggestion to use spectral radiance/irradiance rather than photometric luminance/illuminance in ecological contexts
	Rhythms (e.g., stress, melatonin, immune, recovery, repair)	Detection of light by photoreceptors and non-visual opsins	Scalar irradiance or planar irradiance if only a particular orientation is important (e.g., horizontal or in direction of sight). Spectrum is important.	(Franke *et al.* 2013)
Behavioral	Foraging	Visual detection of food/prey/predator against background.	Radiance map from an imaging system preferable. Scalar irradiance or planar irradiance in the direction of sight can also be	(Baumhardt *et al.* 2014)

			appropriate in some situations.	
		Locating foraging sites based on scene light levels.	Individual: irradiance, spectrum integrated hemispherically or in direction of sight.	(McLaren *et al.* 2018)
	Intra-species visual communication	Contrast, scene brightness (irradiance), radiance (specific areas such as the dewlap of an anole or bill of a toucan).	Planar irradiance (measured in the biologically relevant angle), reflectance of area of interest, radiance (e.g., multispectral band radiance where interpretation depends on species specific spectral response curves).	(Fernández-Juricic *et al.* 2013, 2019)
	Movement (phototaxis/photophobia)	Contrast/color/scene perception.	Radiance map of scene is preferred (hemispherical or spherical for whole environment at location of organism). Radiance map from remote sensing (uncrewed aerial vehicle, satellite). Multiple planar irradiance measures can also be used.	(Vásquez 1994)
		Scene perception (risk assessment); high contrast light-scape obscures ability to see along movement path.		
		Preferred/avoided movement in parts of the landscape with high levels of ALAN.		

	Movement (wayfinding)	Light "landmarks", contrast, spectral/scene perception.	Radiance map of scene (contrast of radiance) to match or assess spectral response curves; sky brightness; polarization.	e.g., regarding species-specific spectral response: (Longcore *et al.* 2018)
	Predator/prey detection	Contrast – detection of object of interest against a backdrop	Spectral radiance map of scene (contrast of radiance) ideally matching visual abilities of the predator and prey. Predator movement along a corridor is likely more appropriately represented by a transect of radiances (from predator eye-level) across the habitat coupled with species-specific spatial acuity and overall light levels of the environment (irradiance).	(Renoult *et al.* 2017; Jechow *et al.* 2019)
	Rhythms	Activity level: light perception by non-visual opsins	Spectral scalar irradiance or radiance map from imaging system (especially for scene perception).	(Johnsen 2016)
		Alter diel activity: night-light niche		
		Scene perception (risk assessment)		

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Figures

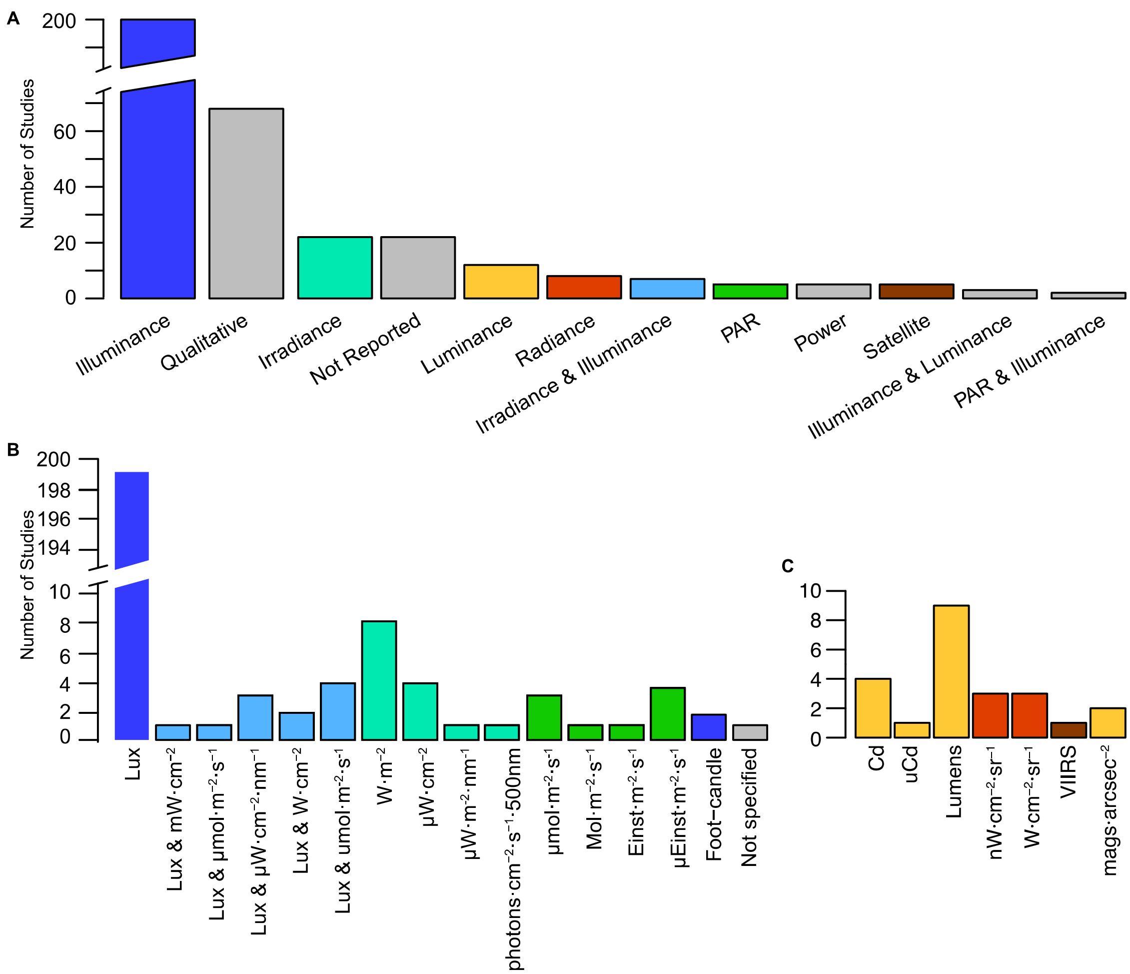


Figure 1. Methods for quantifying light used in prior literature: A) Of the 341 reviewed papers, we find that measurement reported fall into 12 general categories, the number of studies using each category is reported here. A majority measured human-centric illuminance levels (61%, denoted by blue shading) while more than a quarter did not report any light measurement at all (denoted by gray shading). Only 8% of the reviewed studies measured the preferred radiance or irradiance (denoted by red/orange shading). The large number studies using human-centric light metrics, or no quantitative metrics at all, presents a challenge in interpreting the ecological effects of light on non-human species. Additionally, it is difficult to assess the results of any given study that reports only qualitative metrics. B-C) A breakdown of all irradiance and illuminance (B) measurements and of all radiance and luminance (C) reported in the

literature. Ultimately, these data suggest the need for a refinement of the way light is recorded and reported in ecological studies.

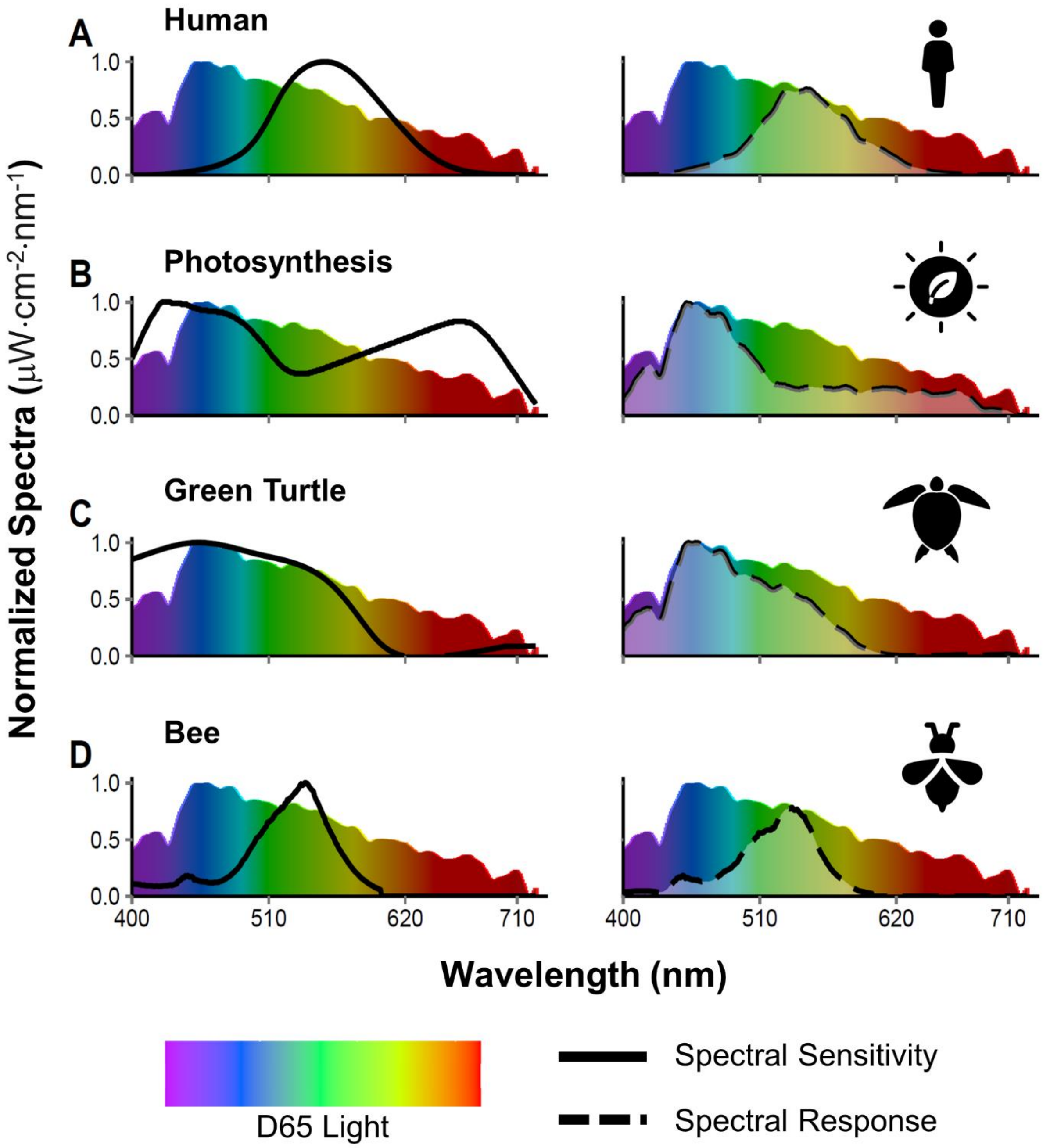


Figure 2. While unbiased light metrics provide information on light present in an environment, it is the interaction between the light present in an environment and what an organism can perceive (i.e., species-specific spectral response) that influences organismal physiology and behavior. Because each species has a unique capacity to perceive different wavelengths of

light, it is important to consider the light perceiving capacity of the study organism. In the leftmost column, a solid black line plots the spectral sensitivity of humans (A, *Homo sapiens)*, photosynthesis (B, *Plantae*), green turtles (C, *Chelonia mydas*), and bees (D, *Apis mellifera*) against a backdrop of daylight (D65 illuminant, a spectra designed to characterize midday light in Europe as defined by the International Commission on Illumination). In the rightmost column, a dashed black line plots the spectral response of each taxon to daylight to illustrate differences among what organisms might functionally perceive. The D65 illuminant and the spectral responses have been normalized and are reported in mW×cm-2×nm-1 as reported in Longcore et al. 2018. While this data could not be converted, it is worth noting that this figure would be better reported in photons×cm-2×nm-1 as photoreceptors count photons, not energy. Icons from the Noun Project ("photosynthesis" by KP Arts, "Human" and "bee" by Adrien Coquet, and "turtle" by Andy Mc)"

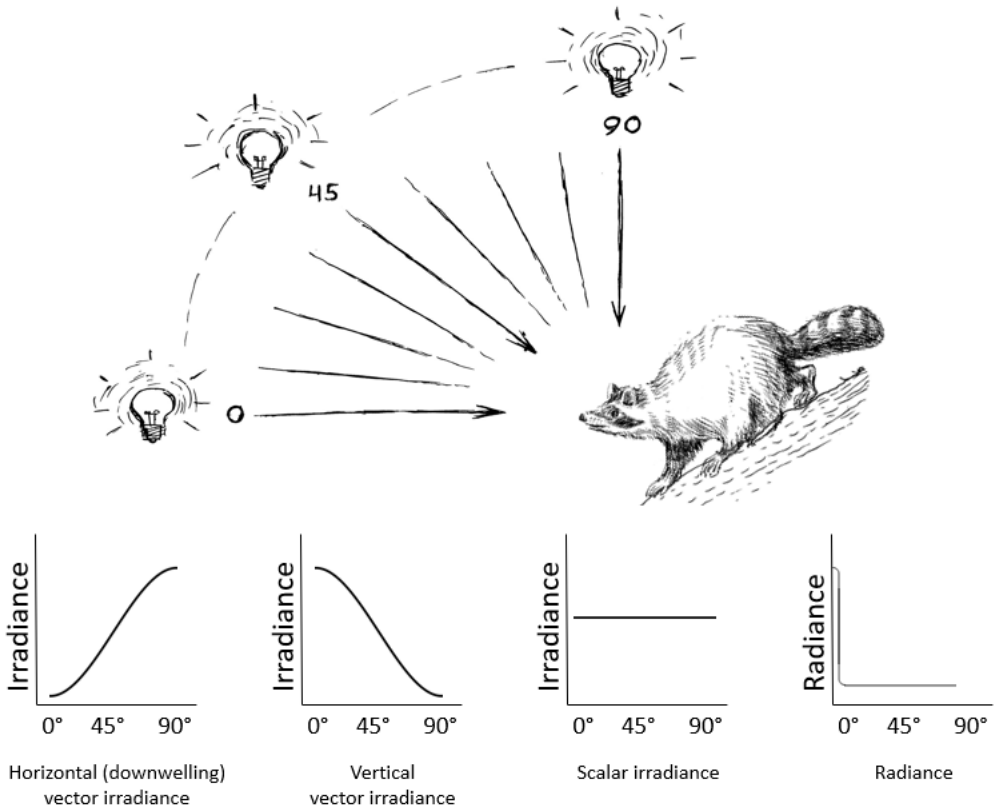


Figure 3. Each light metric is unique and often not correlated. If one were to measure planar irradiance, scalar irradiance, and radiance in the same location (in this case the location of the eye of the pictured raccoon) as a light bulb moved (equidistantly) from directly in front of the pictured animal (0°) to directly overhead (90°) the measured amount of light would be highly dependent upon which of the four standard metrics was used. ***Downwelling (horizontal) planar irradiance***, a specialized form of planar irradiance where a sensor measures light incident on a horizontal surface (e.g., the ground), would theoretically be zero when a distant light is at 0° (i.e., light is arriving perpendicular to the surface of interest) and largest when the light source is directly overhead (i.e., 90°). In contrast, ***vertical planar irradiance*** is largest when the light source is at 0° and zero when the light source is at 90°. ***Scalar irradiance*** is an unbiased metric that considers light arriving from all directions equally – scalar irradiance, in theory, should be the same regardless of where the light source is positioned in space. (In this hypothetical example, one might expect some light to reflect off the ground back into the sensor such that slightly higher values of scalar irradiance would be expected when the light source is directly overhead at 90°. Finally, ***radiance***

only considers light emanating from a restricted portion of an organism’s environment; in this case, radiance values (as measured by a sensor oriented in the same direction that the raccoon’s eye is) would be relatively small until the light source is directly shining into the sensor/eye. Near 0°, the amount of light arriving at the sensor would peak. Art credit: Michael Abelson

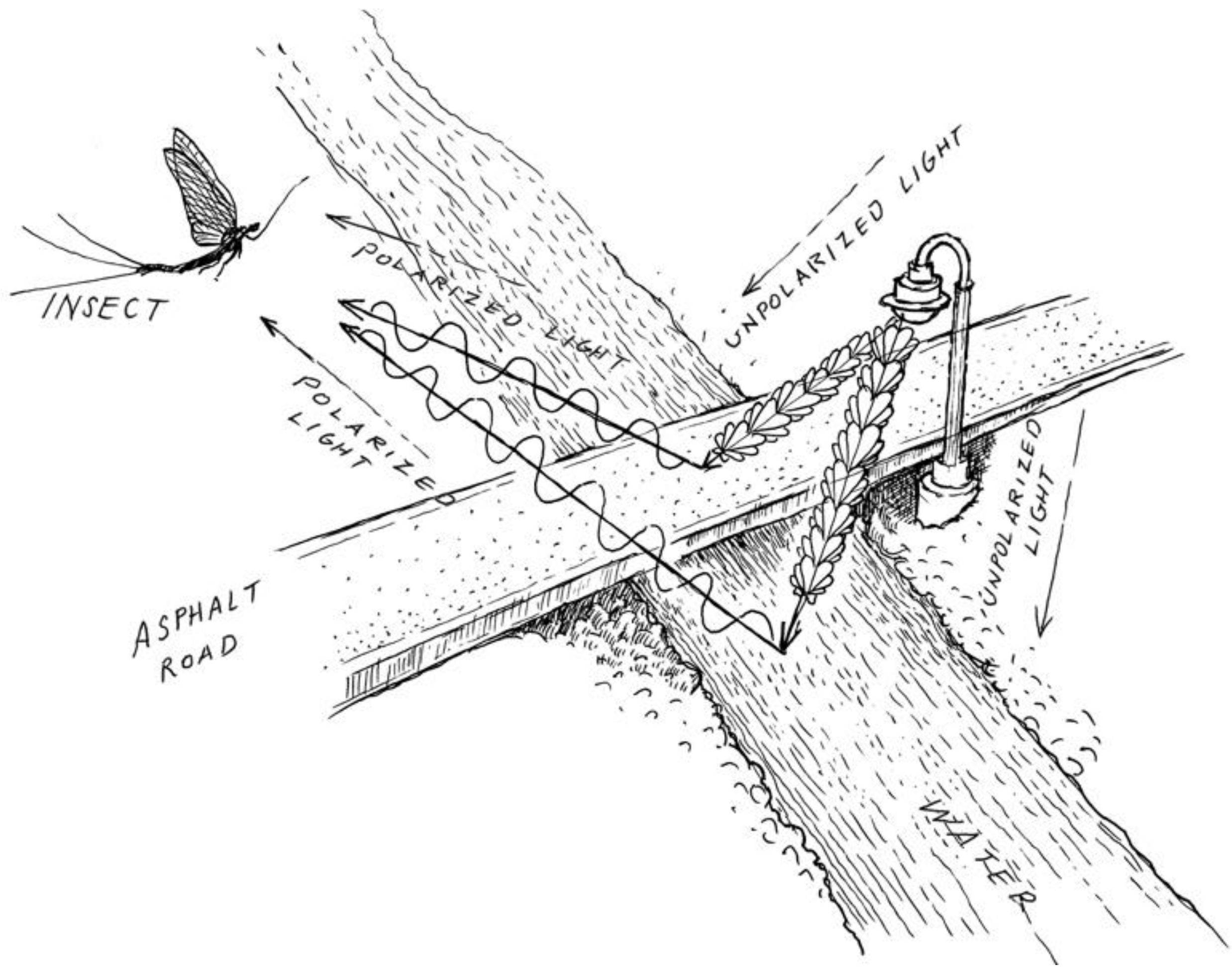


Figure 4. Many organisms detect and modify behavior based on the polarization pattern of light. Many human-made surfaces (e.g., asphalt roads) reflect light that is more highly polarized than reflections from natural surfaces and are a novel source of polarized light pollution. As a result, human-made surfaces that polarize light can disorient and disrupt behaviors. For example, mayflies (Ephemeroptera) lay their eggs on water; identified by the unique signature of polarized light from reflection off water (Horváth *et al.* 2009). In anthropogenically disturbed areas, however, mayflies lay eggs on asphalt roads rather than water as they are likely indistinguishable to these organisms that use the polarization of light for identifying suitable egg-laying habitat. Eggs laid on surfaces other than water will perish, resulting in important ecological consequences for the entire river and riparian environment (Perkin *et al.* 2011). Art credit: Michael Abelson

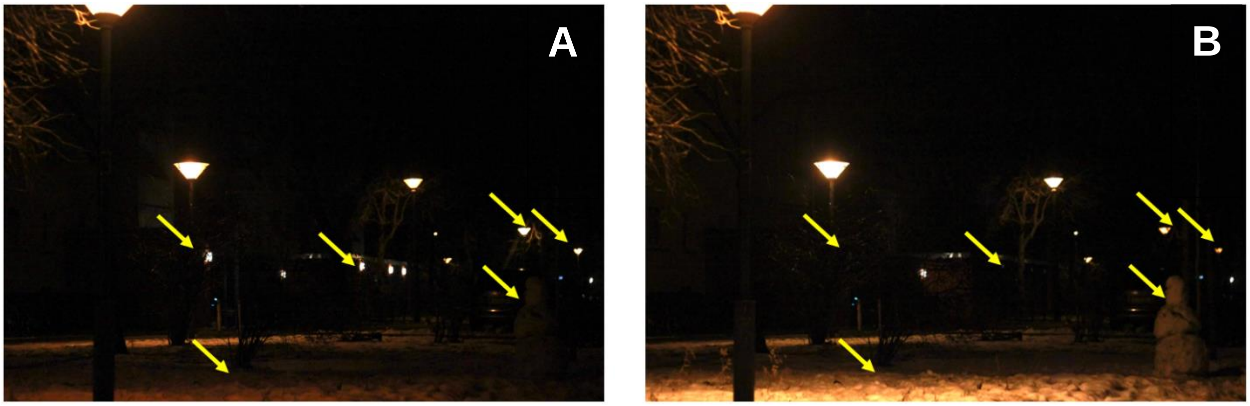


Figure 5. High-speed photographs of a lightscape. Lighting in these images was designed so that, to a human observer, lights would appear to be constantly on with stable light output. However, in reality the light sources are blinking on/off (flickering) and altering the light emissions in any given location. Organisms with a larger critical fusion frequency than humans can see this alternation between light and dark; the resulting flicker results in numerous impacts ranging from altering movement behavior to inducing stress responses. These two photos demonstrate what an animal with a large critical fusion frequency might see with lights blinking on and off and the resulting landscape illumination being well lit and then dark (e.g., in the foreground). Arrows illustrate some of the areas with notable differences between the two photos. Note: a faster shutter speed would be required to see the flicker of some of the lamps pictured as they are overexposed here. The camera settings were: 1 ms exposure, ISO 3200, aperture f2.5. Photo credit: Christopher Kyba

Text box:

Glossary

Contrast: Difference in radiance (or spectra) within a field of view that makes a feature distinguishable in comparison to other features within the same field of view.

Downwelling irradiance: See horizontal planar irradiance.

Flicker: Fluctuations in a light source (or a surface lit by that light source) in which the light dims/brightens or turns on/off.

Glare: Light from a source that causes extreme contrast, because it is much brighter (i.e., has a higher radiance) than the rest of the field of view. Glare results in an uncomfortable or debilitating visual sensation.

Horizontal planar irradiance: A special case of planar irradiance, also termed downwelling irradiance, which includes light from the hemisphere surrounding an upward facing sensor, intended to measure light falling on the ground.

Illuminance: Photometric (i.e., tailored to the human visual system) equivalent of irradiance. Luminous flux per unit area given in lm/m^2.

Integrated light metrics: These metrics report a single value for light intensity that are *tailored to a specific taxon*. Rather than reporting intensity for each wavelength, integrated light metrics sum the energy (or photon count) across many wavelengths of light while applying taxon-specific weighting. While these methods provide a simple metric that indicates brightness to a particular taxon, they result in the loss of wavelength specific information and may not be indicative of the light intensity observed by other species.

Irradiance: The radiant flux per unit area measured in W/m^2 or photons/s m^2.

Scalar Irradiance and Planar Irradiance are both special cases of irradiance. Irradiance can be reported as a single integrated value (spectrally integrated), or as many spectral values with light intensity reported for each of many individual wavelength bins (spectrally resolved).

Light: Electromagnetic radiation that is perceived by photoreceptors; we include radiation outside of human perception, but which can be perceived by organisms, such as ultraviolet or infrared.

Luminance: Photometric (i.e., tailored to the human visual system) equivalent of radiance. Luminous flux per unit area and unit solid angle given in lm/m^2sr – cd/m^2.

Lux: SI unit of illuminance and measures the amount of light perceived by the human eye.

Photoreceptors: Either 1) the anatomical structures within an organism that perceive light or (2) the protein or pigment within a cell that responds to particular wavelengths of light.

Photometric (photometry): Specific case of measuring light tailored to human eye (in daylight conditions).

Polarization: Specific property of an electromagnetic wave. Unpolarized light has the electric field oscillating in all angles equally, while linearly polarized light has the electric field oscillating in a single specific angle (Figure 4).

Radiance: Radiant flux per unit area and unit solid angle given in W/m^2sr or photons/s m^2sr. The number of photons that hit a surface over a period of time that arrives from a specific angular direction. Radiance can be reported as a single (integrated) value or reported with values for each of many spectral (wavelength) bins.

Scalar Irradiance: Special case of irradiance where light from all directions is weighted equally.

Skyglow: The diffuse brightening of the night sky resulting from ALAN. Concentrated skyglow generated by isolated cities creates a light dome.

Spectral power distribution: The distribution of the amount of light energy (per unit area) within each of many wavelength bins.

Spectral response curve: The strength of a particular response (e.g., visual sensitivity, behavioral response) to light of different wavelengths perceptible by a study organism.

Steradian (sr): The SI unit of solid angular measure and is the three-dimensional conical version of the two-dimensional *radian*. There are 4 π steradians in a complete sphere.

Planar Irradiance: Also known as vector irradiance. Special case of irradiance for light incident on a flat surface arriving from the hemisphere surrounding the planar irradiance light meter. Planar irradiance can be taken in any orientation; two commonly used orientations include 1) horizontal planar irradiance (or **Downwelling Irradiance**) when the light meter faces the zenith and 2) and vertical planar irradiance in vertical plane with detector facing the horizon.

Viewshed: The three-dimensional space that is visible from a specific location and is dependent upon an organism's visual ability; also called "visual field".

Spectrum/Spectra (Visual): The continuous range of electromagnetic radiation in which the wavelengths can be perceived as light. The visual spectrum depends on an organism's spectral sensitivity and can start near 300nm and reach past 800nm.

Watt: The SI unit of radiant flux (or optical power).

Wavelength: A photon of specific energies have specific wavelengths. Different wavelengths can be perceived by visual systems with multiple photoreceptors as “color”.

Supplemental Information

- SI 1 - Part I: Inconsistent light metrics and reporting: a review
- SI 1 - Part II: Physics of light pertinent to ALAN research
- SI 2: Literature review data frame

Part I: Inconsistent light metrics and reporting: a review

We identified literature through two approaches: 1) a review yielding 121 ecologically relevant ALAN studies from the ALAN Research Literature Database (“ALAN database Zotero group library” 2022) published between 1 January 2015 and 12 May 2018. All studies on plants or animals listed in the ALAN literature database between October and December 2018 were included in the review, except for studies related to agricultural or aquacultural production. 2) a literature search of manuscripts published between 1 January 1900 to 30 April 2018, yielding 279 publications, using Thompson’s ISI Web of Science and Google Scholar with search terms: ("Light pollution" OR "Artificial Lighting") AND ("Effects on Animals" OR "Effects on Wildlife") (Seymoure *et al.* 2019a).

We reviewed all manuscripts to identify any “effect” from light levels; “effect” was defined as a statistically significant change in the particular biological metric as a function of light level. We included data from empirical studies and reviews. Furthermore, if a publication cited work that was not identified by Web of Science or Google Scholar, we added the study to our database. We constructed a database that included the citation, light measurement(s) used, light meter employed, and units (Supplemental Information 2). We merged the two databases and removed 59 duplicates. We included each light metric reported in any given manuscript (ranging from zero to two metrics); percentages were calculated using the total number of publications (not measurements).

Our review revealed that previous ALAN research used numerous different methods to measure light. A surprising number (n=13; 10.7%) of ALAN studies that we reviewed did not record any light measurements at all, and an additional 32 studies (26.4%) made no mention of which devices were used for the measurements. Light measurement devices are one of the most important pieces of equipment in ALAN research regarding interpreting results. If data on equipment sensitivity and measurement range are not provided directly in the manuscript, it becomes nearly impossible to compare results across studies. Additionally, when no details are given identifying the light measurement device used, pertinent details cannot be looked-up. We suggest that researchers should always provide details for the light measurement equipment used and to ensure that the equipment is capable of accurately measuring ecologically relevant light levels (i.e., well below 1 lx).

In addition, we find great variation in the units reported in studies examining effects of ALAN on biological systems with 17 different types of units reported (see SI 2 – literature review data frame). We found that metrics highly favored lux, the photometric (i.e., human-centric) measurement of illuminance. The second most used “unit” included descriptors that had no objective quantification of light. These included “warm” or “bright” as descriptors of the light source, these descriptors are ineffective for extrapolating the data from of the context of the study. Although there have been hundreds of studies investigating light pollution on organisms, due to variation in reporting and the use of qualitative metrics, only a fraction of these can be used in a meta-analyses as many studies cannot be compared to each other due to differences in measurement type (photometric vs. radiometric), physical property of measurement (irradiance vs. radiance), and then the unit ($W{\cdot}m^{-2}$ vs $W{\cdot}m^{-2}{\cdot}sr^{-1}$).

Photometric quantities and units (illuminance, and luminance; lx, cd/m^2, lm), instead of non-human based measurements such as irradiance and radiance (in W/m^2 or W/m^2sr), were the dominant metrics used in prior ALAN research. We found that, of the 215 studies reporting light values, the majority reported the human-centric illuminance in lx (175/215). The second most common was irradiance (17/215; irradiance was reported in many varieties including both quantal and photon flux). Measuring and reporting only photometric quantities, unfortunately, detracts from the ability to understand the effects of anthropogenic lighting on organisms, as photometric data are not appropriate for most vertebrate visual systems and no invertebrate visual system. Ideally, researchers will, in the future, report values for spectral irradiance and/or spectral radiance as both of these measurements can be used to calculate photometric values as well as any biologically useful weighted measurements (e.g., PAR, clux, etc.).

Part II: physics of light pertinent to ALAN research

Humans, and many animals, perceive different wavelengths (λ) of light as color. The energy of a photon is linked to that wavelength by $E_{phot} = \frac{hc}{\lambda}$, with c being the speed of light and h being Planck's constant. A red photon at λ = 700 nm will only have half the energy of an ultraviolet photon at λ= 350 nm. A certain range of wavelengths is called a *spectral band*. For example, the photopic band (matched to human day time vision) spans from 400 nm (blue) to 700 nm (red), peaking at 555 nm in the green spectrum. This is an important concept in color perception and measuring light because a light detector or a photoreceptor will almost always have a spectral responsivity to different wavelengths and light sources emit light with different spectra.

Radiant flux, irradiance and radiance: Perception of light can be represented in the physics of light as well, where the radiant energy $Q_e = n_{phot} E_{phot}$ is given by the "number of photons" n_{phot} and the photon energy. Radiant flux $\Phi_e = \frac{dQ_e}{dt}$ is the radiant energy per unit time. One example is the total "number of photons per second" emitted by a light source. This is measured in W (watts) and means that a 100W light bulb will emit twice as many photons per unit time than a 50W light bulb.

A light bulb shining on a surface will result in a certain radiant flux per unit area. The *irradiance* $E_e = \frac{d\Phi_e}{dA}$ is all the light incident on a surface and is reported in W/m^2. At night and outdoors, this would include direct and scattered moonlight, starlight and all ALAN sources (e.g., light bulbs) but the irradiance only provides information how much light from all these sources reach the surface, not where they are and how much light comes from each source. Further, there are two main concepts for this physical quantity: 1) *planar irradiance* which can be understood as light incident on a flat surface and where light is weighted based on cosine of angle of incidence and 2) *scalar irradiance* which can be best understood as all light incident on a sphere (or a point in space) and where all light is weighted equally independent of incidence angle (Fig. S1).

Figure S1: Planar irradiance (light incident on a flat surface with cosine weighting) and scalar irradiance (light incident on a sphere or point in space with no angular weighting). Sketch A. Jechow

Now think of looking at or taking an image of a light bulb at night. Your eye (or the camera) will detect light (radiant flux) from an area (the surface of the light bulb) and over some directions (depending on where the light bulb is and how close it is to you or the camera; Fig. SI 2). This is called *radiance*, the radiant flux per unit area and solid angle $E_e = \frac{d\Phi_e}{dA d\Omega}$, reported in W/m²sr. The solid angle Ω is simply the three-dimensional version of a two-dimensional planar angle (reported in degrees) given in steradian (sr) but can also be represented in square-degree - deg^2 or $(°)^2$ (think a two-dimensional plane angle and rotating it to get a cone).

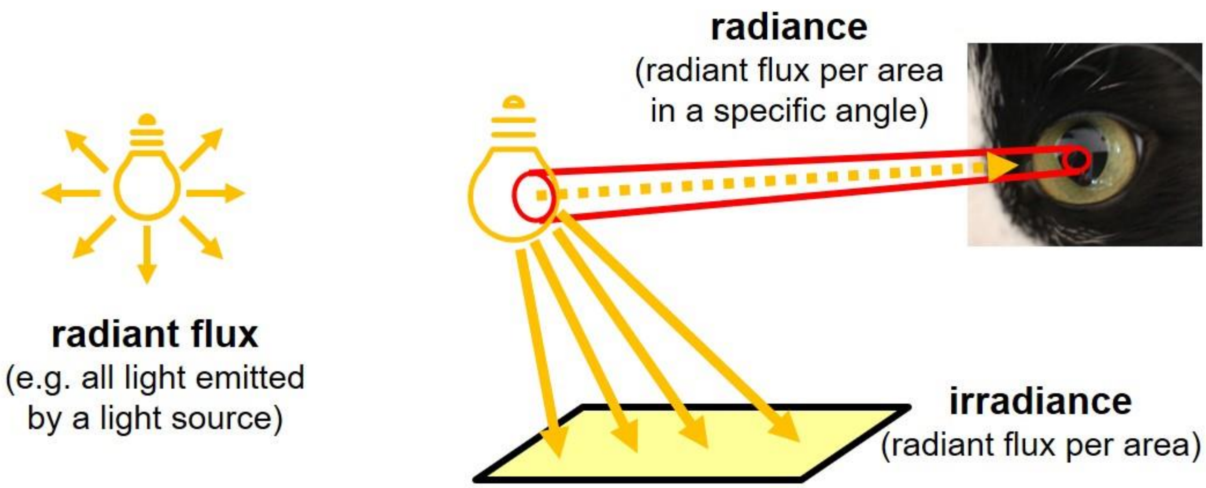


Figure S2: Sketch of radiometric quantities radiant flux, radiance, irradiance. (Figure & image credit: A. Jechow)

A steradian is spanned by a plane angle of about 65.5° (i.e., a cone defined by one sr would have a 65° angle if it were a flat plane), a full sphere covers 4 π steradian (ca. 12.56 sr) and a hemisphere 2 π steradian. A device with 1° field of view will measure light from just 0.00024 sr and the average moon disk is only 0.000064 sr. This means that the measurement device can't resolve the full moon and that the full moon fits about 190.000 times into the celestial hemisphere.

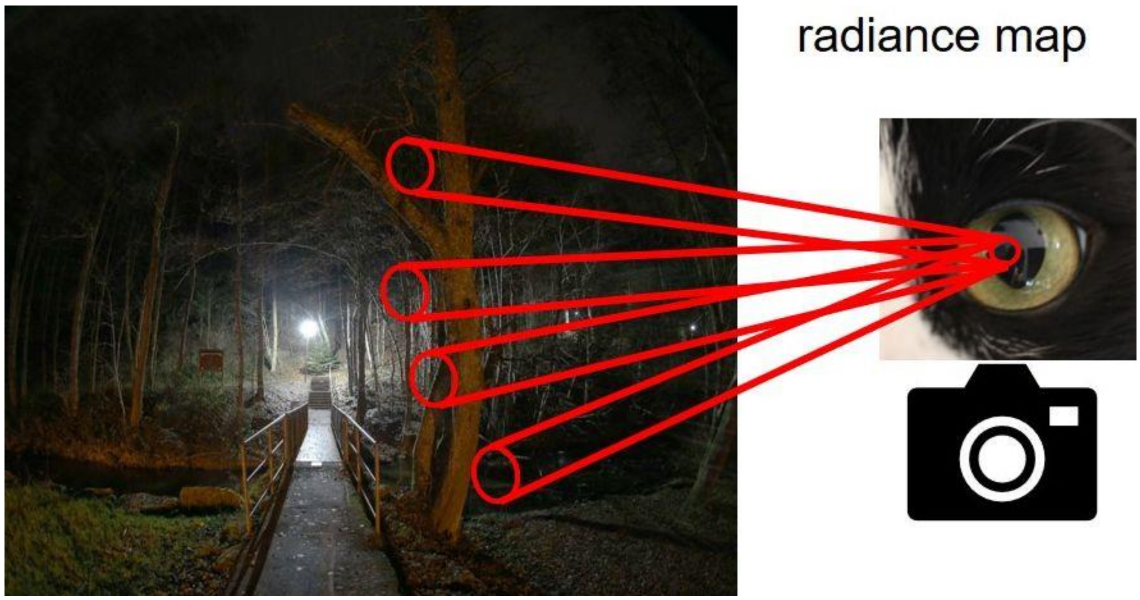


Figure S3: Image of a night-time scene obtained with a camera and how it represents a radiance map (Figure and image credit: A. Jechow).

A camera or an eye provides a spatially resolved radiance distribution (see image in Fig. SI 3) depending on the angular resolution and the field of view. For humans, the angular resolution is about 0.0000006 sr (assuming 0.05° plane angle) and the far peripheral field of view is about 180° x 135° nearly but not exactly covering the full hemisphere. Such a spatial radiance map of a night-time scene with ALAN sources (see Fig. S3 for an example in a forest) might also include the moon and stars and provides information regarding where the light sources are located in space. However, if only a single radiance measurement is performed for some fraction of the scene, the information stored in that radiance measurement is very limited (think of the 1° sensor and moon example above). A special case of imaging is when using a hemispherical optic, i.e., a 180° circular fisheye lens. Mostly this is used in an all-sky geometry (Fig.

S4) but can also be used to obtain information from the full-4 π sphere (Jechow et al. 2019). From such images it is then possible to calculate radiance maps if calibrated (Fig. S4 shows a luminance map) and from these radiance or luminance maps it is possible to calculate irradiance or illuminance.

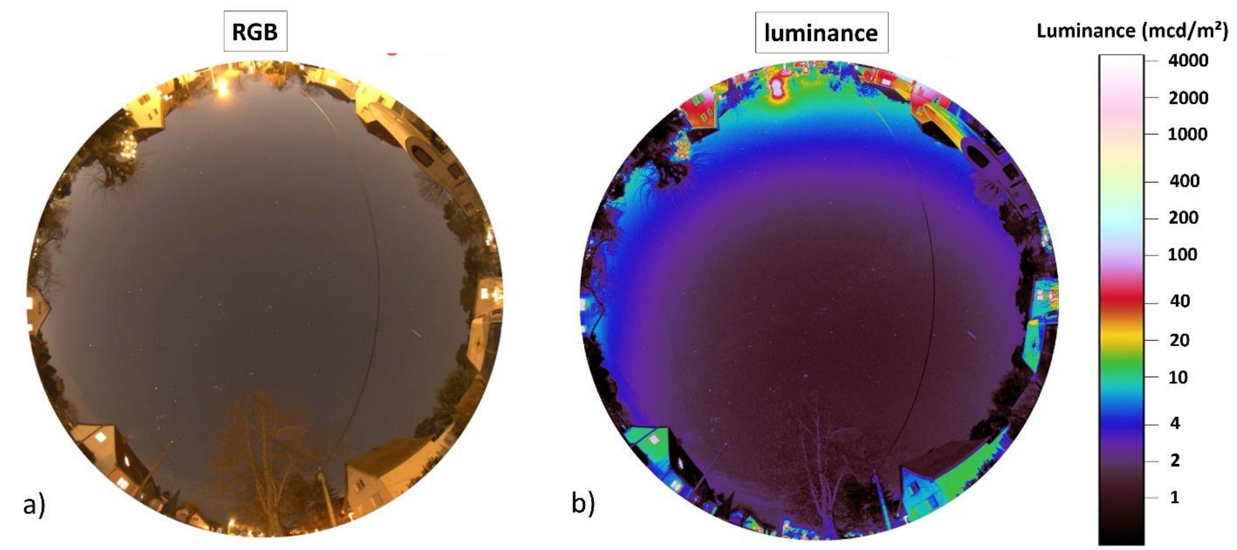
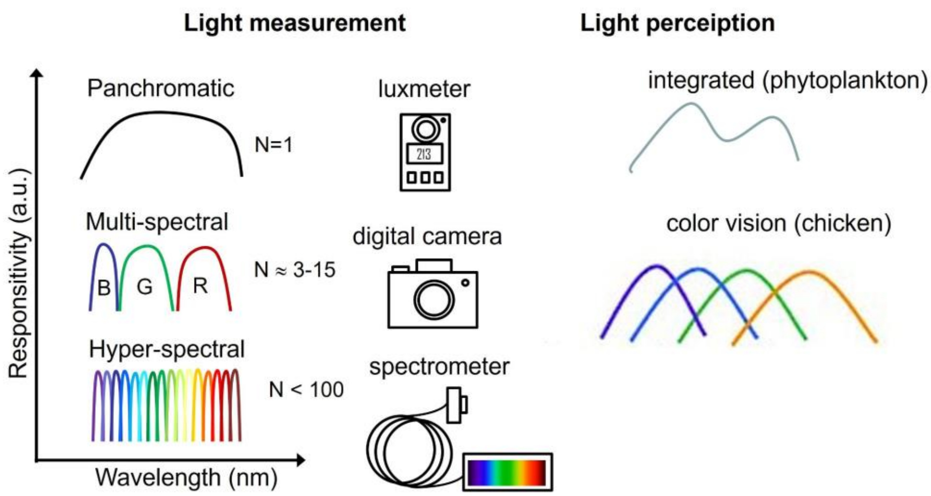


Figure S4: a) RGB all-sky image obtained with a circular 180° fisheye lens and b) luminance map calculated from a). (A. Jechow)

Spectra: A fundamental decision when measuring light is the capability of a detector to resolve wavelength (spectra). On the detector side there are three common ways to distinguish this capability with useful terminology from remote sensing (Figure S5, lefthand panel). A sensor that cannot distinguish wavelengths but integrates over a single large range is called **panchromatic** sensor. Spectrally integrated metrics provide a single radiometric value and could represent a relatively simple and general light metric matched *to a given species*. Two familiar integrated metrics include 1) **photometric** units (e.g., lux) that are specific to the human visual system and 2) PAR (photosynthetically active radiation, see Fig. S5 top righthand side), which consists of wavelengths relevant for plants. If a detector has multiple of such broad “bins” it is called a **multi-spectral** sensor (Fig. S5). This is a digital camera with red, green and blue - RGB “channels” or a species eye that can resolve color like a chicken (see sketch in Fig S5 central righthand side). If the detector has many “narrow bins” this is called a **hyperspectral** device which is also called a spectroradiometer. Such a spectral measurement does not yield a single radiometric value but rather provides such a value for each spectral bin (e.g., ideally 1 nm wavelength bin, covering a range between 300-800 nm, Figure S5).

Generally, a spectrally resolved (hyperspectral) measurement is always preferred to avoid a mismatch between 1) which study species perceive and 2) light measurements recorded. However, there is always a tradeoff between obtaining a radiance map via imaging with high resolution and a large field of view (ideally with a fisheye Fig. S4) or spectral resolution. A hyperspectral camera with fisheye optics is not available at the moment. The combination of a multispectral RGB fisheye imaging system and additional spectral measurements of major light sources in a scene can cover a huge range of measurement problems.



SI Figure 5: Different light measurement systems regarding spectral resolution and how this is linked to color perception. (Sketch A. Jechow)

Converting between light metrics:

Converting between different light metrics is a tedious task but with some care and assumptions, it is possible to convert between similar metrics. Think of different types of ALAN like a streetlight, a shop window, but also the natural and built-up surroundings and the different distances of, for example, the moon vs. a nearby streetlamp and the type of medium (e.g., fog, water, atmosphere) adding complexity. The only exception is the correlation between sky radiance at zenith and horizontal vector irradiance (assuming no obstacles like high-rise buildings or trees), which is called Posch ratio, and can be approximated for overcast skies while clear sky Posch ratios are still ongoing research (Kocifaj *et al.* 2015; Jechow *et al.* 2020; Bará *et al.* 2022).

Converting between the same geometrical unit such as irradiance and illuminance is possible when a full spectral measurement is obtained. In a simple setting (i.e., when only one single lamp type is investigated) it might be possible to convert a human-centric photopic of a taxon-specific measurement to a spectral radiance, and then interconvert those when knowing the spectrum of the dominant light source.