



# A compendium of photopigment peak sensitivities and visual spectral response curves of terrestrial wildlife to guide design of outdoor nighttime lighting

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## ABSTRACT

The presence and proportions of photopigments, which are responsible for the visual and physiological effects of light, vary between taxonomic groups. This leads to differing wavelength sensitivities ranging from ultraviolet (UV; <400 nm) to infrared (IR; >780 nm) and complicates the balancing of spectra used for outdoor lighting to maximize human visual performance while mitigating light pollution effects on wildlife. I developed a database of spectral response information for terrestrial wildlife to create generalized spectral response curves by taxonomic phylum, class, and order. Existing data on species visual sensitivity were collected from previously published research that used behavioral responses, electroretinograms (ERGs), and reflectance within the eye. Resulting summaries of photopigment peak sensitivities ( $n=968$ ) and sensitivity curves ( $n=177$ ) allow for general observations. Overall, longer wavelengths provide the highest possibility for supporting human visual performance at night while reducing intrusive overlap with the vision of other species, because many taxonomic groups are sensitive to light in the blue and into the ultraviolet. Comparison of average response curves at the class level and the spectral power distribution of lamps suggests that spectral tuning might reduce the appurtenance of the lowest correlated color temperature (CCT) lamps to insects, spiders, and non-human mammals the most, with substantial but smaller reductions for reptiles, birds, and amphibians. Spectral tuning, most simply by reducing CCT, should be considered an additional benefit to be used in concert with other mitigation measures such as dimming, shielding, and part-night lighting.

## Introduction

Ecological light pollution has documented adverse impacts on wildlife and their habitats, such as decreased nest habitat quality for a grassland bird (De Molenaar et al., 2006), attraction of insects (Scheibe, 1999), interference with pollination (Macgregor et al., 2017; Macgregor et al., 2019), disruption of sea turtle orientation (Bertolotti & Salmon, 2005), attraction and repulsion of bat species (Stone et al., 2009; Voigt et al., 2018), disrupted migration of fish (Riley et al., 2013), and even altering plant phenology (Massetti, 2018). Mitigating the effects of outdoor lighting, including balancing wildlife needs with roadway safety, is an important avenue of current research (Blackwell et al., 2015; Lee et al., 2021; Long et al., 2022).

The amount of light used to illuminate outdoor spaces is often set by policy, regulators, or risk management considerations. Most jurisdictions follow guidelines adopted by professional organizations such as the Illuminating Engineering Society (IES) or the Commission

Internationale et d'Eclairage (CIE). Roadway lighting in the United States, for example, almost always is designed to be compliant with the IES Recommended Practice: Lighting Roadway and Parking Facilities (ANSI/IES RP-8-21). These standards set illumination levels to be met in specific situations, as measured in lux or lumens. In those locations where lighting has been determined to be necessary, relatively little latitude is available in terms of illumination level, but it is often possible to change the spectrum of light with the intent of maximizing human visual performance while minimizing adverse effects to other species. This paper presents a compilation of terrestrial wildlife visual characteristics that extend far beyond those previously compiled (e.g., Longcore et al., 2018) to guide the choice of color spectrum for lights and ultimately to estimate the potential impact of lights on wildlife species with different visual systems.

Wildlife species have visual systems that differ from humans in their sensitivity to different wavelengths of light. Natural historians and biologists have long recognized the differential effect of portions of the

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light spectrum on different groups and consequently used light color to enhance or reduce the influence of lights. Moths were identified as being sensitive to shorter wavelengths (Cleve, 1964), leading to long-term commercial availability of yellow “bug” lights. Similarly, sea turtle hatchlings are more influenced by shorter wavelengths (Witherington & Bjorndal, 1991; Witherington & Martin, 1996), leading to regulations for turtle-friendly lights with strict limits on shorter wavelength emissions in coastal areas in Florida (rules promulgated under Florida Statutes, 161.163). Through the 20th and into the 21st century, efforts to “tune” outdoor lighting to reduce impacts were done at a coarse scale because a limited number of spectral configurations for lights were available. Outdoor lighting was typically incandescent, mercury vapor, tungsten arc, high pressure sodium, low pressure sodium, metal halide, or induction, each with characteristic spectral outputs, but little adjustability of the spectrum. Even so, yellow and orange lights (low pressure sodium, high pressure sodium) are known for being less attractive to insects, while mercury vapor, with its emissions in the ultraviolet, is extremely attractive to insects (Eisenbeis, 2006; Eisenbeis & Hassel, 2000; van Grunsven et al., 2014). With the advent of LEDs, and the promise of being able to adjust color spectrum, either through use of different colored diodes or through use of phosphor coatings, technological capacity to achieve spectral tuning became more refined (Deichmann et al., 2021; Eisenbeis & Eick, 2011; Longcore et al., 2015; Longcore et al., 2018; van Grunsven et al., 2014).

The approach that has been developed to integrate the role of spectrum into assessment and mitigation of light pollution is to cross-reference the spectral power distribution of light sources with the spectral distribution of the strength of responses by organisms. It has its origins with efforts to evaluate the perception of light by domesticated mammals and birds, matching spectral outputs of lamps with sensitivities of turkey, duck, chicken, cat, rat, mouse, and human vision (Saunders et al., 2008). A similar approach was taken by van Grunsven et al. (2014) to investigate insects, for which they located two insect attraction curves (Cleve, 1964; Menzel & Greggors, 1985), and deemed them to be inadequate when UV light was not present. Longcore et al. (2015) used the same insect curves to predict which configurations of a customizable LED system would attract fewer insects at the same correlated color temperature (CCT) as a conventional LED. Their results showed a significant decrease in insect attraction for the custom spectra selected on this basis. Longcore et al. (2018) formalized an approach to use spectral response curves for species and spectral power distributions from lamps to assess potential impacts by comparing the relative effect of additional lux from the lamp with an additional lux of daylight (the CIE D65 standard) for any particular biological response, similar to Saunders et al. (2008). Longcore et al. (2018) used response curves for insects, including both Cleve and Menzel and Greggors curves in addition to a new curve developed for insects generally (Donners et al., 2018), sea turtles (an average of several curves), a shearwater species (Reed, 1986), and juvenile salmon (Hawryshyn et al., 2010) to measure responses, with the knowledge that additional response curves would need to be found in the literature or developed. The validity of the approach was tested with pre-existing data on the attraction of shearwaters (Longcore et al., 2018). It was further tested in a field study of insects in the Peruvian Amazon Basin, where the calculated attractiveness of different lamps accurately predicted trapping results for three lamp types (one 3000K LED and two different LEDs filtered to reduce blue content characterized as being yellow and amber) (Deichmann et al., 2021). Related efforts to assess the effects of artificial light at night by comparing visual systems to lamp spectral output also support this overall approach (Seymour et al., 2019).

The challenge with using the Longcore et al. (2018) rapid assessment technique for predicting biological responses to different lamp types lies in the current lack of response curves readily available across taxonomic groups. Implementation of the calculations is aided by an open source tool that can be configured to add response curves or lamp emissions spectra, but few digitized response curves are currently available, so

applications are limited to species groups where light responses are consistent across a large number of species and have validated response curves, such as the Donners et al. (2018) curve for insects. Even this approach has its drawbacks, because of the contrasting response of bioluminescent insects to that of insects overall (Deichmann et al., 2021; Owens et al., 2022; Owens & Lewis, 2021) and relatively few studies connecting visual sensitivity with undesirable responses. For development projects with environmental impacts on identified sensitive species, any spectral tuning to mitigate effects of light pollution would need to rely on spectral response curves that are taxonomically close to the target organism or be from a group where there is little variation in spectral sensitivity among different species. Where spectral response curves are not available, information about the peak sensitivity of visual photopigments of the most closely related species could also inform environmental assessments.

In this paper, I report on efforts to locate, digitize, and synthesize spectral response curves for terrestrial wildlife to complement those few already commonly used and to expand on current lists of peak photopigment sensitivity wavelengths. Through a targeted literature review, published response curves describing species responses to light at different wavelengths were located and analyzed. The goal was to discover what patterns arose overall, as well as within groups at different levels of taxonomic classification, so that recommendations can be made for the use of curves that might apply to classes or orders. At a minimum, the compilation should provide more insight into the visual sensitivity of species most closely related to sensitive species for which environmental review is required while analyzing construction and lighting project impacts.

In the following section, additional background information is provided on the types of available spectral response curves and other information to guide understanding of the spectral sensitivity of visual systems. Then the process of locating and extracting curves and other visual information from the literature is described. The results of those efforts are then presented and summarized to provide generalized response curves by phylum, class, and order and compared with the parallel compilation of peak sensitivities of photopigments.

## Background

### Photopigments

Opsins are light-sensitive proteins found in vertebrates and invertebrates, each of which is sensitive to particular wavelengths of light. Stimulation of these opsins, which together with a linked chromophore are known as photopigments, provides the basis for vision and other light-induced physiological responses. There are more than a thousand documented opsins, which fall into eight classes, including melanopsin, which is involved in determining circadian rhythms and pupillary reflex (Terakita & Nagata, 2014). Opsins within taxonomic groups tend to be conserved, leading to the ability to generalize about visual systems among related organisms (Saunders et al., 2008; Shichida & Matsuyama, 2009). Organisms often have more than one photopigment, which allows for different wavelengths of light to be distinguished depending on the sensitivity of each. Humans, for example, have three photopigments that contribute to color vision, with peak sensitivities at blue (419 nm), green (531 nm), and yellow (559 nm; referred to in the literature as “red”) in cones, and one in rods that is sensitive at low light with peak sensitivity of 496 nm.

Photopigments can be isolated in the laboratory and the peak sensitivity determined experimentally using microspectrophotometry, or through genetic analysis to identify opsins and phylogenetic comparisons to determine their peak sensitivity (Rossetto et al., 2023). It is then possible to construct a sensitivity curve for each photopigment that incorporates the structure of the eye and the filtering effects features such as of oil droplets (Dartnall, 1953; Govardovskii et al., 2000; Stavenga et al., 1993) and filtering pigments (Van Der Kooi et al., 2021).

These spectral sensitivity curves derived from the peak wavelength and adjusted for the photopigment type (rods, cones) describe the sensitivity for each pigment, and not for the visual system as a whole. Species also have prereceptoral effects on visual sensitivity from the transmissivity of the lens of the eye, shifting of wavelengths in the eye, and, in some groups, oil droplets that filter light by wavelength before even reaching the photopigment. Without knowing the proportion of different photopigments that an organism has, or their sensitivity relative to each other, and the nature of all of the preceptoral effects, it is not possible to know how they work together to construct a general spectral sensitivity curve for the taxon, let alone behaviors resulting from such perception. For example, a generalized insect behavioral response curve was fit using field data along with the peak sensitivities of the most common insect photoreceptors (Donners et al., 2018), thereby combining different visual sensitivities with the behavioral response of phototaxis. Without such data to fit a model combining individual opsin sensitivities and structural filters and knowledge of the downstream behavioral consequences, the peak wavelengths of the photopigments alone can nevertheless reveal the general spectral sensitivity of different organisms, for example whether they may have ultraviolet vision, and it is for this purpose they are investigated here.

#### Types of spectral response curves

Spectral response curves represent the strength of some organismal or physiological response to light of different wavelengths within the visual spectrum (as defined for the organism, with some falling outside the definition of “light” for humans). The responses are given either in absolute terms (e.g., the brightness of light required to elicit the response by wavelength interval, or the strength of the response to a constant quantal flux by wavelength interval) or in relative terms wherein the response is scaled from 0 to 1 as defined by the strongest and weakest measurement of the behavior or physiological change. Typically, the responses fall into three categories: behavior, electroretinography, and optical reflectance, although other techniques are available to measure responses.

Behavioral responses are measured from live organisms and involve any measurable behavior that can be observed in controlled conditions. For example, the behavior might be a choice in a Y-maze or prey catching behaviors (Przyrembel et al., 1995), movement toward or away from a light (Cohen et al., 2010), or triggering a reward when discriminating a light signal (Maier, 1992; Remy & Emmerton, 1989). The types of behavioral responses vary by organism and usually the tests involve measurement of responses across a discrete number of wavelengths across the visual spectrum, resulting in a series of measurements at 10–50 or more nm increments. The advantage of this approach is that the responses are the outcome of light having been processed through the nervous system of the organism and represent actual outcomes of the exposure. Obtaining behavior curves can, however, be difficult for reasons having to do with the size and other attributes of the organism that may not lend it to repeated experimental exposures to light in a controlled environment. Behaviors may be instinctual, such as positive and negative phototaxis, or trained behaviors reinforced by a reward that involve distinguishing light from an alternative (Arden & Silver, 1962; Cohen et al., 2010; Mészáros et al., 2021). It is possible that one untrained behavior represents sensitivity to one part of the spectrum when other behaviors may be sensitive to other parts of the spectrum, even within the same organism. Trained responses in response to visual discernment are less likely to be vulnerable to this variation.

An electroretinogram (ERG) is measurement of electrical current produced by the retina in response to light (Kantola et al., 2019). Measurements can be taken from live animals by attaching a thin fiber electrode to the cornea. The technique is also used on eyes of invertebrates, both in living organisms and for eyes that have been dissected from the animal and continue to produce electrical signals for a limited time. Tests can be performed on dark-adapted eyes, which will

elicit responses from the rod system in vertebrates, while tests with light-adapted eyes will stimulate the cone system. The response involves a small decline in voltage, followed by an increase in voltage. Different components of these responses can be isolated and their amplitude used to characterize the eye's response to the stimulus (Granit, 1933; Kawamuro et al., 1997). The advantage of this approach is that electrical responses can be precisely measured and in some instances live animals can be tested and released, which is especially important for working with rare or sensitive species (Reed, 1986). The disadvantage is that the measurements only represent the activation of ocular photoreceptors, which do not necessarily correlate with specific behavioral responses. For example, ERGs show that nesting sea turtles are capable of detecting red light, but behavioral assays show that their response to it is minimal when compared with shorter wavelengths. Although live animals can be used in some taxonomic groups, often ERG measurement involves harm or death for the organism (Bernard & Stavenga, 1979).

The third approach to measuring spectral sensitivity of photoreceptor cells is through noninvasive measurement of optical eyeshine or scattering in insect eyes (Bernard et al., 1984; Bernard & Stavenga, 1979). This approach depends on the movement of pigment granules in the eye, which move when light-adapted and increase the reflectance of the eye (Kirschfeld & Franceschini, 1969). The optical approach has been applied to Amphibia (Deutschlander & Phillips, 1995), Lepidoptera (Bernard et al., 1984), and Diptera (Bernard & Stavenga, 1979; McCann & Arnett, 1972).

There are two additional ways to determine visual sensitivity to produce high-resolution response curves: microspectrophotometric measurements (MSP) and single-cell recordings. The MSP approach involves shining lights at specific cones or rods and measuring what is absorbed. It is commonly used in vertebrates and some invertebrates with camera-type eyes (e.g., spiders). Intracellular recordings are like ERGs but only measure one cell.

#### Materials and methods

Two databases were developed, one for peak sensitivity of photoreceptors and another for behavioral, ERG, and optically determined spectral response curves. These inventories were then analyzed and characterized by taxonomic group, lighting condition, and species activity period.

The published literature, including dissertations and theses, was searched by starting with available, thorough reviews of the spectral sensitivity of wildlife (Davies et al., 2013) and insects specifically (Van Der Kooi et al., 2021). Papers referenced in these compendia were obtained and searched for both opsin peak sensitivity values (already compiled by Davies et al., 2013) and any spectral response curves. Then, further searches of the literature were made using Google Scholar and combinations of search terms “spectral response,” “spectral response curve,” “photopigment,” “opsin,” “electroretinogram” and variants, “wavelength AND behavior”, “wavelength AND response”, along with taxonomic identifiers at phylum and class levels to locate relevant studies. Citations were tracked forward and backward from papers and screened by title to locate studies. The databases will be updated on the digital archive Github and amended with additional information as it is located in the literature or shared with the author.

Peak opsin sensitivity values were recorded with species names, taxonomy, and photoreceptor type (rod or cone) if applicable. Review of natural history of each species was used to determine if the species was naturally active at all during the night and active at all during the day.

For spectral response curves, graphs were extracted from digital copies of articles, measured responses were digitized, and curves were fit through the empirically measured response points. Images were captured at high resolution from the underlying digital version or scanned photocopies as screen captures. Then, the image was imported into WebPlotDigitizer 4.5, which is a free tool to digitize graphs. In WebPlotDigitizer, the axes were defined, and all response points were

digitized and exported as a text file. Responses that were defined in log units relative to light were captured as linear responses following Steven's power law (Stevens, 1957) and its application to sensory phenomena (Longcore et al., 2015; Ruchty et al., 2010). This transformation accounts for the fact that the perceived intensity of light for humans increases with the logarithm of the intensity of light and not linearly; we must presume this is true for other organisms as well. Data were then imported into JMP Statistical Discovery Software 17 (SAS Inc., Cary, NC) for further analysis. First, the responses were standardized to 0 to 1 between the minimum and maximum values. Then, a cubic spline was fit through the data with an initial lambda of 0.05. Lambda (determining the stiffness of the spline) was then adjusted so that the curve fit through the data in a manner that matched either any interpretation (often hand drawn) in the original source or had the visual appearance of a typical visual response curve represented as the sum of typical opsin response curves as defined by standard templates (roughly Gaussian). The values of the spline between the minimum and maximum wavelength were then saved and again standardized to 0 to 1. Values between 300 nm and 700 nm were recorded to include the ultraviolet region. Responses to infrared light (heat) were not considered because the sensory pathway is different. If the response value converged on zero at <700 nm, zeros were added to the curve up to 700 nm. Because few curves converged on zero at the lower end of the spectrum, no assumptions were made, and the curves ended at the lowest wavelength value measured. Curves were then added to a database with species names, taxonomy, curve type (behavioral, ERG, optical), and adaptation state (dark or light).

To synthesize the data, peak spectral sensitivity values were visualized by class and nocturnal/diurnal activity status. Response curves were visualized all together, then as means within each taxonomic level.

I then used the response curve database to produce summary curves for the classes of organisms included by fitting cubic spline through the data and adjusting the stiffness to produce a smooth curve. I summarized these class curves by taking the average at each wavelength and then calculated the intersection of these curves with spectral characteristics of a set of light sources compiled previously (Longcore et al., 2018) using the methods described there, which built on the approach of Aubé et al. (2013). This approach allows comparison of the visual effect of an additional lux of light from each lamp relative to an additional lux of

daylight for a species with the average response within each class and the average of classes. These results were then plotted in linear regressions as a function of the CCT, Melatonin Suppression Index, and Star Light Index (Aubé et al., 2013) for each lamp.

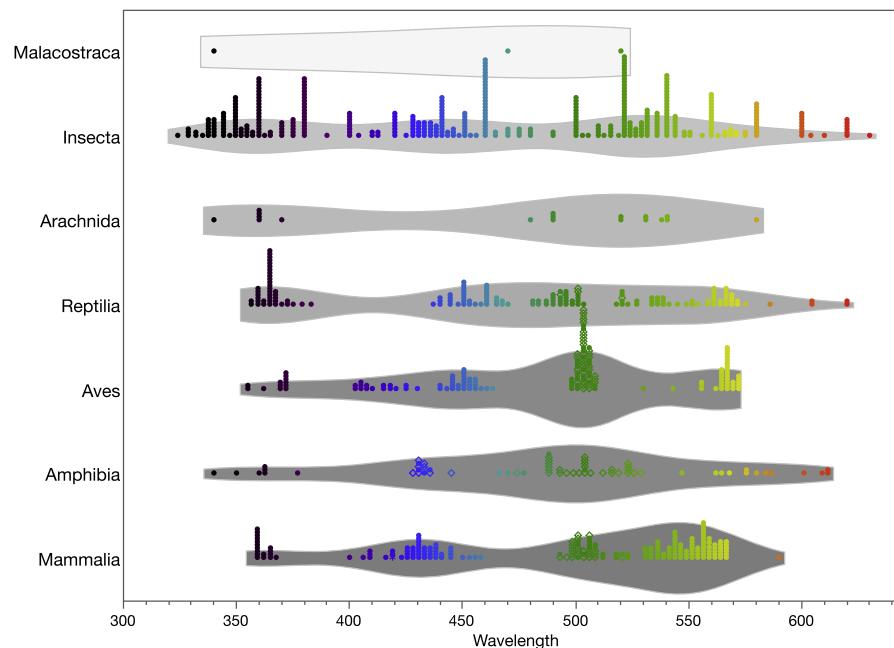
## Results

### Photopigments

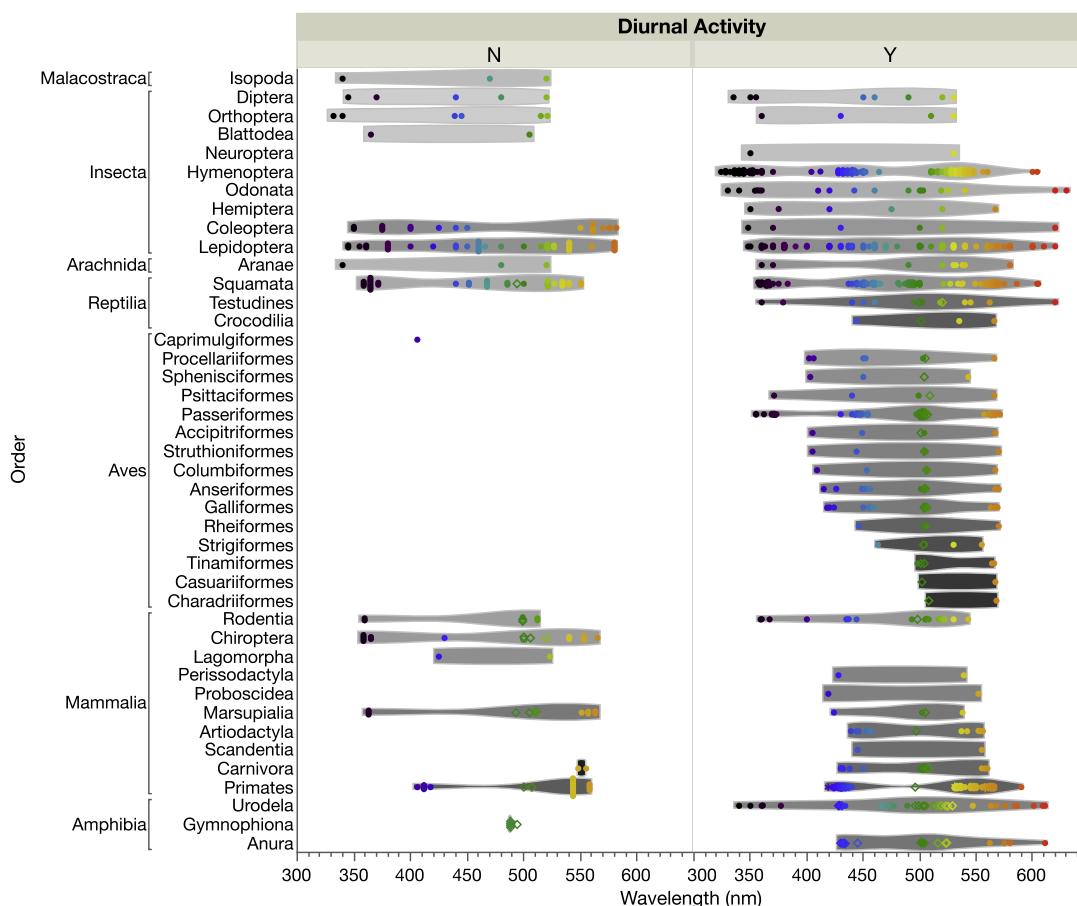
I located measurements of peak sensitivity for 968 photopigments for 320 distinct entities with terrestrial habitats (Fig. 1) (see Appendix A: Table 1). Sea turtles were included because of their use of coastal beaches, while other aquatic species were not. Nearly all these distinct entities were species, while a few subspecific groups were included (e.g., domesticated fowl, male and females, or juveniles distinct from adults). These measurements were 56% from chordates and 44% from arthropods. Insects made up the plurality of measurements by class (41%), followed by mammals (20%), birds (15%), reptiles (14%), amphibians (7%), and spiders (2%).

On average, the median peak sensitivity of the mammalian photopigments was longest (508 nm), followed by birds (503 nm), and amphibians (499 nm), while the median sensitivity of insect photopigments was shorter (460 nm) (Fig. 1). The greatest range in peak sensitivity of photopigments was found in the insects, 306 nm between the longest and shortest peak wavelength. The smallest range in peak sensitivity was found in birds (216 nm) and mammals (232 nm), when excluding the small sample of one species of coastal Malacostraca, the only crustacean in the dataset.

Visual assessment of the distribution of photopigments by class shows how the visual systems of insects are tuned to wavelengths across the spectrum from ultraviolet to red, and indeed include the photopigments most sensitive to the longest wavelengths (Fig. 1). Every species with a pigment with peak sensitivity greater than 580 nm was active during the day. The nocturnal-only species with photopigments with peak sensitivities in the 550–580 nm included species with known use of color vision at night, including bats (foraging), moths (nectaring), and fireflies (mating) (Fig. 2). Overall, the photopigments of species with daytime activity have a slightly greater average light wavelength



**Fig. 1.** Peak sensitivity of visual photopigments by class of terrestrial wildlife. Classes and then orders are sorted from top to bottom by the average wavelength of peak sensitivity of all pigments recorded for the group. Gray scale background reflects density of opsins by wavelength interval and is colored by average peak sensitivity in each group.



**Fig. 2.** Peak sensitivity of visual photopigments by order of terrestrial wildlife and presence of diurnal activity. Classes and then orders are sorted from top to bottom by the average wavelength of peak sensitivity of all pigments recorded for the group. Gray scale background reflects density of opsins by wavelength interval and is colored by average peak sensitivity in each group.

sensitivity of 478 nm compared with 473 nm for species with no daytime activity, but this difference is not statistically significant.

The orders containing the photopigments sensitive to the shortest wavelengths are all arthropods: Hymenoptera (324 and 328 nm), Odonata (330 nm), Orthoptera (332 nm), Hymenoptera again (332 nm), and Diptera (335 nm). A newt with a photopigment with peak sensitivity at 340 nm represents the shortest chordate peak sensitivity. Sensitivity in the ultraviolet (<400 nm) is found across many chordate taxa (rodents, bats, lizards, seabirds, penguins, parrots, passerines, salamanders, turtles, and marsupials all with at least one species with a photopigment sensitivity peak <405 nm), while many other chordate groups lack vision in the ultraviolet. In contrast, none of the arthropod orders included in the dataset lacked ultraviolet sensitivity.

#### Spectral response curves

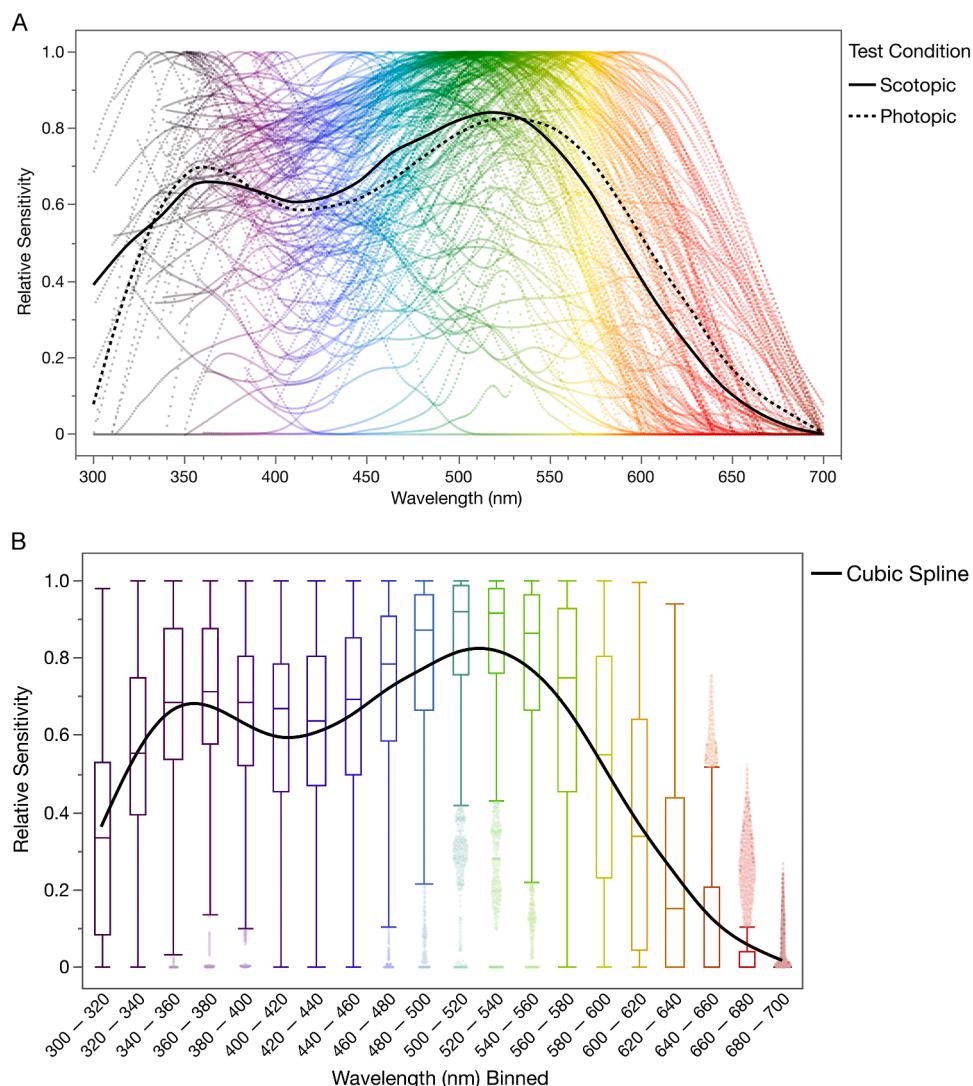
Spectral response data from 177 examples derived from either behavioral assays, ERGs, or reflectance were compiled, digitized, and fit with curves (for list of curves and associated sources see Appendix A: Table 2). Most of these were individual species, although some were provided at the genus or family level when multiple species within a genus or family were tested and showed no differences (e.g., *Aotus*, *Simuliidae*). A beach-dwelling crustacean (*Talorchestia longicornis*), harbor seal (*Phoca vitulina*), and sea turtle species were included because of their use of terrestrial elements of coastal environments. In some instances, both photopic and scotopic curves were available (both were included separately), or different parts of the eye of the same organism. The dataset contains 55% curves from Arthropods and 45% from Chordates. At the class level, the most curves were obtained for insects

(51%), followed by mammals (23%), birds (12%), amphibians (6%), reptiles (4%), and arachnids (3%). Curves were located for 36 orders, with the most coming from the Lepidoptera (21%), followed by Rodentia (13%), Diptera (12%), Coleoptera (7%), and Carnivora (6%). These represented 84 different families.

When averaged over all curves, the peak sensitivity was at 520 nm, where the median sensitivity was 92% of maximum across all species (range 0–100%) (Fig. 3). Peak sensitivity under light conditions was at slightly greater wavelengths than dark conditions, mirroring the Purkinje shift in humans. Median sensitivity declined with increasing wavelengths and by 600 nm the average sensitivity was 40% and by 620 nm, 22%. Shorter wavelength results were derived from only those species where sensitivity was reported and so reflect the values of those species that had non-zero sensitivity, not an average of all species. Most species (85%), however, had results down to 420 nm, at which the median sensitivity was 64%. At shorter wavelengths, median sensitivity increased to a peak of 75% at 360 nm, representing 70 curves of species with ultraviolet vision.

As is well-documented in descriptions of the phylogenetic conservation of visual systems, differences are readily apparent between the two phyla (Arthropoda, Chordata) for which spectral response curves were obtained. Both have a peak sensitivity around 520 nm, with the median sensitivity curve for chordates at 95% and lower for arthropods at 82% (Fig. 4). Arthropods have more species extending into the ultraviolet and for those species, peak sensitivity is around 360 nm. Chordates have a few species with high sensitivity in this region, but far fewer than the arthropods.

Visualization of the response curves at the class level makes apparent both the number of curves available to make inferences, and the degree



**Fig. 3.** (A) Spectral sensitivity curves ( $n=177$ ) compiled from 81 families, fit with a cubic spline and separated by photopic and scotopic test conditions. (B) Box plots show distribution of spectral sensitivities binned into 20 nm increments.

of variation within these large taxonomic groups (Fig. 5A). These curves show differences in the aggregate peak sensitivity, which is 500 nm for amphibians (median sensitivity of 99%), and between 500 and 520 nm for spiders, birds, insects, and mammals. The strongest median visual response for reptiles is around 540 nm (Fig. 5B). Box plots of sensitivities binned into 20 nm increments shows where more and less variation is found, with the least in birds around the peak of 520 nm, and the most for insects in the 500–520 nm range.

Moving to summaries by class, there are many classes for which only one or two curves are available, while many were found for others (Fig. 6; Coleoptera, Diptera, Lepidoptera, Rodentia). Those insect classes consistently sensitive to violet and ultraviolet light are evident, including Blattodea, Coleoptera, Diptera, Ephemeroptera, Hymenoptera, (some) Lepidoptera, Neuroptera, Odonata, Orthoptera, Thysanoptera, and Trichoptera. Frogs show a single peak, while salamanders have a similar peak but also higher sensitivity in the ultraviolet. Passerine birds have remarkably few curves available, but show broad spectral sensitivity, while the one curve for an owl species has a narrow peak around 490 nm. The limited curves for lizards and snakes show significant variation, but little sensitivity in the blue or violet, although this may be an artifact of the range of wavelengths tested.

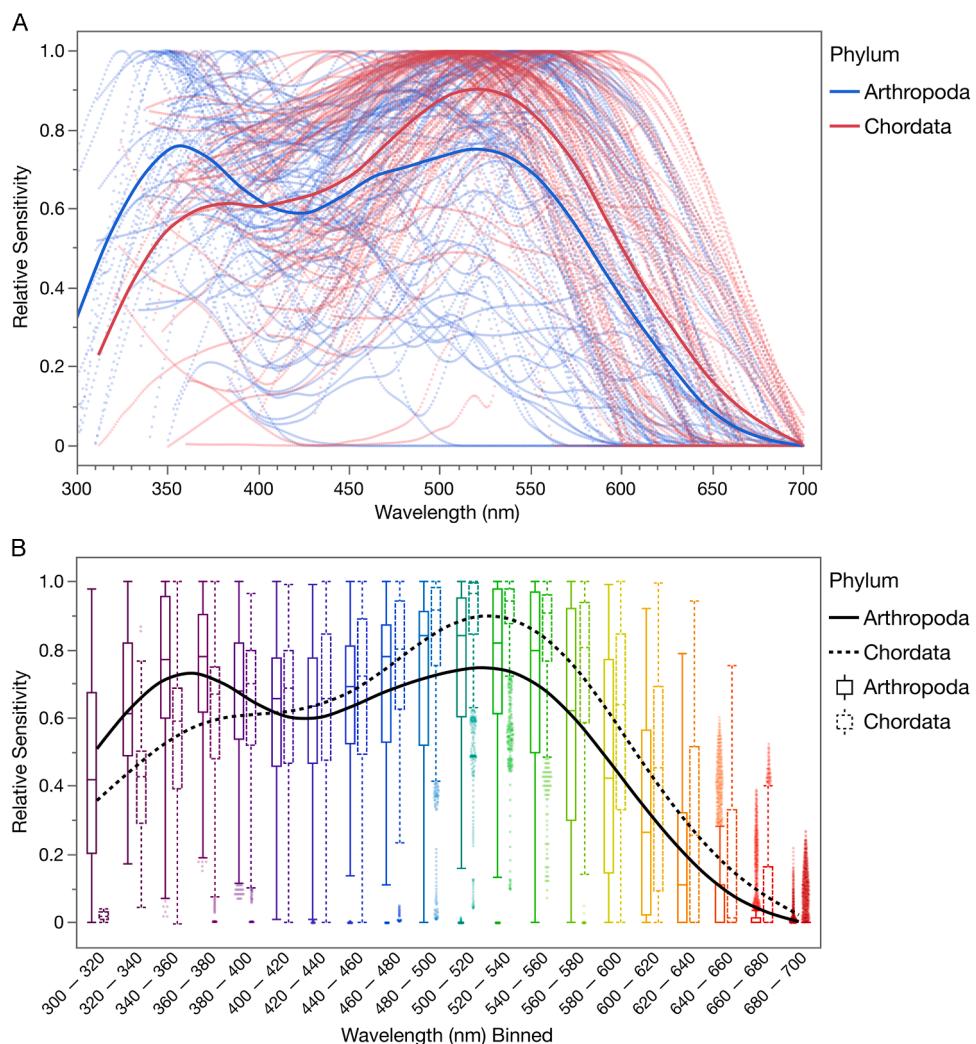
I plotted human scotopic and photopic vision with the aggregate curves by class to illustrate the differences between human vision and

that of different classes of wildlife (Fig. 7). Human photopic vision is more sensitive to longer wavelengths of light than the mean values for other classes. Human scotopic vision has a peak similar to many other species around 500 nm, but under most circumstances when humans are using artificial light outdoors, it is sufficiently bright for photopic vision to be in play, or in the realm of mesopic vision with both systems contributing (CIE, 2020).

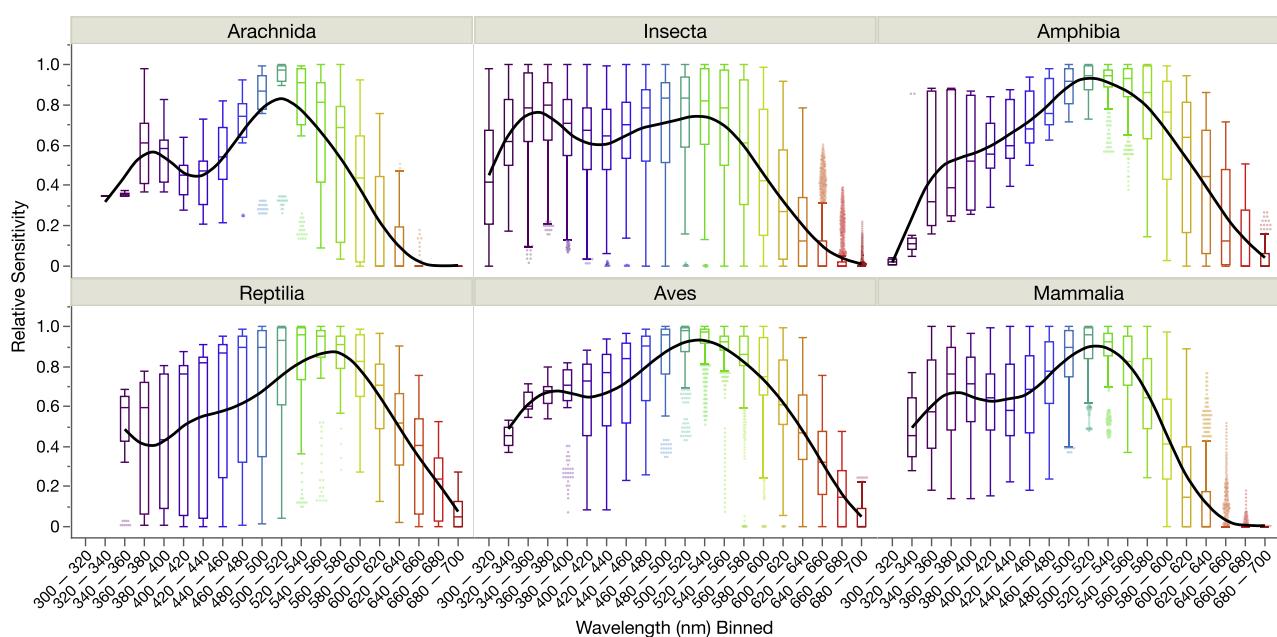
Finally, linear regression of the visual responses for different exemplar light sources against CCT, Melatonin Suppression Index, and Star Light Index showed that potential impacts from light at night increased as each of these summary measures of light spectral composition increased (Fig. 8). The slope of these lines was greatest for insects, mammals, arachnids, and the sole crustacean in the dataset, suggesting sensitivity less than half that of daylight for the lowest CCT lamp (~1200 K of an LED with all blue light filtered out), which also had the lowest melatonin suppression and star light visibility values.

## Discussion

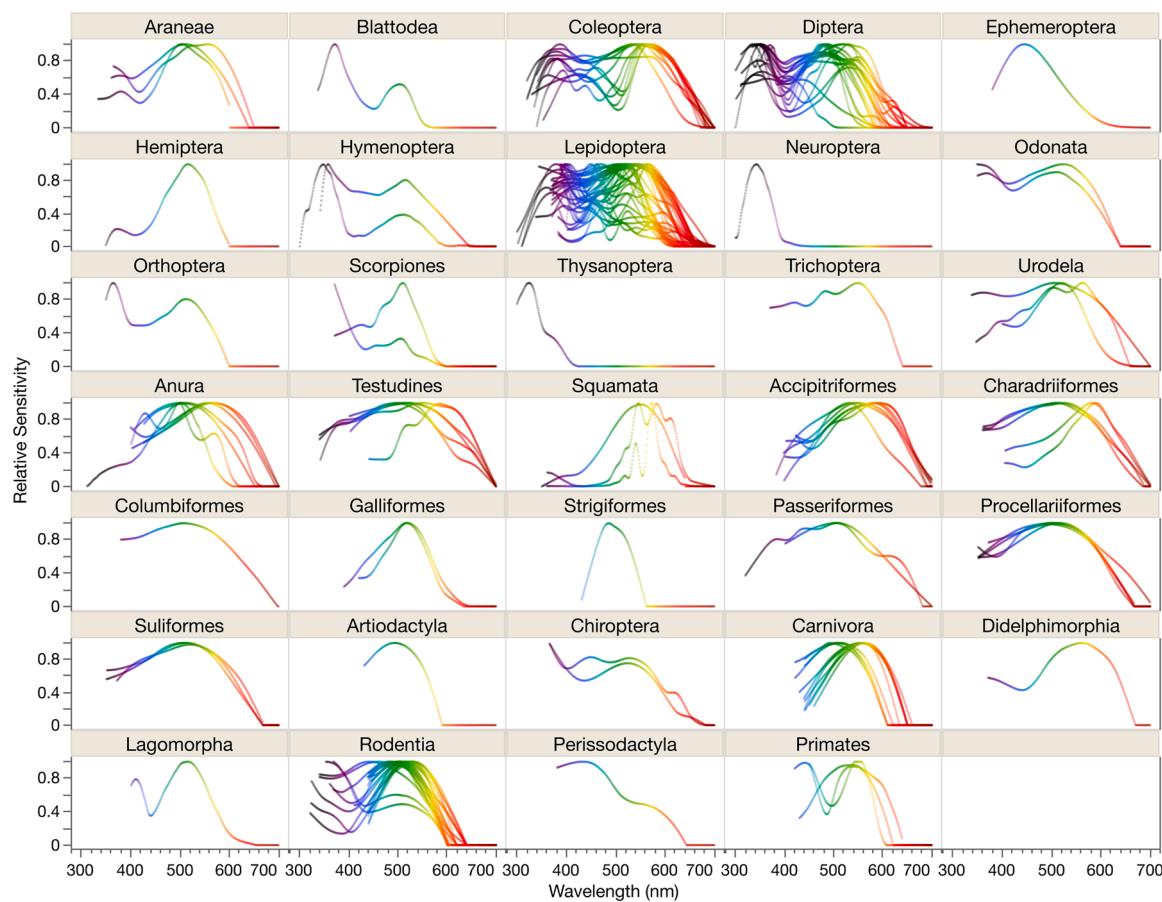
The assembled data provide a basis for evaluating the degree to which different taxonomic groups are sensitive to light across the visible spectrum (as defined by each group). The combined database contains spectral response curves for both photopic and scotopic visions because



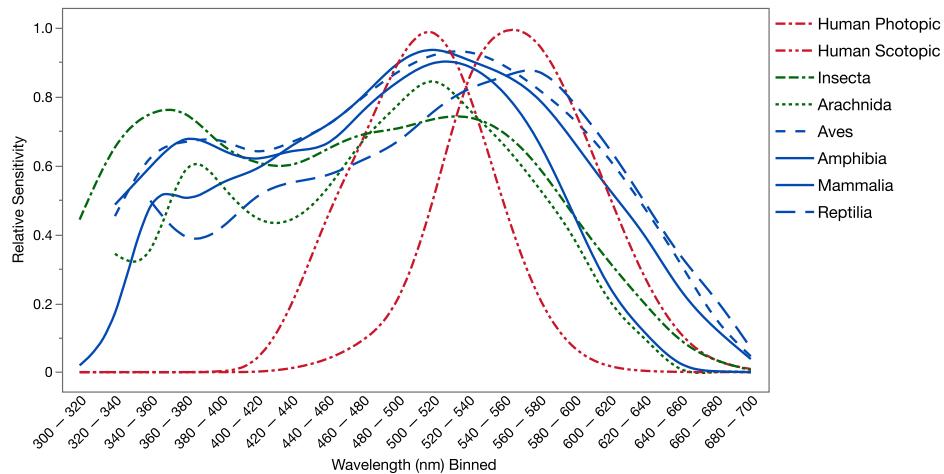
**Fig. 4.** (A) Comparison of spectral sensitivity of chordate ( $n=90$ ) and arthropod ( $n=87$ ) species curves. (B) Box plot comparisons of spectral sensitivity at 20 nm increments. Both graphs are fit with cubic splines.



**Fig. 5.** Box plot comparisons of spectral sensitivity at 20 nm increments for selected classes, with cubic spline.



**Fig. 6.** Spectral sensitivity curves by order. Curves are grouped by class (Araneae, Insecta, Amphibia, Reptilia, Aves, Mammalia).

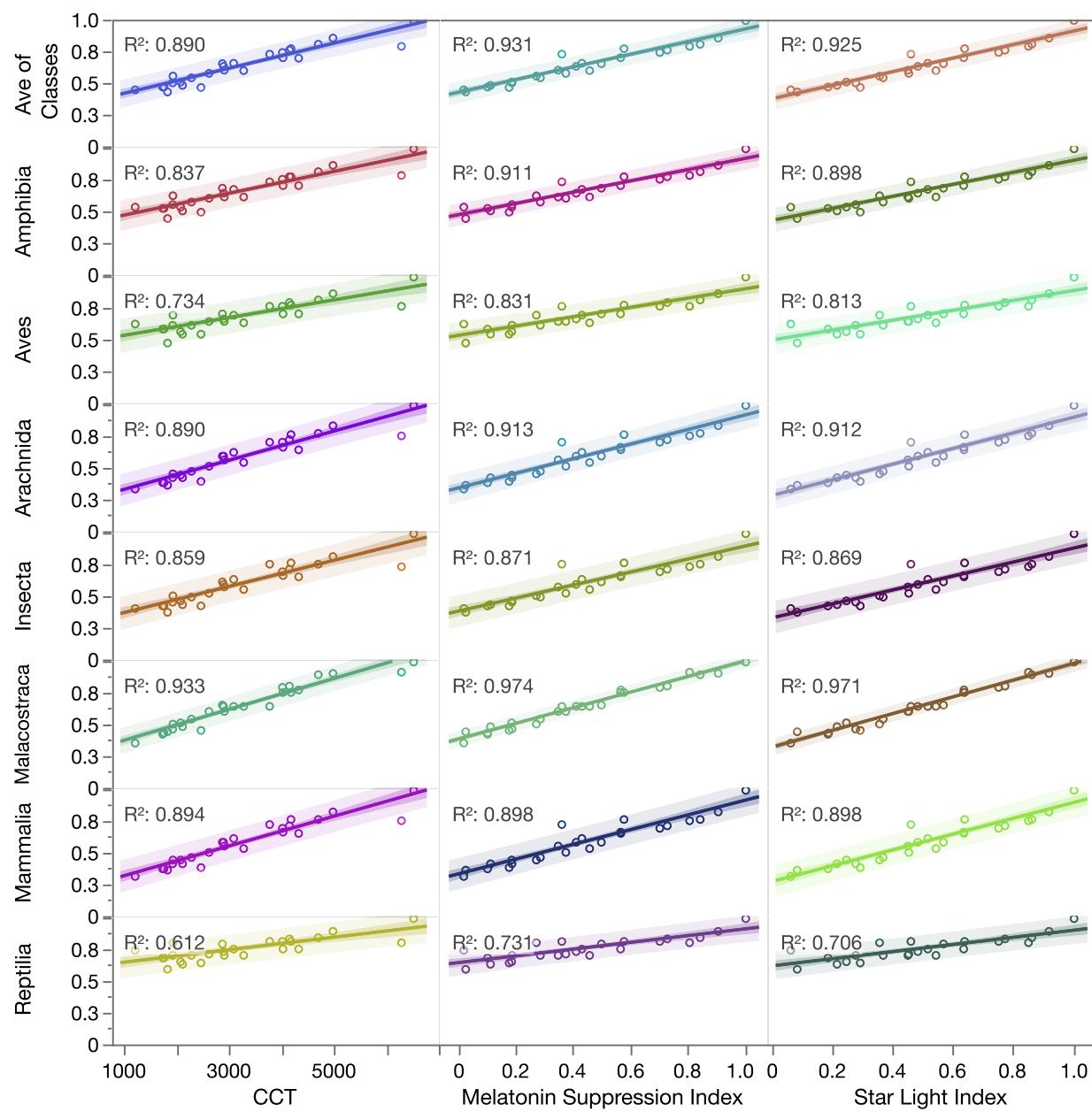


**Fig. 7.** Spectral sensitivity of human photopic and scotopic vision, with aggregate sensitivity for other classes of terrestrial species.

both systems may be implicated when evaluating the potential effects of artificial light at night. The threshold points for conversion from scotopic (achromatic) to photopic (chromatic) vision vary by taxa (Kelber et al., 2002; Kelber & Lind, 2010) so no single threshold can be set to distinguish between the two visual systems when calculating environmental impacts for whole biological communities. Furthermore, insects do not shift from one set of photopigments to another and may have color vision at extremely low light levels (Johnsen et al., 2006). Future research could compile the illumination thresholds for the

transition between photopic and scotopic responses for all the available curves.

The usefulness of these response curves depends on the assumption that species will have a greater response to light that is perceived as being more intense, and that the responses are linear or at least highly correlated with the intensity of the light. For the behavioral curves, this condition is met, but for the ERG and optical reflectance curves no specific behavior is known to be associated with the power of the electrical charge released in response to the light or the energy absorbed by



**Fig. 8.** Linear regression of spectral characteristics of 27 light sources as summarized by correlated color temperature (CCT), Melatonin Suppression Index, and Star Light Index (Aubé et al., 2013) with generalized visual response curves for classes of terrestrial wildlife and the average curve for all classes. Shaded area indicates 95% confidence bands of regression.

it, but some studies do show this correlation (Young et al., 2012). Behavioral response curves have been built through parameterizing the sensitivity of individual opsins using flight-to-light data from the field (Donners et al., 2018) and used to predict attraction to different spectral compositions in the field (Deichmann et al., 2021). There are contradictory studies as well (Pawson & Bader, 2014), so more studies are needed with a well-conceived design and *a priori* prediction of impacts based on the mechanistic approach established by Saunders et al. (2008), van Grunsven et al. (2014), and Longcore et al. (2018). Further research should also investigate behavioral and perceptual responses that involve complex processing such as spectral opponency mechanisms (Jacobs, 2014).

Indeed, more studies confirming that behavioral responses are correlated with visual sensitivity would be beneficial, testing the hypotheses that arise from the ERG and optically derived response curves. It is certain that in some instances response curves will not coincide with

sensitivity, such as shown by the attraction of tiger salamanders to traps with orange glow sticks in them, even though yellow and green glow-sticks would have appeared brighter to them (Liebgold & Carleton, 2020). Behavioral preferences such as these, associated with a species' ecology, must be widespread. The potential of spectral tuning for lighting mitigation is most likely to be realized for impacts where positive or negative phototaxis are at play, or where species are responding to the overall light environment's brightness to assess, for example, whether to forage. In such instances, avoidance of areas of the spectrum where the organism is most sensitive should reduce impacts. Consideration must also be given to those situations where light in an area of the spectrum to which a species has low sensitivity nevertheless interferes with key behaviors such as the discernment of prey items (Briolat, Gaston, Bennie, Rosenfeld, & Troscianko, 2021).

In the absence of additional information, however, the compendium of photopigment sensitivity and quantification of spectral response

averages by taxonomic group still confirms current best practices for reducing impacts from light at night through spectral tuning. The compilation visualizes for the first time that the average arthropod is more sensitive to blue and ultraviolet light than the average chordate (of those for which curves are available at least). The visualizations make clear that it is only with longer wavelengths that it might be possible to provide illumination for humans, while reducing the overlap with the vision of other species. It also demonstrates that longer wavelength light can fall at a sensitivity peak for charismatic groups such as bioluminescent beetles (Lall et al., 1982). The photopigments and response curves show that diurnally active organisms, especially chordates, are more likely to be sensitive to longer wavelengths on average, but they are also more likely to have ultraviolet vision as well.

Although my effort in this paper focused on visual responses to light, the high correlation of the average class-level responses with the melatonin suppression index indicates that efforts to avoid *non-visual* circadian impacts will also reduce visual impacts and vice versa. This relationship was strong, however, only because none of the lamps in the database used in the comparison had emissions in the ultraviolet portion of the spectrum. If ultraviolet had been included, then a lamp could, in theory, have a high visual apparentness to an organism while having a low effect through non-image forming light detection pathways leading to melatonin suppression.

Visual response systems, despite being evolutionarily conserved, still encompass large variability. Consequently, there is no “silver bullet” spectrum that will perfectly provide nighttime visual safety for humans while avoiding impacts on other species. Spectral tuning is an additional benefit that should be pursued in concert with other mitigation measures, such as controlling light power, restricting operating times, dimming, and controlling light direction (Longcore & Rich, 2017). Then, spectral tuning may provide some additional reduction in impacted area, which could be calculated relative to a standard such as the full moon (Ditmer et al., 2021) and use spectral response curves generalized at the lowest feasible taxonomic level that have been compiled here.

Spectral tuning to reduce wildlife responses to light at night should also consider and incorporate the influence of light through non-image forming photoreceptors as equally important as visual responses. Given that light pollution is also a concern for astronomical observation, effects on human nighttime vision as summarized in Aubé et al.’s Star Light Index might also be given equal consideration. Fortunately, each of these metrics leads to the similar design approach of avoiding shorter wavelengths to the degree possible and emphasizing longer wavelengths where human vision will function relatively better than most other species. Such advice is not, however, a license to use unlimited long-wavelength light, because the visual spectral sensitivity of the organisms assessed here decreases logarithmically and many species maintain some sensitivity at these longer wavelengths that can be stimulated by high light levels. My conversion of all response to a 0–1 range, combined with limits on the range of wavelengths tested in studies, results in the potential for very low sensitivity to light at the extremes and beyond the ranges tested to be reported as zero instead of very low. Consequently, the effects of high-intensity long-wavelength light will be underestimated. In addition, lamp types that may have emissions predominantly in the longer wavelengths often also have shorter wavelength emissions. Furthermore, when such lamps are deployed, the preponderance of long wavelength light does not eliminate the effects of shorter wavelength light as a biological signal that increases in strength with the intensity of the light.

Finally, I note that results from the visual response curves are influenced by the range of wavelengths tested by researchers in original studies. Although nearly all studies included a range from 450–575 nm, testing dropped off to half of the studies below 370 nm and above 650 nm. Although one could reasonably safely presume that responses were converging to zero at the upper end of this range, additional responses in the ultraviolet range might have been measured had studies included these wavelengths. Future assessments of visual responses should, if

possible, include light in the near UV (315–400 nm) and at least through 700 nm.

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## Data availability

The compiled datasets of peak spectral sensitivities are available at [http://github.com/tlongcore/photopigments](https://github.com/tlongcore/photopigments) (doi:10.5281/zenodo.8432720) and visual response curves are available at <https://github.com/tlongcore/spectral-response-curves> (doi:10.5281/zenodo.8432683).

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi [10.1016/j.baae.2023.09.002](https://doi.org/10.1016/j.baae.2023.09.002).

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