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Connecting spectral radiometry of anthropogenic light sources to the visual ecology of organisms

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Abstract

Humans have drastically altered nocturnal environments with electric lighting. Animals depend on natural night light conditions and are now being inundated with artificial lighting. There are numerous artificial light sources that differ in spectral composition that should affect the perception of these light sources and due to differences in animal visual systems, the differences in color perception of these anthropogenic light sources should vary significantly. The ecological and evolutionary ramifications of these perceptual differences of light sources remain understudied. Here, we quantify the radiance of nine different street lights comprised of four different light sources: Metal Halide, Mercury Vapor, Light Emitting Diodes, and High-Pressure Sodium and model how five animal visual systems will be stimulated by these light sources. We calculated the number of photons that photoreceptors in different visual systems would detect. We selected five visual systems: avian UV/VIS, avian V/VIS, human, wolf and hawk moth. We included non-visual photoreceptors of vertebrates known for controlling circadian rhythms and other physiological traits. The nine light types stimulated visual systems and the photoreceptors within the visual systems differently. Furthermore, we modelled the chromatic contrast (Just Noticeable Differences [JNDs]) and color space overlap for each light type comparison for each visual system to see if organisms would perceive the lights as different colors. The JNDs of most light type comparisons were very high, indicating most visual systems would detect all light types as different colors, however mammalian visual systems would perceive many lights as the same color. We discuss the importance of understanding not only the brightness of artificial light types, but also the spectral composition of light types, as most organisms have different visual systems from humans. Thus, for researchers to understand how artificial light sources affect the visual environment of specific organisms and thus mitigate the effects, spectral information is crucial.

Introduction

Over 200 years ago Humphry Davy invented arc lamps, beginning an era of drastic changes to nocturnal environments. Since then, our planet has been inundated with electric lighting of numerous types, which alter the natural light cycles and nightscape (Bowers, 1998; Elvidge *et al.*, 2010; Gaston, Duffy & Bennie, 2015a; Falchi *et al.*, 2016). Each light source has unique spectral characteristics that differ from natural light (Elvidge *et al.*, 2010; Johnsen, 2012; Spitschan *et al.*, 2016), thus artificially illuminating the night. Organisms are chronically exposed to artificial lighting, which affects foraging, communication, circadian rhythms, endocrinology, predator-prey interactions, reproduction and other biological functions (Longcore, 2010; Davies, Bennie & Gaston, 2012; Dominoni *et al.*, 2013; Brüning *et al.*, 2015). Ultimately, these changes in animal behavior, physiology and ecology from artificial light at night are due to organismal reception of anthropogenically produced light (Kuenzel, Kang & Zhou, 2014; Alaasam *et al.*, 2018). Millions of different species of organisms have evolved the ability to detect light for visual tasks and as cues for circadian rhythms and phenology, thus altering natural light conditions has grave ecological consequences (Cronin *et al.*, 2014; García-Fernández *et al.*, 2015; Davies & Smyth, 2017; Gaston *et al.*, 2017).

Although numerous studies have investigated behavioral responses to different light sources (Langevelde *et al.*, 2011; van Grunsven *et al.*, 2014; Longcore *et al.*, 2015; Spoelstra *et al.*, 2017), few studies have investigated varied spectral signatures in the environment, see Davies *et al.* (2013); Donners *et al.* (2018); Longcore *et al.* (2018). Davies *et al.* (2013) found that low-pressure sodium lamps emitted the smallest proportion of the light spectrum to which animals are sensitive, whereas metal halides (MH) lamps emitted the largest proportion. Donners *et al.* (2018) and Longcore *et al.* (2018) have devised theoretical models to determine how specific light

sources overlap with the full range of visual sensitivities for organisms. These studies have established an understanding of how different spectra of light sources overlapped with different visual systems, however, these studies combine the overall visual range of organisms and do not investigate artificial light at the photoreceptor level. As conservation and lighting efforts move forward, we must begin to investigate the overlap of artificial light sources on photoreceptors as photoreceptors are ultimately responsible for organismal responses to artificial light.

We are currently in a major transition of lighting technology from older and less efficient light sources to more efficient light emitting diodes (LED) technology (Kyba *et al.*, 2017). Older technology consists of broad spectrum light sources: high pressure sodium (HPS), mercury vapor (MV), and MH (Elvidge *et al.*, 2010). These older lights, as well as LEDs, differ in spectral composition. HPS lamps are long wavelength dominant, both MV and MH have unique spectral peaks that match the human visual system, and LED lamps have a relatively equal distribution of wavelengths, (Elvidge *et al.*, 2010). Thus, during this transition from the older light sources to LEDs, organisms will be exposed to numerous light sources and then eventually only different colors of LEDs (Elvidge *et al.*, 2010; Kyba *et al.*, 2017). To understand the reception, and thus the proximate mechanisms of organismal responses, of these different light sources both within and between visual systems of organisms we must quantify how different visual systems will detect light sources.

The myriad visual systems that detect light at night are very diverse (Briscoe & Chittka, 2001; Hart, 2001; Davies *et al.*, 2013). Visual systems depend upon opsins, proteins that detect light, and different opsins selectively capture photons of specific wavelengths (Cronin *et al.*, 2014). This enables animals to perceive colors in the environment. Animals have evolved diverse sets of opsins and photoreceptors that engender numerous color vision types and most animals have either four (tetrachromacy), three (trichomacy), or two (dichromacy) (Cronin *et al.*, 2014). In addition to the varied color vision of many animals, animals also have non-visual photoreceptors with different opsins that use light as a cue for biological functions, such as circadian rhythms, reproductive timing and sleep (Hattar *et al.*, 2002; Halford *et al.*, 2009; Gaston *et al.*, 2017). These non-visual opsins in photoreceptors in vertebrates (referred to as deep brain photoreceptors) include melanopsin, neuropsin, pinopsin and vertebrate ancient opsin (Kuenzel *et al.*, 2014; Dominoni, 2015). Melanopsin regulates circadian rhythms in vertebrates (Ruby *et al.*, 2002). Neuropsin is an ultraviolet-sensitive opsin controlling seasonal activity patterns (Nakane *et al.*, 2010), whereas pinopsin is involved in pineal function and daily rhythms (Holthues *et al.*, 2004), and the function of vertebrate ancient opsin is still unknown. These non-visual opsins have different spectral sensitivities that are likely to be affected differently by artificial lights at night. Due to the numerous opsins involved in both vision and biological functions, it is likely that anthropogenic lighting affects organisms differently dependent upon light source and opsin composition, which could drastically change hormone production, circadian rhythms, prey detection, reproductive timing and habitat utilization (Longcore & Rich, 2004; Gaston *et al.*, 2012, 2017; Davies & Smyth, 2017).

We calculated how different artificial light sources stimulate the photoreceptors of different visual systems of organisms that are likely to be affected by artificial light at night. We tested if subtle differences in spectral composition of very similar light sources (e.g. high-pressure sodium lamps of different wattages), can disparately affect the same visual system. We measured the radiance of nine common types of city light sources and then calculated how five different animal visual systems would be stimulated at the photoreceptor level. We compared how the different non-visual photoreceptors that occur in the brains of birds and many vertebrates are stimulated by the nine different light types. Lastly, using Just Noticeable Differences (JND) and color space analysis, we tested theoretical chromatic discrimination between different anthropogenic light sources. We predicted that animals should discriminate between different types of sources (e.g. HPS vs. MH), but not between different wattages of the same source (e.g. HPS 400 vs. HPS 100 W). Ultimately, we investigated the underlying reception of artificial lights that organisms will experience in their nocturnal environments to determine if the anthropogenic nightscape is similar for humans and other organisms. Our aim is to lay a foundation for future work to investigate the ecological and organismal consequences of the disparate visual perception of myriad colored lights at night.

Materials and methods

Measurements of artificial light sources

In collaboration with the City of Fort Collins, CO Utilities, we measured four different light sources: LEDS, HPS, MV and MH. Furthermore, we measured five different wattages (referred to as types throughout) of HPS, and two different types of MV, for a total of nine different light types - Table 1 for specific wattage of light sources. We measured radiance, which is the light emitted from a source restricted to a solid angle as this represents how eyes of organisms would be detecting these light sources (Johnsen, 2012). Using a custom-made fiber optic holder that held two lasers on each side of the radiance probe, we were able to confirm that the probe was pointed directly at the intended light source, Fig. 1. The lasers were only on for lens alignment and then were turned off for radiance measurement.

Radiance of the lights was measured 25 m from the light source between 20:20 and 23:50 on September 25, 2017 under clear new moon conditions. We used a LENS-QCOL collimating lens (StellarNet, Tampa, FL, USA) attached via a 1000 μm fiber optic cable (F1000-UVVis-SR-1; StellarNet), to a highly sensitive spectroradiometer (SILVER-Nova-TEC-X2; StellarNet). Each light source was measured three times with the collimating lens focused on the bottom, center, and top of the light source. Using Spectrawhiz software (StellarNet), we recorded radiance in energy flux in watts/m^2/second/nm and measured at a solid angle of 0.002 sr. Twenty-five meters was selected for two reasons: (1) it is more biologically relevant to be at least 25 m from the source as many animals will not be directly next to the source but instead will see the source from

Table 1 Light sources and spectral metrics. Brightness, chroma and hue values for each of the nine different light sources. Means are reported first followed by the standard deviation

Light source	Wattage (Type)	*N*	Brightness	Chroma	Hue
High pressure sodium	70	4	4.38E17 ± 4.52E17	8.75 ± 1.65	1.13 ± 0.11
High pressure sodium	100	4	2.68E18 ± 1.37E18	7.88 ± 0.92	1.04 ± 0.09
High pressure sodium	150	4	2.98E18 ± 1.45E18	9.19 ± 0.53	1.17 ± 0.03
High pressure sodium	250	4	1.88E18 ± 1.04E18	8.04 ± 1.48	1.02 ± 0.09
High pressure sodium	400	4	8.34E18 ± 1.23E19	7.48 ± 0.54	1.06 ± 0.03
Light emitting diode	73	4	2.61E18 ± 2.60E18	2.65 ± 0.15	1.16 ± 0.09
Metal halide	1000	4	8.66E19 ± 7.04E19	6.59 ± 2.22	−1.34 ± 0.15
Mercury vapor	175	4	3.04E17 ± 2.41E17	11.75 ± 1.00	0.78 ± 1.29
Mercury vapor	250	4	4.31E17 ± 2.81E17	11.46 ± 0.76	0.75 ± 1.18

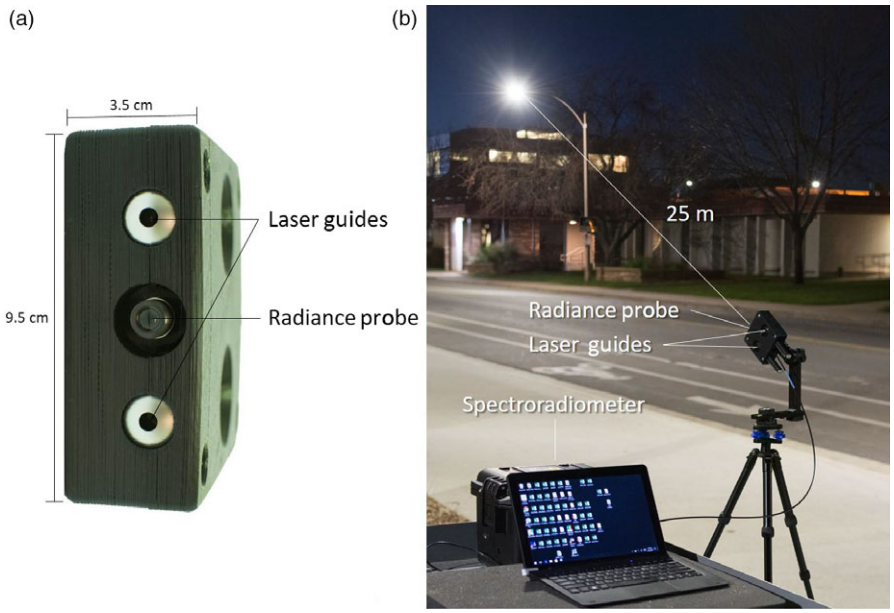

Figure 1 (a) Radiance setup with laser pointer guides and collimating lens housed in 3-D printed block. (b) Field setup using radiance probe, laser guides and panoramic mount.

a distance; and (2) for researcher safety as we needed to be on the other side of the street from the light pole and not in oncoming traffic.

Radiance analysis

All data processing and analysis was performed using the *pavo* package (Maia *et al.*, 2013) implemented in R (Team, 2014). We converted radiance data from radiant flux to photon flux (photons/cm^2/second/sr/nm) (Johnsen, 2012). Furthermore, as the light sources subtended a solid angle of 0.00005 sr, we converted each radiance value from 0.00005 sr to one sr. We compared the spectra of light sources for three different metrics: brightness, chroma and hue, see (Montgomerie, 2006) for complete discussion. Brightness (B_T) is a measure of the total amount of light coming from a unit area of a surface per unit time and was calculated by integrating radiance over all wavelengths (300–700 nm), see equation 1 (Montgomerie, 2006). Chroma (S_8) is a measure of the degree to which a color appears to be pure, and thus composed of a single wavelength of light (Montgomerie, 2006). Chroma was calculated by dividing the difference of the maximum wavelength by the minimum wavelength by the mean brightness, see equation 2 (Montgomerie, 2006). The mean brightness was calculated by dividing the brightness by 400, which is the number of nanometer intervals and thus gives us an average brightness for each wavelength. Hue is the 'color' and indicates which wavelengths contribute most to the total radiance. Due to the many different peaks within one spectrum of artificial light, we used an arctan function of the differences between different ranges of the spectrum to calculate hue, see equation 3 and Montgomerie (2006) for discussion. We then tested for normality with a Q-Q plot assessing multivariate normality, which revealed that the data do not follow a multivariate normal distribution. Thus, we ran a nonparametric equivalent of a MANOVA, the PERMANOVA, using an analysis of variance using

distance matrices (Anderson, 2001; Kabacoff, 2015). The three metrics (brightness, saturation and hue) were the response variables and the light type was the independent variable. A Tukeys HSD was then used to determine differences between each light source for each metric.

$$B_T = \int_{\lambda 300}^{\lambda 700} R_i \quad (1)$$

R_i = Proportional radiance at the ith wavelength

$$S_8 = (R_{max} - R_{min})/B_2 \qquad B_2 = \sum_{\lambda 300}^{\lambda 700} R_i/n_w \quad (2)$$

$$H_4 = \arctan\{[B_y - B_b)/B_T]/[(B_r - B_g)/B_T]\} \quad (3)$$

Visual system stimulation of artificial light sources: spectral sensitivities of select organisms

To determine how the artificial light sources would stimulate myriad visual systems, we calculated quantal catch for each photoreceptor of the selected organisms: an averaged ultraviolet sensitive Passeriformes visual system (UV/VIS) (Hart, 2001; Endler & Mielke, 2005; Maia *et al.*, 2013), an average non-ultraviolet sensitive avian visual system (V/VIS) (Hart, 2001, 2002; Maia *et al.*, 2013), a human (Dartnall, Bowmaker & Mollon, 1983), a Wolf (Jacobs *et al.*, 1993), a hawkmoth (Schlecht, 1979; Briscoe & Chittka, 2001), and we also included the deep brain photoreceptors of birds (Kuenzel *et al.*, 2014).

Specifically, birds have tetrachromatic color vision meaning they have four different classes of photoreceptors that are involved in opponent processing enabling a bird to perceive different colors (Vorobyev & Osorio, 1998; Endler & Mielke, 2005; Ghim & Hodos, 2006; Hart & Hunt, 2007). The difference between the UV/VIS and V/VIS is mostly in the spectral sensitivity of the shortest photoreceptor. UV/VIS is sensitive to ultraviolet light whereas V/VIS is not, but is still sensitive to very short wavelengths of light (i.e. V) (Hart, 2001; Ghim & Hodos, 2006). Furthermore, all birds have two visual photoreceptors not involved in color perception: double cones and rods (Hart, 2001; Cronin *et al.*, 2014). The double cones are an intermediary between the tetrachromatic color vision, which require bright conditions and rods which are only activated in very dim light conditions. Birds also have photoreceptors located within the brain that detect photons from the environment that are transmitted through the bird's diaphanous skull (Wyse & Hazlerigg, 2009; Kuenzel *et al.*, 2014). There are at least four deep brain photoreceptors: neuropsin, melanopsin, pinopsin and vertebrate ancient opsin (Max *et al.*, 1995; Halford *et al.*, 2009; Wyse & Hazlerigg, 2009; Kuenzel *et al.*, 2014).

The human visual system is comprised of three types of cones involved in color vision and one type of rod used for dim-light vision (Dartnall *et al.*, 1983). The Wolf has dichromatic color vision comprised of a short wavelength cone and a long wavelength cone, and the same rod as humans (Jacobs *et al.*, 1993). Lastly, the elephant hawk moth has trichromatic color vision and is currently the record holder for lowest light level color vision in the animal kingdom ((Schlecht, 1979; Kelber, Balkenius & Warrant, 2002; Stöckl, Ribi & Warrant, 2015; Stöckl, O'Carroll & Warrant, 2016)). All photoreceptor sensitivities were calculated using published lambda max values, the peak sensitivity of the photoreceptor, for each visual system and then a Govardovskii template to calculate the complete spectral sensitivity, Table 2 for lambda max values and citations for each visual system (Govardovskii *et al.*, 2000). All spectral sensitivities were calculated using the R plug-in *Pavo* (Maia *et al.*, 2013).

Visual system stimulation of artificial light sources: photoreceptor quantal catch calculations

Several models exist to understand how different spectra are perceived and discriminated by a specific visual system, see Endler, 1990; Vorobyev & Osorio, 1998; Vorobyev *et al.*, 1998; Maia *et al.*, 2013. Most models use the receptor sensitivity of the different photoreceptors to quantify how a given spectrum would stimulate those photoreceptors and the combined effect on color perception. We modified the visual models to enable for an understanding of each light source on each photoreceptor type for each visual system by calculating the number of photons that each photoreceptor would theoretically capture using the known absorbance properties for each photoreceptor and the number of photons at each wavelength for each light source. The number of photons that a photoreceptor catches (Q_i) is referred to as quantum catch and is calculated for a receptor i as follows:

$$Q_i = \int_{\lambda} R_i(\lambda) I(\lambda) d\lambda$$

where λ denotes the wavelength, $R_i(\lambda)$ the spectral sensitivity of receptor i, and $I(\lambda)$ the radiance spectrum (Endler, 1990). Thus, each visual system has several Q_i values and we compared the values of each Q_i for each visual system under the different light sources. We must state that this approach is rarely used, but see Eaton, 2005, as vision is a multivariate process that includes the multiple comparisons and correlations among receptor catches (Kelber, Vorobyev & Osorio, 2003; Maia & White, 2018). However, we aim to test how different light sources stimulate photoreceptors as well as the perception of these light sources. Thus, we first present the stimulations of individual photoreceptors within each visual system, then the ratios of photoreceptor stimulation for each visual system.

Statistical analyses of photoreceptor quantal catches

For each visual system (e.g. avian UV/VIS), we statistically compared the quantum catches (Q_i) between each photoreceptor type and within each photoreceptor type for all nine artificial light sources with MANOVA. The response variables were the different photoreceptor types comprising each visual system (e.g. for the UV/VIS visual system: Q_{UV}, Q_S, Q_M, Q_L,

Q_{DC}, Q_{Rod}). The between factors were the light source (i.e. HPS, LED, MV, & MH), and wattage (e.g. 100W and 250W), whereas the repeated measures were the replicated radiance for each individual light. We checked for normality with a Q-Q plot assessing multivariate normality, which revealed that the data were normally distributed. To determine which specific light sources differed in Q_i, we ran Tukeys HSD comparisons for each Q_i for each visual system.

Visual system stimulation of artificial light sources: just noticeable differences of light sources

To determine if these organisms could perceive light sources as different colors, we first calculated JNDs for each visual system (Vorobyev & Osorio, 1998). JNDs quantify the discriminability of two colors dependent upon the inherent noise of photoreceptors, with JNDs less than one being physiologically indistinguishable by the viewer due to the small signal to noise ratio within the photoreceptor (Vorobyev & Osorio, 1998; Vorobyev *et al.*, 2001; Osorio & Vorobyev, 2005). Two light sources with a JND above one will theoretically be seen as different colors in ideal visual conditions, i.e. bright lighting and non-moving objects. In more natural settings, two colors with a JND of three or less are unlikely to be seen as different (Siddiqi *et al.*, 2004; Langmore *et al.*, 2011; Thurman & Seymoure, 2016). Furthermore, discrimination will depend on both the color (chromatic) and brightness (achromatic) differences between the light sources. However, in this study we focus on the spectral differences as we are concerned with how visual systems will perceive color of these light sources as this will guide further research into proximate mechanisms of anthropogenic lights altering behavior and physiology. Using the quantum catches calculated above, we ran neural noise models with noise set relative to the cone ratios for each visual system with a weber fraction of 0.1 (Table 3; Vorobyev & Osorio, 1998; Olsson, Lind & Kelber, 2017). We report the mean JNDs and the standard error for each light comparison including within light type comparisons.

Lastly, to support the chromatic contrast (JND) analysis, we calculated the color space of each light source for each tetrachromatic and trichromatic visual system (Maia *et al.*, 2013). For color space models, photon catches of all cones involved in chromatic discrimination were set relative to one another to sum to one. Then the maximum stimulation of each cone (*n*) was placed at the vertex of a *n*-1 dimensional polygon that encompasses all theoretical colors that can be perceived by that visual system (Vorobyev *et al.*, 1998; Endler & Mielke, 2005; Maia *et al.*, 2013). Under this color space framework, we calculated color distances as Euclidean distances of the relative cone stimulations. With these Euclidean distances, we calculated polygons of each light type using the four individual bulb values as the vertices of the polygon. Then we calculated the amount of polygon overlap that two light types had and if overlapped occur it is likely that the respective visual system would not perceive these two light types as different colors (Vorobyev *et al.*, 1998). As this overlap approach is descriptive, we did not run statistics on these data and instead inferred whether these visual systems would perceive differences in color of the light types dependent upon polygon overlap.

Table 2 Lambda max values and citations for each species and for each deep brain photoreceptor used in the photon catch models

Species	UV	V	S	M	L	Double cones	Rod	Citations
Avian UV/VIS	372	–	456	544	609	563	506	Hart (2001), Maia *et al.* (2013)
Avian V/VIS	–	416	478	542	607	563	506	Hart (2001), Maia *et al.* (2013)
Human	–	–	420	527	557	–	505	Dartnall *et al.* (1983)
Wolf	–	–	431	–	555	–	505	Jacobs *et al.* (1993)
Hawkmoth	350	–	440	520	–	–	–	Briscoe & Chittka (2001)

Deep brain photoreceptors	λ_{max}	Citations
Neuropsin	360	Kuenzel *et al.* (2014)
Pinopsin	470	Max *et al.* (1995), Kumar *et al.* (2017)
Melanopsin	484	Torii *et al.* (2007), Garcia-Fernandez (2015)
Vertebrate Ancient	490	Young (1962), Hankins *et al.* (2008), Garcia-Fernandez (2015)

Each value represents the peak of the absorbance spectrum for each photoreceptor. Cells without values indicate that the visual system does not have that photoreceptor. We calculated the full spectrum using Govardovskii templates.

Table 3 Relative cone ratios for each visual system used to calculate Just Noticeable Differences

Species	UV	V	S	M	L	Citations
Avian UV/VIS	1	–	2	2	4	Hart (2001)
Avian V/VIS	–	1	2	2	4	Hart (2001)
Human	–	–	4	20	76	Roorda & Williams (1999)
Wolf	–	–	1	–	10	Jacobs *et al.* (1993); Peichl (2005)
Hawkmoth	1	–	1	6	–	White (2003)

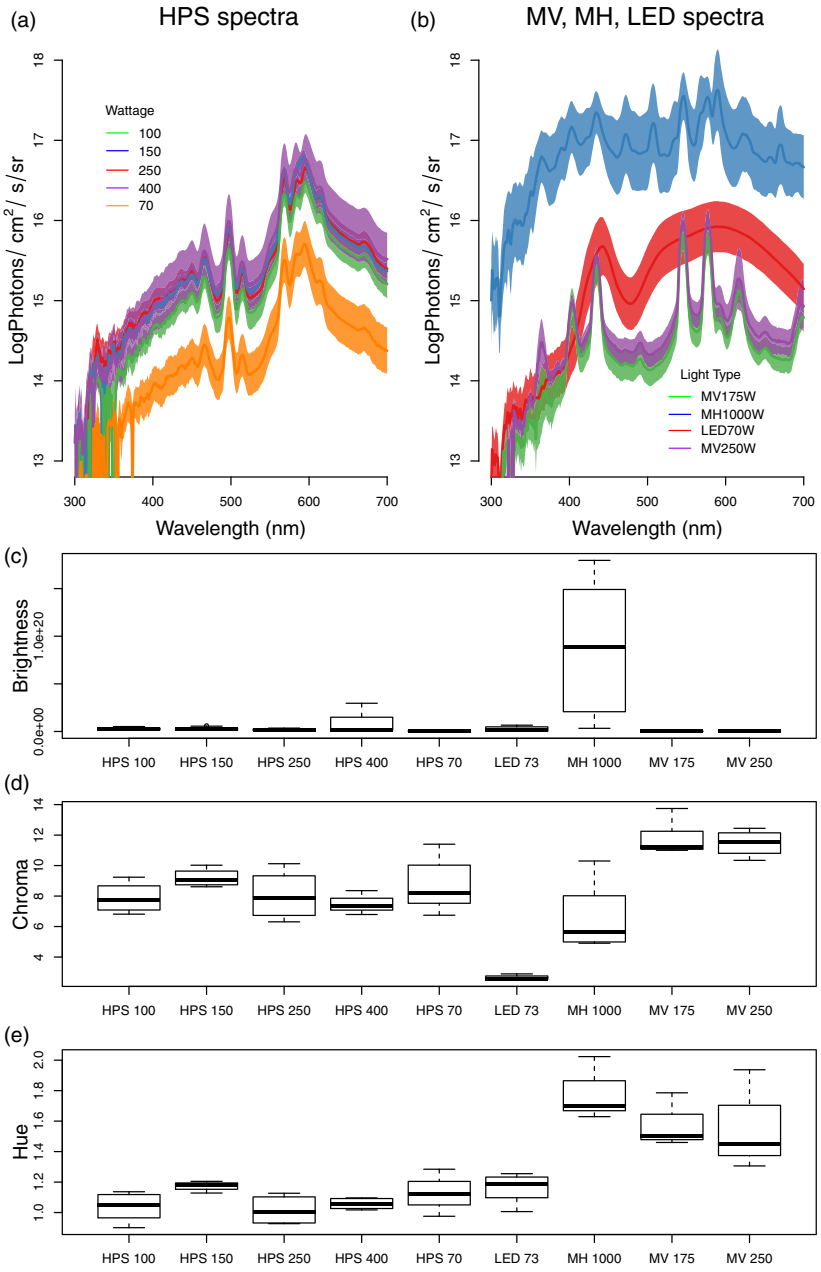

Figure 2 Artificial light at night spectra and boxplots of color metrics. (a and b) The mean spectra (solid line) and the standard error (shading) of the different HPS light sources and non-HPS light sources, respectively. Note that the y axes have been logarithmically scaled to reveal differences in intensity and spectral shape between the different light sources. Not surprisingly, all five HPS spectra are very similar in shape and only differ by intensity, whereas the LED, MH, and MV differ drastically in shape from one another. (c-e) Boxplots of spectral metrics (total brightness, chroma, and hue, respectively) for each of the nine different ALAN sources. Letters represent which groups are significantly different from one another. (c) Only 1000W metal halides (MH) were significantly brighter from the other light sources. (d) The LEDs were the least chromatic (i.e. most broadband), then followed by MH. The mercury vapor and high pressure sodium lights were highly chromatic, indicating that most light is of similar wavelengths (e.g. longer wavelengths for HPS). (e) A greater value of hue represents a spectrum dominant in longer wavelengths, while a lesser value represents a spectrum dominant in shorter wavelengths of light. MH had the greatest composition of short wavelengths while HPS and LEDs had the greatest composition of longer wavelengths of light.

Furthermore, there are inherent assumptions with these visual models: (2) chromatic and achromatic visual channels operate independently of one another; (2) that color is coded by *n*-1 opponent channels; and (3) that the limits to color discrimination are set by noise arising in receptors ((Vorobyev & Osorio, 1998; Kelber *et al.*, 2003; Olsson *et al.*, 2017; Maia &

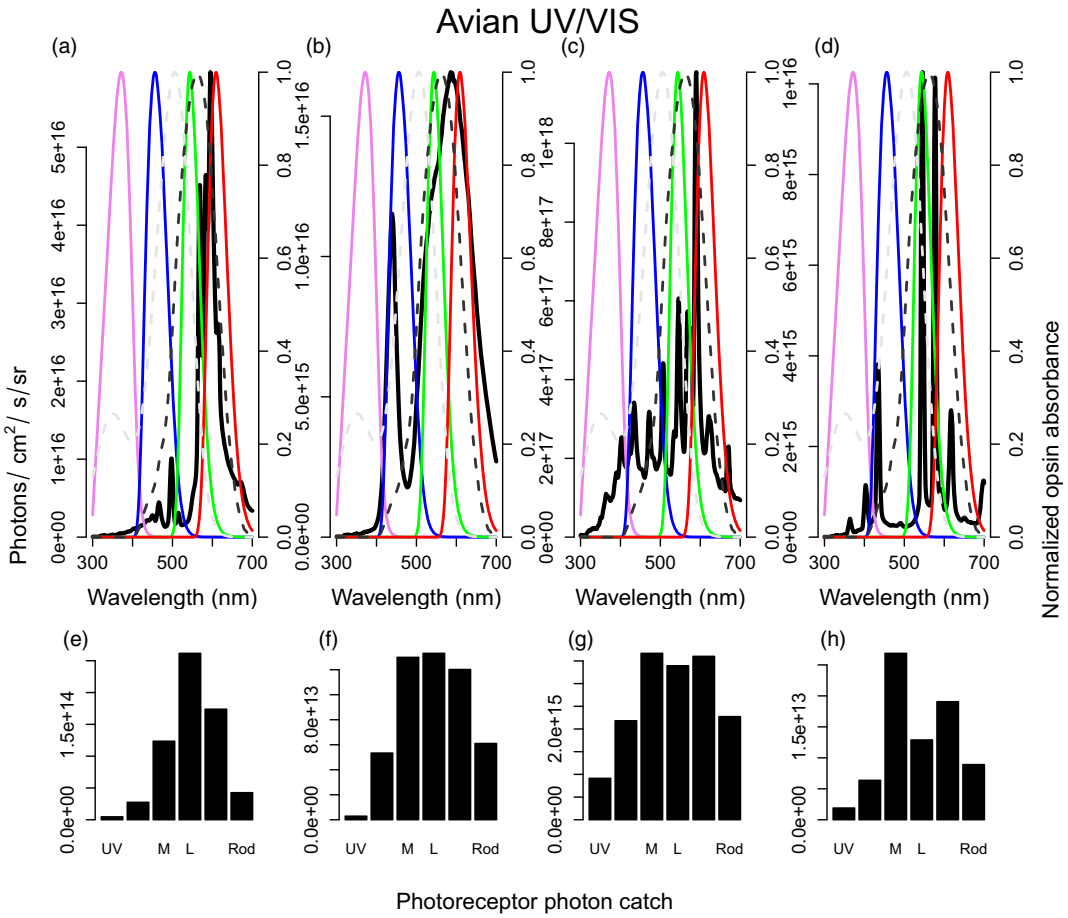

Figure 3 Avian UV/VIS visual system and quantum catches for each photoreceptor for each type of light. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. The radiance spectra are plotted with a continuous black line and the left *y*-axis is the value of photon flux. The colored spectra represent each photoreceptor's normalized absorbance spectra and the normalized absorbance values are plotted on the right *y*-axis. Violet, blue, green and red represent the ultraviolet, short, medium, and long photoreceptors, respectively. The dashed light grey and dark grey spectra represent the rod absorbance and double cones, respectively. These four sub-figures depict how much each light source overlaps with each photoreceptor of the avian UV/VIS visual system. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) metal halides (MH); (h) MV. The figures show how many photons each photoreceptor are likely to catch under illumination from each source. Note that the quantum catch and photon flux scales vary for each light source as light sources can differ by order of magnitudes. Furthermore, although double cones have the highest quantum catch regardless of light type, the quantum catches differ based on light source. High pressure sodium mostly activates the long cones, while mercury vapor mostly activate the medium cones and rods. LEDs and MH activate most cones and rods comparably.

White, 2018). Lastly, our own implementation of these visual models recognizes that we are modeling the perception of light sources against a homogeneously dark background and that eyes and other mechanisms will be adapted for the light intensity of the light sources.

Results

Artificial light sources spectral metrics

The spectra of the different light sources are noticeably different from one another in both intensity and spectral shape, Fig. 2a,b. The robust PERMANOVA revealed that in fact the spectra of the nine different light types differed significantly (PERMANOVA, $F_{8,99} = 12.46$, $P < 0.001$), specific analysis revealed that all three metrics were significantly different: brightness (PERMANOVA, $F_{8,97} = 17.57$, $P < 0.001$; Fig. 2c); chroma (PERMANOVA, $F_{8,97} = 63.01$, $P < 0.001$; Fig. 2d); and hue (PERMANOVA, $F_{8,97} = 24.73$, $P < 0.001$; Fig. 2e).

The MH lights were significantly different from the other light sources in all metrics. For brightness, the only *post hoc* differences were between MH and all other sources, Fig. 2c. This finding was also the case for hue, with only two statistically different groups: MH and all other light types, Fig. 2d. The *post hoc* comparisons for chroma were more complicated with five statistically different groups. LED lights, and the two

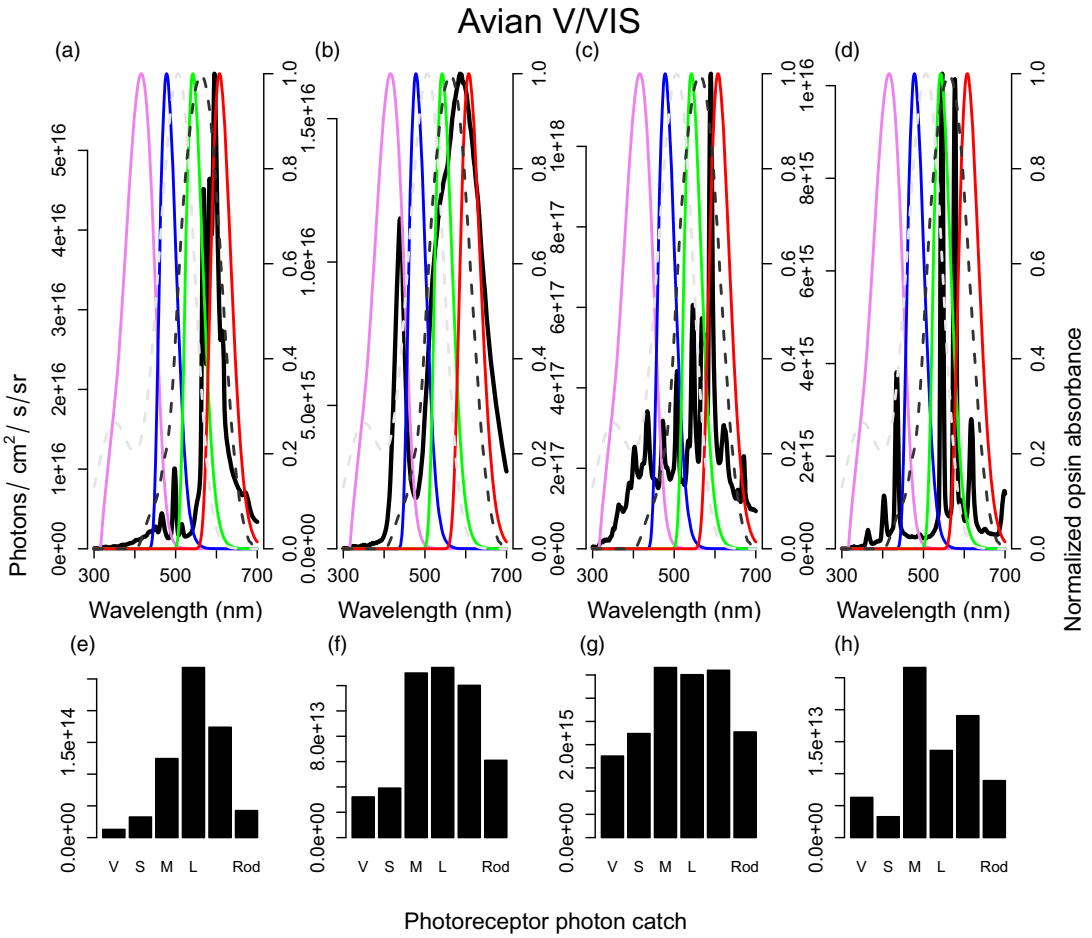

Figure 4 Avian V/VIS visual system and quantum catches for each photoreceptor for each type of light. See Figure legend 3 for specifics on axes. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. Violet, blue, green and red represent the very short, short, medium, and long photoreceptors, respectively. The dashed light grey and dark grey spectra represent the rod absorbance and double cones, respectively. These four sub-figures depict how much each light source (black line) overlaps with each photoreceptor of the avian V/VIS visual system. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) metal halides (MH); (h) MV. The photoreceptors are stimulated differently dependent upon light type. HPS predominately stimulates the long cones; LEDs stimulate the medium cones, long cones, and double cones the most; MH are similar to LEDS except they are even closer to stimulating all cones equally, and mercury vapor predominantly stimulate the middle cones and then to a lesser extent the double cones and long cones.

MV lights were grouped by themselves, whereas there were several overlapping groups of HPS and MH, Fig. 2e for full comparisons. The MV lamps were the most chromatic and LEDs were least chromatic. The other light types (HPS and MH) had intermediate values of chroma.

Photoreceptor quantum catches

As the radiance of each light source is chromatic and thus have an unequal spectral composition of wavelengths, each light source stimulated each visual system's photoreceptors differently, Figs 3–8. Although we did not statistically test for differences between visual systems, a visual comparison of the quantum catches and the relative cone ratios between visual systems (e.g. human vs. hawk moth) reveals that each visual system has a unique response to the different artificial light sources, Figs 3–8; Table 4. The general trends of the different light sources were that most stimulated the longer wavelength photoreceptors most often, although MH stimulated the medium wavelength photoreceptor as well, Figs 3–8; Table 4.

For comparing stimulation of each photoreceptor by the nine different light sources, we found that all photoreceptors for all visual systems had significantly different photon catches. Each visual system had significant differences in photoreceptor quantum catches: UV/VIS (MANOVA, $F_{8,97} = 4.94$, $P < 0.001$, Fig. 3 and Fig. S1); V/VIS (MANOVA, $F_{8,97} = 5.59$, $P < 0.001$, Figs 4 and S2); human visual system (MANOVA, $F_{8,97} = 5.04$, $P < 0.001$, Figs 6 and S4); wolf visual system (MANOVA, $F_{8,97} = 7.20$, $P < 0.001$, Figs 7 and S5); hawk moth visual system (MANOVA, $F_{8,97} = 5.82$, $P < 0.001$, Figs 8

and S6); and the avian deep brain photoreceptors (MANOVA, $F_{8,97} = 4.4024$, $P < 0.001$, Figs 5 and S3). Furthermore, the 1000 W MH stimulated each photoreceptor significantly more than any other light source and at the other extreme, 70 W HPS stimulated each photoreceptor in the UV/VIS system significantly less, Figs S1–6. The other light sources were similar in stimulating the six different photoreceptors, Figs S1–6.

Chromatic contrast (JNDs) between light sources

The chromatic contrast analysis revealed that each of the five visual systems see light types as different colors, even within the same light source (e.g. HPS 70 vs. HPS 400), Table 3. Most visual systems had JNDs under 3 for within light type comparisons (e.g. HPS 70 vs. HPS 70). JNDs differed between visual systems revealing that species have different perceptual abilities for discriminating between these light sources, Table 5. The human visual system had the greatest number of comparisons that would not be perceived as different lights, with most HPS to HPS comparisons as well as MV and LED comparisons have JNDs of less than one, Table 5C. Furthermore, the wolf visual system would also struggle to perceive the MH, MV, and LEDs as different colors as these comparisons had JNDs less than three, Table 5. Only the within HPS 400 comparison was indistinguishable for all visual systems. The avian UV/VIS had the fewest light comparisons with mean JNDs under 3, with avian UV/VIS having JNDs less than three for HPS comparisons and the within LED comparison. Generally, the visual systems had the lowest JNDs for comparisons between HPS light sources and the greatest JNDs for MH compared to other light types, Table 5.

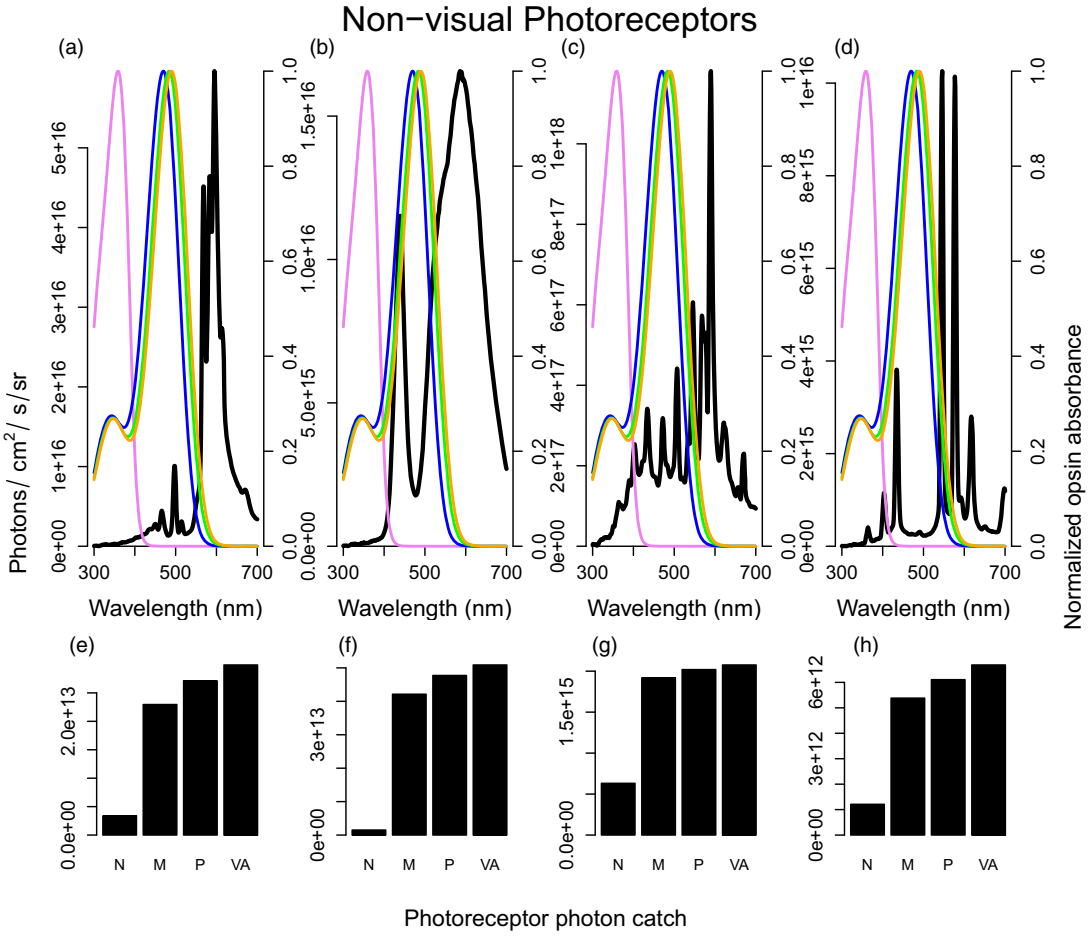

Figure 5 Avian deep brain photoreceptors and quantum catches for each photoreceptor for each type of light. See figure legend 3 for specifics on axes. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. Violet, blue, green and orange represent neuropsin, pinopsin, melanopsin and vertebrate ancient opsin absorbance spectra, respectively. These four subfigures depict how much each light source (black line) overlaps with each deep brain opsin. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) MH; (h) MV. The deep brain opsins are stimulated differently dependent upon light type although all four lights stimulate vertebrate ancient the most, then pinopsin and melanopsin. Neuropsin is minimally stimulated by LEDs and HPS, but is mildly stimulated by MV and MH.

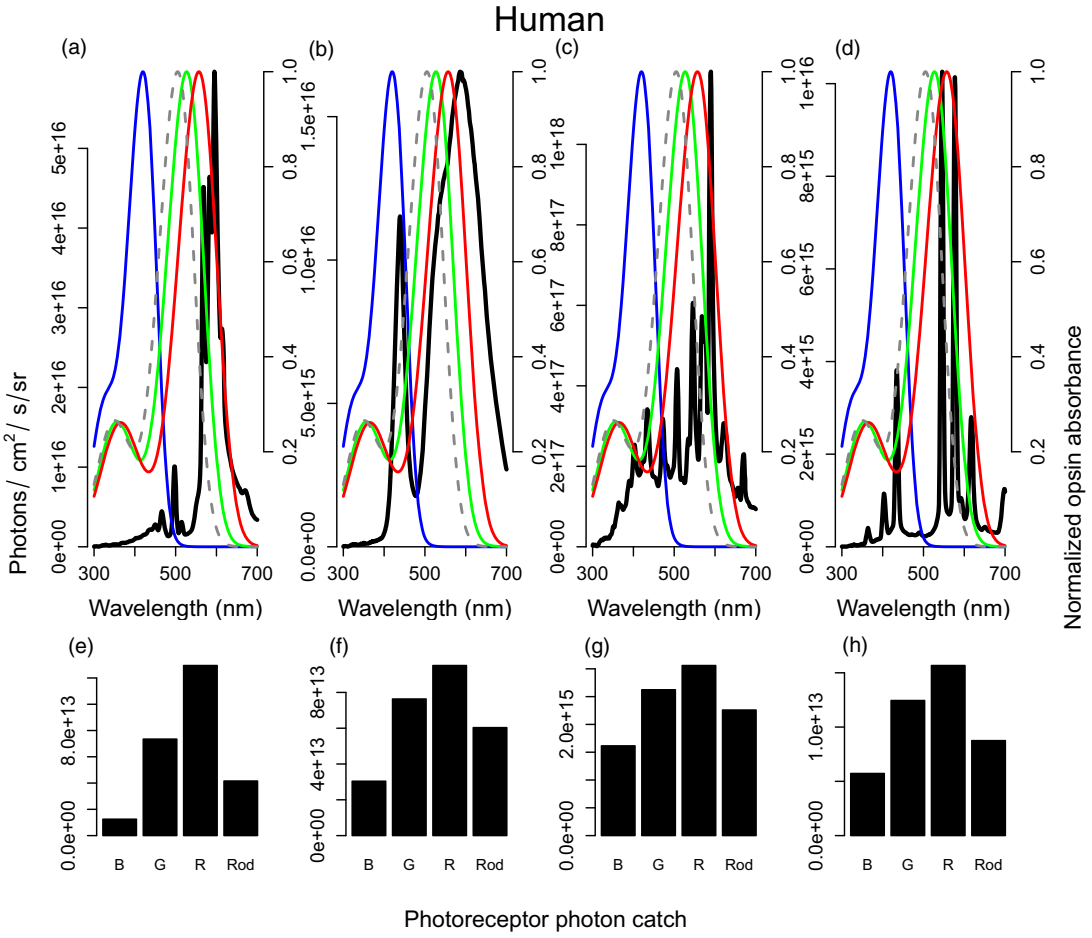

Figure 6 Human visual system and quantum catches for each photoreceptor for each type of light. See figure legend 3 for specifics on axes. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. Blue, green and red represent the short, medium, and long photoreceptors, respectively. The dashed grey spectrum represents human rod absorbance. These four sub-figures depict how much each light source (black line) overlaps with each photoreceptor of the human visual system. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) MH; (h) MV. The photoreceptors are stimulated differently dependent upon light type, however, the pattern is the same for all light types. Each light stimulates the red cones the most, then the green cones, then the rods, and then the blue cones.

The comparison of color space overlap for the different light sources for each visual system corroborate the JND analysis in that most lights should be perceived as different colors, Table 6. Again, the human visual system had the greatest amount of lights overlapping in color space, indicating, that humans would likely perceive all types of high-pressure sodium lamps as the same color and human vision would most likely not be able to discriminate between the two MV lamp types based upon color alone, Table 6. The tetrachromatic UV/VIS avian species had much better discriminability between light types, even between the same light source (e.g. HPS 70 W and HPS 100 W), with only HPS 100 W and HPS 150 W having a very small percentage of overlap. Although the V/VIS avian species also had much better color discriminability than humans, three comparisons of HPS light types and the comparison of MV light types did overlap in the bird's tetrachromatic color space, Table 6. Lastly, the hawk moth also had very good color discrimination between the different light types, with overlap in four comparisons of high-pressure sodium lamps, Table 6.

Discussion

With the photoreceptor catches and the color analyses, we found that visual systems perceive spectral differences not only between light sources, but also between light types of different powers (e.g. 400 vs. 100 W). Most interestingly, humans see a much different nocturnal urban environment than other animals as humans see most lights as the same color, yet birds and insects are likely seeing a myriad of differently colored lights in their environment. Thus, humans have altered the natural nightscape with numerous colors of lights, even though previous research has assumed that within type light sources are the same color (Longcore *et al.*, 2015; Van Langevelde *et al.*, 2017; Donners *et al.*, 2018). All light types varied in overall

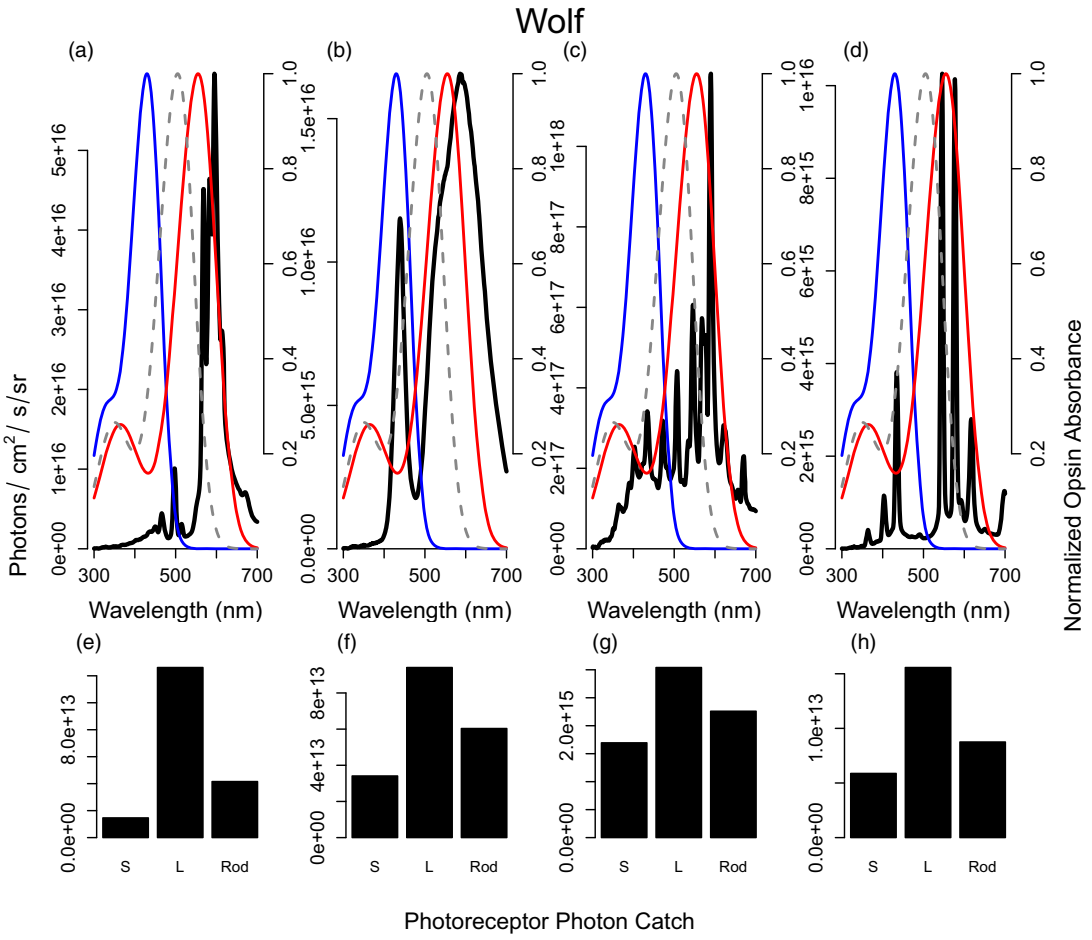

Figure 7 Wolf visual system and quantum catches for each photoreceptor for each type of light. See figure legend 3 for specifics on axes. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. Blue and red represent the short and long photoreceptors, respectively. The dashed grey spectrum represents Wolf rod absorbance. These four sub-figures depict how much each light source (black line) overlaps with each photoreceptor of the Wolf visual system. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) MH; (h) MV. The photoreceptors are stimulated differently dependent upon light type, however, the pattern is the same for all light types. Each light stimulates the long cones the most, then the rods, and then the short cones.

brightness, however, as eyes adapt to light conditions through various mechanisms (e.g. pupil dilation in camera eyes and screening pigment dilution in compound eyes), the subtle variation in brightness is likely visually irrelevant (Cronin *et al.*, 2014). However, the differences in spectral hue and chroma are very visually relevant especially as LED lights were the least chromatic and most likely to stimulate photoreceptors regardless of visual system.

Variation in spectral composition

We corroborate the findings of Elvidge *et al.* (2010) in that different sources and the same source with different wattages (i.e. type) result in different spectra. This is important as current doctrine dictates that similar light sources have the same spectral composition regardless of power (Baumgartner *et al.*, 2012). Research has revealed differences in phototaxis in sea turtles due to spectral differences dependent upon the power of the same light source (Witherington & Bjorndal, 1991). Although our methods systematically measured radiance of each streetlight, there could be very subtle differences in measurement due to fixture height and cleanliness and bulb age. Future research needs to determine the interactions of light power, spectral shape and intensity, and how this affects species behaviors. More specifically, with these data, research can now begin to dive into the mechanisms in which anthropogenic lighting is affecting visually guided behavior and physiology of organisms (Swaddle *et al.*, 2015). Very little is known on how spectral composition alone effects visually guided behavior and physiology.

Photoreceptor quantum catches and perception of different light sources

We found the longest wavelength photoreceptors were stimulated predominantly under most light sources. LED and MH light sources were equally stimulating of the medium, long

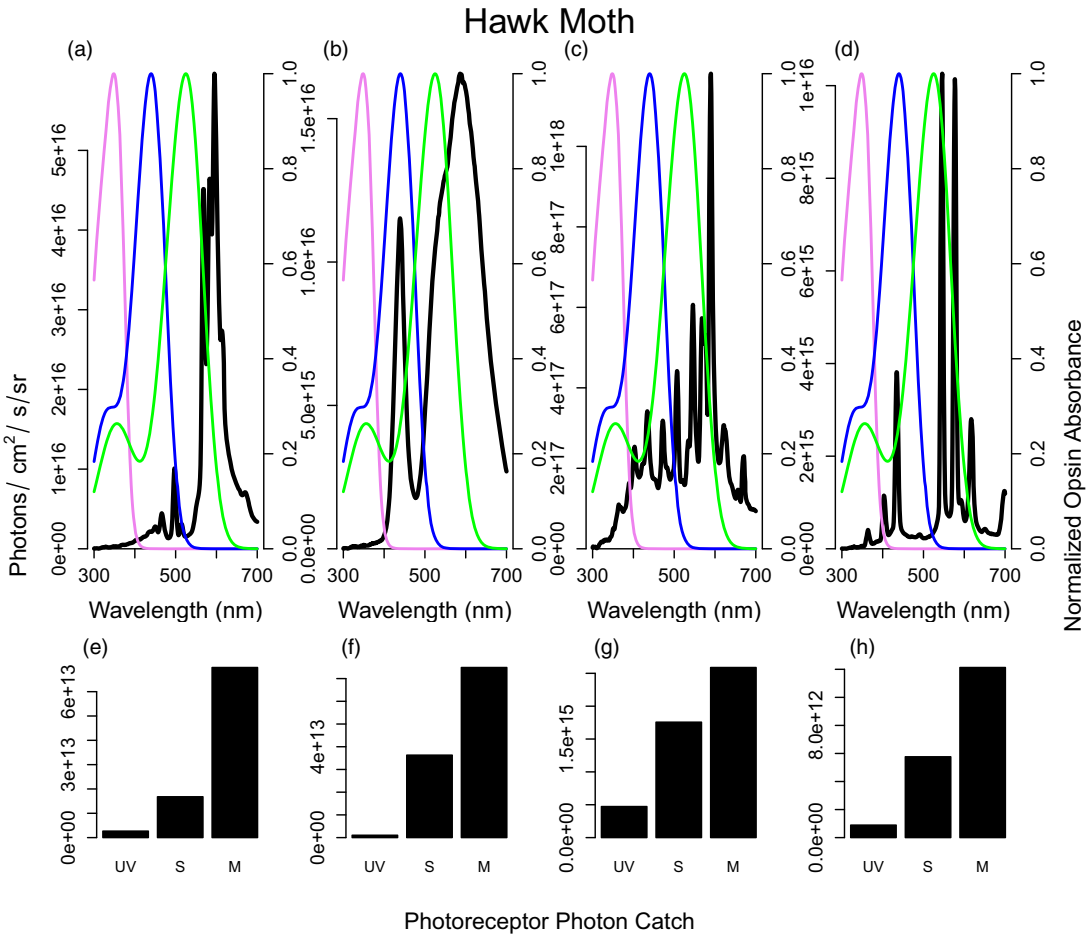

Figure 8 Hawk moth visual system and quantum catches for each photoreceptor for each type of light. See figure legend 3 for specifics on axes. (a-d) Average photon flux for each type of light: (a) High Pressure Sodium; (b) LED; (c) Metal Halide; and (d) Mercury Vapor. Violet, blue and green represent the ultraviolet, short and medium photoreceptors, respectively. These four sub-figures depict how much each light source (black line) overlaps with each photoreceptor of the hawk moth visual system. (e-h) Quantum catch values for each photoreceptor for each light type: (e) HPS; (f) LED; (g) MH; (h) MV. The photoreceptors are stimulated differently dependent upon light type, however, the pattern is the same for all light types. Each light stimulates the medium photoreceptors the most, then the short, and then the ultraviolet photoreceptors.

Table 4 Relative photoreceptor stimulation ratios for each visual system and each average light source

Visuals system	HPS	LED	MH	MV
Wolf	1:9	1:3	1:2	1:3
Moth	1:6:26	1:35:71	1:4:5	1:6:14
Human	1:6:10	1:3:3	1:2:2	1:2:3
V/VIS	1:3:10:21	1:1:4:4	1:1:2:2	1:1:4:2
UV/VIS	1:6:26:56	1:18:45:46	1:2:4:4	1:3:14:7

These ratios are the ratios represented by the bar charts in Figs 3–8. The first value is the shortest wavelength photoreceptor and the last is the longest wavelength photoreceptor. For the wolf the ratio represents S:L, for example the ratio of 1:9 for wolf under HPS represents that the long wavelength photoreceptor receives nine times stimulation to that of the short wavelength photoreceptor. The moth is UV:S:M. The human is S:M:L. For the V/VIS the ratios correspond to V:S:M:L. And for the UV/VIS visual system the ratios correspond to the stimulation of UV:S:M:L.

and double cones of the avian visual systems indicating that different light sources will be perceived as specific colors, which was corroborated by the chromatic contrast analysis. The chromatic contrast analysis and color space overlap revealed that birds and moths can discriminate between different light types based upon color, while humans and wolves would struggle. Furthermore, the stimulation of photoreceptors (relative cone ratio) is quite different between humans and other species. This finding is relevant and timely as our global society switches from older technology (e.g. HPS) to LEDs and use our human vision as a surrogate for how organisms will perceive lights. Our eyes perceive many light sources similarly (e.g. LEDs, MH, MV) due to the spectral peaks matching our photoreceptors resulting in a whitish light. However, many animals are attracted or repelled by specific wavelengths (Somers-Yeates *et al.*, 2013; Stone *et al.*, 2015). For example, millions of migrating birds are attracted to the short wavelength lights of the September 11 Memorial 'Tribute Light'

Table 5 (a-e) Just noticeable differences (JND) for each light type comparison for each visual system

	HPS 70	HPS 100	HPS 150	HPS 250	HPS 400	LED 73	MH 1000	MV 175	MV 250
(a) Avian UV visual system									
HPS 70	3.6 (1.02)								
HPS 100	3.81 (0.76)	4.77 (1.74)							
HPS 150	2.3 (0.45)	2.98 (0.79)	1.12 (0.31)						
HPS 250	2.59 (0.49)	3.01 (0.86)	1.45 (0.11)	1.56 (0.32)					
HPS 400	2.70 (0.47)	2.88 (0.88)	1.26 (0.08)	1.25 (0.15)	0.82 (0.12)				
LED 73	8.79 (0.29)	8.5 (0.40)	7.87 (0.27)	8.14 (0.26)	7.42 (0.27)	3.01 (0.42)			
MH 1000	15.63 (0.69)	14.74 (0.86)	15.93 (0.49)	16.48 (0.48)	16.18 (0.46)	12.99 (0.53)	3.44 (0.85)		
MV 175	13.10 (0.79)	12.77 (0.79)	13.04 (0.77)	13.68 (0.75)	13.21 (0.76)	9.35 (0.81)	7.15 (0.31)	3.97 (1.30)	
MV 250	13.07 (1.18)	12.83 (1.15)	13.03 (1.21)	13.68 (1.20)	13.23 (1.22)	9.94 (1.24)	7.99 (0.54)	5.32 (0.75)	7.5 (1.70)
(b) Avian V visual system									
HPS 70	2.1 (0.57)								
HPS 100	2.47 (0.48)	2.88 (0.99)							
HPS 150	1.54 (0.21)	2.03 (0.49)	0.97 (0.25)						
HPS 250	1.53 (0.20)	1.87 (0.52)	0.96 (0.09)	0.85 (0.16)					
HPS 400	1.75 (0.17)	1.97 (0.47)	0.90 (0.11)	1.01 (0.10)	0.83 (0.16)				
LED 73	7.69 (0.43)	6.93 (0.43)	7.5 (0.35)	7.88 (0.32)	7.31 (0.33)	2.33 (0.35)			
MH 1000	14.10 (0.43)	13.01 (0.55)	13.98 (0.33)	14.27 (0.32)	13.71 (0.34)	6.96 (0.43)	3.85 (1.22)		
MV 175	12.60 (0.58)	12.14 (0.59)	12.61 (0.53)	12.99 (0.52)	12.60 (0.51)	6.97 (0.46)	7.91 (0.42)	3.97 (0.92)	
MV 250	11.91 (0.85)	11.51 (0.84)	11.91 (0.82)	12.30 (0.81)	11.91 (0.81)	6.61 (0.67)	8.34 (0.40)	3.69 (0.56)	4.46 (1.26)
(c) Human visual system									
HPS 70	0.91 (0.28)								
HPS 100	1.03 (0.22)	1.23 (0.44)							
HPS 150	0.55 (0.11)	0.78 (0.24)	0.18 (0.04)						
HPS 250	0.58 (0.10)	0.76 (0.23)	0.21 (0.03)	0.28 (0.06)					
HPS 400	0.58 (0.09)	0.76 (0.23)	0.19 (0.02)	0.23 (0.02)	0.20 (0.02)				
LED 73	2.78 (0.17)	2.37 (0.18)	2.85 (0.10)	2.81 (0.10)	2.74 (0.10)	0.63 (0.11)			
MH 1000	4.50 (0.18)	3.93 (0.24)	4.59 (0.09)	4.54 (0.09)	4.49 (0.09)	1.81 (0.14)	0.60 (0.13)		
MV 175	3.57 (0.17)	3.03 (0.22)	3.66 (0.08)	3.61 (0.08)	3.55 (0.08)	0.89 (0.13)	0.99 (0.11)	0.53 (0.11)	
MV 250	3.31 (0.24)	2.80 (0.26)	3.39 (0.19)	3.34 (0.19)	3.28 (0.19)	0.84 (0.16)	1.31 (0.17)	0.78 (0.09)	1.05 (0.28)
(d) Hawk Moth visual system									
HPS 70	3.4 (1.03)								
HPS 100	3.51 (0.77)	4.68 (1.60)							
HPS 150	2.15 (0.51)	2.66 (0.78)	0.82 (0.24)						
HPS 250	2.43 (0.52)	2.86 (0.78)	1.16 (0.16)	1.6 (0.44)					
HPS 400	2.47 (0.57)	2.67 (0.87)	0.97 (0.11)	0.99 (0.23)	0.49 (0.09)				
LED 73	5.70 (0.55)	5.46 (0.82)	4.36 (0.31)	4.21 (0.34)	3.70 (0.25)	2.13 (0.57)			
MH 1000	6.64 (0.56)	6.44 (0.64)	7.53 (0.26)	7.58 (0.35)	8.06 (0.25)	9.45 (0.43)	1.67 (0.37)		
MV 175	4.2 (0.29)	4.26 (0.45)	3.64 (0.20)	3.64 (0.23)	3.64 (0.23)	4.18 (0.50)	5.52 (0.46)	2.47 (0.55)	
MV 250	4.68 (0.57)	4.62 (0.72)	4.59 (0.61)	4.63 (0.65)	4.74 (0.72)	6.05 (0.91)	4.29 (0.71)	3.64 (0.57)	4.76 (1.19)
(e) Wolf visual system									
HPS 70	1.07 (0.33)								
HPS 100	1.26 (0.26)	1.46 (0.52)							
HPS 150	0.63 (0.13)	0.93 (0.29)	0.80 (0.01)						
HPS 250	0.68 (0.11)	0.87 (0.28)	0.15 (0.03)	0.23 (0.05)					
HPS 400	0.70 (0.10)	0.83 (0.28)	0.17 (0.03)	0.17 (0.03)	0.18 (0.04)				
LED 73	3.21 (0.24)	2.42 (0.30)	3.31 (0.12)	3.20 (0.13)	3.15 (0.13)	0.71 (0.15)			
MH 1000	5.32 (0.24)	4.49 (0.32)	5.42 (0.12)	5.31 (0.13)	5.25 (0.12)	2.10 (0.17)	0.70 (0.16)		
MV 175	4.04 (0.23)	3.21 (0.31)	4.14 (0.10)	4.03 (0.11)	3.97 (0.11)	0.85 (0.15)	1.27 (0.16)	0.59 (0.14)	
MV 250	3.70 (0.31)	2.88 (0.37)	3.80 (0.23)	3.69 (0.23)	3.64 (0.23)	0.85 (0.19)	1.69 (0.23)	0.92 (0.13)	1.24 (0.35)

Dark grey shading represents a JND value of less than one and light grey shading represents a value of less than 3. JND values less than one will be physiological indistinguishable under ideal viewing conditions while JND values of less than three will be difficult to distinguish under most visual conditions.

(Van Doren *et al.*, 2017) and numerous studies have found that different species of arthropods were attracted to different wavelengths of LEDs (Langevelde *et al.*, 2011; Longcore *et al.*, 2015; Spoelstra *et al.*, 2017).

Melanopsin, pinopsin and vertebrate ancient opsin were all highly stimulated by the four light sources while neuropsin was marginally stimulated. These findings are the first to test how different non-visual photoreceptors are stimulated by

Table 6 (a-d) Percentage overlap for each light type in color space for the respective visual system. a) Avian UV/VIS; b) Avian V/VIS; c) Human; d) Hawk moth

	HPS 100	HPS 150	HPS 250	HPS 400	LED 73	MH 1000	MV 175	MV 250
(a) Avian UV visual system								
HPS 70	0	0	0	0	0	0	0	0
HPS 100		1.60E-06	0	0	0	0	0	0
HPS 150			0	0	0	0	0	0
HPS 250				0	0	0	0	0
HPS 400					0	0	0	0
LED 73						0	0	0
MH 1000							0	0
MV 175								0
(b) Avian V visual system								
HPS 70	0	0	0	0	0	0	0	0
HPS 100		3.40E-04	4.32E-06	0	0	0	0	0
HPS 150			6.45E-08	0	0	0	0	0
HPS 250				0	0	0	0	0
HPS 400					0	0	0	0
LED 73						0	0	0
MH 1000							0	0
MV 175								1.97E-02
(c) Human visual system								
HPS 70	20.02	3.25	10.39	2.77	0	0	0	0
HPS 100		0.04	4.93	0.83	0	0	0	0
HPS 150			11.03	12.42	0	0	0	0
HPS 250				9.94	0	0	0	0
HPS 400					0	0	0	0
LED 73						0	0	1.07
MH 1000							0	0
MV 175								10.54
(d) Moth visual system								
HPS 70	0	0	0	0	0	0	0	0
HPS 100		0	4.01	0	0	0	0	0
HPS 150			2.11	1.60	0	0	0	0
HPS 250				4.42	0	0	0	0
HPS 400					0	0	0	0
LED 73						0	0	0
MH 1000							0	0
MV 175								0

numerous anthropogenic light sources and reveal that numerous organisms are at risk for changes to circadian rhythms, seasonal reproduction, hormone cascades and immune function, phenology and migration (Kuenzel *et al.*, 2014; Gaston *et al.*, 2017; Alaasam *et al.*, 2018). We must emphasize that previous research has repeatedly shown that these non-visual photoreceptors are directly responsible for changes in reproduction, physiology, immunity and phenology (Gaston *et al.*, 2017). The non-visual photoreceptors captured millions of photons from these light sources, indicating that even though the light sources are long wavelength shifted, they will still alter organisms' physiology and ecology. Ouyang *et al.* (2015) revealed that birds exposed to shorter wavelengths of light had higher levels of circulating stress hormones. As we have shown here, the non-visual photoreceptors are even more stimulated by LEDs, which is alarming as municipalities switch from HPS to LEDs (Kyba *et al.*, 2017). It is currently unknown how many photons are needed to engender a biological effect from non-visual photoreceptors and this should be a main research aim of future work.

Moving forward: light pollution research and mitigation

Animals with trichromatic or tetrachromatic color vision are likely experiencing an artificially colored night. We have shown here that the perception of these light sources will not be identical and thus organisms may be bombarded with numerous novel stimuli in their environment that could lead to grave consequences. Numerous questions remain as to whether the differences in color perception of lights shown here will have effects on the visual ecology of organisms. Research into the role of color for the underlying mechanisms of distraction, masking and misleading of anthropogenic light will allow for

better management of anthropogenic lighting (Francis & Barber, 2013). For example, will animals be distracted by the numerously different colored LED bulbs along the highway, or will they quickly learn to generalize among the LED bulbs and not be distracted by color differences? How different can light spectra be and still engender a biological effect? Although we show here that these organisms are able to perceive differences within individual light sources, we do not know if these perceptual differences relate to behavioral changes. With this research, we now need to conduct behavioral and physiological research to determine how the visual ecology of organisms is affected by small changes in spectral composition of anthropogenic lights.

As global anthropogenic light at night has been increasing annually (Falchi *et al.*, 2016) and developed countries are upgrading to more efficient technologies such as LEDs (Kyba *et al.*, 2017), we are presented with an opportunity to mitigate the effects of anthropogenic light sources on organisms and implement the best lighting practices. We demonstrate that different light types have differing visual effects dependent upon the viewer and that human vision does not predict how other organisms will perceive artificial lights. Moving forward, we must test how different organisms will not only perceive lights at night through their respective visual systems, but how they will perceive relevant objects in their environment like predators and prey (Bergman *et al.*, 2015; Hutton *et al.*, 2015; Seymoure *et al.*, 2017). Lastly, as LEDs are becoming the preferred lighting technology (Kyba *et al.*, 2017), we have shown here that LEDs are chromatically unique, which can be a major concern for visual guided behaviors as organisms are likely to be more distracted or mislead by a broadband light (Longcore *et al.*, 2015; Seymoure, 2018). Several species are vulnerable to extinction due to light pollution such as species of sea turtles, bats, and moths and future research will likely show that these negative lighting effects are ubiquitous across taxa (Longcore & Rich, 2004; Gaston, Visser & Hölker, 2015b). As we continue to light up the night, the urgency increases for solving the global challenge of illuminating the nocturnal environment while mitigating ecological impacts.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figures S1-S6. Boxplots of photon catch for each of the nine different artificial light sources in: 1) avian UV/VIS visual system; 2) avian V/VIS visual system; 3) avian deep brain photoreceptors; 4) human visual system; 5) wolf visual system; 6) hawk moth visual system. Letters represent which groups are significantly different from one another. Each subpanel represents a different photoreceptor within that respective visual system. Table 1 Percentage overlap for each light type.